

Hunting or habitat degradation? Decline of primate populations in Udzungwa Mountains, Tanzania: An analysis of threats

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ABSTRACT

Hunting and habitat degradation are universal threats to primates across the tropics, thus deciphering the relative impact of threats on population relative abundance is critical to predicting extinction risk and providing conservation recommendations. We studied diurnal primates over a period of nearly 6 years in the Udzungwa Mountains of Tanzania, a site of global importance for primate conservation. We assessed how population relative abundance of five species (of which two are endemic and IUCN-Endangered) differed between two forest blocks that are similar in size and habitat types but contrast strongly in protection level, and how abundance changed during 2004–2009. We also measured habitat and disturbance parameters and, in the unprotected forest, evaluated hunting practices. We found significant differences in primates' abundance between protected and unprotected forests, with the greater contrast being the lower abundance of colobine monkeys (Udzungwa red colobus and Angolan colobus) in the unprotected forest. At this site moreover, colobines declined to near-extinction over the study period. In contrast, two cercopithecines (Sanje mangabey and Sykes' monkey) showed slightly higher abundance in the unprotected forest and did not decline significantly. We argue that escalating hunting in the unprotected forest has specifically impacted the canopy-dwelling colobus monkeys, although habitat degradation may also have reduced their abundance. In contrast, cercopithecines did not seem affected by the current hunting, and their greater ecological adaptability may explain the relatively higher abundance in the unprotected forest. We provide recommendations towards the long-term protection of the area.

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1. Introduction

Global analysis on the status of world mammals shows that primates are the order most threatened by extinction (Schipper et al., 2008). Primates have therefore been used as indicators for investigating vulnerability to threats, the most common ones being habitat disturbance and hunting (Johns and Skorupa, 1987; Marsh and Mittermeier, 1987; Johns and Johns, 1995; Cowlshaw and Dunbar, 2000; Harcourt and Doherty, 2005). In Africa, hunting is a greater threat to primates than habitat degradation (Oates, 1996; Brugière, 1998; Linder and Oates, 2011) because of local people's dependence on bushmeat as a food resource (Milner-Gullanda et al., 2003). Because diurnal primates live at relatively low densities, have slow

life-histories, are highly social and active during the day, they are particularly vulnerable to overexploitation (Cowlshaw and Dunbar, 2000). Species' vulnerability to local extinction is however highly variable: Isaac and Cowlshaw's (2004) meta-analysis shows that primate species' vulnerability to one threat do not predict vulnerability to another, as threat-specific responses are highly influenced by species' particular biological traits, such as diet, social system and body size. In general, large-bodied, slow-reproducing species are more at risk than fast-reproducing species (Kokko et al., 2001; Duncan et al., 2002; Isaac and Cowlshaw, 2004). In addition, species vary in the degree to which they are targeted by hunters, preferred by consumers and susceptible to different methods of hunting (Fa et al., 2002; Kümpel et al., 2008). Deciphering the effects of hunting versus other forms of anthropogenic disturbance, such as forest loss and degradation, on primate abundance, is therefore a critical area of research.

Hunting of primates is the greatest threat to populations in west and central African regions (Oates, 1996; Walsh et al., 2003; Magnuson, 2005; Linder and Oates, 2011), but is less reported,

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and considered less common, in East Africa. General depression of primate population densities due to hunting is widely documented (e.g. Robinson and Bennett, 2000; Waltert et al., 2002; Fa et al., 2002; Peres and Nascimento, 2006), with cases of decline to local extinction, as exemplified by the plight of Miss Waldron's red colobus (Oates et al., 2000; McGraw and Oates, 2002). The impact of habitat degradation, fragmentation and loss on primate populations is also widely documented (Skorupa, 1986; Struhsaker, 1997; Brugière, 1998; Marsh, 2003; Arroyo-Rodriguez and Dias, 2009). In particular, for canopy-dependent species such as the colobine monkeys, analysis of vegetation predictors of abundance have clearly shown that canopy alteration affects local abundances (Medley, 1993; Mboru and Meikle, 2004; Rovero and Struhsaker, 2007).

The Udzungwa Mountains of south-central Tanzania is an area of outstanding importance for primate diversity and conservation (Dinesen et al., 2001; Struhsaker et al., 2004; Marshall, 2007; Rovero et al., 2009). With two strictly endemic monkeys, Udzungwa red colobus (*Procolobus gordonorum*) and Sanje mangabey (*Cercocebus [galeritus] sanjei*), both listed as Endangered (IUCN, 2011), and the very localized, Critically Endangered kipunji (*Rungwecebus kipunji*), the Udzungwa primates have received considerable research attention in the past decade (review in Rovero et al., 2009). Yet, the lack of effective protection of approximately half of the forests (i.e. those not included in the National Park) is a constant problem for the long-term protection of the area (Zilihona et al., 1998; Nielsen, 2006; Museo Tridentino di Scienze Naturali, 2007; Rovero et al., 2010). This study focuses on primates living in one of the most biologically important and unprotected forests in the Udzungwa Mountains: the Uzungwa Scarp Forest Reserve, on which only very scant information has been reported earlier (but see Dinesen et al., 2001; DeFries et al., 2010). By comparing results with those from the ecologically-similar but better protected Mwanihana forest (Rovero and Struhsaker, 2007), we provide the first account of hunting vulnerability of Udzungwa primates and we aim to determine how the interplay of hunting and habitat degradation influences primate populations. Our specific objectives were to (i) assess differences in primate abundance between study forests (hunted and non-hunted); (ii) examine temporal variations of these populations; (iii) review hunting practices and historical changes; (iv) analyse the effect of habitat factors and overall anthropogenic disturbance on primate abundance; and (v) provide conservation recommendations.

2. Methods

2.1. Study area and primate populations

We studied primate populations between February 2004 and October 2009 in two forests in the Udzungwa Mountains: Mwanihana forest (MW) which is inside the Udzungwa Mountains National Park, and Uzungwa Scarp Forest Reserve (USFR), 150 km to the southwest, which is a National Catchment Forest Reserve, where no resource extraction is allowed (Fig. 1). Both forests cover the steep, east-facing escarpment rising from the Kilombero valley to the east and are characterized by continuous cover from lowland, deciduous forest to evergreen moist montane forest (Lovett, 1993). While similar in habitat type, extent (177 and 200 km² for MW and USFR, respectively) and altitudinal gradient (300 to over 2000 m a.s.l.), these forests contrast strongly in protection levels, as MW is regularly patrolled by the National Park's rangers while USFR lacks any law enforcement measures on the ground (Museo Tridentino di Scienze Naturali, 2007). Four species of diurnal primates occur throughout the forests: Udzungwa red colobus, Angolan colobus (*Colobus angolensis palliatus*), Sykes' monkey

(*Cercopithecus mitis cf. monoides/moloneyi*), and Sanje mangabey (Rovero et al., 2009). Yellow baboons (*Papio cynocephalus*) occur at the forest edge. These two forests host the only existing populations of the Udzungwa-flagship Sanje mangabey.

2.2. Data collection

2.2.1. Primate counts

Primates were counted at monthly intervals along line-transects (Rovero et al., 2006). The data presented here are from three transects in each forest, 3.1–4 km in length, sampling lower to mid-elevation zones (300–1000 m a.s.l.) in both forests. Transects were walked once or twice each month by three observers during consecutive periods: A.S.M. (with F.R.) in 2004–2005 (66 and 50 census walks in USFR and MW, respectively), A.S.K. in 2007–2008 (43 and 59 census walks) and again A.S.M. in 2009 (25 and 63 census walks). Walks began at 07:00–07:30 and at each sighting of primates the observer noted the time, position along transect, primate species, number of individuals (when feasible to count them) and perpendicular distance from the transect route. Distance was measured using a laser range-finder. Consistency among observers in species' identification and ability to sight primates was achieved by extensive training prior to the beginning of the study (Rovero et al., 2006).

2.2.2. Sampling of vegetation and human disturbance along transects

All trees greater than 20 cm in diameter at breast height (DBH) were measured and identified along a strip of 5 m width centred on the transect line. The presence of liana coverage on tree stems and canopy was also noted. For MW, data were collected in 2003 and are presented in Rovero and Struhsaker (2007), while for USFR the sampling was conducted in 2004. Details on sampling methods are presented in Rovero and Struhsaker (2007). In contrast to other works (e.g. Skorupa, 1986; Struhsaker, 1997), we choose to measure trees above 20 cm DBH, instead of 10 cm, because (1) the remoteness of USFR constrained fieldwork at this site; (2) regression models of the influence of vegetation parameters on primate abundance using the subsample of trees above 20 cm gave the same results as data based on 10 cm DBH (Rovero and Struhsaker, 2007); and (3) we were targeting the canopy-dwelling species of colobus and aimed to assess their response to canopy structure, which is well represented by trees above 20 cm DBH.

Human disturbance was only measured for USFR as preliminary work showed that in MW there is virtually no disturbance (DeFries et al., 2010), with the exception of firewood collection, which was allowed in MW until June 2011 and did not impact forest canopy. The level of disturbance was measured by (1) counting all signs of encroachment, such as tree and pole cuts, charcoal burning sites, human trails, pit sawing sites and snares set to catch forest ungulates, along a strip width of 5 m centred on the transect line, and (2) by estimating the extension of gaps in the forest canopy cover measured as % of transect length not covered by closed canopy to a minimum width of 50 m each side of the transect (see Rovero and Struhsaker, 2007). Signs of disturbance also included gun shots heard and hunters encountered with dogs. However, as shotguns can be heard from hundreds of metres away, these observations were not referable to a specific transect, and therefore were not used in the analysis.

2.2.3. Hunting survey

Information on the development and nature of hunting in USFR was collected between July and October 2008 by M.R.N. from a sample of cooperating hunters in three villages (Massisiwe, Idagenda and Mbawie) which are located on the plateau 2.5–5 km to the northwest of USFR. These villages were selected as hunters in the lowland villages, i.e. bordering USFR to the east,

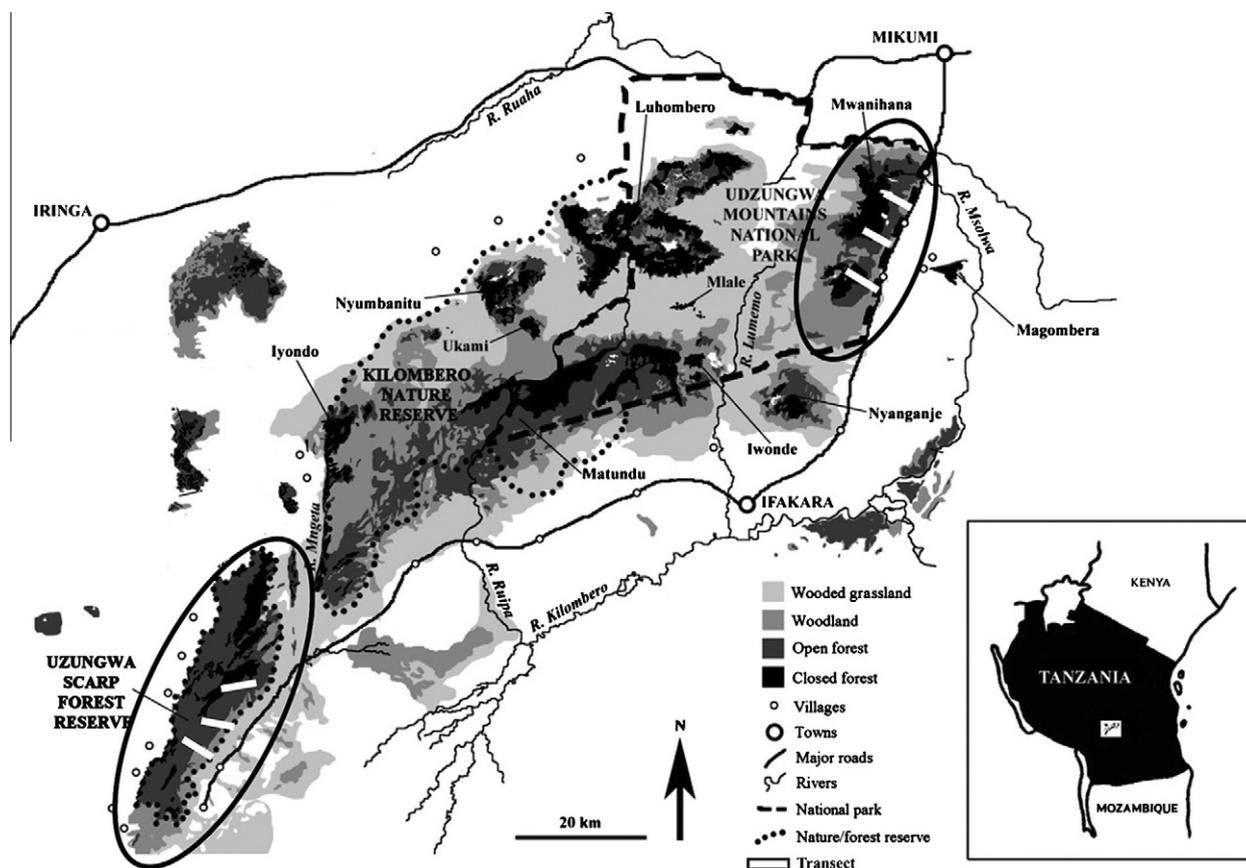


Fig. 1. Map of the Udzungwa Mountains of Tanzania. The two study forests are shown in circles (Mwanihana forest to the northeast and Uzungwa Scarp forest to the southwest), and within them the line-transects used for primate counts are indicated (adapted from Marshall et al., 2010).

are mainly hunting in the Kilombero valley (M.R.N., Unpublished results). Interviews revealed that hunting occurred throughout the forest including in the mid-to-lower elevation zone where the primate survey was done. We therefore considered these results relevant to interpreting results from the primate study. Informants were identified and recruited through the aid of a local assistant using snowball sampling (Patton, 1990). In total 110 individuals were identified as knowledgeable about hunting through having actively hunted, traded or participated in transport of bushmeat or animal products such as hides or ivory. Interviews were conducted through the interpretation of the local assistant residing in one of the villages. Semi-structured interviews were selected as a research approach over more open-ended or structured methods to ensure that the required information was collected while also enabling a measure of flexibility (Bryman, 2004; Lloyd-Evans, 2006). Questions posed assessed the historical development of hunting in USFR in terms of when it was most intense, and how this compared to the intensity of hunting 10 years ago, corresponding to the timing of the 1998 survey in USFR by Topp-Jørgensen et al. (2009), and in 2008. Questions aimed to determine the main reason for hunting (subsistence or commercial), hunting methods used, species caught, items traded, means of transport and end-point of the products in each of these periods. Respondents were also asked about the timing and perceived reason for major changes in diversity and population density of species caught. Obtaining valid and reliable information on bushmeat hunting is difficult in Tanzania because it is a criminal activity. Respondents were naturally reluctant, initially, to share information but the use of a local research assistant and the informal nature of interviews reduced this anxiety. Nevertheless this aspect has to be taken into consideration when analyzing the responses. Key points raised during interviews were furthermore reviewed with the local

assistant immediately after interviews for verification and validation.

2.3. Data analysis

Data from primate censuses were analyzed both as mean encounter rate (groups sighted per km walked) and as the total number of primate groups recorded from all repetitions on segments of 200 m of transects, which allows fine-scale modelling of abundance (Rovero and Struhsaker, 2007). We considered the encounter rate as a reliable index of abundance for intra-specific comparisons within sites and among sites, in line with other primate studies (e.g. Chapman et al., 2000; Mitani et al., 2000; Rovero et al., 2006; Linder and Oates, 2011).

To ensure spatial consistency between primate sighted and habitat features along transect segments, only groups sighted at a perpendicular, cut-off distance equal or less than 40 m were used in the habitat analysis (representing 70% of data, see Rovero and Struhsaker (2007) on details about choosing the cut-off distance). As most data sets to be compared statistically did not have homogeneity of variance, we used the non-parametric Kolmogorov-Smirnov test to assess the differences in primates' relative abundance between forests, and among observers for each forest.

Tree measurements were used to derive the following variables: (i) mean basal area (MBA) and total basal area (TBA) from DBH measurements; (ii) species richness and Shannon's index of diversity from identification and number of stems; and (iii) percentage of trees bearing lianas from the presence of liana coverage. The total number of disturbance signs was computed as an index of disturbance, while canopy cover was estimated by the difference (100%–% of gaps). These variables were then checked for collinearity using Pearson's r values of 0.7 as a threshold. Species richness was

found to be highly correlated with diversity ($r = 0.87$, $n = 107$, $p < 0.001$) and therefore omitted. Lower, but significant correlation was also observed between MBA and TBA ($r = 0.37$, $n = 107$, $p < 0.001$), however both were retained because they contain complementary information (MBA reflects average size of trees while TBA the total basal area irrespective of the size of trees). The proportion of climbers was positively correlated with disturbance ($r = 0.40$, $n = 107$, $p < 0.001$) and negatively with tree cover ($r = -0.30$, $n = 107$, $p < 0.01$). The difference between forests in the vegetative variables was tested using the Kolmogorov–Smirnov test. To assess differences between forests in the floristic composition of the tree community sampled, the difference in the number of stems per each tree species was tested using paired-sample *T*-test.

We used Redundancy Analysis (RDA: ter Braak, 1986), a constrained ordination technique, to analyse the overall primate community response to habitat variables along 200 m segments of transects. RDA was selected over other ordination techniques such as Canonical Correspondence Analysis following an evaluation of the length of the gradient (Ter Braak and Šmilauer, 1998). Significance of the RDA model was tested by using the Monte-Carlo permutation test (9999 permutations) on the first and the sum of all the canonical axes. We used the software CANOCO (ter Braak and Šmilauer, 1998) to run the analysis. To further analyse determinants of abundance in USFR, Generalized Linear Models with Poisson error distribution, which is recommended when the response variables are counts (Maindonald and Braun, 2003), were constructed using the same procedure applied to MW (Rovero and Struhsaker, 2007). We used the software R (<http://cran.r-project.org>) for these regressions. Primate and habitat analysis were only applied to the two colobines and Sykes' monkey as too few observations were made of baboons and Sanje mangabeys and most importantly, because these are predominantly terrestrial species the habitat variables we measured would be mainly irrelevant.

3. Results

3.1. Primates and habitat

During the study period (2004–2009), 180 and 134 transect repetitions were conducted in MW and USFR, totalling 702 and 479 km of transect, respectively. For all primate species, the relative abundance obtained from all counts contrasted distinctly between forests (Table 1). The direction of differences is not the same for all species: abundance of both colobines and baboon is clearly lower in USFR, while Sykes' monkeys and Sanje mangabeys show higher abundance. Overall primate abundance remains significantly lower in USFR than in MW. Analysis of temporal variation shows clear decline in USFR in the abundance of colobines, and, possibly, baboons, while variations in the abundance of mangabeys and Sykes' monkeys do not seem to indicate any temporal trend (Fig. 2 and Table 2). For MW on the contrary, differences are not significant and no evident temporal trend emerges, except for a possible drop of Sanje mangabeys' relative abundance in 2009 relative to previous years (Fig. 2 and Table 2).

Table 1

Mean and standard deviation number of primate groups encountered per km of transect during censuses conducted in Uzungwa Scarp Forest Reserve (USFR, $n = 134$) and Mwanihana forest (MW, $n = 180$) in the Udzungwa Mountains of Tanzania. Results of Kolmogorov–Smirnov tests are also shown.

Species	USFR	MW	H (p)
Red colobus	0.114 ± 0.208	0.463 ± 0.258	104.05 (<0.001)
Angolan colobus	0.050 ± 0.127	0.401 ± 0.292	120.63 (<0.001)
Sykes' monkey	0.560 ± 0.365	0.301 ± 0.257	67.39 (<0.001)
Sanje mangabey	0.155 ± 0.223	0.058 ± 0.125	26.57 (<0.001)
Yellow baboon	0.023 ± 0.086	0.065 ± 0.117	12.49 (<0.001)
All diurnal primates	0.933 ± 0.572	1.302 ± 0.604	22.89 (<0.001)

Variables describing tree species diversity and structure were significantly different between forests, with USFR showing significantly higher total basal area, higher floristic diversity and higher portion of trees bearing lianas (Table 3). Conversely, the extent of canopy cover in USFR was significantly less than in MW (72% versus 88%). Disturbance levels were very high in USFR while no sign of disturbance was observed in MW (Table 3). In USFR moreover, 85% of disturbance signs was recorded along the first 2 km of the two transects that start from the forest edge. Out of 101 tree species, comprising 84 genera, sampled along all transects in both forests, 40 species (39 genera) were recorded in both USFR and MW. The number of tree stems recorded per species was not significantly different between forests, both when considering all tree species (paired-sample *t* test $t = -0.547$, $p = 0.58$) and only those in common ($t = 0.384$, $p = 0.70$).

Redundancy analysis shows that the variables explain 28% of the variation in the species data (sum of all canonical eigenvalues; Table 4). Of this, the first axis alone explains 25.5%. The first three axes display strong species–environment correlations ($r = 0.68$, $r = 0.26$ and $r = 0.25$ respectively). The RDA model was significant: first canonical axis (eigenvalue = 0.255; $F = 33.94$; $p < 0.001$), all axes (Trace = 0.279; $F = 5.470$, $p < 0.001$). The contrast in both primate abundance and habitat variables taken separately are well reflected in the biplot (Fig. 3). The nominal variables MW and USFR (represented by triangles in Fig. 3) show that the two forests were strongly different from each other. USFR is characterized by high values of disturbance and climbers, while MW presents higher cover. Disturbance, TBA, MBA and Shannon index were each other positively correlated but altogether were negatively associated to cover and climbers (opposite arrows on Fig. 3). Red colobus and Angolan colobus (each other positively and strongly correlated) were associated to the greater cover in MW, while the presence of Sykes' monkey was more closely associated with the proportion of climbers, which was higher in USFR.

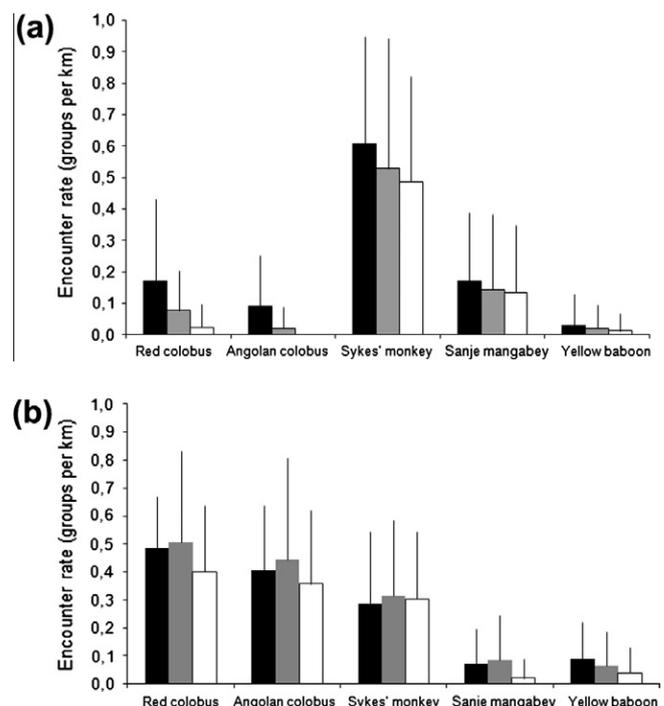


Fig. 2. Temporal variations of primate census results (mean and standard deviation groups' encounter rates) for Uzungwa Scarp (a) and Mwanihana forests (b) in the Udzungwa Mountains of Tanzania. Data were collected in 2004–2005 (black bars), 2007–2008 (grey bars) and 2009 (white bars).

Table 2

Results of Kolmogorov–Smirnov tests (H) for comparisons of primate encounter rates among data-sets for Uzungwa Scarp Forest Reserve (USFR, $n = 134$) and Mwanihana forest (MW, $n = 180$) in the Udzungwa Mountains of Tanzania. In parenthesis are the significance values p (see Fig. 2 for related data collection periods).

Species	USFR ^a	MW ^a
Red colobus	8.62 (<0.02 ^b)	4.154 (=0.125)
Angolan colobus	13.22 (<0.01)	1.132 (=0.568)
Sykes' monkey	2.58 (=0.275)	0.868 (=0.647)
Sanje mangabey	0.311 (=0.734)	8.743 (<0.02)
Yellow baboon	0.648 (=0.723)	5.894 (=0.05)

^a $n = 66, 43, 25$ for USFR and $59, 58, 63$ for MW, for three data collection periods, respectively.

^b Post-hoc comparison of data sets 1 versus 3: $z = 2.29, p = 0.07$.

GLM analysis of colobine monkeys in USFR shows a negative, significant effect of the liana cover and positive, significant effect of TBA for both species (Table 5). The presence of climbers is confirmed to be associated with disturbance and negatively related to canopy cover. For the red colobus the number of disturbance signs has a negative, marginally non-significant effect ($p = 0.117$). Moreover, for the red colobus, MBA has also a negative effect, while for Angolan colobus diversity of trees has a marginally significant, negative effect (Table 5). The deviance explained by the models was 37% for the red colobus and 24% for the Angolan colobus. Models obtained for Sykes' monkey had too low predictive power (<10% of deviance explained) to be meaningful.

3.2. Hunters' interviews

As indicated in Section 2.2.3, hunter surveys were only made in villages near USFR. All respondents belonged to the Wahehe tribe, an ethnic and linguistic group based in Iringa region that has a tradition for hunting. According to respondents (88%, $n = 110$) hunting in USFR had been most intensive in the period 1965–1975 where it primarily was conducted by local people using rifles and pitfalls and oriented towards commercial trade. Bushmeat, elephant tusks and leopard skin were transported at night by porters or hidden between agricultural products on trucks to Iringa town. Regular trade also occurred in Angolan colobus skins that, as far as respondents knew, were sold in Malawi. The disappearance of elephant, buffalo and leopard by the early 1970s (leopard was, however,

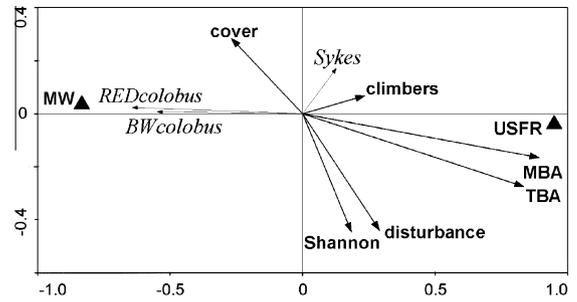


Fig. 3. Biplot of species and environmental variables for Uzungwa Scarp Forest Reserve (USFR) and Mwanihana forest (MW) in the Udzungwa Mountains of Tanzania, based on Redundancy Analysis. See Table 3 for variable abbreviations.

recorded again in 2004 by F.R.) was attributed to the high level of hunting in this period, that also coincided with construction of the TAZARA railway and increased settlement in the Kilombero valley.

A substantial change in hunting practices occurred between 1965–1975 and the mid 1990s. According to respondents, hunters shifted to primarily using snares, traps and dogs and hunted mainly for subsistence with only limited trade within villages. Respondents attributed this change to low profitability of hunting as a result of the disappearance of larger species and only a few medium-sized species remaining, although some mentioned an effect of increased environmental education and law enforcement. These characteristics also describe hunting today, although with notable exceptions. Respondents claimed that they entered the forest less now than ten years ago, and now entered approximately once every three months. According to respondents most natural resource extraction (i.e. timber, poles, firewood, etc.) had shifted from the forest reserve to woodlots and the village forest. This was related to a larger focus on forest conservation through environmental education and preparation for implementation of community-based conservation schemes beginning around year 2000. As a result most respondents indicated that the state of the forest had improved based on their own observations or those of hunters. Hunting was, however, considered the major current threat to the forest (91%) and all acknowledged that hunting, including by using locally produced firearms, takes place in the forest. Thirty-five percentage of respondents considered forest resource extraction

Table 3

Mean (standard deviation) values of vegetation and disturbance parameters (abbreviation and unit in parenthesis) measured along segments of 200 m of transects used for counting primates in Uzungwa Scarp Forest Reserve (USFR) and Mwanihana forest (MW) in the Udzungwa Mountains of Tanzania. The last column shows the results of Kolmogorov–Smirnov comparisons.

Variable	MW ($n = 57$)	USFR ($n = 50$)	H (p)
Mean Basal Area (MBA, m ² /ha)	0.179 (0.072)	0.181 (0.114)	0.925 (0.336)
Total Basal Area (TBA, m ² /ha)	28.3 (14.64)	38.3 (18.51)	9.708 (<0.002)
Diversity (Shannon's index)	1.668 (0.455)	1.937 (0.394)	10.261 (<0.002)
Disturbance (number of signs)	0	5.520 (10.385)	53.738 (<0.001)
Canopy cover (cover, %)	87.94 (27.12)	71.78 (23.92)	25.361 (<0.001)
Stems with climbers (climbers, proportion)	0.346 (0.274)	0.637 (0.241)	24.719 (<0.001)

Table 4

Results of the redundancy analysis (RDA) for primates (Udzungwa red colobus, Angolan colobus and Sykes' monkey) and habitat variables in Uzungwa Scarp Forest Reserve (USFR) and Mwanihana forest (MW) in the Udzungwa Mountains of Tanzania.

Axes	1	2	3	4
Eigenvalues	0.255	0.021	0.003	0.000
Species-environment correlations	0.677	0.255	0.245	0.071
Cumulative percentage variance: species data	25.5	27.6	27.8	27.9
Species-environment relation	91.5	98.9	99.8	100.0

(unspecified) an important activity for their livelihoods and 15% of the rest declared that it was important during times of crisis. No one admitted to practicing hunting but people on average knew of 5–10 individuals in their own village who are active hunters. This is an increase compared to the 5 hunters 10 years before and comparable to the number mentioned in the period 1965–1975 when hunting intensity was perceived as most intensive. Notably, a number of people reported hunting colobus monkeys in the last decade whereas monkeys were rarely mentioned as caught in the previous periods.

4. Discussion

The clear differences we found in the relative abundance of primate populations between the two study forests reinforce earlier findings (DeFries et al., 2010). This study also presents clear evidence of a marked decline of colobines in USFR, calling for urgent protection measures to reduce the risk of local extinction in the near future. We identify species-specific, local drivers that are likely to explain the results. In particular, hunting appears to be the major driver determining the decline of colobines in USFR. Colobus monkeys are arboreal and easily sighted, and hunters (most often using dogs, which are routinely used for chasing ungulates, bush pigs and other terrestrial mammals) can isolate groups in canopy trees where they are easily shot with shotguns. Our results are matched by Oates' (1996) compilation of primate relative abundance in 20 forest sites, demonstrating that as hunting pressure becomes heavier, primate numbers may drop by almost 10-fold. Similarly, surveys in 17 forest sites in French Guiana have shown that hunting pressure was the main factor determining current primate species richness, masking the effects of logging or forest type (de Thoisy et al., 2005).

Gunshots were often heard and hunters with dogs were encountered in USFR during data collection for this and other studies (Topp-Jørgensen et al., 2009; Rovero et al., 2010 and references therein). Differences in protection levels between the two sites clearly underline the much greater disturbance recorded in USFR: MW is inside a well protected National Park where active law enforcement is ensured and no signs of hunting were recorded during our study, even though hunting incidents mainly through finding of snares have been increasingly reported in the last few years. On the contrary, USFR has not received adequate protection (Rovero et al., 2010). Such marked contrast between forests is well highlighted by the community and environment ordination analysis, as the two forests are positioned at the opposite extremes along the axis of major variance. Although to a lesser extent, the two variables indicating forest disturbance are also polarized, with canopy cover intactness pointing towards MW and disturbance signs towards USFR.

Besides indicating an impact of hunting, the lower abundance of colobine monkeys in USFR compared to MW is also related to the greater anthropogenic activity other than hunting and canopy degradation found in USFR. Indeed the effect of these disturbance variables on primates in USFR seems to overwhelm the effect of vegetation structure and floristic composition. Surprisingly however, while MBA is almost equal between forests, both TBA and tree diversity are significantly greater in USFR than MW, and given the positive effect of TBA on both colobus, as demonstrated by the regression analysis (Table 5), this structural variable cannot account for the lower abundance of colobines recorded in USFR. Instead, the higher proportion of trees with climbers in USFR is also retained in the regression models as having a highly negative influence on both species. This variable is an indication of disturbance as climbers mainly occur in the semi-deciduous and regenerating zones (Rovero et al., 2006; Rovero and Struhsaker, 2007), as well

Table 5

Results of Generalized Linear Models^a for the two colobine monkeys in Uzungwa Scarp Forest Reserve. See Table 3 for variable abbreviations.

Species	Variables retained	Z ± SE	p(z)
Udzungwa red colobus	TBA	0.012 ± 0.004	<0.05
	Climbers (angular transformed)	-1.946 ± 0.698	<0.01
	Ln (MBA)	-1.621 ± 0.693	<0.05
	Ln (disturbance signs)	-0.515 ± 0.328	0.117
Angolan colobus	TBA	0.0134 ± 0.006	<0.05
	Diversity	-1.181 ± 0.705	0.094
	Climbers (angular transformed)	-2.864 ± 0.964	<0.01

^a Models were built on $n = 50$ segments of transects of 200 m in length through a GLM with Poisson error distribution following a backward elimination procedure. See section 2.3 for further details.

as around areas where timber is removed. These results are partially discordant with those found for MW using the same analysis (Rovero and Struhsaker, 2007), as red colobus abundance was positively related to MBA (the average size of stems indicating mature forest) while in USFR this variable has a negative effect. This may be an indirect effect of hunting in USFR, forcing the colobus towards sub-optimal areas, where the forest is degraded, i.e. characterized by a large number of small stems.

Although it may be relevant to explaining the lower abundance of colobines in USFR than MW, the habitat analysis remains of limited importance in accounting for the rapid temporal decline of colobines in USFR. Interviews with hunters, however, revealed that hunting has increased during the last decade. Even though relying on hunters' interviews may be problematic, especially for historical trends, results are generally supported by a parallel study that recorded increased density (by 15–19%) of traps targeting small forest ungulates in 2008 (M.R.N., Unpublished results) compared to 1998 (Topp-Jørgensen et al., 2009). The same authors also report a decrease in the relative abundance of ungulates, which is in turn compatible with an increase in primate hunting. Shifting from targeting larger to smaller species is a typical feature in areas where larger species, that generally are preferred and are more vulnerable to hunting pressure (Robinson and Redford, 1986a,b; Fa and Purvis, 1997), have been depleted (Kümpel et al., 2008). The increase in hunting that specifically targets monkeys is consistent with the decreased availability of terrestrial mammals and it is also directly indicated by hunters mentioning colobus monkeys in their catch in the period from 2000 onwards. It remains puzzling that the increased amount of snares reported does not seem to have affected the ground-dwelling Sanje mangabeys. These monkeys may be capable to spot and escape snares. Moreover, they live in large groups, and because we only recorded groups' encounter rates, it is possible that group sizes are being altered by snaring of individuals but this was not detected in our study.

Our results are in line with the results of bushmeat hunting studies from other areas in the tropics, and in particular, they mirror the results of similar studies on primates in central and west-Africa. Canopy-dependent diurnal primates are generally more easily located than ungulates and other ground-dwelling species by hunters in tropical forests because they produce considerable noise when moving or are in social interactions (Bodmer et al., 1988; Oates, 1996). Primates are also often found in groups, which enable a hunter to kill a number of individuals at one time (Peres, 1990; Fitzgibbon et al., 1995). Small forest ungulates, in contrast, tend to be solitary, secretive and partly nocturnal (Bodmer et al., 1988). This may explain the observed tendency of hunters to shift to pursuing primates when harvest rates of duikers drop (Wilkie et al., 1998). The differential impact of hunting among primate

species, with colobines being more affected than cercopithecine monkeys, is also supported by results of other studies (Struhsaker, 2005; Kümpel et al., 2008; Linder and Oates, 2011). Commercial bushmeat markets are well established in the Kilombero valley along the eastern side of USFR. A market survey conducted during 2008–2009 in three villages in the Kilombero valley primarily recorded trade in larger game species hunted in the floodplains of the Kilombero game reserves (M.R.N., Unpublished results). Few forest species were traded in the market but interviews with hunters and traders revealed a demand for colobus monkeys and particularly skins of Angolan colobus, that are traded for approximately 40 US \$ on the local market and transported to Malawi where they are sold at 160 US \$ for uses in traditional medicinal practices.

The relatively higher abundance of Sykes' monkeys and Sanje mangabeys in USFR compared to MW may be due to several reasons. The degree to which hunting impacts primate abundance varies between species (Isaac and Cowlshaw, 2004; Kümpel et al., 2008). Of particular relevance to the higher vulnerability of colobines to hunting may be their limited ecological flexibility as strictly folivorous and canopy-dependent species. Conversely, the more ecologically flexible cercopithecines may be better able to assume niche space left over from hunted species (Struhsaker, 1999; Cowlshaw and Dunbar, 2000; McGraw, 2007). In this respect, Sanje mangabeys and Sykes' monkeys (being mainly frugivorous) use all forest strata, and are much more agile and elusive than colobines. The mangabeys especially, spend as much as 70% of time on the ground (Rovero et al., 2009), making them a difficult target with the hunting technique used for the colobus in USFR while seemingly also capable of avoiding snares set for ungulates. Overall, USFR is also a steeper and rockier escarpment forest, and a large portion of the lower elevation (300–500 m a.s.l.) is characterized by regenerating and degraded forest, while the more intact canopy is found along the distal portions of line transects. These are features that may favour the greater abundance of Sykes' monkeys and Sanje mangabeys. It should also be noted that line-transects are not an efficient method for elusive and ground-dwelling monkeys such as the Sanje mangabeys (Rovero et al., 2006) and therefore our population assessment for this particular species may be inaccurate. Future studies of this IUCN-Endangered and localized species (IUCN, 2011) through focal group follows will be required to estimate population abundance with accuracy. Similarly, continued monitoring will be required to assess the apparent decrease of this species in MW.

4.1. Conclusions and conservation recommendations

Besides the influence of the ecological factors we measured, our results indicate that bushmeat hunting plays a major role in structuring the USFR primate community and that monkey species vary in their degree of vulnerability to hunting, matching results from other studies (Isaac and Cowlshaw, 2004; Linder and Oates, 2011). Thus, while colobines in USFR are threatened by hunting, Sanje mangabeys and Sykes' monkeys do not currently appear to be affected. However, the lower abundance of mangabeys recorded in 2009 compared to previous years deserves further study, as it may be an effect of the escalating overall anthropogenic disturbance in the area. Moreover, while the habitat disturbance from anthropogenic activity in USFR does affect the colobines, there is little evidence of correlation between hunting and other forms of disturbance. Hunters mainly come from the villages neighbouring the higher elevation, western side of the forest, and hunting may therefore be more intense in the mid-to-high elevation portion of the forest. In contrast, as indicated in Section 3.1, most of habitat disturbance signs occur along the lower edge of the forest.

We have presented our results to the Government of Tanzania and other stakeholders (donors, communities, conservation NGOs,

private sector) and encouraged them to join hands towards ensuring effective and long-lasting protection of USFR (Rovero et al., 2010). Key recommendations provided include: (1) increase law enforcement measures, particularly forest patrols that will help decreasing hunting and all other illegal activities recorded which are not permitted by the regulations of Forest Reserves in Tanzania; (2) raise awareness of adjacent communities about forest conservation and the importance of preserving its wildlife, and engage them in monitoring and patrolling initiatives; (3) support communities to establish tree-planting schemes and livelihood alternatives to bushmeat hunting; (4) support the current upgrading from Forest Reserve to Nature Reserve with the financial resources and measures that will effectively result into increased protection (Nature Reserve is a newly-established, IUCN-recognized category of protected areas in Tanzania that should ensure enhanced protection level, even though the current national regulation of Forest Reserves is equally restrictive about resource extraction; URT 2002); and (5) continue to monitor the status of biodiversity and threats. Protection measures should also restore connectivity between USFR and the northern block of protected areas, through the well-researched "Mngeta" conservation corridor (Museo Tridentino di Scienze Naturali, 2007; St. John, 2008).

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