

Modelling fine-scale habitat associations of medium-to-large forest mammals in the Udzungwa Mountains of Tanzania using camera trapping

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We used camera trap data collected in 2013 from 60 locations in the Udzungwa Mountains of Tanzania to determine fine-scale habitat associations for medium-to-large mammal species. The area is outstanding for biodiversity and endemism in Africa, particularly for mammals. Each camera trap sampled for 30 days and the survey yielded 12,911 images of 26 species. We used generalized linear modelling to determine relationships between camera-trapping events and vegetation and other habitat variables, and obtained satisfactory model fit for 9 out of the 11 most recorded species, with explained model deviance up to 63.7%. Results provide novel insights into the ecology of target species. For example, the event count of the IUCN-endangered Abbott's duiker (*Cephalophus spadix*) was positively correlated with distance to the park border, indicating preference for interior forest and avoidance of disturbance. The event count of the Eastern Arc-endemic Lowe's servaline genet (*Genetta servalina lowei*) was positively correlated with diversity of large trees but negatively correlated with visibility and herbaceous cover, indicating preference for mature forest habitat. Our study validates the usefulness of camera trapping to assess communities of forest mammals, especially as related to habitat associations, providing data that are of relevance to their conservation management.

Keywords: camera traps; Eastern Arc; habitat modelling; habitat preferences; tropical forest

Introduction

Forest mammals are a key component of tropical forests in terms of biomass and as indicators of ecosystem health (Ahumada et al. 2011). They are also among the most threatened faunal groups due to habitat loss and degradation (Schipper et al. 2008). Hence, knowledge on their occurrence and factors determining their habitat associations are important for defining conservation strategies (e.g. Wasserman and Chapman 2003; Tobler et al. 2008; Rovero, Zimmerman et al. 2013). Despite such widely recognized importance, however, tropical forest mammals are generally poorly known partly because they are difficult to detect, owing to their nocturnal behaviour, elusiveness and rarity (e.g. Linkie et al. 2007).

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In this context, remotely set, automatic cameras taking pictures of passing animals (camera trapping) have been increasingly used in the last decade for studying mammals all over the world (Karanth and Nichols 1998, 2002; reviews in O'Connell et al. 2011; Fleming et al. 2014). Camera traps are non-invasive, relatively easy to use and cost-efficient (e.g. Rovero, Zimmerman et al. 2013; Fleming et al. 2014). A number of studies (e.g. O'Brien 2008; Ahumada et al. 2011; Ahumada et al. 2013; Rovero, Martin et al. 2014; Rovero, Menegon et al. 2014) have proved the efficiency of camera traps in mammal studies, with a more limited set of studies focusing on habitat associations (e.g. Linkie et al. 2007; Bowkett et al. 2008; Rovero, Collett et al. 2013). These studies have considered single species, or groups of species, to investigate habitat associations (e.g. Bowkett et al. (2008) targeted forest antelopes in the Udzungwa Mountains). Here, we present the results of a study on a community of medium-to-large forest mammals assessed by camera trapping in mountain forest habitat in Tanzania with a focus on fine-scale habitat modelling.

Our study area, the Udzungwa Mountains, is one of the most outstanding sites for biodiversity endemism and conservation in Africa (Rovero, Menegon et al. 2014). The area is particularly rich in mammalian forest fauna (Rovero and De Luca 2007). Forest mammals have been the subject of a number of studies that deployed camera trapping (De Luca and Mpunga 2005; Bowkett et al. 2008; Ahumada et al. 2011; Rovero, Collett et al. 2013; Rovero, Martin et al. 2014). Our study objective was to assess the community of medium-to-large forest mammals as detected through an extensive camera-trapping effort, derive a proxy of species' relative abundance and determine the best predictors of this response variable among a suite of fine-scale vegetation and other habitat factors as potential covariates of relative abundance. In turn, we aimed to provide new insights on habitat associations of several poorly known and/or rare species which are relevant to their conservation management.

Material and methods

Study area

The Udzungwa Mountains in south-central of Tanzania are a system of moist forest blocks interspersed with drier habitats. We conducted the study in Mwanihana forest, eastern Udzungwa Mountains National Park (UMNP; Figure 1). UMNP is centred on 7°46'S, 36°51'E, has a size of 1990 km² and is in the eastern part of the Udzungwa Mountains. Mwanihana is one of the largest forest blocks in the range (192 km² of closed forest habitat) with continuous vegetation cover from 300 to over 2000 m above sea level (Rovero, Collett et al. 2013). The forest habitat is characterized by deciduous forest at lower altitude on the eastern side while evergreen forests are found at higher altitudes on the western side (Lovett et al. 2006). In addition, the lower elevation habitat contains large portions of secondary, regenerating forest as a result of past human activities including logging. The northern part of the upper elevation zone has lower canopy and bamboo forest with rocky and very steep areas. Total rainfall in Mwanihana forest is around 1500 mm per year (data from UMNP). The dry season spans from June to November, with light rains typically falling from November to February and heavy rains from March to June (Tropical Ecology Assessment Monitoring (TEAM) Network, unpublished data).

Data collection: camera trapping

We conducted the camera-trapping survey from 3 July to 11 November 2013 by sampling 60 camera trap locations. Sampling was part of a long-term biodiversity

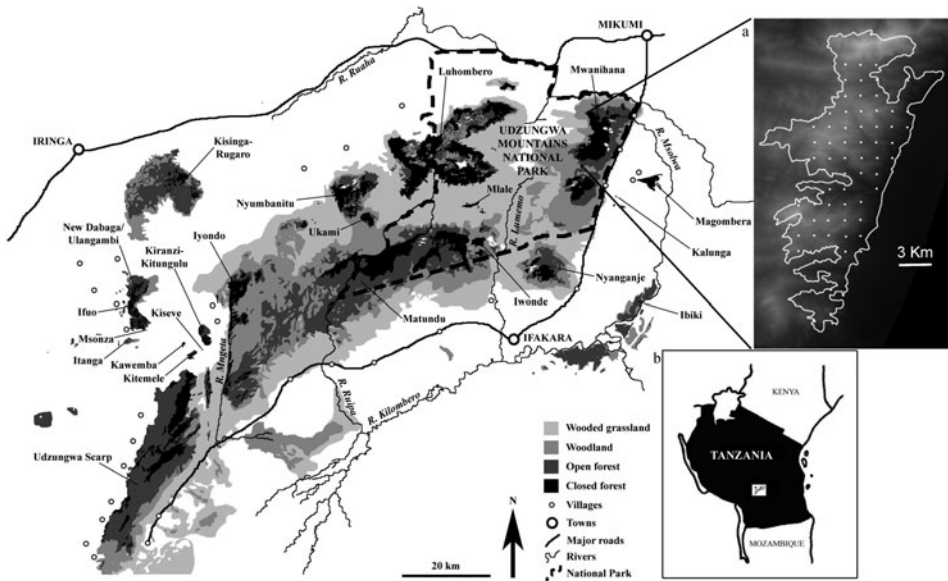


Figure 1. Map of the Udzungwa Mountains showing the main forest blocks with closed canopy forest darker in colour. The study forest was Mwanihana (top right inset) (A) where the 60 camera trap sites are shown as white dots and the background is a black with Digital Elevation Model; (B) shows the location of Udzungwa Mountains in Tanzania. *Source:* Rovero, Martin et al. 2014.

monitoring programme, the TEAM network, of which Udzungwa has been a part since 2009. However, we here used only data for year 2013, as we conducted habitat analysis during the same year. While pooling data for multiple years will have increased the sample size, we preferred not to introduce in our analysis the potential bias due to temporal discordance between animal and habitat data, as well as those due to habitat differences between years. Using ArcGIS 10 (Environmental Systems Research Institute (ESRI) Redlands, CA, USA), we placed camera traps in a pre-designed, regular grid of 60 locations across the forest, at a density of one camera per 2 km². We selected the final camera position as on active wildlife trail located within a maximum of 100 m from the original location using a handheld GPS unit (Figure 1). Due to the number of cameras available and the time needed for the field team to set cameras, we sampled the 60 points by deploying three consecutive arrays of 20 cameras traps (south, central and northern Mwanihana). We used automated digital cameras with infrared flash (Reconyx RM 45 and HC 500 models, Reconyx Inc., Holmen, WI, USA). Cameras were set to take photos with no delay between consecutive triggers and tied to a tree about 2–3 m away from the wildlife trail at an average height of 50 cm and left running for 30 days. As cameras can operate autonomously over such periods, we did not check them so as to avoid unnecessary disturbance. At sampling completion, memory cards were recovered and mammal images extracted for identification using specialized software (DeskTEAM, Fegraus et al. 2011). A single taxonomic authority ([IUCN] International Union for Conservation of Nature, 2014) was used for species identification. Once validated by the TEAM Network secretariat, we downloaded the data package from the open-access repository at <http://www.teamnetwork.org> (data package ID: TV-20140227231705_4591).

Data collection: vegetation sampling

We conducted habitat assessment at all 60 camera trap locations. We adapted a vegetation assessment protocol previously developed in the same area for a camera-trapping study on forest ungulates (Bowkett et al. 2008; Table 1). Thus, we took measurements of vegetation at three spatial scales. At the broadest scale, the 20 nearest trees were measured starting with the tree closest to the camera trap location and moving clockwise until the 20th tree was reached.

Trees were split into two categories: trees with a diameter at breast height (DBH) of 5–10 cm and those greater than 10 cm. For mid-scale, four 3 × 3 m plots were randomly placed within 10 m radius of each camera and the number of stems >5 cm DBH and taller than 1 m recorded within each plot. At the smallest scale, the percent cover of leaves, seedlings and herbs, and bare soil and dead logs was recorded within four, 1-m² plots positioned at the corners of each 3 × 3 m plot, resulting in a total of 16, 1-m² plots around each camera trap.

We recorded the proportion of leaf litter that was at least 5 cm deep in the plots as measured with a ruler. A visibility index of the plot around each camera trap location was calculated by estimating percentage visibility of a 1 × 1 m plastic sheet at a distance of 20 m from the middle of the plot (Bowkett et al. 2008). We randomly repeated this exercise four times by placing the plastic sheet at four different bearings, i.e. north, east, south and west to give a mean value of visibility for each plot. This method was adopted to quantify the density of forest floor vegetation growth not measured by stem density (SD). In addition, the shortest linear distances from each camera trap point to National Park border and forest edge were calculated using geo-processing tools available in ArcGIS 10 software. The distance to the National Park border is negatively correlated with elevation at camera trap sites given the landscape morphology of an east–west escarpment and, together with the distance from forest edge, is considered a proxy of decreasing anthropogenic disturbance (Rovero et al. 2012).

Table 1. Vegetation variables measured in plots centred on camera-trap sites, and used to analyse habitat associations of forest mammals in the Udzungwa Mountains of Tanzania. Redundant variables that were not used in the regression analysis are reported in the footnotes.

Type of plots for the measurements	Variables used in the regression analysis (abbreviation)
20 large trees (>10 cm DBH)	Stem density (SD1) Mean basal area (MBA1) Diversity (Simp1) ^a
20 small trees (5–10 cm DBH)	Mean basal area (MBA2) Diversity (Simp2) ^b
3x3 m plots	Small trees stem density (SD3) Diversity (LogSimp3) ^c
1x1 m plot (forest floor cover)	Herbaceous layer and seedlings (Herbs_Seedl) ^d Sum of deep and very deep leaf litters (SumDepthD_VD) Visibility ^e Distance to the National Park border (DistToNPBorder) ^f Distance to the Forest Edge (DistToForestEdge) ^f

^aSimp1 correlated with richness 1 ($r = 0.9$, $p < 0.01$, $n = 59$).

^bSimp2 correlated with richness 2 ($r = 0.8$, $p < 0.01$, $n = 59$).

^cLogSimp3 correlated with richness 3 ($r = 0.8$, $p < 0.01$, $n = 59$).

^dHerbs_Seedl correlated with leaves ($r = -0.7$, $p < 0.01$, $n = 59$).

^eMeasured 20 m from the centre of the plot.

^fCalculated by using ArcGIS version 10.

Data analysis

TEAM data are.csv files that we analysed using ad-hoc codes in R (R Development Core Team, 2013; see also Ahumada et al. 2011). We derived for each photographed species the number of camera-trapping events as the number of images filtered by 1 h (Rovero, Collett et al. 2013; Rovero, Martin et al. 2014). Hence, instances where the same species were captured by the same camera more than once within 1 h were excluded from the analysis as a compromise between scoring the same individual multiple times and missing individuals (e.g. Bowkett et al. 2008). Following the analytical approach in Bowkett et al. (2008) and Rovero, Collett et al. (2013), we used the number of events, which is standardized by sampling effort as this was constant among sites, as a proxy of relative abundance to determine habitat associations. While this metric is an index that does not account for imperfect detection (O'Connell et al. 2011), and therefore is of limited inference, our choice is supported by studies that show how this index is correlated with true abundance (Carbone et al. 2001; O'Brien et al. 2003; Rowcliffe et al. 2008), including the study by Rovero and Marshall (2009) on Harvey's duiker in the Udzungwa Mountains. We did not oversight the limited value of such index as especially associated with the failure of accounting for potential differences between species due to factors such as trail use, body size, daily range and behaviour (Trolle and Kéry 2003; Kelly and Holub 2008; Rowcliffe et al. 2008; Sollmann et al. 2013); however, we did not aim to compare this index among species. We aimed to analyse species-specific habitat associations; hence, we considered our approach sound for a descriptive assessment of how vegetation features may influence relative abundance.

We derived a species accumulation curve to check if data collection lasted a sufficient number of days to capture the species in the community. The order in which samples were included in the curve was randomized 1000 times and results were used to get confidence intervals around the mean using the package “vegan” in R (Gotelli and Cowell 2001). Even though this approach ignores imperfect detection of individual species, it is useful for comparison with other studies (e.g. Silveira et al. 2003; Tobler et al. 2008).

We derived the following covariates from vegetation data. For the two plots of trees 5–10 and >10 cm DBH, we calculated mean basal area (MBA), total basal area (TBA) and (SD = number of stems divided by the area approximated by a circle of radius equivalent to the distance from camera-trap site of the farthest tree). For the 3 × 3 m plots, we only computed SD. For the 1-m plots, we computed the mean estimated cover of the forest-floor categories and the proportion of plots with deep leaf litter. We used Simpson's reciprocal diversity index (1/D) to calculate plant diversity in each plot.

We then used generalized linear models (GLMs, McCullagh and Nelder 1989) to determine which variables best accounted for variation between the selected species trap events and the habitat covariates at the camera locations. We implemented models in R (www.r-project.org) version 3.1.1 using the packages “lattice” for graph visualizing and “nlme” for running the model (Sarkar 2008; Pinheiro et al. 2014). Before applying the model, we first performed data exploration to check for outliers and collinearity among the explanatory variables (Zuur et al. 2007).

We used dot charts to identify presence of outliers in the explanatory variables. In order to obtain a normalized distribution for explanatory variables, a log transformation was done to correct for the extreme values found for the parameter of SD. Co-plots were used to highlight collinearity among some of the variables. For the covariates that showed high autocorrelation (correlation coefficient $r > 0.6$), only one variable from each

pair was considered for further analysis and this yielded a final set of 12 variables that were used for the model formulation (Table 1).

Since the response variables were counts, which are always non-negative and that tend to be heterogeneous, we chose Poisson GLM owing to its ability to deal with both aspects (Zuur et al. 2010). Whenever over-dispersion was detected in the model (i.e. over-dispersion >1.5), standard errors were corrected using a quasi-Poisson GLM, adding an over-dispersion parameter ϕ to the variance of the response variable (Y_i). Following Zuur et al. (2009), we employed a stepwise backward selection to derive the best model. Since we first performed accurate data exploration and addressed collinearity among the explanatory variables, we were then assured that the algorithm employed could not affect the model selection process.

In order to determine which variable to drop, “Chi” and “F” tests were applied when using a Poisson GLM and quasi-Poisson GLM, respectively (Zuur et al. 2010). The final model, containing only the variables showing significance at 0.05 level, was then validated, looking at the homogeneity of the residuals; these were further plotted against the fitted values and against each explanatory variable in the model, as well as against those covariates that were excluded from the model. In case patterns were found in the variables not included in the models, further analysis was required in order for them to be included in the model (Zuur et al. 2010).

Results

Of the 60 camera traps set, one was stolen, and the remaining accumulated 1818 camera days (mean 30.8), yielding 12,911 images of mammals. Twenty-six species were recorded from all the 59 sites (Table 2). The range of species captured per camera was 1–12 (median 7). Five species were recorded with >100 events in this order: giant pouched rat (*Cricetomys gambianus*), bushy-tailed mongoose (*Bdeogale crassicauda*), red duiker (*Cephalophus harveyi*), suni (*Nesotragus moschatus*) and Sanje Mangabey (*Cercocebus sanjei*). Six species namely grey-faced sengi (*Rhynchocyon udzungwensis*), Tanganyika mountain squirrel (*Paraxerus vexillarius*), tree hyrax (*Dendrohyrax validus*), Abbott's duiker (*Cephalophus spadix*), servaline genet (*Genetta servalina*) and bush pig (*Potamochoerus larvatus*) scored $>20 \leq 100$ events, while the remaining 15 species scored ≤ 20 events, of which seven species scored ≤ 5 events (Table 2). The accumulation of species detected with increasing sampling effort was at first steep, but by 1000 camera days 24 species were recorded, representing 92% of the total number of species detected (Figure 2).

We could only model habitat association for the 11 most camera trapped species (i.e. minimum of 20 events recorded). Out of these, the models did not converge for red duiker and tree hyrax. The deviance explained by the models ranged from 5.8 to 63.7%, and for nearly half of the mammal species deviance explained was $>30\%$ (Table 3; see Appendix 1 for full results of GLMs).

The trapping events for the two carnivore species modelled, servaline genet and bushy-tailed mongoose, were found to be influenced by different variables. For the bushy-tailed mongoose, leaf litter depth and SD were found to be negatively correlated with species' trapping events, with the latter variable being more significant (Table 3). For the servaline genet, instead, the herbaceous cover and visibility index were found to be negatively correlated with its trapping events, while the diversity of large trees was the most significant variable positively correlated. The explained deviances were 21.9 and 43.5% for bushy-tailed mongoose and servaline genet, respectively (Table 3). For the Afrotheria, the model explained 29.8% of deviance of grey-faced sengi's trapping

Table 2. Checklist of mammals camera-trapped in Mwanihana forest, Udzungwa Mountains, Tanzania ordered by decreasing number of events. Naïve occupancy is computed as the number of sites the species was trapped divided by all sites sampled ($n = 59$).

Latin name	Common name	Events per hour	Naïve occupancy
<i>Cricetomys gambianus</i> Waterhouse, 1840	Giant pouched rat	443	0.712
<i>Bdeogale crassicauda</i> Peters, 1852	Bushy-tailed mongoose	419	0.831
<i>Cephalophus harveyi</i> (Thomas, 1893)	Red duiker	394	0.763
<i>Nesotragus moschatus</i> Von Dueben, 1846	Suni	165	0.492
<i>Cercocebus sanjei</i> Mittermeier, 1986	Sanje mangabey	129	0.695
<i>Rhynchocyon udzungwensis</i> Rathbun & Rovero, 2008	Gray-faced sengi	69	0.288
<i>Paraxerus vexillarius</i> (Kershaw, 1923)	Tanganyika mountain squirrel	59	0.322
<i>Dendrohyrax validus</i> True, 1890	Tree hyrax	57	0.305
<i>Cephalophus spadix</i> True, 1890	Abbott's duiker	52	0.458
<i>Genetta servalina</i> Pucheran, 1855	Lowe's servaline genet	37	0.356
<i>Potamochoerus larvatus</i> (F. Cuvier, 1822)	Bush pig	24	0.203
<i>Cercopithecus mitis</i> Wolf, 1822	Sykes monkey	19	0.220
<i>Petrodromus tetradactylus</i> Peters, 1846	Four toed sengi	15	0.034
<i>Mellivora capensis</i> (Schreber, 1776)	Honey badger	12	0.153
<i>Loxodonta africana</i> (Blumenbach, 1797)	African elephant	9	0.119
<i>Nandinia binotata</i> (Gray, 1830)	Palm civet	9	0.119
<i>Syncerus caffer</i> (Sparrman, 1779)	African buffalo	7	0.068
<i>Atilax paludinosus</i> (G.[Baron] Cuvier, 1829)	Marsh mongoose	6	0.085
<i>Colobus angolensis</i> (P. Sclater, 1860)	Black & white colobus monkey	3	0.068
<i>Panthera pardus</i> (Linnaeus, 1758)	Leopard	3	0.034
<i>Procolobus gordonorum</i> (Matschie, 1900)	Udzungwa red colobus monkey	3	>0.051
<i>Mungos mungo</i> (Gmelin, 1788)	Banded mongoose	2	0.034
<i>Tragelaphus scriptus</i> (Pallas, 1766)	Bush buck	2	0.034
<i>Papio cynocephalus</i> (Linnaeus, 1766)	Yellow baboon	1	0.017
<i>Rhynchocyon cirnei</i> Peters, 1847	Chequered sengi	1	0.017
<i>Thryonomys swinderianus</i> (Temminck, 1827)	Marsh cane rat	1	0.017

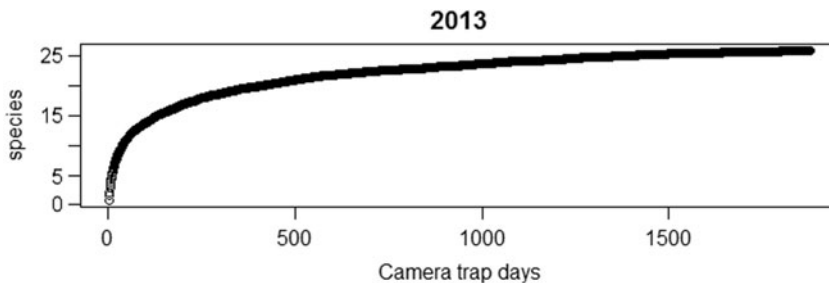


Figure 2. Species accumulation curve with sampling effort for the community of medium-to-large mammals detected by camera trapping in the Udzungwa Mountains of Tanzania.

Table 3. Results of generalized linear models with Poisson error distribution habitat predictors of abundance of nine mammals that had adequate camera trapping events for the analysis (>20). Both the deviance and the significant outcomes of the effects of covariates on trap events are indicated, along with their directionality. See Table 1 for abbreviations of covariates.

Species	Significant covariates	Estimates (SE)	<i>p</i> -value	Deviance (%)
Sanje Mangabey	MBA2	− 510.933 (280.192)	0.074	5.8
Bushy-tailed mongoose	LOGSD3	− 1.675 (0.490)	< 0.05	21.9
	Simp1	0.088 (0.048)	0.072	
	SumDepthD_VD	− 1.365 (0.691)	0.053	
Lowe's servaline genet	DistToNPBorder	0.000 (0.000)	< 0.05	43.5
	LOGSD1	1.937 (1.036)	0.067	
	Simp1	0.239 (0.067)	< 0.001	
	Visibility	− 0.030 (0.015)	< 0.05	
	Herbs_Seedl	−0.052(0.021)	< 0.05	
Giant pouched rat	Simp1	0.110 (0.066)	0.098	30
Tanganyika mountain squirrel	LOGSD1	− 2.260 (1.312)	0.091	14.5
	LOGSD3	3.214 (1.472)	< 0.05	
Gray-faced sengi	Simp2	0.165 (0.080)	< 0.05	29.8
	Simp3	0.190 (0.073)	< 0.05	
Abbott's duiker	DistToNPBorder	0.000 (0.000)	< 0.001	14.5
Suni	DistToForestEdge	− 0.000 (0.000)	< 0.05	30.9
	DistToNPBorder	− 0.000 (0.000)	0.08	
	LOGSD3	− 1.860 (0.846)	< 0.05	
	Visibility	0.030 (0.009)	< 0.01	
Bush pig	DistToNPBorder	0.000 (0.000)	0.055	63.7
	DistToForestEdge	− 0.000 (0.000)	< 0.05	
	LOGSD1	2.221 (1.307)	0.089	
	LOGSD3	−6.141 (1.814)	< 0.001	
	Simp2	−0.468 (0.129)	< 0.001	
	Simp3	−0.316 (1.286)	< 0.05	
	MBA1	2.150 (0.552)	< 0.001	
	Herbs_Seedl	−0.089 (0.034)	< 0.01	

events and showed significant positive correlation with small tree diversity (Table 3). For the primates, the model selected MBA of large trees as the only variable negatively correlated with trapping events of Sanje mangabey with explained deviance of 5.8% (Table 3). For the ungulates, distance to the national park border was the only and most significant variable positively correlated with the trapping event of Abbott's duiker (14.5% of deviance explained), while for suni, with the exception of the visibility index which was positively correlated with the species trapping event, the remaining variables, i.e. SD of small trees, distance to forest edge and National Park border, had negative correlations. Bush pig showed the highest number of variables significantly influencing its trapping events, with 63.7% of explained deviance. These were, from the most significant to the least significant, plant diversity and SD of small trees, distance to the forest edge and herbaceous cover (negative correlation); and MBA of large trees, distance to the National Park border and SD of large trees (positive correlation; Table 3). For the rodents, giant pouched rat's trapping event was positively correlated with large trees diversity, with 30% of deviance explained, while for the Tanganyika mountain squirrel herbaceous cover and SD of large trees negatively correlated with the species-trapping events (14.5% deviance explained; Table 3).

Discussion

We undertook a considerable and systematic camera trap effort comprehensively covering the target area to define the community of medium-to-large forest mammals in the Udzungwa Mountains, and determined habitat associations of selected species based on fine-scale modelling of habitat features at camera trap sites. Our study confirms the usefulness of camera trapping for studying elusive forest mammals, as shown by previous studies in the area (e.g. Rovero, Martin et al. 2014) and elsewhere in the tropics (e.g. Tobler et al. 2008; Ahumada et al. 2011). Our sampling effort was adequate to detect a large (i.e. 87%) proportion of species in the community, as additional camera trapping and complementary knowledge indicates approximately 30 species may in fact be present in the area (Rovero and De Luca 2007; Rovero, Martin et al. 2014). This in turn confirms the need for more than 1000 camera days to describe a complex forest-dwelling community of larger mammals (Tobler et al. 2008; Rovero et al. 2010). While our image event score is an index and does not inform on differences in abundance among species (see Methods), that approximately half of the species were detected with < 10 events does indicate their relative rarity and/or poor detectability by camera traps. Among these are the canopy dwellers such as the two colobine monkeys, namely Udzungwa red colobus and black and white colobus, that rarely come to ground and for which, therefore, camera traps are not a suitable detection method. The remaining species in the forest community were either only detected at low relative abundance, such as leopard, buffalo and elephant, or only live in the marginal areas of the forest, such as yellow baboon and banded mongoose (Kingdon 2008).

The limit of our approach of using an index of relative abundance (see Methods and O'Connell et al. 2011) bears the consequence that we could only implement habitat models for 11 species, while studies adopting inferential approaches that consider detectability may allow extending the analysis to some of the least-detected species. However, Rovero, Martin et al. (2014) used occupancy modelling for a different analysis on the same study system and found that for species with less than 10 events occupancy models did not converge (see also Ahumada et al. 2011). Future analysis, with larger sample size, should capitalize on our results by adopting inferential analytical approaches that account for imperfect detection.

For small carnivores such as the Lowe's genet and bushy-tailed mongoose, we found a strong relationship of their trapping events with plant species diversity. Higher tree diversity occurs in the interior and at mid-elevation forest (Lovett et al. 2006) where prey availability may be optimal for these two forest dwelling species (De Luca and Mpunga 2005). In addition, SD of large trees positively correlated with trapping events of Lowe's genet, indicating their preference for closed canopy, highly sheltered areas (Rovero, Collett et al. 2013). For bushy-tailed mongoose, instead, the model predicted a negative correlation with small SD, which is also concordant with preference for mature, old-growth forest with relatively open lower canopy and understory (Rovero et al. 2012).

Plant diversity of both medium and small trees (i.e. those forming the lower canopy) had a positive and significant effect on the grey-faced sengi's trapping events. This rare species, endemic to Udzungwa Mountains, was described in 2008 (Rovero et al. 2008) and is listed as vulnerable by the International Union Conservation for Nature – IUCN ([IUCN] International Union for Conservation of Nature 2014). Being diurnal, this species may prefer more dense vegetation to avoid detection from aerial predators (Rovero, Collett et al. 2013). For the Sanje mangabey, another Udzungwa-endemic and

IUCN-endangered species ([IUCN] International Union for Conservation of Nature 2014), our model predicted a negative correlation between trapping events and MBA of lower canopy trees. This suggests that the species probably avoids areas with few lower canopy stems, indicative of limited food availability particularly fruits, and high predation risk by raptors particularly African crown eagle (*Stephanoaetus coronatus*) (Rovero et al. 2009). Indeed, the Sanje mangabey's preference for steep, low canopy and densely covered areas is supported by focal group studies (T. Jones, pers. comm.).

For two of the forest ungulates for which the model converged, Abbott's duiker and bush pig, results show that their trapping events were positively correlated with distance to the National Park border, a factor considered as a proxy of anthropogenic disturbance (Rovero et al. 2012). For the endangered and Tanzania-endemic Abbott's duiker, this is an interesting and conservation-relevant finding, and we note that a previous study on forest antelope in the area could not determine the drivers of relative abundance for this species due to insufficient data (Bowkett et al. 2008).

Conversely, Harvey's duiker had a negative association with distance to National Park border, indicating possible tolerance towards disturbance events (Rovero, Martin et al. 2014). The different results found by Bowkett et al. (2008), who found decreasing index of relative abundance with distance from villages, may be partly due to the fact that the latter study had the bulk of its data collected in Matundu, a lowland forest which was reported to be more disturbed with possible hunting from nearby villages. Moreover, in Mwanihana forest local communities were allowed to collect firewood inside the National Park border although this activity was stopped in 2011 (UMNP unpublished data). Our result for Harvey's duiker may also therefore indicate greater use and re-colonization of the lower elevation of Mwanihana by this species to the findings in Bowkett et al. (2008). In contrast, for suni, another forest antelope, trapping events were negatively correlated both with the distances to National Park border and forest edge, and with small SD, which is probably indicative of the species avoidance of the areas where human disturbances are likely to be high such as along the park border and/or forest edge. Comparable results were found by Mugerwa et al. (2012) in Bwindi Impenetrable National Park, Uganda, where higher detection of the yellow-backed duiker (*Cephalophus silvicultor*) from camera trapping was found in the interior forest where human activities were lower than along the park edge. The fact that we found a positive relationship between suni's trapping event and visibility index but negative relationship with small SD does also support this species' sensitivity to disturbances. Poor visibility will likely occur in areas dominated by dense vegetation and lianas along the Park's border due to canopy degradation and predominance of secondary, regenerating forest (Bowkett et al. 2008; Rovero, Martin et al. 2014). Our results also showed negative correlations of bush pig trapping events with sub-canopy tree diversities and stem densities; this response may reflect their opportunistic habits with preference for lower elevation areas, with regenerating vegetation and relatively low tree species' diversity (Simoons 1953). Furthermore, the model predicted the species' habitat preferences to the areas with high percentage of leaf litter coverage, where the content of invertebrates, small vertebrates, insect larvae and carrion constitutes the species' main food (Maberly 1967; Smithers 1983; Kingdon 2008). Only one variable, large tree diversity positively correlated with the trapping events of giant pouched rat. This may likely indicate the species' preference for highly sheltered areas with complex habitat which may in turn mean more food abundance. In contrast, Tanganyika mountain squirrel's trapping events showed a positive relationship with small SD, indicating the species dependence on the

dense forest floor and/or bushy areas not only for food searching but also providing perfect refuges when fleeing from predators particularly raptors.

In general, we found that a number of potential covariates both as proxies of gross habitat, namely the distance to the National Park border, and as fine-scale vegetation features, namely the SD of small trees, appeared to influence habitat associations for most of the selected species. Conversely, few species such as bush pig and Lowe genet appeared to be influenced by a greater set of covariates while a small number of species were only affected by one covariate, such as the Udzungwa-endemic Sanje mangabey (MBA for understory forest) and the Eastern Arc-endemic Abbott's duiker (distance to the National Park border). These species–habitat specific relationships may be of particular relevance to the need of protecting the full array of forest habitat, including the interior in which moist montane forest is found but also the forest edge preferred by other species. Particular emphasis should indeed be given to the areas along the Park border where human activities resulting in severe habitat degradation are higher (Rovero et al. 2012).

Conclusion and recommendations

Our study confirms the usefulness of camera trapping in studying habitat–species associations for elusive forest mammals. Our analytical approach, i.e. the use of an event-based index, has the limits described in the methods, and these should be considered in future studies by adopting inferential approaches. We have provided insights using a habitat sampling approach, i.e. measuring vegetation features at the fine scale that was previously only conducted on forest antelope and on the grey-faced sengi (Bowkett et al. 2008; Rovero, Martin et al. 2014). Our results are of particular conservation relevance for the range-restricted species, such as the Lowe's servaline genet and Abbott's duiker, for which limited ecological data existed before this study. We acknowledge that greater effort would be required to adequately determine habitat associations for a greater portion of species in the community.

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Appendix 1

<i>Bdeogale crassicauda</i>				
Estimate SE <i>t</i> value Pr (> <i>t</i>)				
(Intercept)	– 4.7153	2 2.07066	– 2.277	0.0267*
LOGSD3	– 1.67528	0.49020	– 3.418	0.0012**
Simp1	0.08793	0.04785	1.838	0.0715
SumDepthD_VD	– 1.36536	0.69129	– 1.975	0.0533
<i>Cricetomys gambianus</i>				
Estimate Std. Error <i>t</i> value Pr(> <i>t</i>)				
(Intercept)	1.25240	0.52363	2.392	0.0201*
Simp1	0.11045	0.06562	1.683	0.0978
<i>Cephalophus harveyi</i>				
(Intercept)	2.3895473	0.36 23282	6.595	1.5e-08***
Edge	– 0.0005083	0.0003376	– 1.505	0.138
<i>Cercocebus sanjei</i>				
Estimate SE <i>t</i> value Pr (> <i>t</i>)				
(Intercept)	2.828	1.112	2.544	0.0137*
MBA2	– 510.933	280.192	– 1.824	0.0735
<i>Cephalophus spadix</i>				
Estimate SE or <i>z</i> value Pr(> <i>z</i>)				
(Intercept)	– 1.178e+00	3.556e-01	– 3.314	0.000919***
DistToNPBorder	2.674e-04	7.361e-05	3.632	0.000281***
<i>Dendrohyrax validus</i>				
Estimate SE <i>t</i> value Pr (> <i>t</i>)				
(Intercept)	– 5.478	3.366	– 1.628	0.109
LOGSD1	2.058	1.234	1.667	0.101
<i>Genetta servalina</i>				
Estimate SE <i>t</i> value Pr (> <i>t</i>)				
(Intercept)	– 6.5538390	2.8101742	– 2.332	0.023522*
Border	0.0002665	0.0001043	2.555	0.013524*
LOGSD1	1.9368203	1.0363583	1.869	0.067171
Simp1	0.2792012	0.0672681	4.151	0.000121***
Visibility	– 0.0304681	0.0147306	– 2.068	0.043501*
Herbs_Seedl	– 0.0524114	0.0213909	– 2.450	0.017614*
<i>Potamochoerus larvatus</i>				
Estimate SE <i>z</i> value Pr (> <i>z</i>)				
(Intercept)	– 3.170e+01	1.083e+01	– 2.927	0.003422**
DistToNPBorder	2.792e-04	1.453e-04	1.921	0.054723
DistToForestEdge	– 9.146e-04	4.485e-04	– 2.039	0.041427*
LOGSD1	2.221e+00	1.307e+00	1.699	0.089269
LOGSD3	– 6.141e+00	1.814e+00	– 3.385	0.000711***
Simp2	– 4.675e-01	1.286e-01	– 3.636	0.000277***
Simp3	3.159e-01	1.316e-01	2.401	0.016333*
MBA1	2.150e+00	5.517e-01	3.897	9.73e-05***
Herbs_Seedl	– 8.885e-02	3.433e-02	– 2.588	0.009641**
<i>Paraxerus vexillarius</i>				
Estimate SE <i>t</i> value Pr (> <i>t</i>)				
(Intercept)	6.412	3.411	1.880	0.0654
LOGSD1	– 2.260	1.312	– 1.722	0.0906
LOGSD3	3.214	1.472	2.183	0.0332*

(Continued)

Rynchocyon udzungwensis

Coefficients:

Estimate	SE	t value	Pr (> t)	
(Intercept)		- 2.68711	0.86516	- 3.106 0.00298**
Simp2	0.16537	0.08000	2.067	0.04337*
Simp3	0.19016	0.07308	2.602	0.01184*

Nesotragus moschatus

Estimate SE t value Pr (>|t|)

(Intercept)	0.6440157	0.6224449	1.035	0.30544
Border	- 0.0002310	0.0001025	- 2.253	0.02833*
Edge	- 0.0005118	0.0002880	- 1.777	0.08124
LOGSD3	- 1.8602366	0.8458175	- 2.199	0.03216*
Visibility	0.0304017	0.0094714	3.210	0.00224**
