

Using camera trap data to assess the impact of bushmeat hunting on forest mammals in Tanzania

CARLA HEGERL, NEIL D. BURGESS, MARTIN R. NIELSEN, EMANUEL MARTIN
MARCO CIOLLI and FRANCESCO ROVERO

Abstract Bushmeat hunting is a pantropical threat to rain-forest mammals. Understanding its effects on species richness, community composition and population abundance is of critical conservation relevance. As data on the pre-hunting state of mammal populations in Africa are not generally available, we evaluated the impacts of illegal bushmeat hunting on the mammal community of two ecologically similar forests in the Udzungwa Mountains of Tanzania. The forests differ only in their protection status: one is a National Park and the other a Forest Reserve. We deployed systematic camera trap surveys in these forests, amounting to 850 and 917 camera days in the Forest Reserve and the National Park, respectively, and investigated differences between the two areas in estimated species-specific occupancies, detectabilities and species richness. We show that the mammal community in the Forest Reserve is degraded in all aspects relative to the National Park. Species richness was almost 40% lower in the Forest Reserve (median 18 vs 29 species, highest posterior density intervals 15–30 and 23–47, respectively). Occupancy of most species was also reduced significantly and the functional community appeared significantly altered, with an increase in rodents, and loss of large carnivores and omnivores. Overall, our results show how ineffective reserve management, with almost absent law enforcement, leads to uncontrolled illegal hunting, which in turn has a significant impact on the mammal fauna of globally important sites for conservation.

Keywords Biodiversity conservation, bushmeat, Eastern Arc, poaching, rainforest, Tanzania, Udzungwa

CARLA HEGERL (Corresponding author) Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden. E-mail carlahegerl@gmail.com

NEIL D. BURGESS UNEP–WCMC, Cambridge, UK, and CMEC, The Natural History Museum, University of Copenhagen, Denmark

MARTIN R. NIELSEN Department of Food and Resource Economics, University of Copenhagen, Frederiksberg, Denmark

EMANUEL MARTIN* Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania

MARCO CIOLLI Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy

FRANCESCO ROVERO* Tropical Biodiversity Section, MUSE—Museo delle Scienze, Trento, Italy

*Also at: Udzungwa Ecological Monitoring Centre, Udzungwa Mountains National Park, Tanzania

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Introduction

The hunting of wild animals for household consumption or trade is considered one of the biggest threats to the mammal fauna of tropical rainforests (Fa et al., 2002; Milner-Gulland & Bennett, 2003) and is particularly serious in Africa (Nielsen, 2006; Fa & Brown, 2009; Effiom et al., 2013; Taylor et al., 2015). Rainforests are often defaunated by bushmeat hunting, as harvest rates often exceed reproduction rates where demand for bushmeat is high (Robinson & Bennett, 2004; Rist et al., 2009). Large mammals with slow growth and reproduction rates are usually the first to become locally extinct (Brashares et al., 2001; Poulsen et al., 2011). Medium-sized terrestrial mammals are hunted using non-specific techniques, which can cause shifts in the faunal species composition (Jerozolinski & Peres, 2003). Non-preferred mammals are also affected through bycatch and competitive or predator release (Redford, 1992; Peres & Dolman, 2000; Linder & Oates, 2011), with repercussions for functional plant–animal relations (Wright, 2003) and ecosystem stability (Redford, 1992; Galetti & Dirzo, 2013).

Understanding the effects of hunting on mammal communities is of critical conservation relevance (Cullen et al., 2000; Nielsen, 2006; Bennett et al., 2007) and may be addressed indirectly by comparing forests with similar ecological characteristics and contrasting hunting pressure, because a temporal analysis within one area is often unfeasible because of a lack of data on the pre-hunting state. A robust comparison, however, needs to be based on sufficient ecological similarity of the studied sites and on unbiased estimators of the occurrence or abundance of target species and communities that account for imperfect detection (Yoccoz et al., 2001; Williams et al., 2002). For terrestrial mammals, camera trapping coupled with occupancy analysis meet such requirements (e.g. Ahumada et al., 2011; Rovero et al., 2014a) and are amenable to standardization (Silveira et al., 2003; Tobler et al., 2008; O'Brien, 2011; Rovero et al., 2013).

We conducted our study in the Udzungwa Mountains of Tanzania within the Eastern Arc, a region of outstanding value for biological endemism and biodiversity conservation

(Burgess et al., 2007; Rovero & De Luca, 2007; Rovero et al., 2009, 2014b). The human population on the eastern lowland margins of the forest has been increasing in recent decades as the fertile land facilitates commercial production of sugar cane and rice (National Bureau of Statistics, 2013). Bushmeat hunting is illegal in all reserves within the Udzungwa range but is still widespread in reserves with ineffective management regimes (Nielsen, 2006; Topp-Jørgensen et al., 2009). The aim of this study was to understand whether and how intensive hunting altered the mammal community of a Forest Reserve with low management effectiveness, in comparison to a well-protected forest area within a National Park where hunting does not occur but which has comparable elevation range, forest type and rainfall patterns. We used camera trapping to collect data on the presence of mammals. The occupancy analytical framework we adopted corrects occupancy, or probability of presence, for potential bias as a result of varying species- and site-specific detectabilities (MacKenzie et al., 2002, 2005). This facilitates a sound comparison of hunted communities, unlike previous studies on the effects of bushmeat hunting in this area, which were based on raw indices of abundance (Topp-Jørgensen et al., 2009; Rovero et al., 2012). Specifically, we aimed to compare the mammal communities of the two forests from three perspectives: (1) species richness, (2) species-specific occupancy and detectability, and (3) functional composition.

Study area

Uzungwa Scarp Forest Reserve and Mwanihana Forest are the two largest continuous forest areas within the Udzungwa Mountains and are critical for the conservation of most of the mammalian diversity in Udzungwa forests (Shangali et al., 1998; Rovero & De Luca, 2007; DeFries et al., 2010; Rovero et al., 2012). Mwanihana Forest covers an area of 177 km² within the north-eastern part of Udzungwa Mountains National Park (1,990 km²; Fig. 1), which was established in 1992. Uzungwa Scarp Forest Reserve covers 200 km² and lies c. 150 km south-west of the National Park; it was gazetted in 1929 and is currently a proposed Nature Reserve. Both forests are located on the eastern slopes of steep escarpments of the Udzungwa Mountains and have similar ecological characteristics (Table 1): both sites are covered by continuous forests, from lowland deciduous to submontane and montane evergreen forests, on an elevational gradient of c. 300 to > 2000 m. They receive similar amounts of rainfall (2,000–2,500 mm per year), have similar temperature ranges throughout the year and grow on ancient mountains with a common geological history (Lovett, 1993; Rovero et al., 2012).

The forests differ, however, in their conservation effectiveness (Table 1): as a part of Udzungwa Mountains

National Park, Mwanihana Forest is managed by Tanzania National Parks, the well-resourced National Parks agency, and therefore hunting is rare here (Museo Tridentino di Scienze Naturali, 2007; Rovero et al., 2014a). Uzungwa Scarp Forest Reserve is managed by the Tanzania Forest Service, with few resources and lower effectiveness. A 2011 survey on the conservation state of protected areas within the Eastern Arc highlighted that illegal bushmeat hunting is the main threat to biodiversity in the Reserve, whereas it has little or no impact in the National Park (Eastern Arc Mountains Conservation Endowment Fund, 2013). The survey also suggested that indicators of conservation effectiveness are an appropriate way to approximate hunting pressure, as evidence suggests that poor law enforcement is the main reason for increased hunting activity (Nyundo et al., 2006; Topp-Jørgensen et al., 2009; Rovero et al., 2012).

Many large-bodied mammals (> 4 kg), including elephant *Loxodonta africana*, buffalo *Syncerus caffer* and leopard *Panthera pardus*, were locally extinct in the Reserve by the early 1970s as a result of intensive hunting for bushmeat trade (Rovero et al., 2012). As a consequence, hunters shifted their practices towards subsistence hunting, and snares and pitfall traps are now the most commonly used tools. Hunters increase the probability of catching preferred species by adapting the size of the snares and placing them on the trails used by target species. Although there is some variation in hunters' preferences, evidence from snare counts along line transects and interviews with hunters suggest that forest-dwelling, small- to medium-sized ungulates (Abbott's duiker *Cephalophus spadix*, Harvey's duiker *Cephalophus harveyi*, blue duiker *Cephalophus monticola* and suni *Neotragus moschatus*) are the preferred species (Topp-Jørgensen et al., 2009; Rovero et al., 2010, 2012). Other species, such as giant pouched rat *Cricetomys gambianus*, are also caught occasionally, and predominantly arboreal primates are driven by dogs into isolated trees and then shot (Rovero et al., 2012).

Methods

Data collection

In Uzungwa Scarp Forest Reserve two grids of 15 digital camera traps (UOVision IR+, UOVision Technology, Shenzhen, China) were set sequentially at a density of 1 camera per km². The first grid was located in the northern, remote part of the Reserve (Fig. 1), at 1,653–1,848 m, and was active during 15 December 2013–14 January 2014. The second grid was located in the southern part of the Reserve and was active during 20 January–25 February 2014, at 372–1,564 m (Supplementary Fig. S1). Each camera was set on a tree to record a trail c. 2 m away. The area within the sensor field of the camera was cleared of ground vegetation

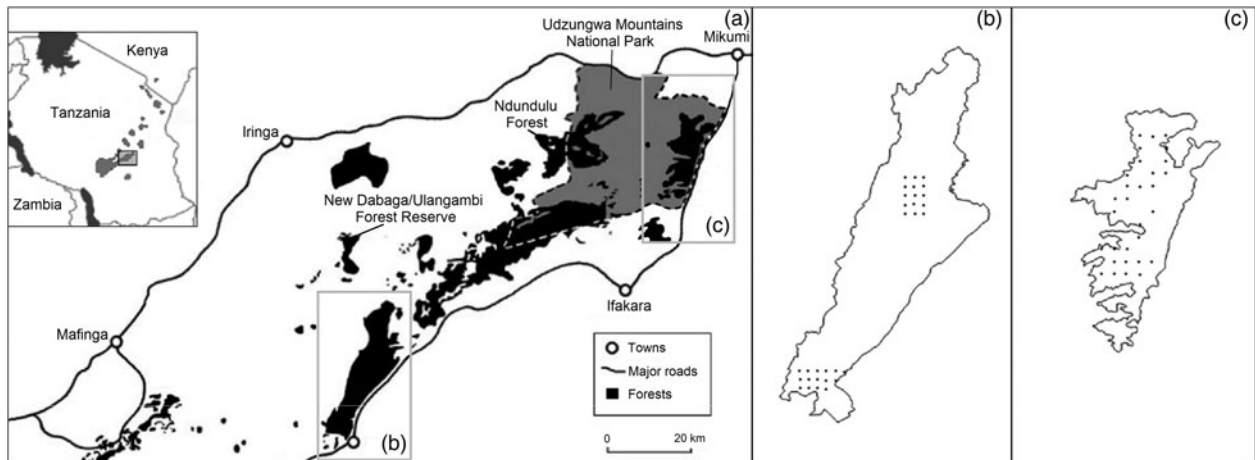


Fig. 1 Location of Uzungwa Scarp Forest Reserve and Mwanihana Forest in the Udzungwa Mountains of south-central Tanzania (a), and the location of camera traps in the Reserve (b) and Mwanihana Forest (c).

for better visibility. Elevation, canopy cover (open, closed) and the size (i.e. width) of the adjacent trail (small, medium, large) were recorded at each camera site. The distance to the forest edge (which coincides with the Reserve border) was calculated using *QGIS v.2.2.0* (OSGeo, Beaverton, USA). To account for variation in camera trap models used in the Reserve and in Mwanihana Forest we set one camera of each model one above the other on the same tree at two sites in the Reserve and compared the event count per species recorded by each model using a Wilcoxon test. The results indicated a marginally significant trend towards higher event counts with the cameras used in Mwanihana Forest (Wilcoxon test, $n = 8$, $P = 0.062$). However, we consider this trend unlikely to influence our results, as our analyses are based on presence and absence of species rather than their relative event count.

Camera trap data collected in Mwanihana Forest in 2013 were available through the Tropical Ecology Assessment and Monitoring (TEAM) Network project. According to a standardized protocol for monitoring terrestrial vertebrates (TEAM Network, 2011) 60 Reconyx RM45 camera traps (RECONYX, Holmen, USA), distributed over three sequential arrays of 20 cameras, were placed at a density of 1 camera per 2 km^2 for a minimum of 30 days. Camera trapping was conducted during July–November 2013. To improve comparability between data from the Reserve and Mwanihana Forest 30 of the 60 cameras were selected according to the following criteria: all cameras at $> 1,600 \text{ m}$ ($n = 4$) were included and the remaining 26 were chosen at random from all cameras located at $> 800 \text{ m}$. We proceeded in this way to improve the comparability in elevation range between the camera sites in the Reserve and Mwanihana Forest: on average the 60 camera trap sites in Mwanihana Forest were located at lower elevations than those in the Reserve.

Data analyses

We used the raw data (image count) to derive standard descriptors, as follows: we counted all photographs of a species taken within an hour as one event (hourly event count), a commonly used interval to reduce the effect of multiple counts of lingering individuals (e.g. Bowkett et al., 2008; Tobler et al., 2008; Rovero & Marshall, 2009). We calculated a relative abundance index (species-specific number of events per 100 days of camera trapping) and naïve occupancy (proportion of all sites occupied by a species) as raw indices of abundance for basic comparisons between the two sites and with other similar studies in the area. All descriptive statistics were calculated using *PAST v. 2012* (Hammer et al., 2001).

To compare the species richness at both sites we estimated the number of species present in each forest according to the model developed by Dorazio et al. (2006), which accounts for imperfect detection and solves the ambiguity between absence and non-detection (MacKenzie et al., 2005; Dorazio et al., 2006). Specifically, this multispecies occupancy analytical approach models heterogeneity in species occurrence and detectability by considering species-specific random intercepts (i.e. mean occupancy/detectability on the linear predictor with a logit link) drawn from a normal distribution with community-level parameters (the mean and variance of the normal distribution). The outcome is a posterior Bayesian distribution of species richness. We used the *R2WinBUGS* package in *R v. 3.0.3* (R Development Core Team, 2013) to execute simulations with five Markov chains, 55,000 iterations for each chain, discarding 5,000 iterations at the beginning (burn-in) and setting the thinning rate to 50; this returns 5,000 samples from the posterior distributions. Species accumulation curves with cumulative sampling effort (i.e. camera days)

TABLE 1 Summary of ecological characteristics and indicators of conservation effectiveness in Uzungwa Scarp Forest Reserve and Mwanihana Forest in the Udzungwa Mountains of Tanzania (Fig. 1), based on a dossier by the Government of Tanzania (2011) and a report by the Eastern Arc Mountains Conservation Endowment Fund (2013) on the conservation state of the protected areas of the Udzungwa.

Characteristics & indicators	Uzungwa Scarp Forest Reserve	Mwanihana Forest
Ecological factor (Lovett, 1993; Government of Tanzania, 2011)		
Area	200 km ²	177 km ²
Altitudinal range	300–2,068 m	300–2,100 m
Mean annual rainfall	1,800–2,000 mm	1,750–2,000 mm
Temperature range	19–27°C	21–31°C
Forest types & elevation (m)	Woodland; 150–300 m Lowland forest; 300–800 m Submontane forest; 800–1,400 m Montane forest; > 1,400 m	
Management effectiveness indicator (Eastern Arc Mountains Conservation Endowment Fund, 2013)		
Vehicles (cars & motorbikes)	None	Several
Annual budget	USD c. 1,000	USD c. 400,000
METT score*	52%	82%
Permanent staff	1	78
Infrastructure (buildings, etc.)	None	Considerable
Relevant Ministry	Natural Resources & Tourism	Natural Resources & Tourism
Government agency	Tanzania Forest Service	Tanzania National Parks
Status	Forest Reserve (being upgraded to Nature Reserve status)	National Park (1992); formerly Forest Reserve

*METT (Management Effectiveness Tracking Tool) is a standardized measure of conservation effectiveness developed by WWF and the World Bank, which in this case included 30 factors with conservation relevance (METT < 30%, poor; 31–45%, average; 45–60%, good; > 60%, very good effectiveness; Eastern Arc Mountains Conservation Endowment Fund, 2013)

were calculated for both sites to check if the sampling effort captured a substantial portion of the species in the community (Rovero et al., 2014a). Instead of showing the quantile-based credible intervals we used the *coda* package in R to calculate the highest posterior density intervals (Chen et al., 2000) of the posterior distributions of species richness, given these are skewed distributions.

We modelled species-specific detectabilities (p , probability of detection) and occupancies (ψ , proportion of sites occupied by a species), using single-species occupancy models (MacKenzie et al., 2006). Splitting the total number of trapping days into 5-day intervals, we used repeated samplings to estimate p . We performed two sets of occupancy analyses using the *unmarked* package in R (Fiske & Chandler, 2011): firstly, we computed basic null models for species with more than five events, to compare the estimates between the two sites; secondly, we modelled ψ and p with relevant habitat covariates for species with 10 or more events for Uzungwa Scarp Forest Reserve. An equivalent analysis for Mwanihana Forest using data from the TEAM Network project (i.e. 60 camera trap sites) was conducted by Rovero et al. (2014a) and we used it for reference in the comparison of potential drivers of abundance of selected species. For the Reserve, the following habitat covariates were included: (1) the distance to the forest edge, coinciding with the Reserve border (affecting p and ψ), assuming that species are influenced by higher hunting pressure in central forest areas and by higher habitat degradation towards the

forest edges (Rovero et al., 2012); (2) the size of the trail where the camera trap was set (affecting p), assuming that species seek to avoid snares, which are preferably placed along animal trails; and (3) the canopy cover (affecting ψ), assuming that species have preferences regarding the openness of their habitat. Models were executed for all combinations of the selected covariates and ranked according to the Akaike information criterion (AIC) as a standard index for model comparison (Burnham & Anderson, 2002; MacKenzie et al., 2006). We used model averaging to identify the critical covariates from the top-ranked models with similar AIC ($\Delta\text{AIC} < 2$; Burnham & Anderson, 2002). We calculated the relative importance of the model parameters using the package *AICcmodavg* in R (Mazerolle, 2012).

To compare the functional community composition between the two sites we grouped species into five functional guilds (carnivores, herbivores, insectivores, omnivores and rodents; Table 2) and counted the number of events within each guild. We tested for differences in the proportional event count of each guild between the two forests by using a χ^2 test.

Results

Sampling effort was 850 (mean per camera 28.3) and 917 (mean per camera 30.6) camera days in Uzungwa Scarp Forest Reserve and Mwanihana Forest, respectively, yielding

TABLE 2 Medium-to-large mammals detected by camera trapping in Uzungwa Scarp Forest Reserve (USFR) and Mwanihana Forest (MF), Tanzania (Fig. 1), with mass, functional guild, no. of events, relative abundance index, and naïve occupancy (no. of occupied sites divided by total no. of sites).

Species	Mass (kg)	Functional guild	No. of events		Relative abundance index		Naïve occupancy	
			USFR	MF	USFR	MF	USFR	MF
Afrotheria								
Tree hyrax <i>Dendrohyrax validus</i>	2.95	Omnivore	3	41	0.35	4.47	0.10	0.37
African elephant <i>Loxodonta africana</i>	3,900	Herbivore		5		0.55		0.10
Four-toed sengi <i>Petrodomus tetradactylus</i>	0.19	Insectivore		1		0.11		0.03
Chequered sengi <i>Rhynchocyon cirnei</i>	0.49	Insectivore	76		8.94		0.60	
Grey-faced sengi <i>Rhynchocyon udzungwensis</i>	0.80	Insectivore		42		4.58		0.27
Carnivores								
Marsh mongoose <i>Atilax paludinosus</i>	3.30	Carnivore		4		0.44		0.10
Bushy-tailed mongoose <i>Bdeogale crassicauda</i>	1.55	Carnivore	49	169	5.76	18.43	0.37	0.77
Lowe's servaline genet <i>Genetta servalina lowei</i>	1.06	Carnivore	37	17	4.35	1.85	0.53	0.37
Honey badger <i>Mellivora capensis</i>	8.50	Omnivore	1	8	0.12	0.87	0.03	0.17
African palm civet <i>Nandinia binotata</i>	1.90	Carnivore	17	7	2.00	0.76	0.27	0.17
Leopard <i>Panthera pardus</i>	52	Carnivore		3		0.33		0.07
Primates								
Sanje mangabey <i>Cercocebus sanjei</i>	8	Omnivore	23	81	2.71	8.83	0.20	0.77
Sykes' monkey <i>Cercopithecus mitis</i>	5	Omnivore	8	5	0.94	0.55	0.23	0.17
Udzungwa red colobus <i>Procolobus gordonorum</i>	10	Omnivore		2		0.22		0.07
Rodents								
Giant pouched rat <i>Cricetomys gambianus</i>	1.24	Rodent	384	247	45.18	26.94	0.83	0.70
Tanganyika mountain squirrel <i>Paraxerus vexillarius</i>	0.68	Rodent	57	27	6.71	2.94	0.33	0.43
Greater cane rat <i>Thryonomys swinderianus</i>	4.6	Rodent		1		0.11		0.03
Ungulates								
Harvey's duiker <i>Cephalophus harveyi</i>	12	Herbivore	23	188	2.71	20.50	0.48	0.73
Blue duiker <i>Cephalophus monticola</i>	6.3	Herbivore	6		0.71		0.21	
Abbott's duiker <i>Cephalophus spadix</i>	56	Herbivore	10	32	1.18	3.49	0.28	0.57
Suni <i>Neotragus moschatus</i>	6.5	Herbivore	16	88	1.88	9.60	0.21	0.50
Bush pig <i>Potamochoerus larvatus</i>	48.78	Omnivore	4	8	0.47	0.87	0.07	0.17
African buffalo <i>Syncerus caffer</i>	580	Herbivore		5		0.55		0.10
Bushbuck <i>Tragelaphus scriptus</i>	43	Herbivore		1		10.11		0.03

1,698 photographs (714 in the Reserve, 984 in Mwanihana) of 15 and 23 species in the Reserve and Mwanihana Forest, respectively (Table 2). The species accumulation curves reached a plateau by 200 and 250 camera days in the Reserve and Mwanihana Forest, respectively (Supplementary Fig. S2).

Estimated species richness differed significantly between the two sites, with a median of 18 (mean 19.3, highest posterior density interval 15–30) and 29 species (mean 31.5, highest posterior density interval 23–47) in the Reserve and Mwanihana Forest, respectively (i.e. mammal richness was almost 40% lower in the forest with hunting pressure; Fig. 2). At the species level, null models could be fitted for seven species detected in both forests (Harvey's duiker, suni, giant pouched rat, Tanganyika mountain squirrel *Paraxerus vexillarius*, Sanje mangabey *Cercocebus sanjei*, bushy-tailed mongoose *Bdeogale crassicauda* and palm civet *Nandinia binotata*; Table 3) and ψ was lower in the Reserve for all of them except the giant pouched rat and the palm civet.

The lowest estimates of ψ in the Reserve relative to the Forest were found for Sanje mangabey (Reserve: 0.23; Mwanihana: 0.83), suni (Reserve: 0.25; Mwanihana: 0.51) and bushy-tailed mongoose (Reserve: 0.42; Mwanihana: 0.78), whereas the opposite pattern was found for the giant pouched rat (Reserve: 0.84; Mwanihana: 0.70); for Harvey's duiker the model did not converge (Table 3). Detectability was lower in the Reserve for Harvey's duiker (0.12 vs 0.55), suni (0.22 vs 0.41) and bushy-tailed mongoose (0.28 vs 0.43), and higher for Tanganyika mountain squirrel (0.44 vs 0.18) and palm civet (0.28 vs 0.12); for the giant pouched rat and the Sanje mangabey there was no difference in detectability between the two sites.

For five of the six species that were present at both sites and for which there were too few capture events for occupancy models, the relative abundance index was lower in the Reserve compared to Mwanihana Forest (tree hyrax *Dendrohyrax validus*, 0.25 vs 4.47; honey badger *Mellivora capensis*, 0.12 vs 0.87; Harvey's duiker, 2.71 vs 20.50;

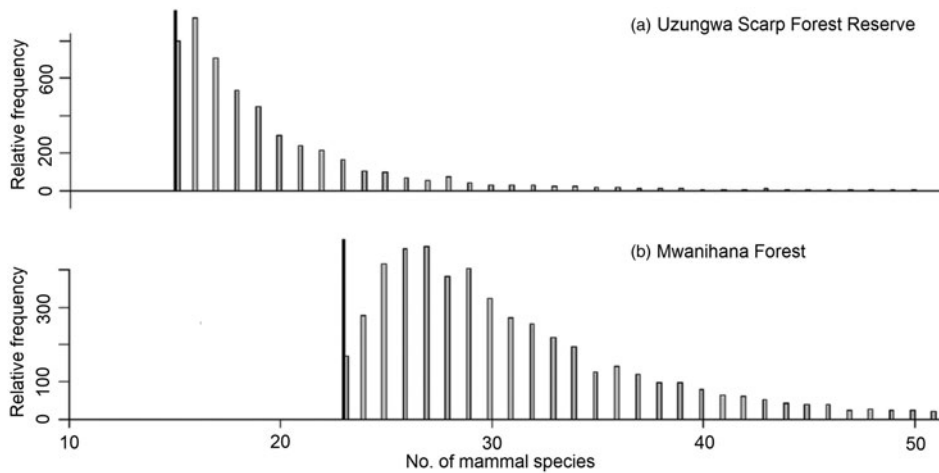


FIG. 2 Bayesian posterior distribution of species richness in (a) Uzungwa Scarp Forest Reserve and (b) Mwanihana Forest (Fig. 1). The analysis follows Dorazio et al. (2006); the vertical black line is the observed species richness, 15 and 23 in the Reserve and Mwanihana Forest, respectively, whereas the estimated median richness is 18 (mean 19.3, highest posterior density interval 15–30) and 29 species (mean 31.5, highest posterior density interval 23–47), respectively.

Abbott's duiker, 1.18 vs 3.49; bush pig *Potamochoerus larvatus*, 0.47 vs 0.87); only Sykes' monkey *Cercopithecus mitis* showed the opposite pattern (0.94 vs 0.23).

Occupancy models with habitat covariates for the Reserve could be fitted for the seven species that were found at both sites, as well as for Lowe's servaline genet *Genetta servalina lowei* and the chequered sengi *Rhynchocyon cirnei* (see Table 4 and Supplementary Table S1 for details of model selection). For all species at least one covariate affected p or ψ ; specifically, p was affected by the distance to the forest edge, the trail size or both, whereas canopy cover did not have a significant effect for any species. The Tanganyika mountain squirrel and chequered sengi were the only species for which distance to the forest edge had a positive effect on ψ .

The functional community composition in the Reserve was significantly different from that in Mwanihana Forest (χ^2_4 ($N_{\text{Reserve}} = 714$, $N_{\text{Forest}} = 984$) = 292.18, $P < 0.001$). All functional guilds were affected and the biggest differences were found for rodents, which were more abundant in the Reserve, and herbivores, which were less abundant (Fig. 3).

Discussion

We have shown the potential of camera trapping in the study of bushmeat hunting, when standardized and unbiased metrics of richness and relative abundance are required. Camera trapping has only rarely been used in research on the intensity and effects of bushmeat hunting (but see Coad et al., 2013). Previous studies in the Udzungwa Mountains have been based on line transects, and dung and track counts (Topp-Jørgensen et al., 2009; Nielsen & Treue, 2012); these methods do not facilitate accurate species identification (Bowkett et al., 2013) and do not consider detectability. Our results are therefore more likely to reflect accurately the effects of bushmeat hunting on the mammal community in Uzungwa Scarp Forest Reserve.

Our comparison between the two study sites is based on the assumption that both forests originally held equivalent communities of mammals, given their similar ecological and climatic characteristics (Table 1). The Udzungwa-endemic Sanje mangabey is found only in these two forests, and many large-bodied mammals that were once present at both sites became locally extinct in the Reserve following intensive hunting in the 1970s (Rovero et al., 2012). We therefore argue that differences in the mammal communities are largely attributable to differences in hunting pressure. Two exceptions are the grey-faced sengi *Rhynchocyon udzungwensis*, which is found only in Mwanihana (and western Udzungwa; Rovero et al., 2008), and the blue duiker, which is found in the Reserve and a few other forests but not in Mwanihana (Rovero & De Luca, 2007). The absence of these species in one of the two forests may be attributable to biogeographical reasons. Our results indicate that hunting has significantly altered the mammal community in the Reserve, and the loss of 40% of mammal species there demonstrates that the level of hunting pressure is not sustainable and may lead to ecological destabilization, as ecosystem resilience and stability are connected to biodiversity (Terborgh et al., 2008; Wilkie et al., 2011; McCauley et al., 2012; Effiom et al., 2014). With fewer species, webs of ecological interactions are reduced in complexity (Solé & Montoya, 2001) and the system's resilience in response to disturbances decreases (Peterson et al., 1998; Galetti & Dirzo, 2013). Furthermore, studies in various locations have highlighted the negative implications of loss of access to bushmeat as an essential source of protein and micro-nutrients for human welfare, and for children in particular (Fa et al., 2003, 2015; Golden et al., 2011), and the loss of essential non-timber forest products indirectly as a result of altered seedling demographics over time (Muller-Landau, 2007; Wright et al., 2007a; Poulsen et al., 2013; Schaafsma et al., 2014).

TABLE 3 Summary of null-model parameter estimates from occupancy modelling on the seven species recorded > 10 times by camera traps in both Uzungwa Scarp Forest Reserve (USFR) and Mwanihana Forest (MF), in the Udzungwa Mountains of Tanzania (Fig. 1), with estimates of occupancy (ψ) and detectability (p).

Species	$\psi \pm \text{SE}$		$p \pm \text{SE}$	
	USFR	MF	USFR	MF
Harvey's duiker	0.85 ± 0.26	0.73 ± 0.08	0.12 ± 0.04	0.55 ± 0.04
Suni	0.25 ± 0.10	0.51 ± 0.09	0.22 ± 0.08	0.41 ± 0.05
Giant pouched rat	0.84 ± 0.07	0.70 ± 0.08	0.60 ± 0.04	0.62 ± 0.04
Tanganyika mountain squirrel	0.34 ± 0.09	0.59 ± 0.15	0.44 ± 0.06	0.18 ± 0.05
Sanje mangabey	0.23 ± 0.09	0.83 ± 0.09	0.27 ± 0.07	0.31 ± 0.04
Bushy-tailed mongoose	0.42 ± 0.11	0.78 ± 0.08	0.28 ± 0.06	0.43 ± 0.04
Palm civet	0.30 ± 0.10	0.29 ± 0.17	0.28 ± 0.07	0.12 ± 0.07

TABLE 4 Summary of results of occupancy analyses with habitat covariates for mammals detected in Uzungwa Scarp Forest Reserve, Tanzania (Fig. 1). Models tested the influence of canopy cover on occupancy ψ (canopy [coverage]), distance to the forest edge on occupancy ψ (edge), distance to the forest edge on detectability p (edge), and trail size on detectability p (trail [size]), with significant factor levels (i.e. small/medium/large trail size, open/closed canopy) of factorial covariates in []. A significant ($P < 0.05$) influence of a covariate is indicated by – for a negative and + for a positive effect. A marginally significant influence ($P < 0.10$) is shown in ().

Species	ψ (canopy [coverage])	ψ (edge)	p (edge)	p (trail [size])
Harvey's duiker			–	
Suni				[small] (–) [medium] (–)
Giant pouched rat			–	[small] (–)
Tanganyika mountain squirrel		+	(+)	
Sanje mangabey			–	
Bushy-tailed mongoose			–	[small] (–)
Palm civet				[small] (+)
Lowe's servaline genet				[small] (–)
Chequered sengi		(+)		[small] (+)

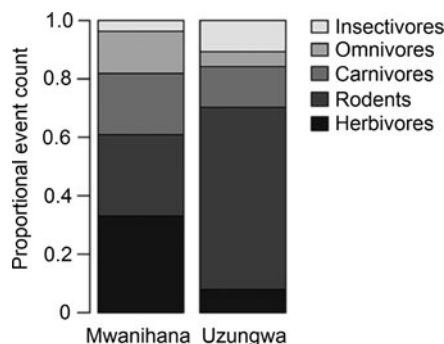


FIG. 3 Proportional event count for each functional guild in Uzungwa Scarp Forest Reserve and Mwanihana Forest (Fig. 1). The community composition is significantly different between the two sites ($\chi^2_4 (N_{\text{USFR}} = 714, N_{\text{MF}} = 984) = 292.18, P < 0.001$).

For the majority of species, occupancy estimates were lower in the Reserve than in Mwanihana Forest, and for five of the six species with too few captures to estimate occupancy both the relative abundance index and naïve occupancy were lower in the Reserve. Species' responses to hunting are influenced by species-specific vulnerabilities

(Isaac & Cowlshaw, 2004; Linder & Oates, 2011), and indirectly by the alterations of interspecific interactions (i.e. competitive and/or predator release; Peres, 2000). Not surprisingly the relative abundance index for all preferably hunted species still present in both forests was substantially lower in the hunted forest. The number of hourly events was too low for model convergence for several of these species, such as Abbott's duiker, blue duiker and tree hyrax. The occupancy estimate for suni in the reserve was half that estimated for Mwanihana Forest. For the Udzungwa-endemic Sanje mangabey, occupancy in the Reserve was nearly a quarter of that in Mwanihana Forest, contrary to an earlier study that reported this species as common in both forests as a result of its ecological adaptability (Rovero et al., 2012). The study was based on line transect counts mainly in the lower zones of the forests but our results are based on a more robust method and cover a more representative area, and therefore may be more accurate. The occupancy of species not preferred by hunters, such as the bushy-tailed mongoose, also differed between the two forests; this may reflect indirect effects such as competitive and/or predator release. Such processes, which are difficult to study, may be

common in hunted rainforests (Peres & Dolman, 2000; Wright, 2003); for example, a study based on repeated transect surveys in the adjacent Kilombero nature reserve found declining densities of Abbott's duiker and bush pig associated with increased densities of blue and Harvey's duikers, interpreted as a likely effect of competitive release (Nielsen, 2011).

The interpretation of differences in detectability between forests is not straightforward, as it may be influenced by a range of factors (Rovero et al., 2014a). It highlights the importance of accounting for detectability when comparing populations, and how assessments based on raw indices (e.g. Topp-Jørgensen et al., 2009; Rovero et al., 2012) may lead to biased results; for example, lower detectabilities for the hunted Harvey's duiker and suni in the Reserve may be explained by decreased mobility and/or reduced home ranges as a result of higher levels of human disturbance (Newing, 2001; Mockrin, 2010). Furthermore, hunting avoidance behaviour may explain the influence of the size of animal trails on the detectability of several species, as hunters in the Reserve prefer to set their snares on wide animal trails (M.R. Nielsen, unpubl. data). Studies on behavioural adaptations to hunting are rare, although some evidence exists for duikers and primates in Gabon and Ivory Coast (Bshary, 2001; Croes et al., 2007). Weckel et al. (2006) and Harmsen et al. (2010) found that medium-sized mammals avoided larger trails when facing a higher risk of encounters with predators, indicating that mammals adapt their behaviour to specific dangers.

The differences in functional composition of the two communities appeared to be explained by the hunting levels in the Reserve: whereas the variance in the relative abundances of all five guilds was low in Mwanihana Forest (0.01), the Reserve was dominated by rodents at the expense of all other guilds except insectivores, and the variance was six times higher (0.06, Fig. 3). These findings match those of Ahumada et al. (2011), who compared several mammal communities and showed how markedly functional guilds can differ in their responses to human disturbance. Such changes in community composition may also affect plant-animal interactions in the Reserve (Fjeldså & Lovett, 1997), including seed predation and dispersal, seedling survival and plant regeneration (Wright, 2003; Muller-Landau, 2007; Wright et al., 2007a,b).

Two potential confounding factors need to be considered when interpreting our results. Firstly, besides hunting, logging and firewood collection may also affect mammal abundance and eventually lead to local extinction of some species (Laurance et al., 2006; Arroyo-Rodríguez & Dias, 2010; Rovero et al., 2012) and increased density of others (Nummelin, 1990; Wilkie & Finn, 1990). Intensive logging occurs mainly towards the lower edge of the Reserve, and therefore we placed camera traps in the forest interior, 231–4,586 m from the forest edge, where logging does not

occur and hunting is likely to be more intense (Rovero et al., 2012; C. Hegerl, unpubl. data). Secondly, the differences in sampling season and area coverage between the two sites may be a source of bias in our results. However, we believe that seasonal fluctuations in species' abundance and detectability cannot account for the differences we found, as despite extensive work in both forests no seasonal movements in or out of the forest area have been documented for the medium-sized forest-dwelling species considered in this study. Furthermore, preliminary results from a study that compared occupancy and detectability between wet and dry seasons in Mwanihana Forest indicate that neither parameter changed significantly (E. Martin & F. Rovero, unpubl. data). The surveying of a smaller area in the Reserve compared to Mwanihana Forest was a result of logistical constraints related to the accessibility and roughness of the terrain in the former relative to the latter. Furthermore the 2 km grid cell size adopted by the TEAM protocol in Mwanihana Forest is mainly relevant to large mammals with home ranges larger than the grid cell size, whereas our study focused on small- to medium-sized mammals with home ranges that we assumed to be smaller than the grid cell size.

Although our study was limited to some extent by sample size, we provide evidence of the impact of bushmeat hunting on the mammal community in one of the most biologically important forests within the Udzungwa Mountains and the whole Eastern Arc. Enforcement of existing regulations prohibiting hunting is important, but evidence from the adjacent Kilombero Valley indicates that the availability of alternative income-generating options has a greater effect on the decision whether or not to engage in hunting (Nielsen et al., 2014). The study found that 90% of the actors in the bushmeat value chain would cease their illegal activities if an alternative job paying c. USD 3 per day was available. Local communities must be given the expertise and power to take an active part in the implementation of conservation measures, as long-term changes will only be possible if local livelihoods are not negatively affected (Nielsen & Treue, 2012).

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Biographical sketches

CARLA HEGERL is interested in applied conservation and ecological modelling. NEIL BURGESS works at the interface between science and policy and has managed large-scale conservation projects in Tanzania. MARTIN NIELSEN works on the human dimensions of wildlife management, focusing on bushmeat hunting and the design of management strategies. EMANUEL MARTIN's research focuses on the use of camera traps for studying temporal and spatial variations of forest mammals in the Udzungwa Mountains. MARCO CIOLLI is a forest ecologist whose research focuses on the application and development of geographical information systems, and on forestry and ecological planning in mountain environments. FRANCESCO ROVERO is a zoologist and conservation ecologist who focuses on ecological modelling of tropical forest mammals, and uses camera trapping extensively.