Estimating population size and habitat suitability for mountain nyala in areas with different protection status

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Short title: Conservation of mountain nyala

Abstract

Many species of large herbivores are declining in numbers as a consequence of direct persecution or habitat loss. In the Ethiopian highlands rapid human population growth has resulted in an expansion of human settlements and farmland, threatening many endemic species such as the mountain nyala (*Tragelaphus buxtoni*). Despite being listed as an endangered species it is still the most important trophy hunting species in Ethiopia. We counted faecal pellets of mountain nyala within plots distributed along transects to estimate population size. Further, we determined focal habitats of mountain nyala by developing resource selection functions that identify key environmental variables associated with the presence and abundance of faecal pellet groups. The total mountain nyala population was estimated at 3756 (95% CI: 2506 – 7135) individuals, mainly occupying woodlands while avoiding areas under significant human influence. The total suitable area was estimated at 8333 km^2. Only 31.6% of the population lived within a national park, while 53.5% of the total population was found in two controlled hunting areas in the eastern mountains. Abundance was 3.7 times higher in areas patrolled by wardens regardless of being in a national park or hunting area, suggesting that formal protection must be followed by patrolling to avoid poaching and habitat destruction. From our analyses of spatial variation in abundance we found no negative correlation with trophy hunting. Yet, it is too early to conclude that trophy hunting is sustainable as it has only recently been initiated in the studied populations.

Key words: mountain nyala, habitat suitability; resource selection functions; trophy hunting; population size estimation

Introduction

Many populations of large herbivores are directly persecuted through legal or illegal hunting and/or have lost much of their original habitat (Gordon, 2009). As much as 84 out of a total of 175 species of large herbivores are today classified as vulnerable, endangered or critically endangered (Gordon, 2009). Pressure on large herbivore populations is particularly heavy in many African countries. Here, pastoralists have moved their livestock into areas where large herbivore populations are present, often accompanied by extensive poaching (Hilborn *et al.,* 2006) and over-exploitation for meat (Wato, Wahungu & Okello, 2006). Due to the decrease of many sub-Saharan wildlife populations, there is a need to gain basic knowledge about the many poorly known species. The first crucial step in wildlife conservation is to obtain population estimates and information on the spatial distribution of a species (Dawson *et al*., 2008). Secondly, it is vital to know how a species interacts with its habitat and particularly its sensitivity to human disturbance (Araujo & Guisan, 2006). Habitat selection is commonly quantified through resource selection functions (RSF) such as logistic regression (Manly, 2002) and can be spatially extrapolated to highlight potential suitable habitats beyond the known range (Guisan & Thuiller, 2005). This information is important when evaluating the suitability of areas for protection (Araujo *et al.,* 2004).

The highlands of Ethiopia comprise the major part of Conservation International's Eastern Afromontane hotspot (Brooks *et al.,* 2004). The rapid human population growth followed by extensive cultivation and overgrazing threatens the endemic fauna and flora of the area. The mountain nyala, *Tragelaphus buxtoni* (Hillman & Hillman, 1987) is one of the endemic flagship species of the Ethiopian highlands. Due to its restricted distribution and assumed decline in numbers, the species has been listed as endangered by the IUCN Red List (Sillero-Zubiri, 2008). The Bale mountains (Fig. 1) harbours by far the largest mountain nyala population (Evangelista *et al*., 2008), while remnant populations are found in the highlands of Chercher, Arussi and Kuni- Muktar (Evangelista, Swartzinski & Waltermire, 2007; Kingdon, 1997). Bale Mountains National Park (BMNP) was established in 1970, primarily to protect the Ethiopian wolf *Canis simensis* and the mountain nyala (Waltermire, 1975). Despite being protected since 1970, the mountain nyala is the primary target for trophy sport hunters in Ethiopia, providing the majority of an annual local hunting industry worth about USD 1.4 million (Lindsey *et al*., 2007a; Lindsey, Roulet & Romanach, 2007b). Poaching is also expected to influence the abundance of mountain nyala (Yalden & Largen, 1992), especially in areas that are not effectively patrolled by wardens.

Several studies have estimated the population size of the mountain nyala (East, 1999; Malcolm & Evangelista, 2004; Refera & Bekele, 2004; Evangelista, 2006; Sillero-Zubiri, 2008), but the estimates differ by a factor of four and have been based on little quantitative data. Information on the ecology of the species is scarce, in particular on its sensitivity to human presence and habitat choice (Evangelista *et al*., 2008). In this study we used field data to assess the conservation status of the mountain nyala. Firstly, we estimated the population size (including confidence interval, CI) of mountain nyala in the Bale Mountains using faecal pellet counts calibrated with visual counts in open areas. Secondly, RSF models were used to estimate habitat selection and the total suitable area for mountain nyala in the Bale Mountains. Finally, we investigated whether mountain nyala abundance was higher in areas patrolled by wardens preventing livestock grazing and other human activities (either as part of BMNP or in hunting concessions) than in unpatrolled areas.

Material and methods

Study area

The study area consists of areas above 1800 m.a.s.l. in the Bale mountains (Fig. 1; N 6° 40'; E 39° 40') of South-Central Ethiopia (14 775 km^2). This is the expected lowest elevation where the mountain nyala is found (Evangelista *et al*., 2008). Based on field surveys we delineated 10 discrete areas containing populations of mountain nyala. We also randomly selected 13 areas (each 30 km^2) within the study area (by selecting random points taken to be the centre of each area; Hawth's Tools [Beyer, 2004]). Although the distribution of mountain nyala was only partly known *a priori*, pellet surveys in all random areas confirmed absence (see below) and they are henceforth termed “areas without mountain nyala” (Fig. 1).

All areas with mountain nyala are formally protected within the boundaries of BMNP (i.e. Gaysay area, the BMNP headquarters, Web Valley, Senetti Plateau and Harenna Forest) or belong to a Controlled Hunting Area (i.e. Hanto, Hora, Abasheba Demaro, Besmena-Odo Bulu, Shedem-Berbere and Dodola). Frequent patrolling by wardens is limited to the Gaysay area, the BMNP headquarters, and two hunting concessions Abasheba Demaro and Besmena-Odo Bulu. Gaysay area is a 31 km^2 area containing three scout stations where three wardens are on daily duty. The situations in Abasheba and Odobullu are similar. The presence of scouts effectively prevents tree cutting and shepherding in these fairly small areas. Human settlements are abundant in much of the Bale Mountains, particularly in the north-eastern half of the range (Fig. 1).

GIS environmental variables

The supervised classification method (Dean & Smith, 2003) was used to classify pixels in a SPOT satellite image (resolution 10 m; from 2007) into the following seven land cover categories: Forest, Erica shrub, Grassland, Bushland, Agriculture, and Human settlement (Table S1) using the software ERDAS Imagine (Fig. 2; ERDAS, 1994). The map was validated with 944 ground truth locations (Congalton, 1991) and classification accuracy of the map was 88% (Anderson *et al*., 1976). The slope, aspect and elevation values of the plots were derived from a 90 m resolution Digital Elevation Model (DEM) by using Spatial Analyst in ArcGIS 9.3 (ESRI, USA).

Pellet sampling along line transects

Within each area (with or without mountain nyala) line transects were established at regular intervals (200 m; Krebs, 1989). Along each transect we randomly selected points in proportion to the area to be sampled (4 points per km^2 area). On each point a 4 x 5 meter rectangle (termed “plot” hereafter) was censured for presence of mountain nyala pellets (Carvalho & Gomes, 2004) and the number of pellet groups were counted. A total of 1515 plots in mountain nyala areas and 1553 plots in areas without mountain nyala were sampled.

Estimating population size

The density of animals was calculated from pellet count transects using Eqn 1, where Da= density of the animal, Ds= total number of pellet pellets encountered per area, Pi= mean time to degradation of the pellets and I= defecation rate (Homyack *et al*., 2006; Periago & Leynaud, 2009).

$Da = Ds/Pi*I$ Eqn 1

Pellet group degradation rate (Pi) was estimated by marking fresh pellet groups (observed being defecated) followed by daily monitoring until all the pellets in a group was completely decayed. Sixty pellet groups were marked during the wet season when we did the pellet count across all the mountain nyala localities. The mean degradation rate for pellet groups in the wet season varies depending up on the cover of the area where the pellets were dropped. Average degradation rate of pellet groups in open areas (33.5 days; n= 31, sd= 8.6) was significantly faster than for pellets in closed habitat (44 days; n= 29, sd= 12; Mann-Whitney U= 243, Z= -3.06, p= 0.002). When estimating population size, the decay time was taken as the linear combination of the estimated open and covered decay times weighted with the proportion of open and closed habitat for each locality (Table 1). The proportion of cover and open areas in each locality was estimated from a 10m resolution SPOT image by supervised classification using the ERDAS imagine software.

We estimated the defecation rate (I) from Eqn. 1 by using the maximum density estimate (25 individuals/km^2) obtained from 6 repeated total visual counts (range in estimated density: 23-25) of the mountain nyala in the Gaysay area. The 31 km^2 area was divided into 10 blocks with clear demarcation to avoid double count during the visual count. The mountain nyala defecation rate was estimated at 22.3 pellet groups per day per animal, which is very close to the defecation rate of 24.8 pellet groups per day estimated for the similar-sized greater kudu (*Tragelaphus strepsiceros*; Ellis & Bernard, 2005). Finally, defection rate in an independent, smaller data set from a forested area (Headquarter area of BMNP) was estimated at 20.0 pellet groups per day, indicating that our estimate of defecation rate is robust. To estimate the confidence intervals (CI) for the size of each population we used a Monte Carlo error propagation method (Press *et al.*, 1992) assuming Poisson distribution in each parameter on the right hand side of Eqn. 1 (see electronic appendix A1).

Resource selection functions and habitat suitability

We modelled habitat selection in two steps. A case control logistic regression was used to analyse environmental differences between the mountain nyala areas (cases; n=10) and the randomly selected areas without mountain nyala (controls; n=13). This step was conducted to identify characteristics of empty areas in order to censor areas with similar characteristics from the final habitat suitability map. Due to the low sample size we compared a range of univariate models (Table 2). The most parsimonious model based on the AIC (Burnham & Anderson, 1998) was tested against a null model with a Likelihood ratio test (Hosmer & Lemeshow, 1989).

The second modelling step investigated how the probability of detecting mountain nyala (pellets) varied within mountain nyala areas. First we checked linearity and modality of each single predictor variable using Generalized Additive Models GAM (Fig. S1). We fitted logistic mixed models (using function lmer in R library lme4, R Development Core Team, 2010) with presence of pellets within the plots as a binomially distributed response variable, and mountain nyala area as a random intercept. As fixed effects we included combinations of the variables: 1) habitat as a factor variable with 5 levels (forest, Erica tree/shrub, grassland, bushland and human influenced habitats [agriculture and settlements]), 2) slope (in degrees; log-transformed to stabilize variance), and 3) elevation (standardized; fitted both as first order and second order to investigate potential optimums along the elevation range). Co-linearity between predictor variables was checked by calculating the Variance Inflation Factor (VIF) (Zuur, Leno & Elphick, 2010). The top competing models (within ΔAIC=4 of the top model; Table 3) were included in model averaging. The habitat suitability map was constructed by extrapolating the averaged model onto all pixels within the study area. See electronic appendix A2 for a discussion of using faecal sampling to assess habitat selection.

Estimating the effect of guarding and hunting

To investigate the correlation between efficient patrolling by wardens on the probability of mountain nyala occurrence, we created a dummy variable assigned 1 if patrolled and 0 if not. We compared the AIC of the previous best model with a model including patrolling as a factor and quantified how much patrolling increased the probability of mountain nyala occurrence as the odds ratio between patrolled and unpatrolled populations. Similarly, the effect of trophy hunting on the current abundance was assessed by creating a dummy variable for “hunting” (hunting=1; no hunting=0). The statistical software R was used in all analyses (R Development Core Team 2010).

Results

Population size and distribution

The total mountain nyala population in the Bale mountains was estimated at 3756 individuals (95% CI: 2506 – 7135) (Table 1). The largest numbers of mountain nyala were found in Besmena-Odo Bulu (n=1025), Abasheba Demaro (n=986) and Gaysay area within the BMNP (n=776; see Table 1 for estimates of all areas including 95% CI). We found that the BMNP only included 31.6% of the mountain nyala in the Bale mountains, while Controlled Hunting Areas in Besmena-Odo Bulu and Abasheba Demaro harboured 53.5% of the population. A sensitivity analysis for the standard deviation in the defecation rate showed that when the standard deviation was increased twofold (from 2.5 to 5), the total upper 95% CI increased by 24% while the lower limit decreased by 11 %. This indicates that the lower limit of the population estimate, which is important with regards to conservation, is robust.

Habitat suitability

Human influence was the primary factor differing between the mountain nyala areas and the randomly selected areas confirmed not to contain mountain nyala. The most parsimonious model for the presence of mountain nyala included the proportion of human-influenced habitat as a predictor variable (ΔAIC=5.6 lower than the strongest competing model; AIC_{weight}=0.87; Table 2). The effect of humans was strongly negative (Fig. 3; Likelihood ratio test with a 0-model; $p<0.001$). Mountain nyala was never present in areas exceeding 50% human influence, but there was data-deficiency between 6% and 50% because the mountain nyala tended to stay in areas with no humans and the randomly selected areas were always heavily inhabited by humans (Fig. 3). For the habitat potential map we therefore present a "best case" (censoring areas >50% human influence) and a "worst case" (censoring > 6% human influence) map. The censored area (best case; >50% human influence) covers 6442 km^2 (44% of the Bale mountains; coloured red in Fig. 4). Excluding localities with higher than 6% of human influence (worst case; the highest human density with nyala presence in our study area), censors 11525 km^2 which is 78% of the Bale mountains (Fig. S2).

A model containing only habitat type was the most parsimonious model for explaining variation in pellet abundance within the mountain nyala areas, but adding first and second order elevation and slope resulted in competing models (ΔAIC<4; Table 3). These variables were, therefore, included in the final averaged model (Table 4). The highest mountain nyala abundances occurred in forest (2.1 times more likely than in the reference type grassland) while the lowest abundances were in bushland (0.30 times as likely as occurrence in grassland (Table 4). Accounting for the effect of habitat, the abundance of mountain nyala increased marginally with elevation and slope (but the 95% CI did in all cases overlap zero indicating no significant effect; Table 4).

The averaged model provided the probability of mountain nyala occurrence in all pixels of the map where the probability was not set to zero in the first analysis step (all other colours than red in Fig. 4). When extrapolating the model geographically using the "best case" scenario (censoring only areas with > 50% human influence), the total suitable area for mountain nyala in the Bale mountains was estimated at 8333 km^2. The distribution of probabilities of mountain nyala occurrence was tri-modal and we defined the probability groups as rare (2-5% probability of pellet occurrence per plot; 2980 km^2), intermediate (6-10%; 2183 km^2) and common (16-20%; 3169 km^2; Fig. 4).

The effect of patrolling and hunting on mountain nyala abundance

A model including patrolling by wardens as a factor variable performed better than the model with only habitat (AIC with=1041.2; AIC without=1045.6; ΔAIC=4.4; Likelihood ratio test: Chisq= 6.43; p= 0.0112). The probability of mountain nyala occurrence in a plot was 3.7 times higher in the patrolled areas Gaysay area, Besmena-Odo Bulu and Abeshaba Demaro, as compared to unpatrolled areas. The effect of about 10 years of trophy hunting on abundance was, on the other hand, insignificant (AIC with the factor hunting= 1047.42; AIC without= 1045.63; Likelihood ratio test: Chisq= 0.2151; p= 0.6428).

Discussion

Here we report the conservation status of the endemic mountain nyala based on extensive field data in the last stronghold of its range, the Bale Mountains in the Ethiopian highlands. The total population size was larger than expected because many mountain nyala were found in densely forested regions where quantitative surveys have not previously been conducted. Although the mountain nyala has lost much of its original habitat to humans, populations exist in forested refuges outside the BMNP, in pockets of land that at least currently are not used for human settlement and agriculture.

Higher population size than previously found

Successful conservation and management of wild animals require reliable population estimates (Ogutu *et al.*, 2006). Our population estimate of around 3800 individuals in the Bale mountains is higher than estimates reported in earlier studies, which vary by a factor of nearly four (1000 by Refera & Bekele, 2004; 1,500 to 2,000 by Sillero-Zubiri, 2008; 1450 by Malcolm & Evangelista, 2004; 2650 by East, 1999; over 4000 by Evangelista, 2006 [similar to our estimate but also including Arussi mountains]). The reported differences are most likely due to low sampling coverage of field data, in particular from the forested habitats where we report the highest numbers.

Due to lack of comparable data it is not possible to address the population trends over time in the entire Bale Mountains. However, our estimate of 982 individuals combined in Gaysay area and the headquarter of BMNP indicates that this population is back to the same level as before 1991 when it was reduced to about 200 individuals due to illegal hunting (Woldegebriel, 1996).

Habitat suitability – avoiding humans in forested refuges

No meaningful model of mountain nyala habitat suitability can be built without knowledge of the species' sensitivity to human activity (Araujo & Guisan, 2006). Indeed, the presence of mountain nyala was strongly affected by human influence as defined by agricultural land and human settlements. Areas exceeding 50% human influence were never inhabited by mountain nyala. The exact threshold for acceptable human influence is likely to be much lower, but because areas tended to have either very high or very low occupancy of people, we were not able to make a more precise threshold for the tolerance level of humans (Fig. 3). Even with a "best case" scenario (threshold of 50% human influence) as much as 44% of the total area in the Bale Mountains was censored as potential mountain nyala habitat, primarily areas in the North-East and the North-West of the Bale mountains (Fig. 4). In the "worst case" scenario excluding areas with more than 6% human influence, as much as 78% of the area was censored (Fig. S2).

With the best case scenario, we estimated the total suitable habitat to cover an area of 8333 km^2 while the highest probability class was restricted to an area of 3169 km^2. The area of suitable habitat for mountain nyala has been quantified in one earlier study (Evangelista *et al*., 2008). Compared to our study, they concluded that a much larger area of the Bale Mountains was suitable mountain nyala habitat. The discrepancy is likely due to differences in elevation thresholds of suitable mountain nyala habitat, the spatial resolution of environmental variables and that we censored habitats with strong human influence. In our model, forest provides the most suitable habitat for the mountain nyala, with the forest belt in the escarpment running East-West of BMNP (Fig. 2) standing out as a particularly suitable area (Fig. 4). In accordance with this finding, the mountain nyala were restricted to steep woodland areas unsuitable for human settlement or farming in the western parts of the Bale Mountains (Malcolm & Evangelista, 2004). Forested ecosystems provide concealment opportunities, critical cover for thermal regulation and a wide selection of available forage (Evangelista, Swartzinski & Waltermire, 2007).

Habitat suitability modelling is tightly linked to the niche concept (Guisan & Thuiller, 2005). The fundamental niche is composed of all the suitable habitats a species can occupy, while the realized niche is what is actually observed in nature (Pulliam, 2000). The mountain nyala seems to have a wider fundamental niche than observed in most parts of the study area. First, Brown (1969) suggested that the ericaceous belt provided the best potential habitat for the mountain nyala. Since then much of the Erica forest has been converted to agricultural land (Evangelista *et al.,* 2008), and we found that the remaining pockets are less frequently selected than other forest types. Increased hunting pressure may have contributed to this shift from Erica to preference for the denser forests. In the well-patrolled Gaysay area within the BMNP, the mountain nyala spend the daytime in exposed open areas without shelter, which is not the case outside this protected area. The realized niche is, therefore, likely to be restricted by human disturbance in most of the distribution range.

Higher abundance in areas patrolled by wardens

The mountain nyala abundance was 3.7 times higher in areas that were patrolled by wardens, either as part of the BMNP (Gaysay area) or in hunting concessions (Abeshaba Demaro and Besmena-Odo Bulu). This indicates that intensified protection may decrease the negative impact of humans, including poaching (Hilborn *et al*., 2006). We did not find a negative effect of trophy hunting on the mountain nyala abundance. However, hunting has taken place in our study populations only for a period of 10 years. A thorough analysis of the effect of trophy hunting would require trends over time in hunted and protected populations. In addition other traits than abundance may be affected, such as changes in sex and age composition, as well as genetic effects of hunter selection of males with large horns (Coltman et al., 2003; Ginsberg & Milner-Gulland, 1994; Milner-Gulland *et al*., 2003). Trophy hunting is increasingly used as a tool for wildlife conservation in the sub-Saharan African countries (Lindsey, Roulet & Romanach, 2007b), but must be biologically sound and sustainable in order to be an effective conservation tool (Sparrowe, 1990).

Conservation implications

This field survey revealed that the total population size of the mountain nyala in the Bale Mountains was higher than previously expected. By quantifying and including avoidance of humans in a habitat suitability model we report that the suitable area for mountain nyala is only around half of what has previously been suggested. It is worrying that as much as 55% of the total population were found to live within Controlled Hunting Areas. Within these areas we recommend that there is continued monitoring of trophy hunting through annual estimation of population size by using the standardized faecal pellet count method presented here. Mountain nyala abundance was almost 4 times higher in areas patrolled by wardens. Intensive patrolling by wardens is likely to be an efficient tool for preventing population decline of endangered species in areas with strong human-wildlife conflicts.

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Table 1. Population estimates (PE) including lower (LCI) and upper (UCI) 95% confidence intervals based on pellet counts in mountain nyala populations in areas throughout the Bale mountains. The decay time was taken as a linear combination of the estimated open (34.5 days) and covered decay times (44 days) in the population estimate.

	AR	% OP	% CR	No. PS	PAI	DR	PE	LCI	UCI
Besmena Odo Bulu	71	8	92	285	0,278	43,24	1025	645	2125
Abasheba Demaro	34	10	90	144	0,557	43,05	986	627	2015
Gaysay area	31	49	51	130	0,437	39,35	776	528	1290
Dodola	26	14	86	98	0,179	42,48	245	159	493
Harenna Forest	74	6	94	291	0,040	43,43	152	95	319
Shedem Berbere	24	26	74	109	0,100	41,53	129	85	237
Hanto	23	18	82	115	0,080	42,29	97	63	188
Hora	21	7	93	113	0,080	43,34	87	54	181
Web Valley	26	40	60	120	0,020	40,20	29	20	51
Senetti Plateau	22	45	55	110	0,018	39,73	24	16	41
Headquarter[3]	1	-	-	-	-	-	206	216	197
Total	353			1515			3756	2506	7135

AR= Area estimated in km^2, % OP= Percentage of open area in the locality, %CR= Percentage of cover of the locality, No. PS= number of plot sampled, PAI= Pellet per plot/ Pellet abundance index, PE= Population estimate, UCI= Upper 95% confidence interval, LCI= Lower 95% Confidence Interval, DR= Degradation rate estimate.

[3] In the Headquarter of the BMNP (in italics) the population estimate was based on visual counts

Table 2. Model selection of large-scale presence and absence of mountain nyala.

Model	AIC	ΔAIC	AICweight	AUC
Habitat type[4]				
Prop. of human influenced habitat (settlement and agriculture)	20.1	0	0.871	0.9
Prop of shelter habitat (Forest and Erica)	25.7	5.56	0.054	0.85
Prop. of Erica	31.4	11.29	0.003	0.758
Prop. of forest	31.9	11.77	0.002	0.689
Slope				
Slope**b**	27	6.86	0.028	0.85
Elevation				
Elevation**c**	28.3	8.16	0.015	0.819
Elevation (spline function; k=3)	28.1	7.99	0.016	0.835
Elevation + Elevation²	29	8.89	0.01	0.804

[a]All habitat variables are included as the proportion covering each area (range 0 to 1). The most parsimonious model (*in italics*)

[b]Slope is measured in degrees and log-transformed.

[c]Elevation was normalized for easier interpretation of the relative importance of first versus second order term.

Table 3. Model selection among candidate models for predicting the presence of mountain nyala pellets in 4 by 5 meter plots as a function of environmental variables.

Model name	Parametersa	AIC	ΔAIC	AICweight	AUC
m1e	Habitatb	1045.6	0	0.39	0.761
m6	Habitat + Slope (ln-transformed)	1046.59	1	0.24	0.766
m4	Habitat + Elevation + Elevation²	1047.6	2	0.14	0.764
m5	Slopec	1090.6	44.9	0	0.724
m0	Null model (only intercept)	1091.39	45.8	0	0.718
m3	Elevationd + Elevation²	1091.7	46	0	0.722
m2	Elevation	1093	47.3	0	0.719

[a]Locality is always fitted as a random intercept.

[b]Habitat is fitted as a factor variable with 5 levels (Forest, Erica tree/shrub, Grassland, Bushland and human influenced habitats [agriculture and settlements]).

[c]Slope is measured in degrees and log-transformed.

[d]Elevation was normalized for easier interpretation of the relative importance of first versus second order term.

[e]The most parsimonious models included in later model averaging is presented *in italics*

Table 4. The most parsimonious model[a] predicting the presence of mountain nyala pellets in 4*5 meter plots as a function of environmental variables.

	Coefficient	SE	Lower 95% CI	Upper 95% CI
Intercept	-2.33	0.473	-3.26	-1.4
Habitat (Erica - Grassland)	-0.283	0.42	-1.11	0.541
Habitat (Forest - Grassland)	0.766	0.373	0.0338	1.5
Habitat (Human influenced habitats - Grassland)	-1.33	0.806	-2.91	0.253
Habitat (Bushland - Grassland)	-1.2	0.44	-2.06	-0.333
Slope (ln transformed)	0.0458	0.0865	-0.124	0.215
Elevation (normalized)	0.0366	0.081	-0.122	0.195
Elevation^2 (normalized)	-0.0119	0.0377	-0.0859	0.062

[a]The model is averaged across all competing models (within ΔAIC < 4)

Figure legends

Fig. 1. The study area in the Bale Mountains, South Ethiopia. The black polygons are areas with mountain nyala. Striped squares are randomly selected areas (n=13; each area 30 km^2) where no evidence of mountain nyala presence was found (no pellets). Grey polygons represent the major human settlements. The black line outlines the Bale Mountains National Park (BMNP).

Fig. 2. Land cover map of the Bale Mountains in Ethiopia showing the distribution of five vegetation types in addition to human settlements and water.

Fig. 3. Probability of presence of mountain nyala with increasing proportion of human-influenced habitat (major human settlement or agricultural land). The area of each point is proportional to sample size. Note the data deficiency between 6% and the line at 50% human influence which occurs because mountain nyala were found in areas with low human occurrence while the random locations (n=13) tended to be heavily inhabited, due to the large human population in the area.

Fig. 4. Habitat suitability map for mountain nyala. Red colour resembles unsuitable areas (zero probability of occurrence) defined according to the “best case” scenario as areas with more than 50% influence of humans (6442 km^2). In the rest of the area the distribution of probabilities is tri-modal and we defined each probability group as rare (brown; 2-5% probability of pellet occurrence per plot; 2980 km^2), intermediate (yellow-green; 6-10%; 2183 km^2), or common (blue; 16-20%; 3169 km^2).

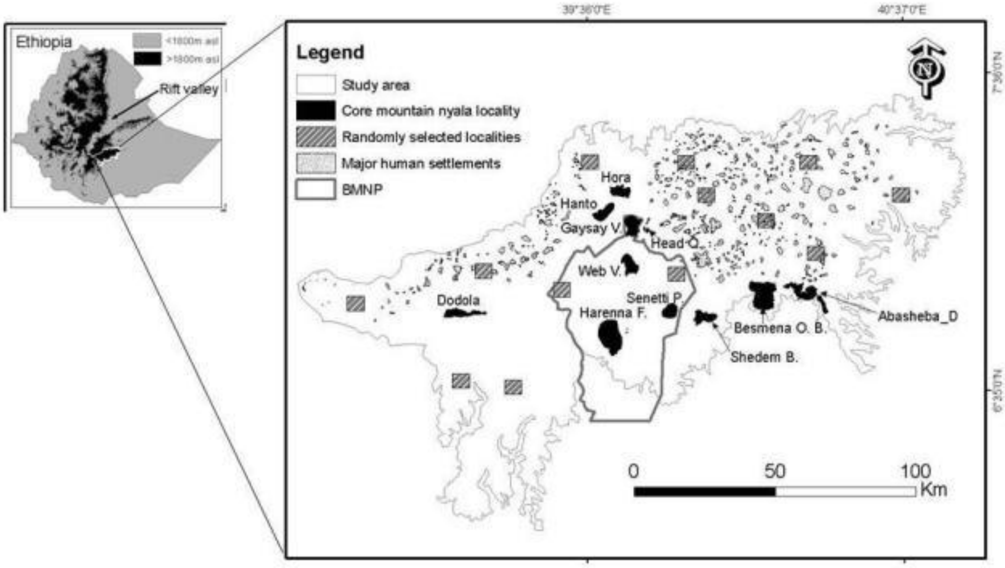
Ethiopia
Rift valley
Legend
Study area
Core mountain nyala locality
Randomly selected localities
Major human settlements
BMNP
Hora
Hanto
Gaysay V.
Head Q.
Web V.
Senetti P.
Harenna F.
Dodola
Besmena O. B.
Abasheba_D
Shedem B.
0
50
100
Km

Fig. 1.

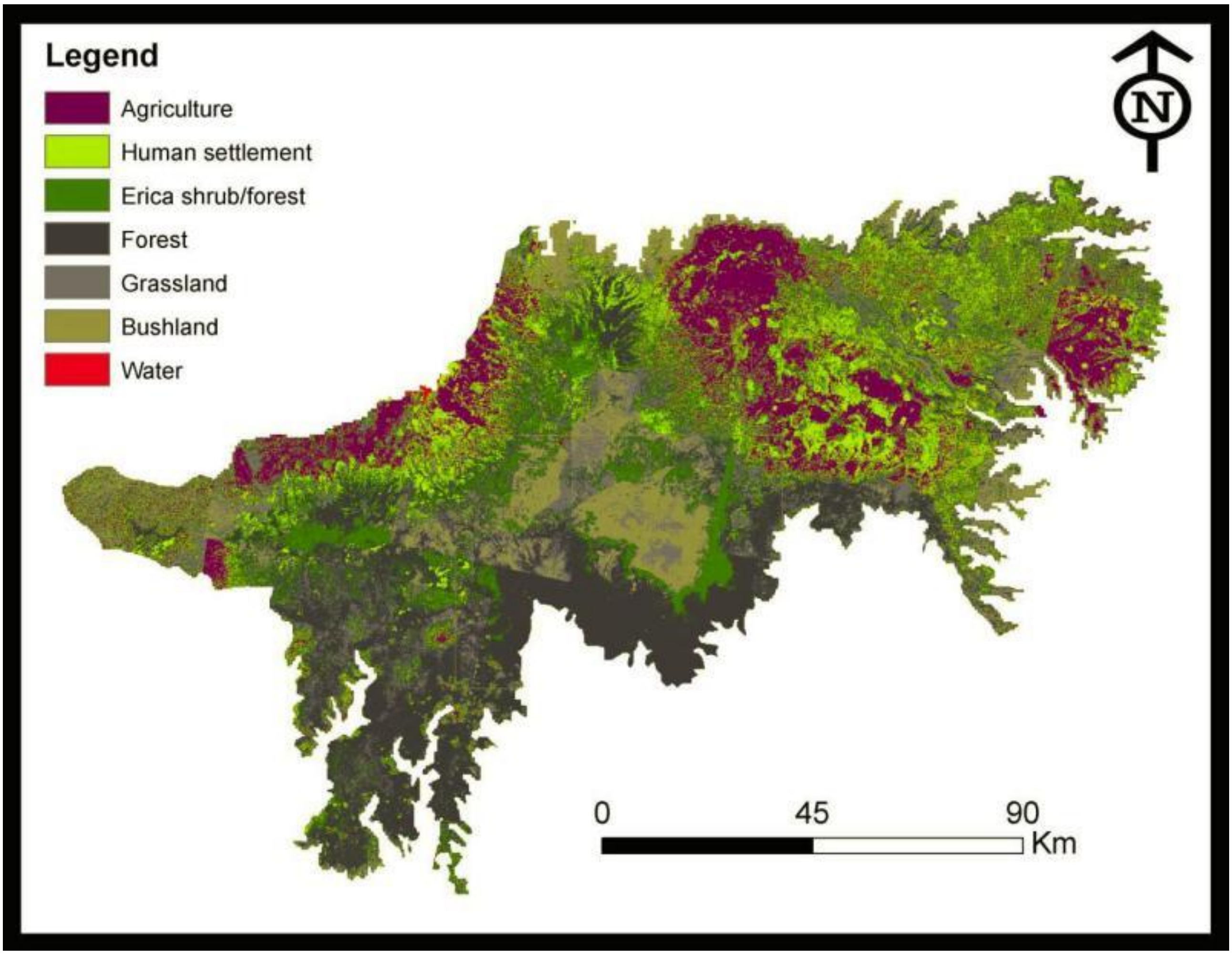
Legend
Agriculture
Human settlement
Erica shrub/forest
Forest
Grassland
Bushland
Water
N
0
45
90
Km

Fig. 2.

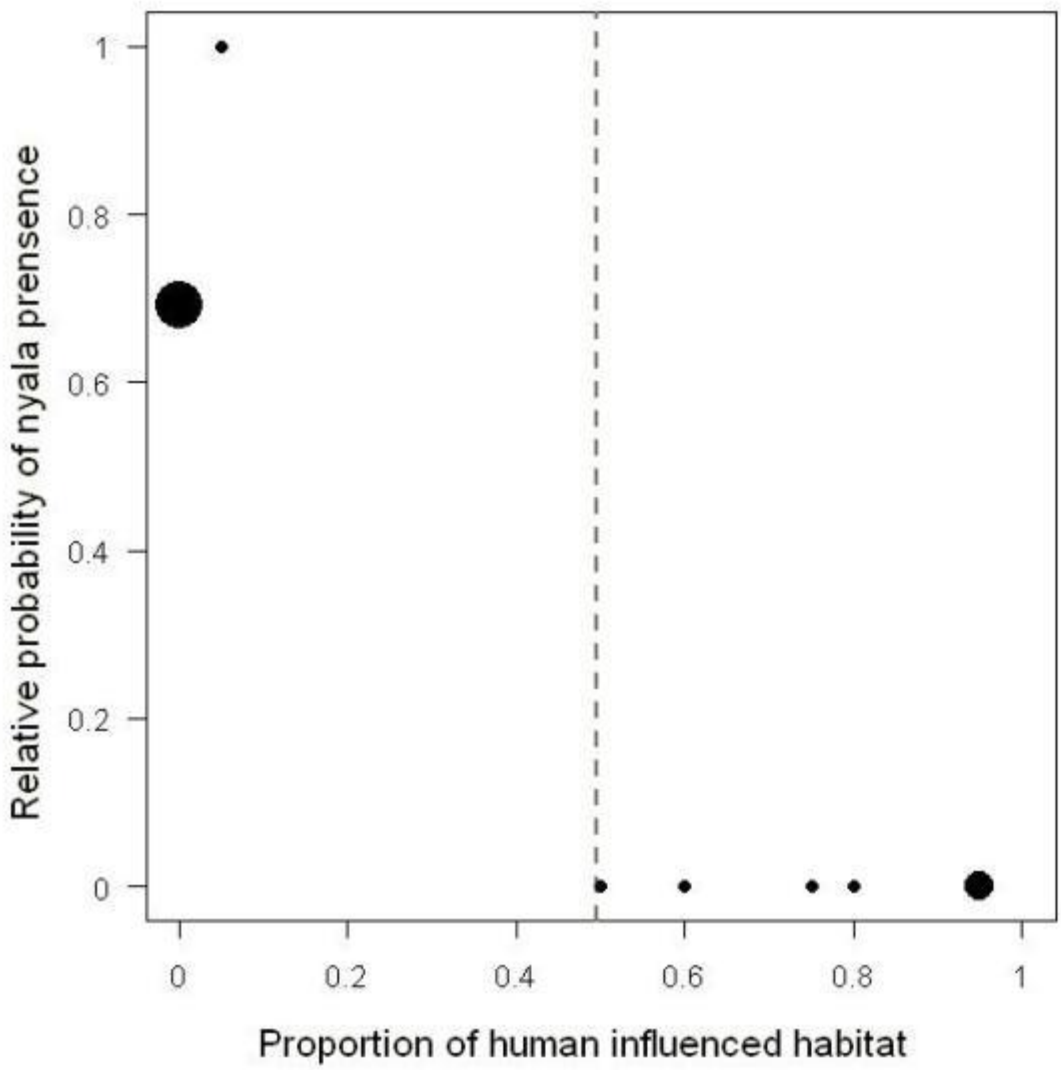
Relative probability of nyala prensence
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
Proportion of human influenced habitat

Fig. 3.

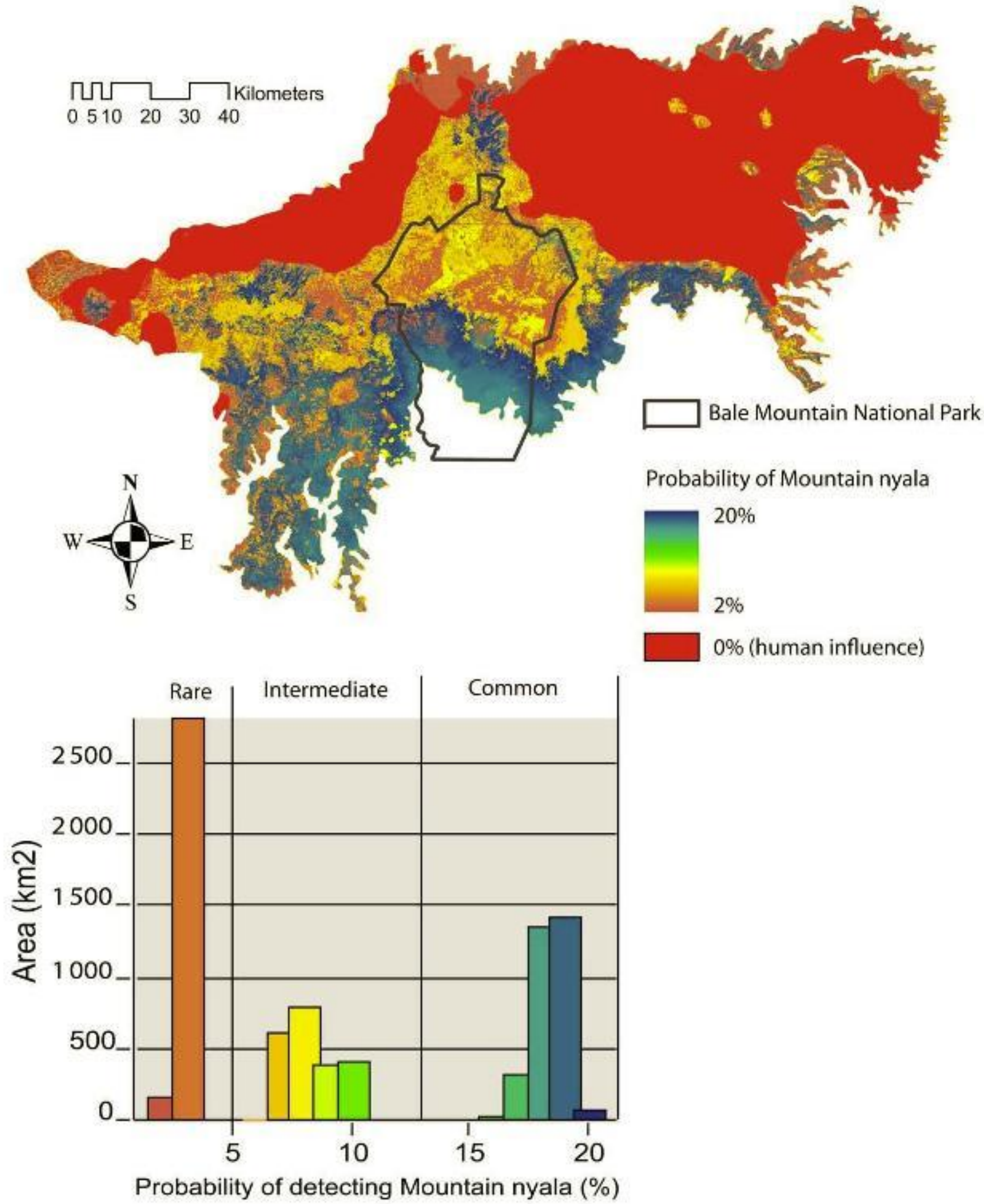
Kilometers
0 5 10 20 30 40
N
W
E
S
Bale Mountain National Park
Probability of Mountain nyala
20%
2%
0% (human influence)
Rare
Intermediate
Common
Area (km2)
2 500
2 000
1 500
1 000
500
0
5
10
15
20
Probability of detecting Mountain nyala (%)

Fig. 4.

Electronic Supplementary Material

A1. Calculating confidence limits and testing for bias in the population estimate
We performed a Monte Carlo simulation with the aim of calculating confidence limits and testing for bias in population size estimates. The standard deviation in the mean decay time (Pi; Eqn 1) was estimated at 8.6 in open areas and 12 in areas with cover. Finally, the standard deviation in defecation rate (I) is unknown, but to get a reasonable estimate of the total CI an error term in the defecation rate had to be included. We therefore assumed that the standard deviation in the defecation rate is 2.5 (see below for estimation of bias in the model). A Monte Carlo simulation for each locality using 100000 random draws from these distributions was propagated to the population estimate through Eqn 1.

When testing for bias we used the following approach. In this simulation we follow each individual pellet and allow the probability of decay to increase with the square of the age of the pellet. Decay rates are variable depending on the cover but on average the decay time was 39.2 days. Each individual mountain nyala is expected to have daily variations in defecation rate and size of the pellet (which is proportional to the decay probability as small pellets have a larger chance of decaying). Our analysis allows for some individuals to have higher average defecation rate than others (but in a fraction which gives a mean defecation rate of 22.3) that might reflect differences in mountain nyala size and habitat. We follow individual pellets accumulated from 100 simulated mountain nyala. We keep track of the pellets for a fixed time of 100 days. This is long enough to reach the equilibrium, because a steady state is reached after about 60 days (with about 86000 pellets at steady-state). From these simulations we did not find any signs of bias due to individual variations. We conclude that our method is fairly stable with the current data. Note however, that bias due to immigration and emigration is not included in this simulation and could potentially introduce some minor bias.

A2. Using faecal sampling to assess general habitat selection
We use faecal pellet sampling to draw general inferences of mountain nyala habitat use. This relies on the assumption that defecation of pellets is proportional to habitat use. Faecal sampling is frequently used in other studies as a proxy of general habitat use (e.g., Herrera, Comparatore & Laterra, 2004; Shimano et al., 2006) and Loft and Kie (1988) found corresponding ranks of relative habitat use when comparing faecal sampling with radio triangulation. However, we cannot entirely exclude a bias in selection towards the habitat types used more frequently during night time resting or shortly after resting [due to higher defecation frequency at these times]. For the mountain nyala this is expected to be sheltered habitat.

Table S1. Description of habitat types in the Bale Mountains, Ethiopia

Habitat type	**Description**
Forest	Habitat with natural and plantation trees including Hagenia abyssinica, Podocarpus falcatus, Rapanea melanophloeos, Discopodium penninervum, Maytenus obscura, Bersama abyssinica, Hypericum revolutum, Dombeya torrida, Juniperus procera, Pittosporum viridiflorum, Conyza vernonioides, Euphorbia abyssinica, Arundinaria alpine, Afrocarpus falcatus, Prunus africana, Schefflera abyssinica and other bigger tree species excluding Erica forest.
Erica tree/shrub	Habitat dominated by one of the two species Erica arborea and Erica trimera, either in tree or shrub form.
Grassland	Area dominated by grass species including Festuca abyssinica, Carex spp, Poa schimperiana, Andropogon abyssinicus, and grass species mixed with other herbs lower than 10 cm of height, including Crepis carbonara, Dichrocephala chrysantemifolia, , Cerastium afromontanum, Merendera schimperiana, Trifolium burchellianum, Trifolium multinerve, Carduus camaecephalus, Geranium arabicum , Lobelia minutula, , Alchemilla abyssinica, Kraterostigma plantagineum and others.

Bushland	Habitat dominated by woody herbs and shrub species forming a closed layer including Acanthus sennii, Achyrantes aspera, Artemisia afra, Carduus nyassus, Conyza steudelii, Echinops ellenbeckii, Helichrysum formosissimum, Helichrysum citrispinum, Helichrysum splendidium, Senecio myriocephalum, Senecio ochrocarpus, Solanum giganteum, Veronica persica, Verbascum sinaiticum, Hebenstretia dentate, Delphinium welbyi, Kniphofia foliosa, Thymus schimperii, Leonotis ocymifolia, Swertia abyssinica, Plectanthrus barbatus, Rosa abyssinica Euphorbia dumalis and others.
Agriculture	Area for cultivation and land being prepared for growing crops (barley).
Human settlement	Area with human settlements in the form of village or town.

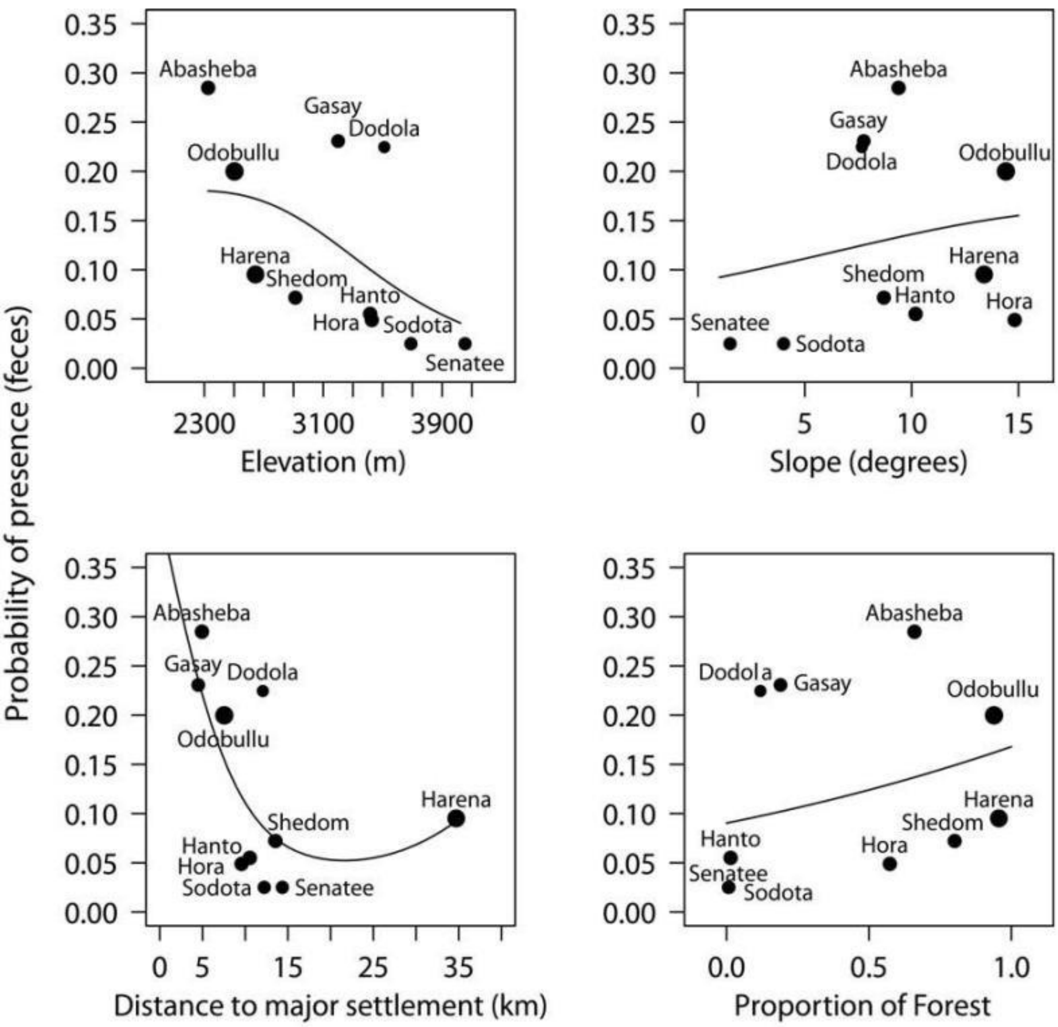

Fig. S1. Univariate relationships between the probability of detecting pellets in 4*5 meter plots within mountain nyala areas and the four predictor variables elevation, slope, distance to major human settlement and proportion of forest. Predicted lines are derived from univariate Generalized Additive Models (GAM).

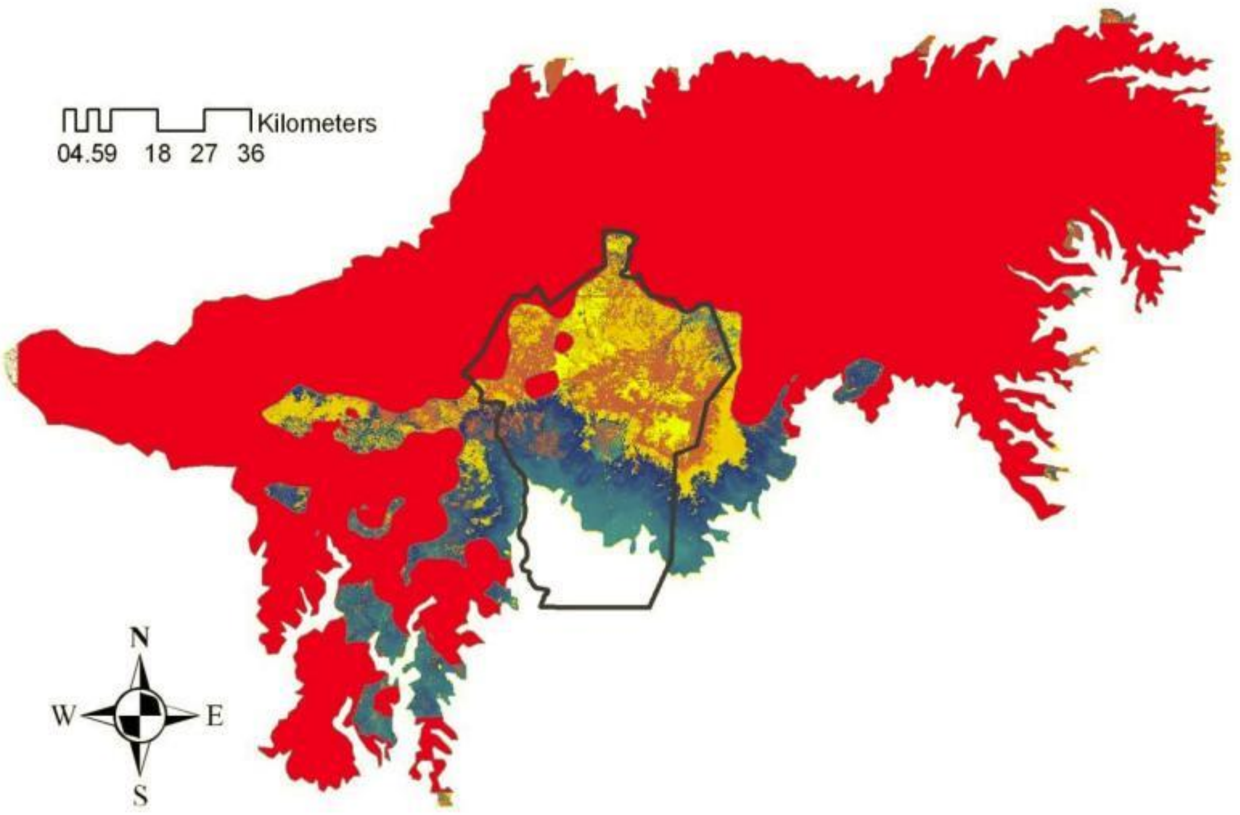

Fig. S2. Habitat suitability map for mountain nyala when defining areas with more than 6% human density (the "worst case"scenario) as unsuitable (red colour; 78 % of the total area; 11525 km^2). In the rest of the area the distribution of probabilities is tri-modal and we defined each probability group as rare (brown; 2-5% probability of pellet occurrence per plot), intermediate (yellow-green; 6-10%), or common (blue; 16-20%).