Distribution, occupancy, and habitat associations of the gray-faced sengi (Rhynchocyon udzungwensis) as revealed by camera traps

Authors: Rovero, Francesco, Collett, Leah, Ricci, Silvia, Martin, Emanuel, and Spitale, Daniel

Distribution, occupancy, and habitat associations of the gray-faced sengi (*Rhynchocyon udzungwensis*) as revealed by camera traps

Francesco Rovero,* Leah Collett, Silvia Ricci, Emanuel Martin, and Daniel Spitale

Tropical Biodiversity Section, MUSE—Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38123 Trento, Italy (FR, SR, DS)
Udzungwa Ecological Monitoring Centre, Udzungwa Mountains National Park, P.O. Box 99 Mang'ula, Tanzania (FR, EM)
Department of Life Sciences, Animal and Environmental Research Group, Anglia Ruskin University, East Road, Cambridge CB1 1PT, United Kingdom (LC)

* Correspondent: francesco.rovero@muse.it

Three of the 4 species of giant sengis or elephant shrews (genus *Rhynchocyon*) have restricted geographic distributions in eastern Africa and are threatened by anthropogenic habitat loss. However, little is known about their ecology and habitat relationships. We used remotely triggered cameras to detect the gray-faced sengi (*Rhynchocyon udzungwensis*), which is endemic in the Udzungwa Mountains of Tanzania, with the aim of defining distributional limits, estimating occupancy patterns, and determining habitat requirements. We deployed 183 camera stations over 6 years and accumulated 4,600 camera trapping days. We refined the area of known occurrence to be 390 km^2, thus confirming the species' restricted range and vulnerability. We estimated the average occupancy at 56% of sites occupied on sites sampled, and found that occupancy was best predicted by the forest habitat type, with interior, closed-canopy forest supporting highest estimated sengi occupancy. Terrain slope and distance to the nearest park boundary were less important covariates, but nevertheless included among the best models. Camera-trapping rate (photographic events by day) was significantly correlated with subcanopy tree coverage. Combined, these habitat features may provide optimal conditions for antipredation vigilance (vegetation cover), and for nest-building and/or foraging on invertebrates in the thicker leaf litter on gentle slopes. Our results offer new insights into the ecology of giant sengis and confirm the potential utility of camera trapping for occupancy analysis of small, forest-dwelling mammals.

Key words: camera trapping, distribution, elephant shrew, habitat model, habitat use, Macroscelidea, occupancy analysis, *Rhynchocyon udzungwensis*, Udzungwa

Sengis, or elephant shrews, include 18 species (Order Macroscelidea) that are endemic to Africa (Corbet and Hanks 1968; Dumbacher et al. 2012). They belong to the mammalian super-cohort Afrotheria, along with elephants, sea cows, hyraxes, the aardvark, golden moles, and tenrecs (Corbet and Hanks 1968; Stanhope et al. 1998). Despite being relatively specialized and uniform in their morphology and social structure, sengis occupy a range of terrestrial habitats, from coastal deserts to montane forests (Rathbun 2009). The 4 species of giant sengis (genus *Rhynchocyon*) occur in eastern and central African forests, including coastal thickets, dry woodlands, secondary forests, and moist evergreen forest, habitats that are generally threatened by human exploitation. Three species of *Rhynchocyon*, especially those with restricted ranges, are currently of conservation concern (Rathbun 2009;

IUCN 2012). Unfortunately, we know little about the distributions and habitat associations of these species.

On the basis mainly of a study of the golden-rumped sengi (*Rhynchocyon chrysopygus*) in coastal Kenya (Rathbun 1979), giant sengis are thought to be diurnal and monogamous. They construct nests of dead leaves on the forest floor in which they spend the night and give birth. A large portion of their active time is spent foraging for invertebrates on the forest floor (Rathbun 1979). The paucity of data on the ecology of giant sengis stems from their shy nature combined with the difficulties of working in dense forests. Indeed, the only

www.mammalogy.org

detailed studies of habitat associations of sengis were conducted on the golden-rumped sengi by FitzGibbon (1994) and FitzGibbon and Rathbun (1994). On the basis of radio-tracking combined with an assessment of habitat features associated with nests, these authors found that the variables that best predicted nest densities of golden-rumped sengis were related to the amount of vegetation cover. Secondarily, areas with deep leaf litter and where tree trunks were closely spaced were also preferred. The association with deep leaf litter presumably reflected high prey density, whereas dense tree-trunk spacing was thought to provide greater overhead cover from aerial and terrestrial predators.

In recent years, camera trapping has been used to study giant sengis (Rovero and Rathbun 2006; Andanje et al. 2010), with the potential of gathering and analyzing more quantitative information (Rovero and Marshall 2009; O'Connell et al. 2011), including habitat associations (e.g., Linkie et al. 2007; Bowkett et al. 2008). For giant sengis in particular, the advantage of camera trapping over alternative detection methods, such as nest counts, is that it eliminates observer bias associated with detecting nests. It also allows for sampling of the entire activity area, whereas surveys of nests may be limited to particular portions of the home range or specific habitats. A potential problem of camera trapping is the recording of false absences, i.e., cameras not taking images where animals are present, a bias that can be addressed by occupancy analysis (MacKenzie et al. 2002; O'Connell and Bailey 2011).

Rhynchocyon udzungwensis was described as a new species of giant sengi in 2008 from the Udzungwa Mountains of Tanzania, where it is endemic (Rovero et al. 2008). The mountains are one of the continental hot spots for biodiversity conservation (Burgess et al. 2007), especially for mammals (Rovero and De Luca 2007). Gray-faced sengis occur mainly in moist evergreen forests covering steep mountain slopes, in contrast with the coastal drier forests, where the golden-rumped sengi occurs (FitzGibbon 1994). Our research objectives were to further define the distribution of the gray-faced sengi; determine, at a fine scale, the vegetation characteristics that are most correlated with camera-trapping rate, a crude index of sengi abundance; and determine, at a broader scale, habitat correlates of sengi occupancy.

Materials and Methods

Study area and data collection.—The Udzungwa Mountains (7°40′–8°40′S, 35°10′–36°50′E) are a mosaic of forest blocks interspersed with drier habitats. The gray-faced sengi occurs solely in 2 of the largest, continuous tracts of these forests (Fig. 1): Ndundulu/Luhomero (300 km^2) and Mwanihana (180 km^2). The Ndundulu/Luhomero Forest extends from 1,300 to 2,300 m above sea level (asl), whereas Mwanihana Forest covers an escarpment slope and ranges from 300 to 2,000 m asl. These 2 forests are separated by approximately 25 km of woodland and wooded grassland inside the Udzungwa Mountains National Park. Whereas Ndundulu/Luhomero Forest is inscribed within

a larger matrix of protected habitat, Mwanihana Forest borders to the east, at its foothills, the vast Kilombero Valley, which is heavily populated and intensively farmed.

We conducted 7 camera-trapping surveys between September 2005 and February 2011, deploying 183 camera stations overall (see Table 1 for details of sampling periods). We used 2 different sampling designs. The 1st design, an opportunistic approach in both forests, utilized 103 camera stations spatially lumped at several sites (Fig. 1) and was aimed at refining the distributional limits of the gray-faced sengi, with a focus in Mwanihana Forest where the eastern limit had not been determined; and determining microhabitat associations by conducting vegetation assessment at a subset of these camera sites. The 2nd design, a systematic approach in central-northern Mwanihana Forest, consisted of a regular grid of 40 camera traps at a density of 1 camera per 2 km^2 that included the entire known gray-faced sengi range in this forest. Cameras were deployed sequentially using 2 arrays of 20 camera stations each in central and northern Mwanihana, respectively. Sampling on this grid was conducted in 2009 and 2010 by setting cameras at the same position in each year, and aimed at estimating gray-faced sengi occupancy and determining larger-scale habitat associations of occupancy. This latter sampling was part of a long-term monitoring of terrestrial mammals (Tropical Ecology, Assessment and Monitoring [TEAM] program—TEAM Network 2011), using occupancy analysis (Ahumada et al. 2011).

We used 2 different camera-trap types. For opportunistic sampling, we used film cameras (Vision Scouting and Deercam, NonTypycal Inc., Green Bay, Wisconsin), with 36-exposure film (Kodak 200 ISO) set to take photos with a minimum interval of 1 min between consecutive triggers. For systematic sampling and occupancy analysis, we used digital cameras (Reconyx RM45, Reconyx Inc., Holmen, Wisconsin), set to take photos without delay between consecutive triggers. Cameras were tied to trees at an average height of 50 cm along wildlife trails and run for an average of 27.7 days. Additional observations of sengis and their nests taken during both visual and camera-trap surveys by us or other researchers were also included to refine distributions.

We conducted vegetation analyses in plots centered on 40 of the 103 camera-trap sites deployed for the opportunistic surveys. Of these cameras, two did not function and 33 of the remaining 38 cameras captured the sengi. The spatial design of this subset of plots compromised between including adequate habitat variability and constraints associated to the relative extensive effort needed to measure the vegetation plots. Hence, plots were concentrated in 2 areas, the eastern Luhomero Forest (plots measured in 2008) and along the elevation gradient of cameras set in central Mwanihana Forest (plots measured during 2 surveys, in January 2009 and in January 2011, respectively; Fig. 1). We used a vegetation assessment protocol previously developed in the same area for forest antelope (Bowkett et al. 2008) that we adapted to variables we expected to be relevant for gray-faced sengis. Overall, given the species' habit of foraging on leaf litter and
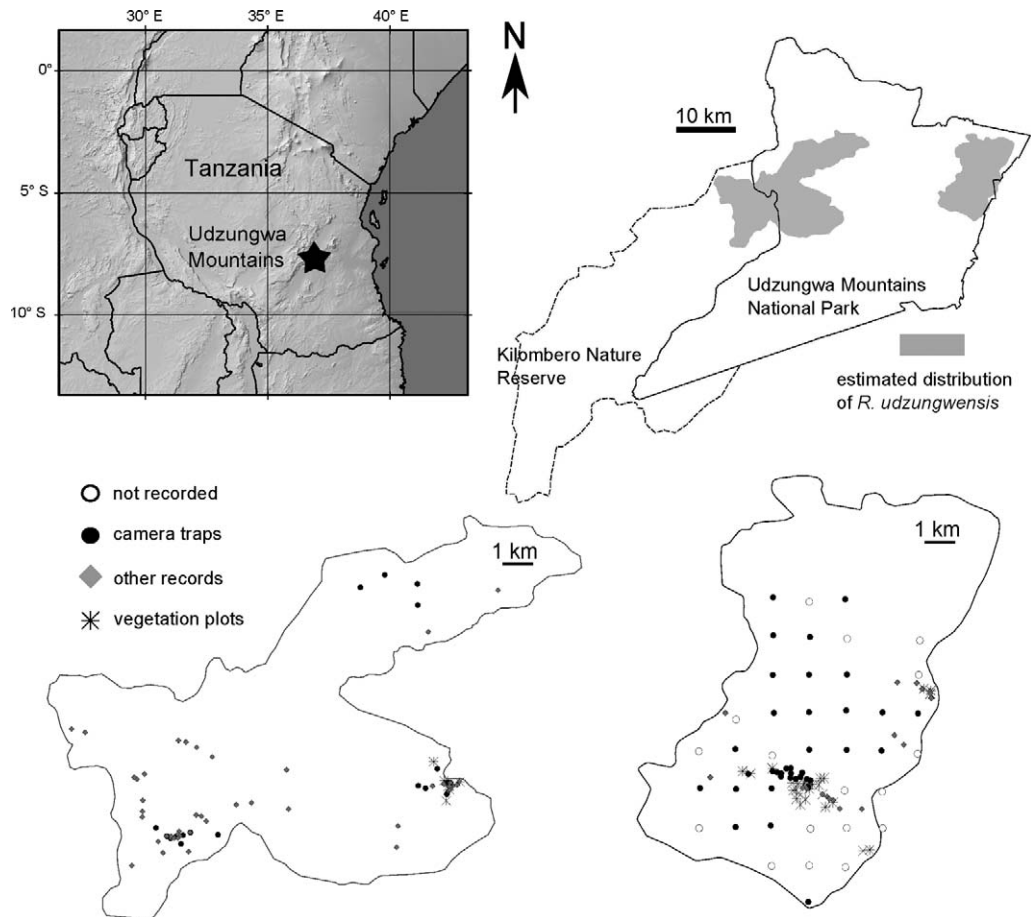
FIG. 1.—Top left inset shows the location of the Udzungwa Mountains in Tanzania. Top right: map of the estimated area of occurrence (gray shading) of the gray-faced sengi, *Rhynchocyon udzungwensis*, in northern Udzungwa Mountains, Tanzania, as derived from multiple survey methods. Bottom: enlargements of the 2 forest blocks where the species occurs and black dots show localizations. The western portion (left) of the distribution extends over the whole Ndundulu/Luhomero Forest, whereas the eastern portion (right) extends over the mid- to northern portion of Mwanihana Forest. In this forest, the camera-trap sites that failed to record the sengis within a regular grid of 40 camera-trap sites are also shown.

sheltering in vegetation when alerted, our sampling aimed to determine vegetation cover, from canopy and understory to the forest floor, by using structural variables (stem density and basal area), with attention to forest-floor coverage, particularly the leaf-litter depth.

Vegetation measurements were taken at 3 spatial scales. At the broadest scale, tree stem measurement was recorded for the 20 nearest trees to a camera trap in 2 categories: trees with a diameter at breast height (DBH) of 5–10 cm and those greater than 10 cm. For mid-scale, 4, 3- × 3-m plots were randomly

TABLE 1.—Summary of locations, altitude range, sampling effort, and trapping results for 7 camera-trapping surveys targeting the gray-faced sengi, *Rhynchocyon udzungwensis*, in the Udzungwa Mountains of Tanzania. The majority of sites were in submontane and montane evergreen forest, except for the survey in Mwanihana (2008–2009) that was in lowland, deciduous to semideciduous forest.

Site (sampling period)	Elevation range (m above sea level)	Number of cameras set (cameras functional)	Total (mean) camera days	Number of successful cameras	Number of sengi events	Mean (*SD*) camera-trapping rate (events/day)
Opportunistic surveys: Ndundulu (September–October 2005 and March 2006)	1,360–1,440	13 (10)	265 (26.5)	5	10	0.103 (0.064)
Mwanihana (June–July 2006)	980–1,660	16 (14)	418 (29.9)	12	55	0.167 (0.159)
Luhomero (October–November 2008)	1,430–1,860	13 (11)	333 (25.6)	11	47	0.195 (0.144)
Mwanihana (December 2008–January 2009)	400–640	26 (21)	552 (26.3)	9	14	0.068 (0.039)
Mwanihana (December 2010–February 2011)	900–1,500	35 (34)	535 (15.7)	26	66	0.159 (0.137)
Systematic surveys: Mwanihana (August–December 2009)	380–1,800	40 (39)	1209 (31.0)	14	47	0.113 (0.100)
Mwanihana (August–December 2010)	380–1,800	40 (40)	1285 (32.1)	18	82	0.143 (0.139)
All surveys combined	380–1,860	183 (169)	4597 (26.7)	95	321	0.135 (0.111)

placed within 10 m of a camera trap within which the number of stems was recorded for all trees < 5 cm DBH and taller than 1 m. At the smallest scale, the percent cover of leaves, seedlings and herbs, and bare soil and dead logs was recorded within 4, 1-m^2 plots positioned at the corners of each 3- × 3-m plot, resulting in a total of 16, 1-m^2 plots around each camera trap. We recorded the proportion of these plots with leaf litter that was at least 5 cm deep, as measured with a ruler.

To assess habitat covariates related to gray-faced sengi occupancy, we derived 3 habitat features of presumed relevance at each of the 40 TEAM camera-trap sites: straight distance to the eastern forest edge (DEE), which coincides with the nearest park boundary; forest habitat type; and maximum slope. DEE was estimated with Quantum GIS software (Quantum GIS Development Team 2012). We considered this variable to be an indicator of human disturbance on the forest, which is greatest near the park border, especially in form of firewood collection (Rovero et al. 2012). The forest habitat type was quantified using a land cover map derived from LANDSAT (Fisher et al. 2011) and assigning to each camera trap a habitat category depending on their location: closed canopy interior forest, transitional semideciduous zone, and lowland deciduous forest. Hence, this categorical variable quantifies the shift in forest habitat from deciduous lowland to evergreen montane forest (Lovett 1993), the latter of which is assumed to represent higher-quality habitat for gray-faced sengis (Rovero et al. 2008).We derived slope from a National Aeronautics and Space Administration digital elevation model (Farr et al. 2007) with a spatial resolution of 30 m by using GRASS GIS (Neteler and Mitasova 2008). We considered it to be a proxy for habitat quality, under the assumption that leaf litter depth, which is critical for feeding and building nests, is greater in areas with little or no slope. This assumption is partially supported by the negative correlation between litter depth at the vegetation plots and slope derived from a digital elevation model at these plots (Spearman's $r = -0.299$, $P = 0.068$, $n = 38$). In turn, there is evidence that litter depth affects diversity and abundance of some invertebrates (e.g., Bultman and Vetz 1982).

Data analysis.—The location records that we collected since Rovero et al. (2008) allowed us to update the area of occurrence for gray-faced sengis. Using Quantum GIS software (Quantum GIS Development Team 2012), we plotted all records on a background map of vegetation derived from LANDSAT (Fisher et al. 2011). We then used the closed-forest vegetation category boundaries to estimate the maximum extent of the gray-faced sengi distribution outside the known range.

We computed the camera-trapping rate (camera-trapping events by day) for each survey as the number of images per unit sampling time (the number of days that cameras were operational, i.e., from deployment until camera retrieval or until memory or film saturation). All images were date and time stamped, and we used only images separated by at least 1 h to eliminate biases caused by the same individual pausing in front of the camera (e.g., Bowkett et al. 2008). Camera-

trapping rate was considered an index of relative abundance (O'Brien 2011); for forest ungulates in the same area, camera-trapping rate was shown to be a valid index of density through calibration to independent density estimates (Rovero and Marshall 2009). We therefore used the camera-trapping rate as the response variable for the habitat preference analysis described below.

Table 2 shows the vegetation variables we derived from measurements. Data from the 38 plots, where cameras functioned, were used for the analysis. As mentioned previously, sengis were not captured in 5 of these plots. For the 2 plots of trees 5–10 and > 10 cm DBH, we computed mean basal area and total basal area (TBA), and stem density (ST = number of stems divided by the area approximated by a circle of radius equivalent to the distance from the camera-trap site of the farthest tree). For the 3- × 3-m plots, we only computed ST. For the 1-m plots, we computed the mean estimated cover of forest-floor categories and the proportion of plots with deep leaf litter.

We used binomial generalized linear model (GLM) to determine which variables best accounted for variation in camera-trapping rate at the 38 opportunistic camera sites. Since we detected overdispersion, we corrected the standard errors using a quasi-GLM model (Zuur et al. 2009). Variables were first checked for collinearity using a Spearman's correlation matrix: we excluded a priori 2 variables that were highly correlated with other variables (Table 2). This yielded a final set of 9 variables, which were included in the model.

For occupancy analysis, we followed a procedure described by Ahumada et al. (2011) and conducted in R software (R Development Core Team 2011). Occupancy was defined as the proportion of points in a site where a species was expected to occur, and was estimated using a likelihood-based method (MacKenzie et al. 2002). We first built an occupancy matrix that aligned data for 2009 and 2010, and consisted of 40 camera traps × 83 sampling days, which is the overall period from August through December in each year when the 2 sequential arrays of cameras were used. The resolution of the matrix, or sampling occasion, was 1 day. We then estimated gray-faced sengi occupancy and detection probability using the package "unmarked" in R (Fiske and Chandler 2011; see also Ahumada et al. 2011). To ensure that our inferences were robust (i.e., minimizing the probability of false absence to an acceptable level), we pooled data from 2009 and 2010, assuming that occupancy did not vary between consecutive years ("closure assumption"). To test this assumption, we used a multiseason occupancy model (MacKenzie et al. 2003). In this type of model, the dynamic processes governing changes in the occupancy state variable are the colonization (γ) and extinction (ε) probability. Because closed populations do not experience either colonization or extinction, we fit a model with year-dependence parameters: Ψ(year) γ(year) ε(year) p(year). Results of this model showed that the processes of both colonization and extinction were not significant ($P > 0.9$) and that detection probability (p) was similar in the 2 years (0.157 and 0.154 in 2009 and 2010, respectively). Estimates of

TABLE 2.—Vegetation variables measured in plots, centered on 38 camera-trap sites, to analyze microhabitat associations of the gray-faced sengi in the Udzungwa Mountains of Tanzania. Redundant variables not used in the regression analysis are reported in the footnotes.

Type of plot for measurements	Variables used in the regression analysis (abbreviation)
20 large trees (> 10 cm diameter at breast height [DBH])	Mean basal area (MBA1)[a]
	Stem density (ST1)
20 small trees (5–10 cm DBH)	Mean basal area (MBA2)
	Total basal area (TBA2)[b]
3- × 3-m plots	Stem density (ST3)
1- × 1-m plot (forest floor cover)	Leaves
	Logs/bare soil
	Seedlings/herbs
	Leaf litter depth

[a] Correlated with total basal area ($r = 0.93$, $P < 0.01$, $n = 38$).
[b] Correlated with stem density of small trees ($r = 0.58$, $P < 0.01$, $n = 38$).

occupancy probability (Ψ) in the 2 years were derived from the estimates of 1st-year occupancy and the 2 parameters governing the dynamics, that is, colonization and extinction. Calculations yielded an occupancy of 0.303 ± 0.135 *SE* in 2009 and 0.402 ± 0.110 *SE* in 2010. Thus, since colonization and extinction were irrelevant in these 2 years and occupancy did not change significantly, we are confident that the closure assumption held.

We then modeled both occupancy and detection probability with and without covariates, applying a single-season occupancy model on the pooled data set. We tested the importance of DEE as potential covariate of detection probability (other than of occupancy) because sengis were expected to be more elusive near the forest edge, where anthropogenic disturbance is higher. Once standardized, we included covariates both individually and in combination. We used the Akaike information criterion (AIC) to rank candidate models and calculate their Akaike weights (Burnham and Anderson 2002). In the case of top-ranked models with similar AIC (and weight > 0.01), we applied a model-averaging technique to estimate occupancy from these multiple models (Burnham and Anderson 2002). The relative importance of the model parameters were calculated with the R package "AICmodavg" (Mazerolle 2012).

RESULTS

Overall, we photographed gray-faced sengis at 95 camera sites and obtained 321 independent photographs. Of the 183 camera traps we deployed throughout the study, 14 malfunctioned (7.7%), whereas the remaining 169 operated over 4,597 camera-trap days, for a mean of 26.7 ± 5.5 *SD* days of sampling per camera trap (Table 1). TEAM sampling in 2009–2010 (2,494 camera days) accounted for over half of the sampling effort, whereas opportunistic surveys provided a range from 265 to 552 camera days per survey (see Table 1). We revised the estimated area of occurrence from 300 km² (Rovero et al. 2008) to 390 km², of which 268 km² was in Ndundulu-Luhomero Forest (elevation range 1,300–2,500 m) and 122 km²was in Mwanihana Forest (elevation range 400–2,200 m; Fig. 1). The new estimate was based on a total of 171 georeferenced records of gray-faced sengis from 80 camera traps, 17 specimens, and 74 visual sightings.

The lowest camera-trapping rates occurred at lower elevations in Mwanihana ($\bar{X} = 0.068$; Table 1), whereas higher camera-trapping rates were at mid- to high altitude in both Mwanihana (0.159–0.167) and Ndundulu-Luhomero (0.103–0.195). Although this comparison pools data from different surveys and different cameras, camera-trapping rate did not differ between digital and film cameras (2-sample *t*-test: $t = -0.23$, $P = 0.82$), indicating similar performance by camera types at detecting passing sengis. The regression analysis of the influence of habitat variables on camera-trapping rate at the 38 camera stations that were set opportunistically and where vegetation was recorded (of which 33 detected sengis) resulted in only 1 significant variable at $P < 0.01$: TBA of subcanopy trees (TBA2; Table 3). This was also maintained after removing the nonsignificant terms to avoid overfitting. For the systematic grid of cameras in Mwanihana, we detected gray-faced sengis at 22 of 40 camera traps, yielding a naïve occupancy estimate of 55% of sites occupied on sites sampled. Occupancy analysis indicated that no single model was demonstrably better than the others, since AIC scores varied continuously. For clarity, we only reported the top 4 models with AIC < 2 (Table 4). There are several common features among the top-ranked models. The model that included DEE and closed forest in occupancy and DEE in detection probability ranked highest, suggesting little support for the constant model $\Psi(\cdot) \, p(\cdot)$. The summed model weight for DEE with respect to detection probability was 87% and detection probability increased linearly with this covariate. In terms of occupancy probability, on the basis of rankings and AIC model weights, the results suggested a leading role for closed forest (98%) over DEE (57%) and slope (31%), with a linear relationship that was positive for the former and negative for DEE and slope. The average occupancy model was 0.551 ± 0.095 (*SE*); Fig. 2 shows the estimated occupancy probabilities at the 40 systematic camera-trap sites.

DISCUSSION

Our results increased the estimated area of occurrence for the gray-faced sengi by 30% (90 km²) compared with the 1st published estimate (Rovero et al. 2008). This increase was mainly due to new records from lower elevations (from 1,000 to 400 m asl) in the eastern Mwanihana Forest that includes deciduous lowland forest. The updated range, however, probably will not alter the species' current Vulnerable status on the International Union for Conservation of Nature Red List (Rovero and Doggart 2008) because it remains confined to only 2 forests and our results suggest that most of the revised range is in what is considered to be suboptimal habitat for gray-faced sengis.

TABLE 3.—Results of binomial generalized linear models testing the effect of vegetation variables on the camera-trapping rate of the gray-faced sengi at 38 camera traps in the Udzungwa Mountains of Tanzania. Variable abbreviations are in Table 2. Statistically significant outcomes ($P < 0.01$) are highlighted in bold.

Variable	Estimate	SE	z	$P(> |z|)$
ST1	1.008	6.716	0.150	0.881
MBA1	−0.110	0.220	−0.499	0.618
TBA2	0.668	0.262	2.625	**0.009**
MBA2	−39.370	29.555	−1.332	0.183
ST3	−0.063	0.103	−0.605	0.545
Leaf litter depth	0.576	0.509	1.132	0.258
Logs/bare soil	0.401	2.864	0.140	0.889
Leaves	−0.137	1.183	−0.116	0.908
Seedlings/herbs	3.553	3.381	1.051	0.293

The limits and potential of camera-trapping rate as an index of relative abundance have been assessed (Rovero and Marshall 2009; O'Brien 2011; see also below). Taking these caveats into account, our results broadly indicate lower sengi abundance at lower elevation in Mwanihana, and higher abundance at mid- to high-elevation sites in both forests. Our results for Mwanihana, where the greatest elevation range occurs, support the pattern of higher occupancy in closed-canopy interior and evergreen forest. Occupancy too is considered an index of abundance (MacKenzie and Nichols 2004), and because it accounts for detection probability, it represents an unbiased estimate of animal occurrence (O'Connell and Bailey 2011).

We acknowledge that the opportunistic cameras only covered a fraction of the whole extent of forest habitat where sengis occur; despite this sampling design caveat, we are confident that the results provide good indication of micro-habitat associations by the gray-faced sengi, particularly in view of the relatively broad altitudinal range covered by plots in Mwanihana Forest (409–1,823 m asl). We also assumed that vegetation conditions did not change over the period plots were measured. The regression analysis of trapping rate on habitat features clearly indicated that the total amount of subcanopy tree cover had a positive influence on trapping rate, suggesting a preference by gray-faced sengi for forest understory that is densely covered. Such modeling implicitly accounts for variability in the relationship between trapping rate and abundance, and the actual influence of vegetation characteris-

tics on this species' abundance. Because these 2 quantities are summed, the lack of significant relationship for variables other than TBA2 that may be important could partly reflect the unknown relationship between true abundance and trapping rate. This intrinsic problem would be avoided in future studies by sampling vegetation at the same sites used for occupancy analysis and hence incorporating the vegetation variables in the analysis as occupancy covariates. A larger sample size, with the inclusion of a broader range of sampled habitats (i.e., including areas outside those known to be occupied by sengis), may also reveal more clearly the microhabitat associations of sengi. In addition, assessing sengis' prey availability would also be recommended in future studies.

However limited, our analysis identified useful predictors of sengi activity. Because gray-faced sengi are diurnal (Rovero et al. 2008), closed subcanopy coverage may permit vigilance at the forest floor and overhead shelter from predators. Our findings mirror those reported for the golden-rumped sengi, for which nest densities were highest in areas with substantial understory vegetation cover (FitzGibbon 1994). Our results also are similar to those from a preliminary study on the black and rufous sengi, *Rhynchocyon petersi*, from the South Pare Mountains in Tanzania, which reported greater density of nests in areas with higher shade than expected in the lowest (< 5 m) canopy layer (Coster and Ribble 2005).

Results from our occupancy analysis indicated that gray-faced sengi were more abundant in evergreen forest than in dry lowland forest, which follows an elevation-dependent gradient of increasing extent of closed-canopy, old-growth forest and increasing tree basal area (Lovett et al. 2006). Sengis also tended to avoid steep areas, which seemingly have thinner leaf litter and therefore may be less suitable to foraging and/or nest building. In addition, results did not directly support our assumption that human disturbance may affect sengi occupancy, as DEE (which was assumed to be positively related to disturbance) had a negative sign in the model outcome, albeit its model weight was much lower than the habitat one. Models with p(DEE) ranked higher than models with $p(\cdot)$, supporting our assumption of a possible influence of DEE on detectability of gray-faced sengis. Lower detectability of gray-faced sengis in camera traps set near the edge could reflect both disturbance-driven shyness of sengis and the compressed field of view of cameras in the denser

TABLE 4.—Estimated occupancy (Ψ) and detection probability (p) of the top-ranked models for the gray-faced sengi in Mwanihana forest, Udzungwa Mountains, Tanzania. Change in Akaike information criterion (ΔAIC) is the difference in AIC values between each model with the lowest AIC model, *n*Pars is the number of parameters in the model, w_i is the AIC model weight, and DEE is the distance to the eastern edge of the forest.

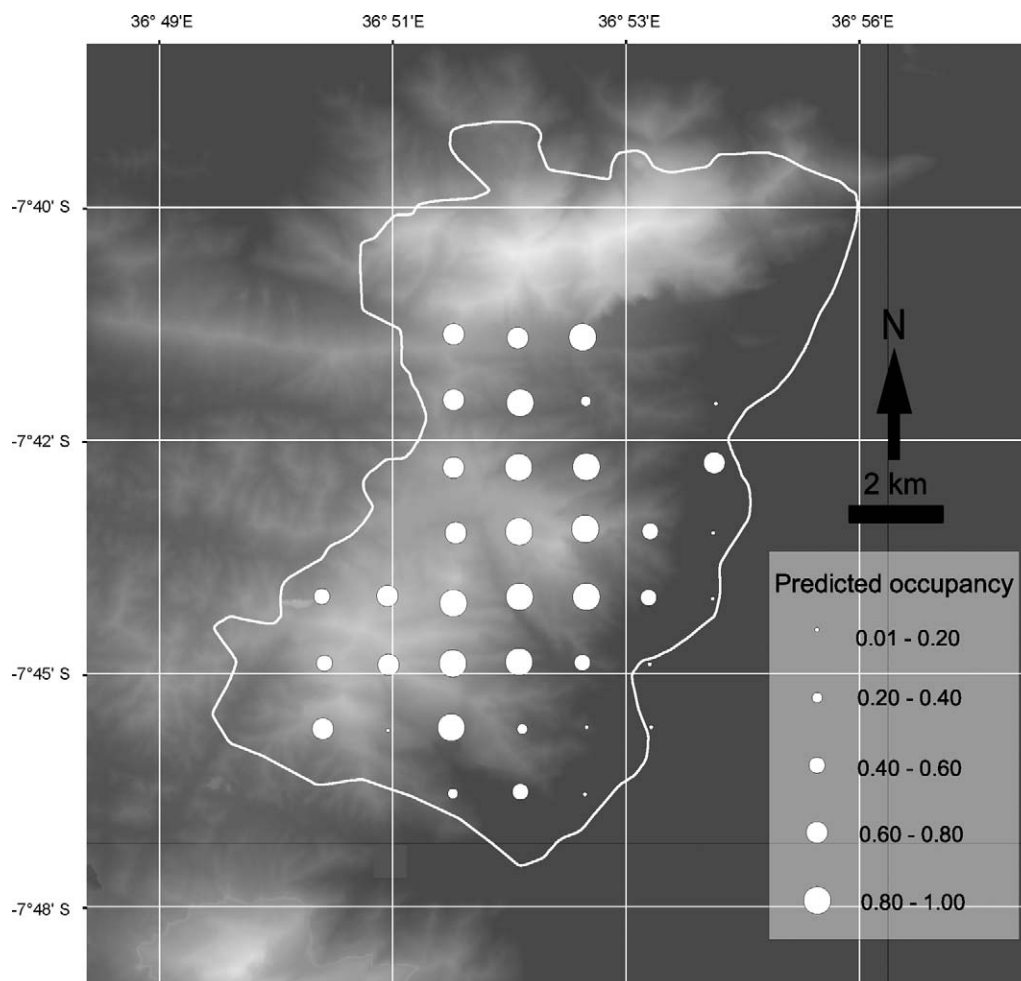| Model	AIC	ΔAIC	nPars	w_i	Ψ ($\pm$ SE)	P
Ψ(DEE + closed forest) p(DEE)	685.9	0.00	5	31%	0.552 ± 0.097	0.127
Ψ(closed forest) p(DEE)	686.4	0.48	4	24%	0.546 ± 0.093	0.128
Ψ(DEE + slope + closed forest) p(DEE)	687.3	1.35	6	16%	0.557 ± 0.097	0.127
Ψ(slope+ closed forest) p(DEE)	687.6	1.70	5	13%	0.552 ± 0.093	0.128
Model average					0.551 ± 0.095	

F IG. 2.—Map of the distribution of the gray-faced sengi in the mid- to northern portion of Mwanihana Forest, Udzungwa Mountains, Tanzania, with locations of camera traps shown as dots of size proportional to its estimated occupancy. The background layer is a digital elevation model (dark is low elevation). The gray-faced sengi's occupancy peaks in forest interior, evergreen forest habitat. See Fig. 1 for location of Mwanihana.

forest floor found in the lower-elevation areas with secondary and regenerating vegetation.

By coupling camera-trapping methods with habitat assessment, we revealed new insights into the ecology of gray-faced sengis that could be applied to other giant sengi species. Our results suggest that gray-faced sengis are most abundant in moist montane forest with adequate cover of understory vegetation and deep leaf-litter forest floors in gentle slopes. These habitat preferences match those highlighted for the golden-rumped sengi, which inhabits lowland forests along coastal Kenya and has a similarly restricted distribution. This suggests that despite the remarkable variation of forest habitats colonized by giant sengis (Rathbun 2009), their habitat requirements may be relatively conserved.

The restricted range of the gray-faced sengi remains intriguing, and likely reflects the complex biogeography of the Udzungwa Mountains, holding other range-restricted, endemic species whose origins are associated with the postulated ancient persistence and climatic stability of the montane forest cover (e.g., Dinesen et al. 1994; Stanley et al.

2005). The gray-faced sengi shares with other endemics a rapidly increasing conservation concern that is associated with increasing human pressure, especially in the least-protected forests of the range (Rovero et al. 2012). Hence, ensuring long-lasting and effective management of the full extent of the moist montane forests where the species occurs is of critical conservation relevance.

Last, our study confirms the potential of camera trapping for studying giant sengis and presumably similar forest-dwelling mammals, with an emphasis on determining occupancy and environmental drivers (Linkie et al. 2007; Tobler et al. 2009; Ahumada et al. 2011). Relative to alternative detection methods (i.e., sightings or counts of signs), camera trapping allowed us to achieve sufficiently high detection probabilities ($P > 0.10$) for deriving precise models. However, the systematic sampling protocol was designed for the whole community of medium to large mammals (TEAM Network 2011), and modifications might need to be made for it to be optimal, i.e., yield higher detection probability, for any particular species.

LITERATURE CITED

AHUMADA, J., ET AL. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2703–2711.

ANDANJE, S., B. R. AGWANDA, G. W. NGARUYA, R. AMIN, AND G. RATHBUN. 2010. Sengi (elephant-shrew) observations from northern coastal Kenya. Journal of East African Natural History 99:1–8.

BOWKETT, A. E., F. ROVERO, AND A. R. MARSHALL. 2008. The use of camera trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. African Journal of Ecology 46:479–487.

BULTMAN, T. L., AND G. W. VETZ. 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia (Berlin) 55:34–41.

BURGESS, N. D., ET AL. 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation 134:209–231.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference. A practical information–theoretic approach. 2nd ed. Springer, New York.

CORBET, G. B., AND J. HANKS. 1968. A revision of the elephant shrews, Family Macroscelididae. Bulletin of the British Museum (Natural History), Zoology 16:47–111.

COSTER, S., AND D. O. RIBBLE. 2005. Density and cover preferences of black-and-rufous elephant-shrews *Rhynchocyon petersi* in Chome Forest Reserve, Tanzania. Belgium Journal of Zoology 135(Suppl.):175–177.

DINESEN, L., T. LEHMBERG, J. O. SVENDSEN, L. A. HANSEN, AND J. FJELDSÅ. 1994. A new genus and species of perdicine bird (Phasianidae, Perdicini) from Tanzania: a relict form with Indo-Malayan affinities. Ibis 136:2–11.

DUMBACHER, J. P., G. B. RATHBUN, A. SMIT, AND S. J. EISEB. 2012. Phylogeny and taxonomy of the round-eared sengis or elephant-shrews, genus Macroscelides (Mammalia, Afrotheria, Macroscelidea). PLOS One **7**:e32410.

FARR, T. G., ET AL. 2007. The shuttle radar topography mission. Reviews of Geophysics 45:RG2004 / 2007. URL http://www2.jpl.nasa.gov/srtm/. Accessed 1 January 2013.

FISHER, B., ET AL. 2011. Measuring, modeling and mapping ecosystem services in the Eastern Arc Mountains of Tanzania. Progress in Physical Geography 35:595–611.

FISKE, I., AND R. CHANDLER. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43(10):1–23. URL http://www.jstatsoft.org/v43/i10/. Accessed 1 January 2013.

FITZGIBBON, C. D. 1994. The distribution and abundance of the golden-rumped elephant shrew *Rhynchocyon chrysopygus* in Kenyan coastal forests. Biological Conservation 67:153–160.

FITZGIBBON, C. D., AND G. B. RATHBUN. 1994. Surveying *Rhynchocyon* elephant-shrews in tropical forest. African Journal of Ecology 32:50–57.

IUCN. 2012. IUCN red list of threatened species. http://iucnredlist.org. Accessed 24 July 2012.

LINKIE, M., Y. DINATA, A. NUGROHO, AND I. A. HAIDIR. 2007. Estimating occupancy of a data-deficient mammalian species living in tropical rainforests: sun bears in the KerinciSeblat region, Sumatra. Biological Conservation 137:20–27.

LOVETT, J. C. 1993. Eastern Arc moist forest flora. Pp. 33–55 in Biogeography and ecology of the rain forests of Eastern Africa (J. C. Lovett and S. K. Wasser, eds.). Cambridge University Press, Cambridge, United Kingdom.

LOVETT, J. C., A. R. MARSHALL, AND J. CARR. 2006. Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. African Journal of Ecology 44:478–490.

MACKENZIE, D. I., AND J. D. NICHOLS. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461–467.

MACKENZIE, D. I., J. D. NICHOLS, J. E. HINES, M. G. KNUTSON, AND A. B. FRANKLIN. 2003. Estimating site occupancy, colonization, and extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MACKENZIE, D. I., J. D. NICHOLS, G. LACHMAN, S. DROEGE, J. ANDREW ROYLE, AND C. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MAZEROLLE, M. J. 2012. AICcmodavg: model selection and multi-model inference based on (Q)AIC(c). R package version 1.26. http://CRAN.R-project.org/package=AICcmodavg. Accessed 1 January 2013.

NETELER, M., AND H. MITASOVA. 2008. Open source GIS: a GRASS GIS approach. 3rd ed. Springer, New York.

O'BRIEN, T. G. 2011. Abundance, density and relative abundance: a conceptual framework. Pp. 71–96 in Camera traps in animal ecology: methods and analysis (A. F. O'Connell, J. D. Nichols, and K. U. Karanth, eds.). Springer, New York.

O'CONNELL, A. F., AND L. L. BAILEY. 2011. Inference for occupancy and occupancy dynamics. Pp. 191–205 in Camera traps in animal ecology: methods and analysis (A. F. O'Connell, J. D. Nichols, and K. U. Karanth, eds.). Springer, New York.

O'CONNELL, A. F., D. NICHOLS, AND K. U. KARANTH. 2011. Camera traps in animal ecology: methods and analysis. Springer, New York.

QUANTUM GIS DEVELOPMENT TEAM. 2012. Quantum GIS geographic information system. Open Source Geospatial Foundation Project, http://qgis.osgeo.org. Accessed 1 January 2013.

R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, www.R-project.org. Accessed 1 January 2013.

RATHBUN, G. B. 1979. The social structure and ecology of elephant-shrews. Zeitschriftfur Tierpsychologie 20(Suppl.):1–77.

RATHBUN, G. B. 2009. Why is there discordant diversity in sengi (Mammalia: Afrotheria: Macroscelidea) taxonomy and ecology? African Journal of Ecology 47:1–13.

Rovero, F., and D. W. De Luca. 2007. Checklist of mammals of the Udzungwa Mountains of Tanzania. Mammalia 71:47–55.

Rovero, F., and N. Doggart. 2008. *Rhynchocyon udzungwensis*. The IUCN Red List of threatened species, http://www.iucnredlist.org/details/136309/0. Accessed 1 January 2013.

Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1011–1017.

Rovero, F., A. Mtui, A. Kitegile, and M. Nielsen. 2012. Hunting or habitat degradation? Decline of primate populations in Udzungwa Mountains, Tanzania: an analysis of threats. Biological Conservation 146:89–96.

Rovero, F., and G. B. Rathbun. 2006. A potentially new giant sengi (elephant-shrew) from the Udzungwa Mountains, Tanzania. Journal of East African Natural History 95:111–115.

Rovero, F., et al. 2008. A new species of giant sengi or elephant-shrew (genus *Rhynchocyon*) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. Journal of Zoology (London) 274:126–133.

Stanhope, M. J., et al. 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proceedings of the National Academy of Sciences USA 95:9967–9972.

Stanley, W. T., M. A. Rogers, and R. Hutterer. 2005. A new species of *Congosorex* from the Eastern Arc Mountains, Tanzania, with significant biogeographical implications. Journal of Zoology (London) 265:269–280.

TEAM Network. 2011. Terrestrial vertebrate monitoring protocol, v. 3.1. TEAM Standardized Monitoring Protocols. Conservation International. http://www.teamnetwork.org/protocols/bio/terrestrial-vertebrate. Accessed 24 July 2012.

Tobler, M. W., S. E. Carrillo-Percastegui, and G. Powell. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. Journal of Tropical Ecology 25:261–270.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Submitted 17 September 2012. Accepted 19 March 2013.

Associate Editor was Paul T. Stapp.