Home Range and Habitat Selection of Female Mountain Nyalas (Tragelaphus Buxtoni) in the Human-Dominated Landscape of the Ethiopian Highlands

Anagaw Atickem (anagawam@gmail.com)  
Addis Ababa University

Matthias Klapproth  
Deutsches Primatenzentrum GmbH - Leibniz-Institut fur Primatenforschung

Martha Fischer  
Saint Louis Zoo

Dietmar Zinner  
Deutsches Primatenzentrum GmbH - Leibniz-Institut fur Primatenforschung

Leif Egil Loe  
Norwegian University of Life science

Research article

Keywords: Mountain nyala, Home range, Habitat selection, Human settlement

DOI: https://doi.org/10.21203/rs.3.rs-21274/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License. Read Full License
Abstract

**Background:** Human settlement and agricultural activities restrict increasingly the range of large mammals in many cases contributing to declining numbers of ungulates. Here, we studied home range size and habitat selection of female mountain nyalas in the northern end of the Bale Mountains National Park (BMNP) (31 km$^2$) surrounded by human settlement. We collected data on space use of seven adult female mountain nyalas equipped with Global Positioning System (GPS) collars. Home range size was estimated using fixed kernel density and habitat selection was determined by resource selection functions.

**Results:** We found that female mountain nyalas have much smaller (5.7 km$^2$) home ranges than the 19 km$^2$ home range size predicted for a 170 kg, group-living species living in mixed habitats. Home ranges were 30% larger in night time than daytime. We suggest that the night time extension beyond the park boundaries were caused by both push and pull effects. The presumably high livestock and other ungulates grazing pressure within the protected area may cause forage-driven excursions out of the park, in particular during agricultural crop seasons. In addition, mountain nyalas are probably attracted by humans as shields against hyena predation. Resource selection index indicates bush land and forest habitat are the most preferred habitat types while agriculture and human settlements are least preferred habitats.

**Conclusions:** Given that mountain nyalas are found in high density (24 individuals/km$^2$) and the size of the northern part of the Bale Mountain National Park, which is currently under protection by the park authorities for the mountain nyala conservation, is too small for the predicted home range size of large ungulates, we suggest protecting additional area may be needed for the long-term conservation of the endangered mountain nyala.

**Background**

Home ranges and activity pattern of animals can be affected by the availability and quality of food and other resources, population densities of the respective species, the presence of competitors, risk of predation and climate [1–4]. Increasingly, human activities and human caused landscape alteration and fragmentation affect animal home range size, habitat use, activity and movement patterns [1, 5, 6].

As a rule of thumb, the size of a home range is expected to increase with the body size of the respective species, mediated also by habitat type and quality (e.g., open, mixed, closed) and the species’ social organization (e.g., solitary or group living) [7–9]. The influence of humans is expected to be higher for large mammals because of their higher space requirements [10, 11]. Furthermore, since humans are mainly diurnal they interfere with wildlife more during daytime than during night time, pushing many mammal species towards a more nocturnal activity [12].
A greater understanding of the human impact on activity and movement patterns, home ranges and habitat use constitute important baseline data for conservation management [13, 14, 5]. This is of particular importance for endangered species whose populations and ranges have already been reduced [15]. Ecological information on home range size, activity pattern and habitat use are essential for wildlife management and design of protected areas.

Mountain nyalas, *Tragelaphus buxtoni*, are endangered antelopes endemic to the south-eastern highlands of Ethiopia [16]. The largest mountain nyala population (n = 1100) exists in a forest-dominated landscape of the Bale Mountains National Park (BMNP) [17]. The park was established during the 1970s primarily to protect mountain nyalas and another endemic species, the Ethiopian wolf, *Canis simensis* [18]. Currently, about 90% of the mountain nyala population of the park is confined to its northern part, the Gaysay Area [17]. Human settlement and livestock grazing, however, is increasing outside and inside the park, resulting in competition for space and food with wild large herbivores, such as the mountain nyala [19].

In this study we equipped seven female mountain nyalas with GPS collars to investigate their activity and movement pattern, home range size and habitat use. Given the strong human encroachment in the area surrounding the Gasay Area, we predict that the home ranges of mountain nyala are smaller than expected from theory [20] and that diurnal habitat selection and movement patterns are influenced by human infrastructure. Based on our findings, we discuss whether the current size of the protected area and conservation measures are sufficient for long-term conservation of mountain nyala.

**Materials And Methods**

**Study area**

The study was carried out in the Gaysay Area (31 km$^2$) of the BMNP and its surroundings outside of the national park. Unlike large parts of the BMNP, which are dominated by human settlements and herds of livestock, the Gaysay Area is patrolled by rangers as protection from livestock grazing but the extent of illegal grazing is still extensive [19]. The climate of the Bale Mountains is characterized by a 4-month dry season (November to February) and 8-month rainy season (March to October).

We defined our study area as the 100% minimum convex polygon containing the all locations (fixes) of all collared female mountain nyalas (number fixes = 31,649) which corresponds to an area of about 133 km$^2$ (Fig. 1).

**Mountain nyala GPS-data**

We equipped seven female mountain nyalas with Global Positioning System (GPS) collars (Followit Holding AB, Sweden) between 25/05/2008 and 29/05/2008[21]. The females were immobilized using a remote injection system and collared. The GPS units were programmed to take fixes every other hour, i.e. 12 fixes per day. We downloaded data from the GPS collars remotely by an external telemetry receiver,
and transferred respective location data onto a computer with a Tellus Project Manager. The collars lasted on average 402 days before failure (SD = 215, range 212–681 days). The immobilization and animal handling was carried out with the permit and Ethical guidelines of Ethiopian Wildlife Conservation Authority [21].

**Habitat classification**

We defined habitats as grassland, forest, heath (dominated by *Erica* sp.), bushland, agriculture and human settlement. The habitat map was classified from SPOT images (2 m resolution) by using a supervised classification (ERDAS Imagine) based on 220 ground truthing locations [22, 23]. Elevation and slope values were derived from 90 m Digital Elevation Model (DEM). Geographic positions of households (settlements) adjacent to the Gaysay Area were recorded by using handheld GPS (24, for more details on habitat classification).

**Statistical analyses**

**Home range estimation**

We conducted home range analyses using fixed kernel density estimation. The bandwidth \( h \) was determined with the rule-based *ad hoc* approach [25]. Home range contours were calculated at the 95\% isopleth level. The most intensively used portion of a home range is defined as the core area, i.e. areas where individuals are found with greater probability within the home ranges, and was determined at the 50\% isopleth level [26, 27]. In addition, we calculated the extent of total area using the minimum convex polygon (MCP) method (determined at the 100\% isopleth level) for habitat utilization analysis. Home ranges and core areas were estimated with the R package “rhr” [28].

**Home range and body size**

To predict the home range size of a species of body size 170 kg [20, 29], living in mixed habitat and with a mean group size of seven we followed Ofstad et al. [9, Eq. 1].

Eqn 1: \( HR = \exp(-10.28 + 1.44*\log(BM) + 0.3*\log(\text{group size}))/100 \)

where \( HR \) refers to home-range, BM to body mass (measured in grams), group size in number of individuals. Note that the constant (-10.28) is specific for species living in mixed habitats.

**Habitat selection analysis**

The habit preference within our study area was carried out by using Generalized Linear Models (GLMs) with a use-availability design in R [30–32]. We used animal location as the sample unit in all analyses.
Each used location was paired with one random location in the following way: the random location copied all the non-spatial variables from the used point (ID, season, day time/night time) before adding new spatial covariates (distance to humans, habitat class) from the random location [33]. The response variable is binomially distributed and consists of used points (GPS points of respective mountain nyalas, coded 1) and randomly sampled available points (coded 0).

To account for temporal autocorrelation among observations we estimated robust standard errors using the approach of Forester et al. [34], i.e. we clustered the data based on the lag of the temporal autocorrelation and placed every other cluster in a second data set. The robust standard errors were calculated by averaging the covariance matrices for both subsets of data, while the parameter estimates represent fitted values from the full-data set.

The sample size differed among individuals. To prevent individuals with larger samples from influencing the results more than individuals with smaller samples, we weighted the contribution of each data point by a vector $W = \text{the lowest sample size across all individuals} / \text{sample size of focal animal in the GLM using the weights argument}$. Parameter estimates of this analysis are log odds of use relative to reference categories of categorical variables and zero values of continuous variables.

**Results**

**Home range size**

A total of 31,649 GPS fixes were obtained from the seven females with an average of 4,521 GPS fixes [SD = 2368] per female. The GPS collars recorded fixes with an overall success rate, successful records of GPS record in 2 hrs interval, of 92.1% (range between 82.8–96.3%). The mean home range size of a female was $5.7 \pm 4.4 \text{ km}^2$ and mean core area size was $1.1 \pm 0.79 \text{ km}^2$ (Table 1). This is only about 1/3 of the 19 km$^2$ home range size expected from Eq. 1.
Table 1
Size (km²) of home ranges (HR) and core areas (core) of female mountain nyalas (fixed kernel estimate home range 95%; core area 50%).

| ID | size    |         |         |      |         |      |      |         |      |      |         |      |
|----|---------|---------|---------|------|---------|------|------|---------|------|------|---------|------|
|    |         | annual  |         |      |         |      |      |         |      |      |         |      |
|    |         | core    | HR      | core | HR      | core | HR   |         |      |      |         |      |
| F1 | 0.8     | 4.2     | 1.0     | 4.7  | 1.3     | 5.7  |      |         |      |      |         |      |
| F2 | 0.6     | 3.6     | 0.6     | 3.7  | 0.6     | 3.4  |      |         |      |      |         |      |
| F4 | 1.2     | 7.1     | 1.2     | 7.5  | 0.7     | 3.5  |      |         |      |      |         |      |
| F5 | 1.1     | 6.5     | 1.0     | 6.1  | 0.9     | 4.3  |      |         |      |      |         |      |
| F7 | 2.8     | 14.4    | 2.5     | 13.9 | 1.7     | 9.9  |      |         |      |      |         |      |
| F8 | 0.5     | 2.6     | 0.4     | 2.0  | 0.4     | 2.7  |      |         |      |      |         |      |
| F9 | 0.7     | 5.2     | 0.7     | 5.9  | 0.9     | 4.9  |      |         |      |      |         |      |
|    | mean ± SD | 1.1 ± 0.8 | 5.7 ± 4.4 | 1.1 ± 0.7 | 6.3 ± 3.8 | 0.9 ± 0.4 | 4.9 ± 2.4 |

During night time females were significantly more often located outside the protected area (30% ± 33%) than during daytime (13% ± 18%, V = 2, n = 7, p = 0.021). However, females showed large inter-individual difference on the proportion of GPS fixes outside the protected area during the night which varied from 2.26 to 99.39% of the total GPS fixes of the night time (Table 2, see also 24). On average, 70% (SE = 30%, range: 22–100%, Table 3, Fig. 1) of the home range of the females was located inside the protected area, but there were large individual differences.
Table 2
Proportion (%) of GPS fixes outside and inside the protected Gaysay Area during day and night.

| ID | total fixes | day/night fixes | out/in | day    | night   |
|----|-------------|-----------------|--------|--------|---------|
|    |             | day             |        |        |         |
| F1 | 7561        | day             | out    | 28.0   | 76.7    |
|    |             | night           | in      | 72.1   | 23.3    |
| F2 | 7650        | day             | out    | 1.8    | 2.3     |
|    |             | night           | in      | 98.2   | 97.7    |
| F4 | 5574        | day             | out    | 2.4    | 18.3    |
|    |             | night           | in      | 97.6   | 81.7    |
| F5 | 2631        | day             | out    | 2.6    | 22.9    |
|    |             | night           | in      | 97.4   | 77.1    |
| F7 | 2917        | day             | out    | 9.7    | 9.5     |
|    |             | night           | in      | 90.4   | 90.5    |
| F8 | 3114        | day             | out    | 0.5    | 0.6     |
|    |             | night           | in      | 99.6   | 99.4    |
| F9 | 2202        | day             | out    | 48.8   | 77.6    |
|    |             | night           | in      | 51.2   | 22.4    |
| total | 31649    | day             | out    | 13.4 ± 18.3 | 29.7 ± 33.4 |
| mean ± SD |   | night           | in      | 86.6 ± 18.3 | 70.3 ± 33.4 |
Table 3
The proportion (%) of the 95% home range estimate within the Gaysay Area.

| ID | proportion |
|----|------------|
| F1 | 38.1       |
| F2 | 100.0      |
| F4 | 83.5       |
| F5 | 66.4       |
| F7 | 77.7       |
| F8 | 100.0      |
| F9 | 22.0       |
| mean (± SD) | 69.7 ± 30.0 |

Habitat use and habitat selection

The Gaysay Area consists of grassland (45.5%), forest (22.9%), bush land (19.4%), heath (5.5%) and others including water bodies, roads, and settlements (6.8%). The buffer zone of the Gaysay Area is dominated by human settlement and agricultural fields.

Habitat selection of the female mountain nyalas differed between seasons and between night and day for some, but not all, habitat types. Heath was avoided both day and night in both seasons. Bushland and grassland were preferred daytime habitats, but avoided during night (with the exception of bushland in wet season). Forest is the strongly selected daytime habitat and moderately preferred night time during dry season, while preference of forest is neutral both in day and night in wet season (Fig. 2, Table 4). All seven females tend to avoid human settlements and agriculture.
Table 4
A Generalized Linear Model for habitat selection of female mountain nyalas. Parameter estimates are log odds of use relative to reference categories of categorical variables and zero values of continuous variables. Spatial autocorrelation and different sample size is accounted for (see material and methods).

|                         | Estimate | robust SE | z     | p       |
|-------------------------|----------|-----------|-------|---------|
| Intercept               | -176.5900| 11.1220   | -15.88| < 0.001 |
| Vegetation (Heath-Forest)| -1.4953  | 0.2958    | -5.06 | < 0.0000|
| Vegetation (Grassland-Forest)| -0.4430 | 0.1188    | -3.73 | 0.0002  |
| Vegetation (Bushland-Forest)| -0.4442 | 0.1454    | -3.06 | 0.0022  |
| Vegetation (Settlement-Forest)| -3.9325 | 0.6202    | -6.34 | < 0.0001|
| Vegetation (Agriculture-Forest)| -4.5864 | 0.6839    | -6.71 | < 0.0001|
| Slope (steep-flat)      | -0.4618  | 0.2604    | -1.77 | 0.0762  |
| Elevation               | 0.1087   | 0.0070    | 15.57 | < 0.001 |
| Elevation2              | 0.0000   | 0.0000    | -15.21| < 0.001 |
| Distance to house       | -0.0003  | 0.0003    | -1.00 | 0.3197  |
| Distance to house2      | 0.0000   | 0.0000    | 2.15  | 0.0312  |
| Season (Wet-Dry)        | -1.2041  | 0.1861    | -6.47 | 0.0000  |
| Light (Night-Day)       | 1.3873   | 0.1983    | 7.00  | < 0.0000|
| Distance to house x Season | 0.0009 | 0.0004    | 2.41  | 0.0160  |
| Distance to house2 x Season | 0.0000 | 0.0000    | -1.35 | 0.1784  |
| Vegetation (Heath-Forest) x Season | 0.0729 | 0.2934    | 0.25  | 0.8037  |
| Vegetation (Grassland-Forest) x Season | 0.6888 | 0.1242    | 5.55  | < 0.0001|
| Vegetation (Bushland-Forest) x Season | 0.8109 | 0.1509    | 5.37  | < 0.0001|
| Vegetation (Settlement-Forest) x Season | -0.0834| 0.3057    | -0.27 | 0.7850  |
| Vegetation (Agriculture-Forest) x Season | 0.6875 | 0.2438    | 2.82  | 0.0048  |
| Vegetation (Heath-Forest) x Light | 0.4053 | 0.2843    | 1.43  | 0.1539  |
| Vegetation (Grassland-Forest) x Light | -0.4619| 0.1146    | -4.03 | 0.0001  |
| Vegetation (Bushland-Forest) x Light | -0.1751| 0.1358    | -1.29 | 0.1971  |
| Vegetation (Settlement-Forest) x Light | 2.5837| 0.6112    | 4.23  | < 0.0001|
| Vegetation (Agriculture-Forest) x Light | 3.6086| 0.6735    | 5.36  | < 0.0001|
Discussion

The Gaysay Area at the northern end of the BMNP has been the stronghold of mountain nyalas for over four decades and is home for 90% the mountain nyala population in the park. The Gaysay Area is, however, small in size [31 km$^2$] with many herbivore wildlife species and is under livestock grazing pressure [19]. With this study, we demonstrated the home range size of the female mountain nyalas is by far less than the home range size predicted for group living species living in mixed habitat. Bush land and forest are the most preferred habitat types by female mountain nyalas and these habitats combined are much smaller (13 km$^2$) suggesting the need for additional protected area free from human and livestock grazing impact. Hence, we recommend extending the protection of the Gaysay Area habitat against human settlement and livestock grazing beyond the current 31 km$^2$ area towards southern range of the mountains. During 1986, this area was used intensively by mountain nyalas and used as corridor to the eastern escarpments of the Bale Mountains [35].

The mean 95% of the home range estimate (5.3 km$^2$) was only 28% of the home range expected for a 170 kg, group-living species living in mixed habitat. The comparatively small and largely overlapping home ranges of female mountain nyalas may be due to the dense human population surrounding the park. It is reported that human-dominated landscapes surrounded by a matrix exploited by agriculture or human settlement limits the ranging pattern and adversely affects the fitness of wildlife [1, 5, 34]. There is reason to expect a large cumulate impact on the suite of large herbivores in the Gaysay Area. In addition to the mountain nyala population which is estimated to be about 840 individuals [17], the Gaysay Area is home for many other herbivores including about 400 Bohor reedbucks Redunca redunca [35], ca 600 common warthogs Phacochoerus africanus [36] and an unknown number of Menelik's bushbucks Tragelaphus scriptus and grey duikers Sylvicapra grimmia. In addition, there is extensive illegal grazing of domestic cattle [19]. The carrying capacity of the Gaysay Area may limit further population growth of the herbivore community including mountain nyalas.

Protected areas are the primary biodiversity conservation strategy used across the globe to avert biodiversity loss [37]. Effectiveness of the protected areas however becomes controversial as wildlife population decline from several protected areas [11, 38 – 44]. The decline is in particular severe for large mammals where Craigie et al. [45] reported a 59% decline in large mammal population abundance in Africa's Protected Areas in less than 40 years. Understanding the ecological requirement of large mammals and available resources in the protected area is key for reversing the currently observed decline of wildlife species [46, 47]. During the night time, mountain nyalas spend a relatively higher proportion of their time outside the park than during the daytime. During the wet season, mountain nyalas may move out of the park for foraging on the barley crop, but they also move toward human settlements to avoid hyena predation [24], known as the human shield strategy [48]. While mountain nyalas are very shy in much of their range in the eastern escarpments of the Bale Mountains where legal and illegal hunting may occur, they are more tolerant for human presence in the protected Gaysay Area [24]. Therefore range contraction due to human infrastructure may be expected to be stronger than in other areas inhabited by mountain nyalas.
For large herbivores, habitat selection is often a trade-off between foraging and avoidance of predators [49]. Many prey species resolve this by selecting predator-safe habitat during the time the predator is active and foraging habitat while the predator is inactive [50]. The mountain nyalas moved out of the park, in particular during the dry season when no crop for forage is available, to avoid hyena predation [24].

Resource selection index indicates bush land and forest habitat are the most preferred habitat types for mountain nyalas while agriculture and human settlements are least preferred habitats. Heath bushland, one of the most important habitats for mountain nyalas [51], is part of the Gaysay Area and was found to be among least used and least preferred habitats during this study. From the geographic scale resource selection of mountain nyalas [17], forest areas were found to be the most preferred habitat with largest mountain nyala population while mountain nyalas avoid human influenced area (agriculture and human settlement). The mountain nyala population of the Gaysay Area may be established due to its protected status rather than its habitat quality for forage in the first place. Mountain nyalas were not reported in the Gaysay Area during Brown survey in 1969 [51]. Following the establishment of the park in 1970, the mountain nyala population dramatically increased from few individuals [52] to 1,100 in 1986 [35]. While the population may have increased through births, the rate of increase likely represents high emigration from the surrounding mountains due to pressure from the human population and attraction to the protected status of the area. Since 1991, humans and their livestock have encroached upon BMNP leaving the Gaysay Area as last stand refuge for the mountain nyala population [53].

**Conclusion**

Our study suggests, the currently protected area of the northern end of the Bale Mountains National Park, Gaysay area, is too small for the mountain nyala conservation. Given with large number of other herbivores and continued livestock grazing, the future long term conservation of the endangered mountain nyala need additional protected area free from human and livestock grazing impact.

**Abbreviations**

GPS: Global Positioning System; CEES: Centre for Ecological and Evolutionary Synthesis.

**Declarations**

**Acknowledgements**

We are very grateful for Dr. David V. Cooper for his help in immobilizing of mountain nyala individuals and fixing GPS collars. We thank Ethiopian Wildlife Conservation Authority for giving permit to carry out the project.

**Authors' Contributions**
AA and LEL designed the study. AA and LEL collected the data, LEL and MK analyzed the data. AA drafted a first manuscript which was improved by MF and DZ. All authors read, comment and approved the final manuscript.

**Funding**

Saint Louis Zoo funding the field work and Centre for Ecological and Evolutionary Synthesis (CEES).

**Availability of data and materials**

Data is available at Dryad, Dataset, https://doi.org/10.5061/dryad.fttdz08pv.

**Ethics approval and consent to participate**

Immobilization of mountain nyala was carried out with the guideline and permit of the Ethiopian wildlife conservation authority.

**Consent to publish**

Not applicable. Here we confirm that the data is collected with the ownership of the authors and have no any restriction to publish the results.

**Competing interests**

The authors declare that they have no competing interests.

**Author details**

1 Department of Zoological Sciences, Addis Ababa University, PO Box 1176, Addis Ababa, Ethiopia.  
2 Cognitive Ethology Laboratory, German Primate Center (DPZ), Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany.  
3 WildCare Institute Center for Conservation in the Horn of Africa, Saint Louis Zoo, St. Louis, Missouri, USA.  
4 Leibniz Science Campus Primate Cognition, Göttingen, Germany;  
5 Department of Primate Cognition, Georg-August-University of Göttingen, Göttingen, Germany.  
6 Departments of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Aas, Norway.

**References**
1. Kie JG, Bowyer RT, Nicholson MC, Boroski BB, Loft ER. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology. 2002;83:530–544.

2. Willems EP, Hill RA. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. Ecology. 2009;90:546–555.

3. Ochiai K, Susaki K, Mochizuki T, Okasaka Y, Amada Y. Relationships among habitat quality, home range size, reproductive performance and population density: Comparison of three populations of the Japanese serow (Capricornis crispus). Mamm Study. 2010;35:265–276.

4. Van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? J Anim Ecol. 2011;80:771–85.

5. Knüsel MA, Lee DE, König B, Bond ML. Correlates of home range sizes of giraffes, Giraffa camelopardalis. Anim Behav. 2019;149:143-151.

6. Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali A H, Allen AM et al.. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science. 2018;359:466.

7. Mysterud A, Pérez-Barbería-Francisco FJ, Gordon IJ. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia. 2001;127:30–39.

8. du Toit JT. Home range - body mass relations: a field study on African browsing ruminants. Oecologia. 1990;85:301–303.

9. Ofstad EG, Herfindal I, Solberg EJ, Saether BE. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proc R Soc B: Biol Sci. 2016;283:20161234.

10. Mclean S, Rumble MA, King RM, Baker WL. Evaluation of resource selection methods with different definitions of availability. J Wildl Manage. 1998;62:793–801.

11. Tucker MA, Ord TJ, Rogers TL. Evolutionary predictors of mammalian home range size: Body mass, diet and the environment. Global Ecol Biogeogr. 2014;23:1105–1114.

12. Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. The influence of human disturbance on wildlife nocturnality. Science. 2018;360:1232–1235.

13. Rhodes JR, Mcalpine CA, Lunney D, Possingham, HP. A spatially explicit habitat selection model incorporating home range behavior. Ecology. 2005;86:1199–1205.

14. Harless ML, Walde AD, Delaney DK, Pater LL, Hayes WK. Home range, spatial overlap, and burrow use of the desert tortoise in the West Mojave Desert. Copeia. 2009;2:378–389.

15. Rechetelo J, Grice A, Reside AE, Hardesty BD, Moloney J. Movement patterns, home range size and habitat selection of an endangered resource tracking species, the black-throated finch (Poephila cincta cincta). PLoS ONE. 2016;11:e0167254.

16. Sillero-Zubiri C. Behavioural ecology of the Ethiopian wolf, Canis simensis. 1994 PhD thesis. University of Oxford, Oxford.

17. Atickem A, Loe LE, Langangen Ø, Rueness EK, Bekele A, Stenseth NC. Estimating population size and habitat suitability for mountain nyala in areas with different protection status. Anim Conserv.
18. Waltermire, R. A national park in the Bale Mountains. Walia. 1975;6:20–23.

19. Atickem, A., Loe LE. Livestock-wildlife conflicts in the Ethiopian highlands: assessing the dietary and spatial overlap between mountain nyala and cattle. Afr J Ecol. 2013;52:343–351.

20. Walther, FR. Spiral-horned antelopes. In: Parker SP, editor. Grzimek's Encyclopedia of Mammals. New York: McGraw-Hill; 1990. p. ??

21. Atickem A, Cooper DV, Kock R, Rueness EK, Fischer M, Bekele A, Loe LE, Stenseth NC. Immobilization of Mountain nyala (Tragelaphus buxtoni) in the Bale Mountains, Ethiopia. Gnusletter 2016;33: 6–7.

22. Dean AM, Smith GM. An evaluation of perparcel land cover mapping using maximum likelihood class probabilities. Int J Remote Sens. 2003;24:2905–2920.

23. Erdas. 1994. ERDAS Field Guide. Version 8.1.

24. Atickem A, Loe LE, Stenseth NC. Individual heterogeneity in use of human shields by mountain nyala. Ethology. 2014;7:715–725.

25. Kie, JG. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Anim Biotelemetry. 2013;1:13. doi:10.1186/2050-3385-1-13

26. Bingham BB, Noon BR. Mitigation of habitat "take": application to habitat conservation planning. Conserv Biol. 1997;11:127–139.

27. Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA. Effects of sample size on kernel home range estimates. J Wildl Manage. 1999;63:739–747.

28. Signer J, Balkenhol N. Reproducible home ranges (rhr): a new, user-friendly R package for analyses of wildlife telemetry data. Wildl Soc Bull. 2015;39. doi:10.1002/wsb.539.

29. Raethel H. Keeping mountain nyala (Tragelaphus buxtoni) in the Berlin Zoo, 1932-1943. Zoo Report, Berlin Zoo. 1980;4:55–62.

30. R Development Core Team. R. A language and environment for statistical computing. 2011Vienna: R Foundation for Statistical Computing.

31. Guisan A, Zimmermann NE. Predictive habitat distribution models in ecology. Ecol Model. 2000;135:147–186.

32. Johnson DS, Thomas DL, ver Hoef JM, Christ A. A General Framework for the analysis of animal resource selection from telemetry data. Biometrics. 2008;64:968–976.

33. van Beest FM, Mysterud A, Loe LE, Milner JM. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. J Anim Ecol. 2010;79:910–922.

34. Alfred R, Ahmad AH, Payne J, Williams C, Ambu LN, How PM, Goossens B. Home range and ranging behaviour of Bornean elephant (Elephas maximus borneensis) females. PLoS ONE. 2012;7:e31400.

35. Forester JD, Im HK, Rathouz PJ. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology. 2009;90:3554–3565
36. Afework B, Bekele A, Balakrishnan M. Population status, structure and activity patterns of the Bohor reedbuck *Redunca redunca* in the north of the Bale Mountains National Park, Ethiopia. Afr J Ecol. 2010;48:502–510.

37. Hillman JC. Bale Mountains National Park Management Plan. 1986 Report to Ethiopian Wildlife Conservation Organization. EWCO, Addis Ababa.

38. Deribe E, Bekele A, Balakrishnan M. Population status and diurnal activity patterns of the common warthog (*Phacochoerus africanus*) in the Bale Mountains National Park, Ethiopia. Int J Ecol Environ Sci. 2008;34:91–97.

39. Chape S, Harrison J, Spalding M, Lysenko I. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Phil Trans R Soc Lond B Biol Sci. 2005;360:443–55.

40. Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, et al. Global biodiversity: indicators of recent declines. Science. 2010;328(5982):1164–1168.

41. Ottichilo WK, de Leeuw J, Skidmore AK, Prins HHT, Said MY. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. Afr J Ecol. 2000;38:202–216.

42. Brashares JS, Arcese P, Sam MK. Human demography and reserve size predict wildlife extinction in West Africa. Proc R Soc B: Biol Sci. 2001;268:2473–2478.

43. Jetz W, Carbone C, Fulford J, Brown JH. The scaling of animal space use. Science. 2004;306:266–268.

44. Estes RD, Atwood JL, Estes AB. Downward trends in Ngorongoro Crater ungulate populations 1986–2005: conservation concerns and the need for ecological research. Biol Conserv. 2006;131:106–120.

45. Scholte P. Towards understanding large mammal population declines in Africa’s protected areas: A west-central African perspective. Trop Conserv Sci. 2011;1:1–11.

46. Ogutu JO, Piepho HP, Said MY, Ojwang GO, Njino LW, Kifugo SC, Wargute PW. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? PLoS ONE. 2016;11: e0163249.

47. Craigie ID, Baillie JEM, Balmford A, Carbone C, Collen B, Green RE, Huttone JM. Large mammal population declines in Africa’s protected areas. Biol Conserv. 2010;143:2221–2228.

48. Gaston KJ, Jackson SF, Cantú-salazar L, Cruz-piñón G. The ecological performance of protected areas. Annu Rev Ecol Evol Syst. 2008;39:93–113.

49. Cattarino L, Mcalpine CA, rhodes JR. Spatial scale and movement behaviour traits control the impacts of habitat fragmentation on individual fitness. J Anim Ecol. 2016;85:168–177.

50. Berger, J. Fear human shields and the redistribution of prey and predators in protected areas. Biol Lett. 2007;3:620–623.

51. Godvik IMR, Loe LE, Vik JO, Veiberg V, Langvatn R, Mysterud A. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology. 2009;90:699–710. doi:10.1890/08-
0576.1

52. Lone K, Mysterud A, Gobakken T, Odden J, Linnell J, Loe LE. Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. Oikos. 2017;126:624–632. doi:10.1111/oik.03486

53. Brown CL, Hardy AR, Barber JR, Fristrup KM, Crooks KR, Angeloni LM. The effect of human activities and their associated noise on ungulate behavior. PLoS ONE. 2012;7:e40505.

54. Malcolm J, Evangelista P. The range and status of the mountain nyala. Technical Report to the Ethiopian Wildlife Conservation Department, Oromia Rural Land and Natural Resource Department. 2004.

55. Stephens PA, dSa CA, Sillero-Zubiri C, Leader-Williams N. Impact of livestock and settlement on the large mammalian wildlife of the Bale Mountains National Park, southern Ethiopia. Biol Conserv. 2001;100:307–322.

Figures
Figure 1

Study area in the northern part of the Bale Mountain National Park, Gaysay Area, and 95% kernel home ranges of the seven female mountain nyala.

Figure 2

Predicted log odds of use with increasing elevation. Predicted values are for flat slopes (0-20 degrees), 2000 m from human households, vegetation type grassland and for daytime in the wet season. Elevation is modelled as a second order polynomial with no interactions with light (day and night) or season.