Global Ecology and Conservation 32 (2021) e01900

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Human activities increase vigilance, movement and home range size of the endangered mountain nyala (*Tragelaphus buxtoni*) at the cost of foraging and resting

Ejigu Alemayehu Worku [a,*], Anagaw Atickem [b], Jakob Bro-Jørgensen [c], Afework Bekele [b], Paul Evangelista [d], Nils Chr. Stenseth [a]

[a] *Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066, Blindern, 0316 Oslo, Norway*
[b] *Department of Zoological Sciences, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia*
[c] *Mammalian Behaviour and Evolution Group, Department of Evolution, Ecology and Behaviour, University of Liverpool, Neston CH64 7TE, UK*
[d] *Natural Resource Ecology Laboratory, Colorado State University, B254 NESB, Fort Collins, CO 80523, USA*

ARTICLE INFO

Keywords:
Activity budget
Home range
Human activities
Mountain nyala
Restorative behaviors
Vigilance

ABSTRACT

Behavioral responses in wildlife due to human activities may often go unnoticed but have significant effects on population viability. This is a particular concern with endangered species characterized by small population sizes. From June 2016 to May 2017, we measured the effects of human activities on daily the activity budget and home range size of mountain nyala (*Tragelaphus buxtoni*), an endemic antelope of the Ethiopian highlands. We tracked two groups of mountain nyala from two study sites that differ in the level of human activities; Adaba-Dodola Community Conservation Area (Adaba-Dodola CCA) and Arsi Mountains National Park (Arsi Mountains NP). Our results showed that the time spent on vigilance and movement was dramatically higher in Adaba-Dodola Community CCA, where human presence is significant, than in Arsi Mountains NP, whereas the opposite was true for time spent foraging and resting. In addition, mean home range size (95% KDE) was significantly larger for the Adaba-Dodola CCA group (13 ± 7.4 km^2) than for the Arsi Mountains NP group (6.3 ± 2.7 km^2) covering larger areas during the dry season (18.7 ± 6.9 km^2) than the wet season (4.9 ± 1.0 km^2). The finding that increased investment in vigilance and movement trade-off against the restorative behaviors of foraging and resting in human-disturbed areas have implications for conservation managements; specifically, it underscores the need to (i) establish the fitness consequences of behavioral changes, and (ii) monitoring behavioral change in the disturbed population with the aim of bringing it closer to the undisturbed baseline. The study highlights the importance of protected areas, limiting human activities and monitoring the behavioral change of endangered species in human-disturbed areas.

1. Introduction

Human activities can severely threaten the well-being of wildlife, not only by causing habitat loss and direct mortality, but also by altering the wildlife's behavior (Wilson et al., 2020). This is particularly critical for large mammals (Blom et al., 2004). For example,

* Corresponding author.
E-mail addresses: ejiguaw@student.matnat.uio.no, yismake1998@gmail.com (E.A. Worku).

https://doi.org/10.1016/j.gecco.2021.e01900
Received 22 June 2021; Received in revised form 22 October 2021; Accepted 29 October 2021
Available online 2 November 2021
2351-9894/

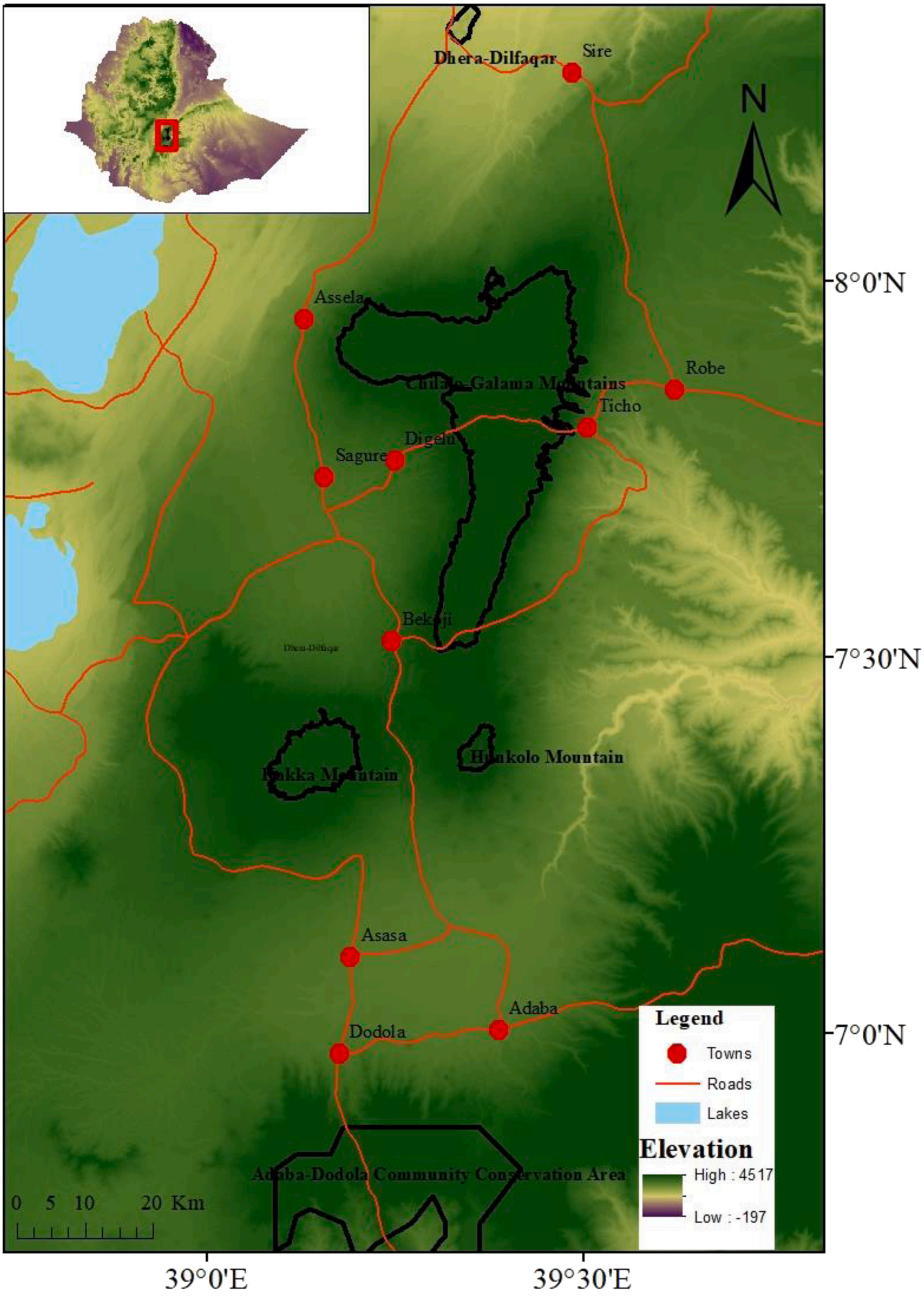

Fig. 1. Elevation map of the Adaba-Dodola CCA and Arsi Mountains NP in southeast highlands of Ethiopia.

previous studies on ungulates have documented human activities affecting escape responses (Stankowich, 2008), activity budgets (e.g. impala *Aepyceros melampus*; Wronski et al., 2015), habitat use (e.g. mountain gazelles *Gazella gazelle*; Manor and Saltz, 2003, 2005), and home range size (e.g. giraffes *Giraffa camelopardalis*; Knüsel et al., 2019). These changes in behavioral responses can have severe consequences. For example, Ciuti et al. (2012) showed that increased vigilance behavior caused by human activities can result in reduced reproductive success. This may be explained by a trade-off between the time and energy spent being alert and the time spent for foraging (Wang et al., 2011).

Understanding activity budgets and home range requirements are vital for effective conservation and management planning (Cooke, 2008; Tadesse and Kotler, 2013; Allen and Singh, 2016; Knüsel et al., 2019; Tang et al., 2019). The differences in the activity budget result from a trade-off between foraging activity, reproductive opportunities, and environmental constraints (Shi et al., 2003). Human activities and presence in the environment inevitably cause changes in the surroundings (Mangiacotti et al., 2013), including changes in forage availability and quality. The change in quantity and quality of forage affect activity budget, and behavioral changes associated with changes in environmental conditions serve as indicators of habitat status (Morris et al., 2009). Quantifying home range size also provides ecological information and is influenced by the human presence and anthropogenic changes to the environment (Viana et al., 2018). The anthropogenic changes in the environment reduce food availability cause species to disperse to meet their dietary needs, varies across sites due to resource availability, which aids in the conservation planning of endangered species (Plotz et al., 2016).

The mountain nyala (*Tragelaphus buxtoni*) is an endemic antelope listed as Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2016). The species is known to inhabit the Afroalpine and montane vegetations of the Bale, Arsi, and Ahmar Mountains in the southeast highlands of Ethiopia (Blower, 1968; Brown, 1969; Evangelista et al., 2008, 2012). However, livestock grazing, deforestation (Kubsa and Tadesse, 2002; Tadesse et al., 2014), agricultural expansion (Kindu et al., 2015), and rapid land conversion (Tadesse et al., 2014; Young et al., 2020) have resulted in significant habitat loss. In addition, growing human populations and intensified activities are known to affect mountain nyala population dynamics (Mamo et al., 2010), population densities (Bunnefeld et al., 2013), distribution patterns (Atickem et al., 2014) and abundance (Atickem and Loe, 2014). As a result, the species has been driven out of much of its former range, and at present, only exists in fragmented and isolated populations (Evangelista et al., 2015). Few prior studies have been conducted on the effect of sex-age class and seasonality on the activity budget of mountain nyala in a dry Afromontane forest, plantation and cleared-vegetation habitat (Tadesse and Kotler, 2013) and the foraging behavior of the species (Atickem and Loe, 2014), with the emphasis on sexual variations. The proportion of time spent on vigilance, moving, and feeding varies by season, with vigilance being highest in the wet season and moving highest in the dry season. During the dry season, vigilance was likewise highest in cleared vegetation compared to Afromontane forest and plantation habitat. Neither of these studies, however, assessed the effect of human activities on the species' activity budget and estimated home range size in its typical Ericaceous habitat.

In this study, we aimed to investigate the effect of human activities on the activity budgets and home range size of an endangered species, the mountain nyala, and its possible variations over seasons. Specifically, we (1) compared the activity budget between two mountain nyala study groups, i.e. from the Adaba-Dodola Community Conservation Area (Adaba-Dodola CCA), where human activities are significant, and the Arsi Mountains National Park (Arsi Mountains NP), where human activities are strictly regulated, (2) determined the home range size of the mountain nyala in the two study sites.

2. Materials and Methods

2.1. Study areas

2.1.1. Adaba-Dodola Community Conservation Area

The Adaba-Dodola Community Conservation Area (Adaba-Dodola CCA) is located between 6°41' to 6°52' N latitude and 39°5′ to 39°24' E longitude (Fig. 1). The Adaba-Dodola CCA covers 499 km^2 with elevations ranging from 2400 to 3764 m a.s.l. (Bogale, 2011). The area has a bimodal rainfall distribution with annual mean precipitation ranging from 878 mm to 1089 mm (Gelashe, 2017), while mean minimum and maximum temperature recorded are 4 °C and 24 °C, respectively (Nega, 2014).

The Adaba-Dodola CCA vegetation is characterized by Afroalpine and subalpine vegetation at higher elevations (> 3200 m above sea level) (Uhlig, 1988; Friis et al., 2010; Ameha et al., 2014a) and dry Afromontane forest at the lower elevation (Gelashe, 2017; Asefa et al., 2020). The Afroalpine vegetation is distinguished by short vegetation (Vial et al., 2011) and home to endemic plants such as the giant *Lobelia rhynchopetalum* (Miehe and Miehe, 1994; Asefa et al., 2020). The dry montane forest is dominated by *Juniperus procera* and *Podocarpus falcatus* (Friis et al., 2010).

Since 1995, the Adaba-Dodola CCA has been supported by the Integrated Forest Management Project (IFMP), a joint project of Ethiopian and Germany's governments (Kubsa and Tadesse, 2002; Watson, 2013). The IFMP has developed a conservation approach known locally as WAJIB ("WAJIB" is an abbreviation for "Forest Dwellers' Association" in Afan Oromo language), which is a joint management organization that considers residents as a key conservation stakeholders (Borrini-Feyerabend et al., 2004). This type of management grants exclusive user rights to the recognized members (Kubsa and Tadesse, 2002), ensures the sustainability of forest resources (Tefera, 2011), and helps to share the benefit of wildlife conservation with the local communities (Tessema et al., 2010). However, habitat loss from agricultural expansion, illegal human settlements (Kubsa and Tadesse, 2002; Gelashe, 2017), livestock grazing, and high demand and uncontrolled access to the forest (Ameha et al., 2014b; Wilder, 2016) are threatening wildlife conservation and the survival of mountain nyala. Trophy hunting for mountain nyala has been permitted in the Adaba-Dodola CCA since 2011, where up to three bulls are allowed to be harvested annually. The federal Ethiopian Wildlife Conservation Authority governs this licensed trophy hunting in partnership with regional governments (Fischer et al., 2015).

2.1.2. Arsi Mountains National Park

Arsi Mountains National Park (Arsi Mountains NP) covers 939 km^2 in the southeast highlands of Ethiopia (Fig. 1). The park is located between 7°18' to 8°22' N latitude and 39°1′ to 39°33' E longitude. The government established Arsi Mountains NP to preserve threatened species and the fragile ecosystem. The park has four fragmented blocks (Young, 2012): Chilalo-Galama, Kaka, Hunkolo, and Dhera-Dilfaqar. The average annual rainfall ranges from 779 mm to 1090 mm, and the average monthly minimum temperature of 11 °C and maximum of 22 °C (Girma et al., 2018).

The vegetation at the lower elevation (upper limit at about 3300 m a.s.l.) belongs to the dry evergreen Afromontane forest dominated by *Juniperus procera* and *Hagenia abyssinica* (Hedberg, 1971). The vegetation above 3300 m a.s.l. are referred to as the subafroalpine and Afroalpine vegetation (Hedberg, 1971; Miehe and Miehe, 1994). Despite its designation as a national park, Arsi Mountains NP is subjected to intense human activity (Kostin et al., 2019). The main activity in Arsi Mountains NP is livestock grazing, which often includes the intentional burning of Erica to increase forage production. In recent years, the expansion of human settlement

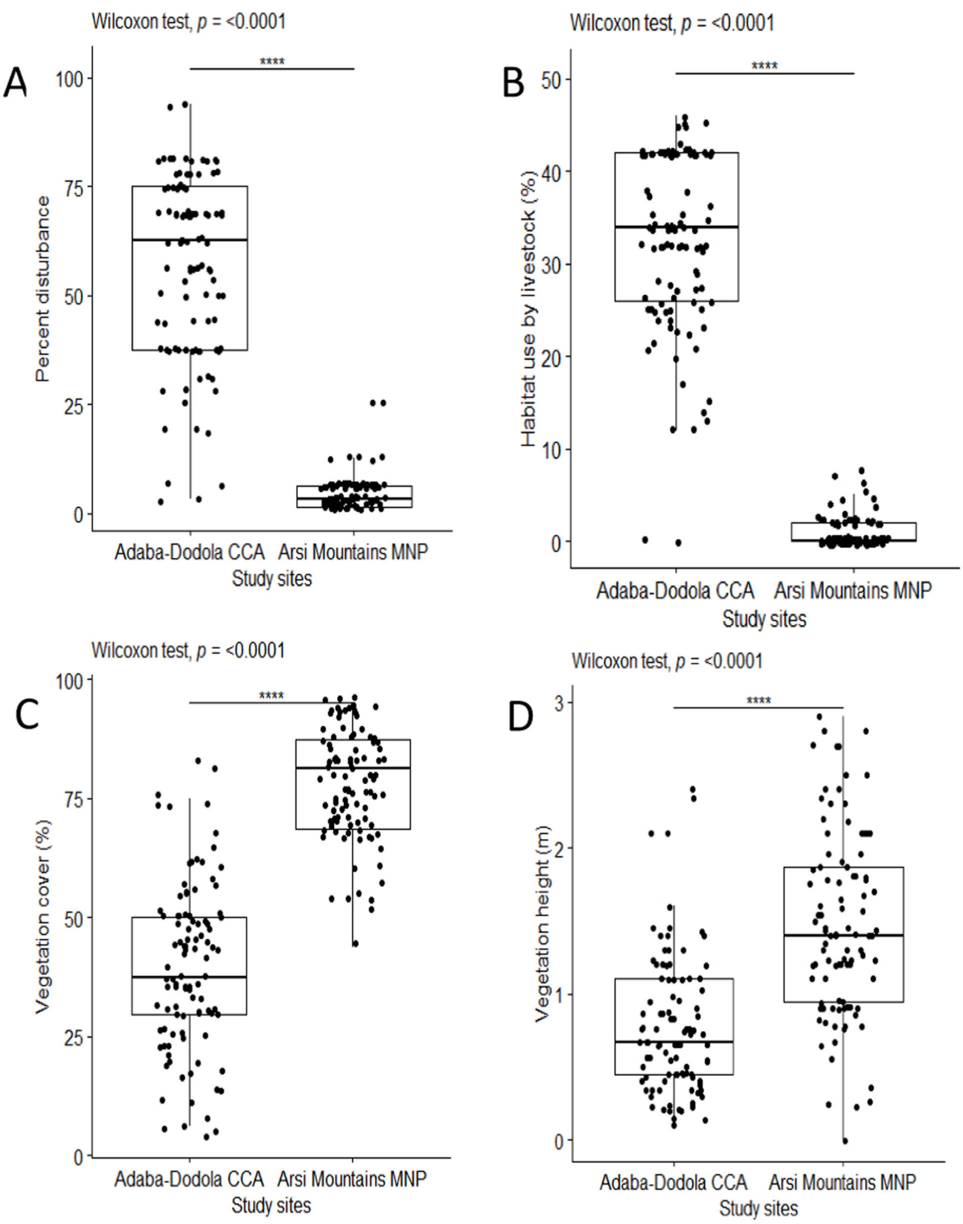

Fig. 2. Habitat characteristics of Adaba-Dodola CCA and Arsi Mountains NP study sites. (A) Human disturbance level, (B) habitat use by livestock, (C) average vegetation cover, and (D) average vegetation height.

and associated agriculture in higher elevations pose conservation challenges in the national park. The mountain nyala population status is known from short-term studies (Evangelista et al., 2007). Between 2000 and 2003, the population was estimated to be 130 individuals (Malcolm and Evangelista, 2011), and currently estimated to be 108 individuals (Ejigu Alemayehu Worku, unpublished result).

2.2. Assessment of human activities

We established 14 line transects and randomly generated 200 plots (5 m x 20 m) to quantify the level of disturbance, the frequency of livestock dung piles, vegetation cover and height. The field survey was conducted using Intensive Modified-Whitaker (I-MW) nested plot design (Barnett and Stohlgren, 2003), with 100 plots in Adaba-Dodola CCA and 100 plots in the Arsi Mountains NP (Supplementary Fig. 1 and Fig. 2). The I-MW plot is framed within an outer 100-m^2 plot (5 m x 20 m) with four 1-m^2 subplots (0.5 $\times$2 m^2) in a fixed location within its perimeter and one 10-m^2 (2 m x 5 m) subplot in the center. In each plot, we recorded the data on anthropogenic disturbance noting any sign of habitat use by livestock, fodder collection and forest uses such as woodcutting. We also recorded the vegetation cover and height for the four 1 m^2 subplots. In addition, the number of people traveling on foot and riding horses and was counted during the behavioral observations (cf. Section 2.3) (Manor and Saltz, 2003) and was also used as a proxy for human activity (Wronski et al., 2015). We also continuously recorded the number of livestock herds passed through each study site during the behavioral observations.

2.3. Study groups and behavioral observations

We selected two mountain nyala study groups. The study groups had relatively stable number of individuals throughout the year, with 13 individuals in Adaba-Dodola CCA and 12 individuals in Arsi Mountain NP. The nearly equal group size between the two study sites aids in avoiding the 'the many-eyes effect' as group size with other environmental factors influences activity budgets. The study groups comprise adult females and offsprings. When the study groups split, the observers followed the larger sub-group during the behavioral observation.

Before the actual data collection, we habituated the study groups to the data collectors, taking care not to disturb the animals before or during the actual behavioral observations. We conducted field observations from early morning (06:00 h) to late afternoon (18:00 h) for five days each month from June 2016 to May 2017. We used instantaneous scan sampling (Altmann, 1974) of up to five minutes long at 15-minute intervals to determine the proportion of time spent on various behavioral activities. The behavioral states were observed with the aid of Nikon 10 $\times$ 50 binoculars and reported as (1) foraging (actively ingesting or chewing food); (2) vigilance (scanning their surroundings with ears erect position, head raised, and ears focusing in different directions); (3) resting (inactive, ruminating or sleeping); (4) movement (head-upright locomotion either walking or hurrying); (5) other (other activities that do not fit in any of the above behaviors performed with very low frequencies). For each study group, we calculated the percentage of time spent on each behavioral activity (excluding records that were not visible). We also pooled activity records into monthly periods and seasons to compare activity budgets between the study groups.

During our observation period, we recorded the study groups' spatial position every hour using a Global Positioning System (GPS) for five days each month, making 60 all-day follows per study group. A total of 1440 locations were obtained in both study sites. The GPS location points were collated for each group and used to estimate home range sizes. We subdivided the locations into dry (October to January), intermediate (February to May), and wet (June to September) seasons.

2.4. Statistical analyses

All statistical analyses were performed using the statistical software R version 4.0.4 (R Development Core Team, 2021) and the spatial analyst extension in ArcGIS 10.8.1 (ESRI, 2020). The Mann-Whitney-Wilcoxon test was used to compare the two study sites in terms of human activity, average animal dung pile count, vegetation cover and vegetation height.

The proportion of time spent in each of the five behavioral categories (i.e., foraging, vigilance, resting, moving and other) was calculated for each study group by dividing the number of occurrences of a particular activity by the total number of sightings. The Mann-Whitney-Wilcoxon test was used to compare the proportions of time spent foraging, moving, vigilance, and resting between the two study groups, and the Kruskal–Wallis test was used to compare between seasons. We also used the Pearson Correlation to test the relationship between the behavioral activities and human activity. We also used a general linear mixed-effects model from the package lme4 to analyze time spent on behavioral activities, and we log transformed the response variable (percent of time spent on behavioral activities) to prevent model fit problems.

We used Kernel Density Estimations (KDEs) with 'href' smoothing parameter using the package 'adehabitatHR' to estimate home range size (Calenge, 2015). KDEs measure utilization distribution and are the most widely used techniques for home range size analysis (Plotz et al., 2016). We used 95% kernel isopleths (95% KDE) and 50% kernel isopleths to depict core areas (50% KDE) of the two study groups (Worton, 1989) to estimate seasonal home range sizes. We used the Mann-Whitney-Wilcoxon test to compare the 95% and 50% KDE between the two study groups and linear models to compare seasonal changes in 95% and 50% KDE for each group separately.

3. Results

3.1. Assessment of human activities

Comparatively high level of human activities and habitat use by livestock were observed in the Adaba-Dodola CCA compared to the Arsi Mountains NP. We found a significant difference in the level of human activities (Wilcoxon test, $p < 0.05$, effect size $r = 0.84$) between the study sites, with an average total disturbance of 56.7% ($\pm$ 21.1) in Adaba-Dodola CCA relative to the Arsi Mountain NP (4.76 $\pm$ 3.9). Habitat use by livestock also varied between the two study sites (Wilcoxon test, $p < 0.05$, effect size $r = 0.87$). We also found a significant difference in average vegetation height (Wilcoxon test, $p < 0.05$, effect size $r = 0.56$) and cover (Wilcoxon test, $p < 0.05$, effect size $r = 0.79$) between the two study sites (Fig. 2).

3.2. Daily activity budget

We obtained 7755 individual activity records for Adaba-Dodola CCA and 9583 individual activity records for Arsi Mountain NP, totaling 17,338 individual activity records from 3468 scan samples. In total, mountain nyala groups were observed for 867 h in both study sites (Table 1).

The time observed with each behavioral category for mountain nyala in the Adaba-Dodola CCA was foraging 35.3% ($\pm$ 0.9), vigilance 32.3% ($\pm$ 0.9), moving 23% ($\pm$ 0.8), resting 5.7% ($\pm$ 0.4) and other 3.8% ($\pm$ 0.3). However, mountain nyala in Arsi Mountains NP spent 55.2% ($\pm$ 1.1) of their time foraging, moving 16.1% ($\pm$ 0.6), vigilant 14.5% ($\pm$ 0.5), resting 10.9% ($\pm$ 0.1) and others (3.2 $\pm$ 0.4%) (Fig. 3). The time spent on foraging, moving, vigilance, and resting represented more than 95% of the total observation time. Other behavioral categories performed with low frequency accounted for less than 4% of the observations.

The percentage of time mountain nyala spent foraging, moving, vigilance, and resting differed significantly between the two study groups. We found a statistically significant difference in vigilance (Wilcoxon test, $p < 0.05$, effect size $r = 0.84$) and moving (Wilcoxon test, $p < 0.05$, effect size $r = 0.85$) percentages between the two study groups, with greater percentages observed at the Adaba-Dodola CCA relative to the Arsi Mountain NP. We also found a significant difference in the foraging (Wilcoxon test, $p < 0.05$, effect size $r = 0.85$) and resting (Wilcoxon test, $p < 0.05$, effect size $r = 0.65$), with greater percentages observed at the Arsi Mountain NP relative to the Adaba-Dodola CCA.

Mountain nyala diurnal activity budgets showed significant seasonal variation in the proportion of time spent foraging (Kruskal-Wallis $\chi^2 = 8.3$, $d.f. = 2$, $P = 0.01$), with this activity being more common during the dry season than during the wet season. Significant seasonal variation in the proportion of time spent vigilant ($\chi^2 = 8.7$, $d.f. = 2$, $P = 0.01$), moving (Kruskal-Wallis, $\chi^2 = 6.1$, $d.f. = 2$, $P = 0.03$) and resting ($\chi^2 = 8.3$, $d.f. = 2$, $P = 0.01$) in the Adaba-Dodola CCA were also observed (Fig. 4 A). Time budgets for mountain nyala in Arsi Mountains NP were similar between wet, intermediate and dry seasons for moving ($\chi^2 = 2.6$, $d.f. = 2$, $P = 0.3$), vigilant ($\chi^2 = 2.6$, $d.f. = 2$, $P = 0.3$), and resting ($\chi^2 = 3.9$, $d.f. = 2$, $P = 0.1$) except foraging (Kruskal-Wallis $\chi^2 = 8.8$, $d.f. = 2$, $P = 0.01$) (Fig. 4B).

The number of humans per day was found to be negatively correlated with foraging (R= -0.68, $P < 0.05$, $n = 60$, Fig. 5A) and resting (R= -0.48, $P < 0.05$, $n = 60$, Fig. 5D), with decreasing activities and with increasing human movements. By contrast, the number of humans observed was found to be positively correlated with vigilance (R= 0.8, $P < 0.05$, $n = 60$, Fig. 5B) and movement (R= 0.45, $P < 0.05$, $n = 60$, Fig. 5C). We found that number of humans and livestock in the mountain nyala range affects the behavioral activities of the species (Supplementary Table 1).

Table 1
Information for behavioral scanning of mountain nyala in Adaba-Dodola CCA and Arsi Mountains NP.

Month	Adaba-Dodola CCA			Arsi Mountains NP		
	No. of observation hours	No. of individual scans	No. of activity records	No. of observation hours	No. of individual scans	No. of activity records
June	28.45	113.8	569	39.05	156.2	781
July	29.1	116.4	582	42.25	169	845
August	23.8	95.2	476	38.75	155	775
September	33.15	132.6	663	39.3	157.2	786
October	40	160	800	38.85	155.4	777
November	43.75	175	875	37.45	149.8	749
December	33.65	134.6	673	37.8	151.2	756
January	38.55	154.2	771	41.25	165	825
February	28.95	115.8	579	43.45	173.8	869
March	32.1	128.4	642	40.35	161.4	807
April	28.05	112.2	561	40.9	163.6	818
May	28.2	112.8	564	39.75	159	795
Total	387.75	1551	7755	479.15	1916.6	9583
Average	32.3	129.25	646.25	39.93	159.72	798.58
SD	5.1	23.4	116.8	1.79	7.14	35.72

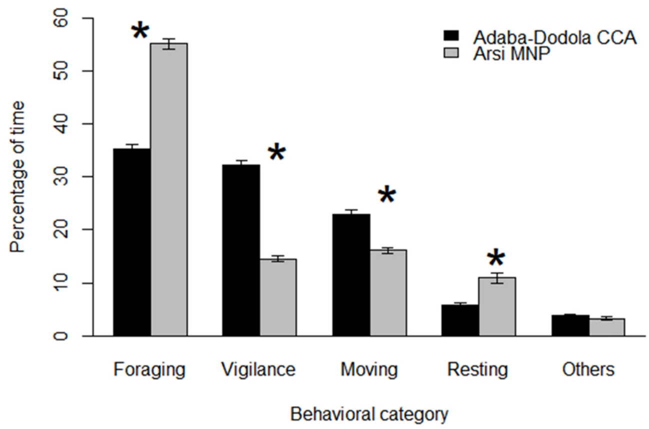

Fig. 3. Mean percentage of time (± SE) devoted to each of the behavioral categories in the Adaba-Dodola CCA and Arsi Mountain NP. An asterisk indicates significant differences for that activity category, as demonstrated through the non-parametric Mann-Whitney test.

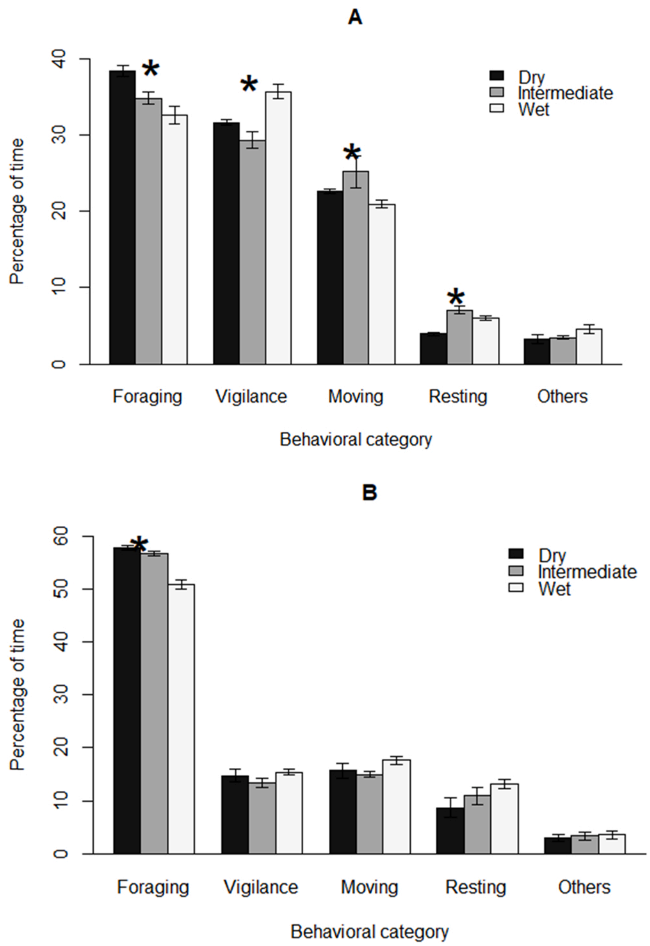

Fig. 4. Seasonal variations in time budgets of mountain nyala for various activity categories in (A) Adaba-Dodola CCA and (B) Arsi Mountains NP at different seasons.

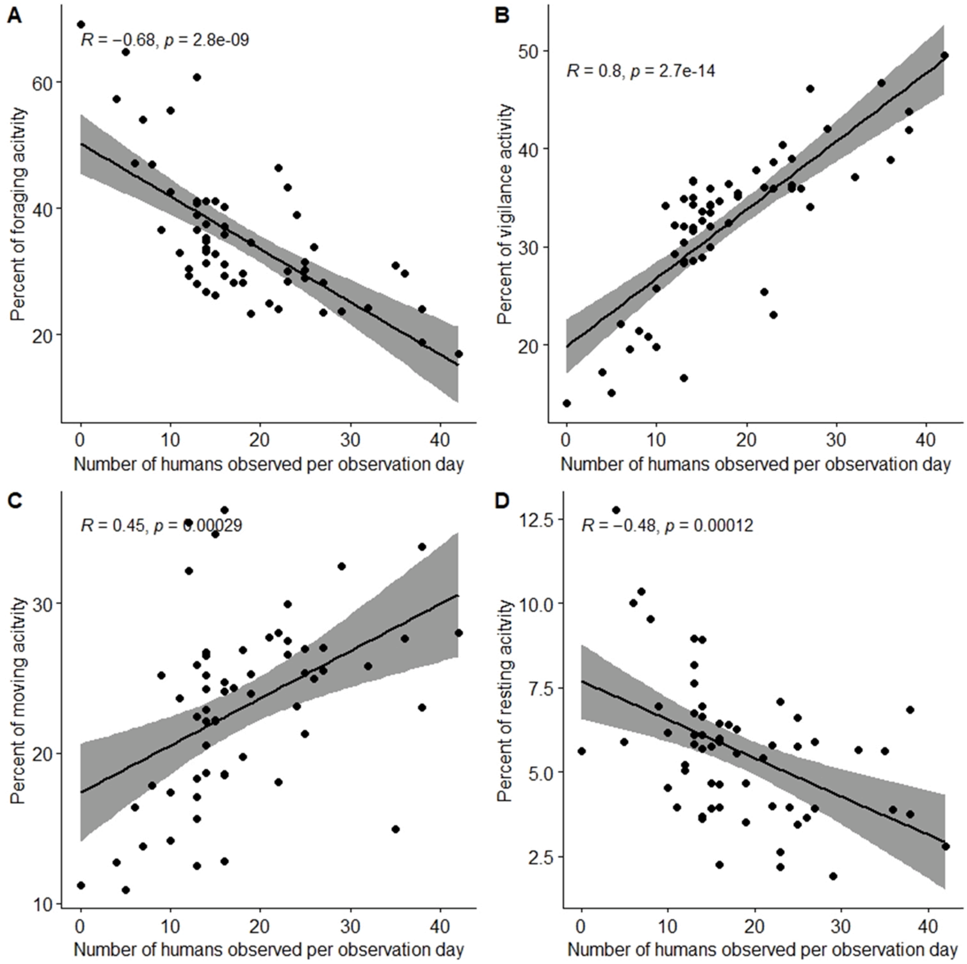

Fig. 5. Mountain nyala foraging (A), vigilance (B), moving (C) and resting (D) activity in relation to the number of humans observed per day.

3.3. Home range sizes

During the one-year study period, we recorded 1440 GPS locations for the two study groups (Adaba-Dodola CCA = 720; Arsi Mountain NP = 720). The means ± *SD* of the 95% and 50% KDE home range sizes across the three seasons were 13 ± 7.4 km^2 and 3.3 ± 1.8 for Adaba-Dodola CCA, and 6.3 ± 2.7 and 1.7 ± 0.9 for Arsi Mountain NP, respectively (Fig. 6; Table 2).

We found a significant difference in 95% KDE and 50% KDE (Wilcoxon test, W = 112.5, $p < 0.021$) between the study groups, with greater home range size observed at the Adaba-Dodola CCA relative to the Arsi Mountains NP. The 95% and 50% KDE were also significantly affected by seasonality except for the intermediate season range of Adaba-Dodola CCA (Supplementary Table 2).

4. Discussion

4.1. Daily activity budget of mountain nyala

From the monitoring of the two study groups for one year, significant differences in the percentages of time spent foraging, vigilance, moving, and resting were found between the two study groups. The differences in behavioral activity budgets can largely be attributed to the high human activities and livestock grazing. The level of human activities in the Adaba-Dodola CCA was significantly higher than in the Arsi Mountains NP (Fig. 2), and this was primarily due to direct human presence and livestock grazing. The high level of human activities increased the time spent on vigilance and movement and decreased the time spent on foraging and resting (i.e., restorative behaviors) in the mountain nyala population. This elevated vigilance and movement level (i.e., costly behavioral activities) entail a foraging cost (Fortin et al., 2004), given that vigilance and foraging are the two main behavioral activities of mountain nyala (Tadesse and Kotler, 2013). Additionally, our results showed that mountain nyala decreased resting time. Other studies also showed that human activities increase the amount of time spent in vigilance and movement in mountain gazelle (*Gazella gazella*) (Manor and Saltz, 2003), red deer (*Cervus elephus*) (Jayakody et al., 2008), and impala (*Aepyceros melampus*) (Setsaas et al., 2018).

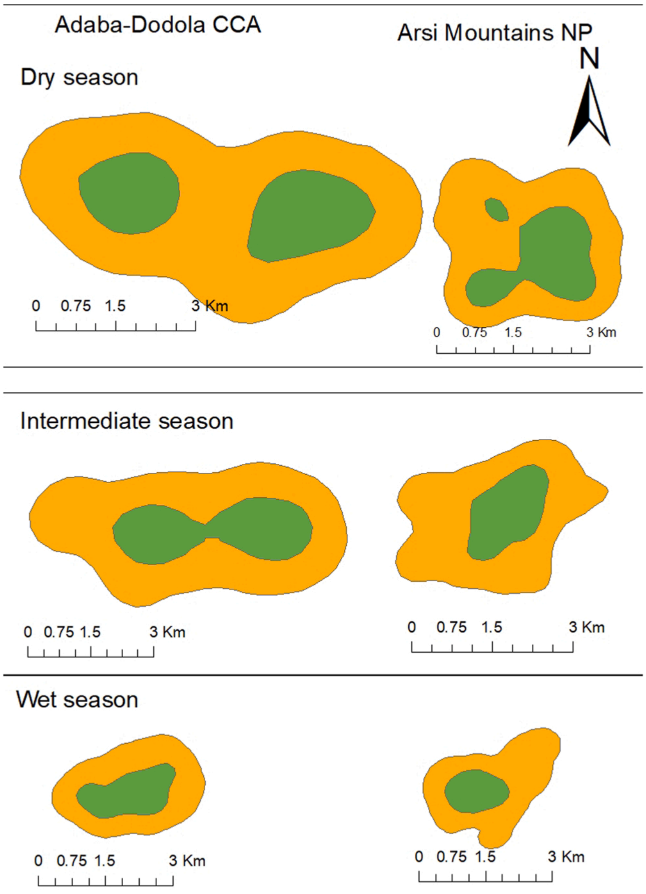

Fig. 6. Map showing home range estimates for the two mountain nyala study groups in the Adaba-Dodola CCA and Arsi Mountains NP, Ethiopia. Orange refers to the 95% and green to the 50% Kernel density estimate (KDE) for the dry, intermediate, and wet seasons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Home range sizes of mountain nyala study groups in Adaba-Dodola CCA and Arsi Mountains NP, Ethiopia estimated based on 95% fixed kernel density estimator (95% KDE) and core area (50% KDE).

Study sites	Seasons	95% KDE ($km^2 \pm$ SD)	50% KDE ($km^2 \pm$ SD
Adaba-Dodola CCA	Dry	18.7 ± 6.9	4.6 ± 1.5
	Intermediate	16.2 ± 3.1	4.1 ± 1.5
	Wet	4.9 ± 1.0	1.5 ± 0.4
	Mean	13 ± 7.4	3.3 ± 1.8
Arsi Mountains NP	Dry	9.1 ± 1.0	2.7 ± 0.4
	Intermediate	6.2 ± 0.8	1.7 ± 0.3
	Wet	3.4 ± 1.8	0.9 ± 0.4
	Mean	6.3 ± 2.7	1.7 ± 0.9

Due to the high human and livestock presence and the relatively low vegetation cover in the Adaba-Dodola CCA, mountain nyala may reduce their daytime feeding durations or shift their foraging times from day to night. Other studies have also found that southern bushbuck (*Tragelaphus scriptus*) and blue duiker (*Philantomba monticola*) performed most of their activity at night in response to anthropogenic disturbances (Smith et al., 2019). More than 500,000 head of livestock seasonally graze within the Adaba-Dodola CCA (Kubsa and Tadesse, 2002), and this disturbance may ultimately affect the mountain nyala population persistence.

The proportion of time spent foraging in both study sites varies with seasons, foraging more time during the dry than the wet season (Fig. 4A and B). The high level of human activities and livestock grazing, together with low quality and quantity of forage, may have forced mountain nyala to spend on foraging during the dry season. Conversely, the reduced foraging behavior of mountain nyala during the wet season is probably due to the increased forage availability and quality. This may reflect the species behavioral response to differences in the seasonal and spatial variation of food availability (Shi et al., 2003). Several studies have also shown that foraging increases during the dry season (Owen-Smith, 1979), a time when food resources are scarce in terms of both quality and quantity.

4.2. Home range sizes of mountain nyala

The effects of human activities were not limited to changes in activity budget but also observed to significantly impact home range sizes. Our results showed that the mountain nyala home range size in the Adaba-Dodola CCA (13 ± 7.4 km^2) was larger than the Arsi Mountains NP study group (6.3 ± 2.7 km^2) (Table 2 and Fig. 6). The size of home ranges varies with the level of human disturbance, where larger home range sizes were recorded in areas subjected to more severe disturbance (Hovick et al., 2014). The larger home range may also be related to reduced habitat quality (Mueller and Fagan, 2008; Viana et al., 2018), where animals move across large areas to meet their energy requirements and vegetation cover (Fischer and Linsenmair, 2001). Studies have also shown that large herbivores in human-disturbed habitats are known to use a larger home range to meet nutritional demands in giraffes (*Giraffa camelopardalis*) (Knüsel et al., 2019) and female red deer (*Cervus elaphus*) (Jeppesen, 1987) than in protected habitats. These disturbances, including livestock grazing, are likely to reduce resource availability and cover, forcing individuals to increase their movements to obtain resources (Knüsel et al., 2019).

The livestock pressure has negative impacts on the mountain nyala population (Mamo and Bekele, 2011), *Erica* vegetation regeneration (Gebre Kidan, 1996), and a common conservation threat in the majority of protected areas in Ethiopia (Stephens et al., 2001). On the other hand, mountain nyala are better protected from human activity and livestock grazing in Arsi Mountains NP. More research is needed, however, to understand the types of human activities that have a major effect on activity budgets and home range size because some disturbances are more likely to have a greater effect than others.

Our results showed that the mean and seasonal home range sizes vary; the smallest are during wet, then smaller during intermediate, and the largest are during dry seasons (Table 2; Fig. 6). This is in line with the findings of Sillero-Zubiri (2013), who found that home ranges in the dry season were much larger than in the wet season. Similar results were also reported in nyala (*Tragelaphus angasii)* (Hart et al., 2013) and female kob antelopes (*Kobus kob kob*) (Fischer and Linsenmair, 2001) with a larger dry season home range when moving to meet food and shelter requirements. Variations in local weather also impact home range size (Rivrud et al., 2010). The home range size and precipitation are also negatively correlated in giraffe (*Giraffa camelopardalis*) (Knüsel et al., 2019), and precipitation appears to be a predictor of seasonal home range size (Janse van Rensburg et al., 2018). Furthermore, because precipitation is seasonal in the current study area, it is likely to be a major determinant of plant phenology and, as a result, food availability (Janse van Rensburg et al., 2018). Animals in forage-rich areas have smaller home ranges than those in forage-deficient areas (Rivrud et al., 2010). Similarly, variations in topography also influence the size of home ranges as movement in sloppy areas is more energetically costly (Mcloughlin and Ferguson, 2000; Anderson et al., 2005).

To conclude, we found that extensive human activities appeared to affect the activity budget and home range size of mountain nyala in the Ericaceous habitat. Our analysis found that human presence and vigilance were shown to be positively correlated, while human presence and foraging were found to be negatively correlated. The effects of human activities and livestock grazing in the region result in foraging and resting costs from high level of vigilance and movement. We do, however, suggest more study and continuous behavioral monitoring aimed at combining behavioral responses with physiological aspects of the species in order to provide detailed information for conservative management.

4.3. Implications for conservation

Understanding how human activities impact behavioral patterns and home range size is essential for conservation efforts. Overall, our findings indicate that intensive human activities increased vigilance, movement, and home range size in mountain nyala. Mountain nyala adjusted their activity budget and home range size to survive in the highly disturbed habitat. Hence, this research adds to our understanding of the adaptive behavioral ecology of the species, and future research should prioritize the fitness cost associated with human activities as well as measures that conservationists might employ to lower these foraging costs. Hence, the high level of human activities, livestock grazing, and human encroachment in and around Adaba-Dodola CCA should be regulated. In light of these results, we suggest a decrease in human activities in the Adaba-Dodola CCA as it affects the time budget of mountain nyala, and a decrease in human activity is expected to an increase in foraging time. Direct and uncontrolled exploitation of resources from the Adaba-Dodola CCA makes the habitat vulnerable and could be minimized. Understanding the effects of intensified human activities on the mountain nyala population will help the management authorities and stakeholders for conservation and management of mountain nyala areas.

Funding

This work was supported by Rufford Small Grant for Nature Conservation (RSG reference 20813-2), Saint Louis Zoo (USA) and Norwegian State Educational Loan Fund (Norway).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The financial support to Ejigu Alemayehu Worku from the Norwegian State Educational Loan Fund (Lånekassen) under the Quota Scheme is indebted. This research received logistic and institutional support from the Centre for Ecological and Evolutionary Synthesis (CEES) of the University of Oslo, Norway. We are grateful to the Ethiopian Wildlife Conservation Authority and Oromia Forest and Wildlife Enterprise for permitting us to conduct this research. We thank research assistants Abebaw Limenh and Jemal Kedir for their valuable help.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01900.

References

Allen, A.M., Singh, N.J., 2016. Linking movement ecology with wildlife management and conservation. Front. Ecol. Evol. 3, 155.
Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–266.
Ameha, A., Larsen, H.O., Lemenih, M., 2014a. Participatory forest management in Ethiopia: learning from pilot projects. Environ. Manag. 53, 838–854.
Ameha, A., Nielsen, O.J., Larsen, H.O., 2014b. Impacts of access and benefit sharing on livelihoods and forest: case of participatory forest management in Ethiopia. Ecol. Econ. 97, 162–171.
Anderson, D.P., Forester, J.D., Turner, M.G., Frair, J.L., Merrill, E.H., Fortin, D., Mao, J.S., Boyce, M.S., 2005. Factors influencing female home range sizes in elk (Cervus elaphus) in North American landscapes. Landsc. Ecol. 20, 257–271.
Asefa, M., Cao, M., He, Y., Mekonnen, E., Song, X., Yang, J., 2020. Ethiopian vegetation types, climate and topography. Plant Divers. 42, 302–311.
Atickem, A., Loe, L.E., 2014. Livestock-wildlife conflicts in the Ethiopian highlands: assessing the dietary and spatial overlap between mountain nyala and cattle. Afr. J. Ecol. 52, 343–351.
Atickem, A., Loe, L.E., Stenseth, N.C., 2014. Individual heterogeneity in use of human shields by mountain nyala. Ethology 120, 715–725.
Barnett, D.T., Stohlgren, T.J., 2003. A nested-intensity design for surveying plant diversity. Biodivers. Conserv. 12, 255–278.
Blom, A., Van Zalinge, R., Mbea, E., Heitkönig, I.M., Prins, H.H., 2004. Human impact on wildlife populations within a protected Central African forest. Afr. J. Ecol. 42, 23–31.
Blower, J., 1968. The wildlife of Ethiopia. Oryx 9, 276–285.
Bogale, A., 2011. Valuing natural forest resources: an application of contingent valuation method on Adaba-Dodola Forest Priority Area, Bale Mountains, Ethiopia. J. Sustain. For. 30, 518–542.
Borrini-Feyerabend, G., Pimbert, M., Farvar, M.T., Kothari, A. & Renard, Y. (2004) Sharing power: learning-by-doing in co-management of natural resources throughout the world IIED and IUCN/ CEESP/ CMWG, Cenesta, Tehran, Earthscan.
Brown, L.H., 1969. Observations on the status, habitat and behaviour of mountain nyala *Tragelaphus buxtoni* in Ethiopia. Mammalia 33, 545–597.
Bunnefeld, N., Edwards, C.T., Atickem, A., Hailu, F., Milner-Gulland, E.J., 2013. Incentivizing monitoring and compliance in trophy hunting. Conserv. Biol. 27, 1344–1354.
Calenge, C. (2015) adehabitatHR: A collection of tools for the estimate of animals home range. R package version 0.4. 14.
Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS One 7, e50611.
Cooke, S.J., 2008. Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. Endanger. Species Res. 4, 165–185.
ESRI, E.A. (2020) Release 10.8. 1. *Redlands, CA, USA: Environmental Systems Research Institute.*
Evangelista, P., Swartzinski, P., Waltermire, R., 2007. A profile of the mountain nyala (Tragelaphus buxtoni). African Indaba 5 (2).
Evangelista, P., Young, N., Swift, D., Wolde, A., 2015. Demographic observations of mountain nyala Tragelaphus buxtoni in a controlled hunting area, Ethiopia. J. Biodivers. Endanger. Species 3, 1000145.
Evangelista, P.H., Norman, J., Berhanu, L., Kumar, S., Alley, N., 2008. Predicting habitat suitability for the endemic mountain nyala (Tragelaphus buxtoni) in Ethiopia. Wildl. Res. 35, 409–416.
Evangelista, P.H., Norman III, J., Swartzinki, P., 2012. Assessing habitat quality of the mountain nyala Tragelaphus buxtoni in the Bale Mountains, Ethiopia. Curr. Zool. 58, 525–535.
Fischer, A., Tibebe Weldesemaet, Y., Czajkowski, M., Tadie, D., Hanley, N., 2015. Trophy hunters' willingness to pay for wildlife conservation and community benefits. Conserv. Biol. 29, 1111–1121.
Fischer, F., Linsenmair, K.E., 2001. Spatial and temporal habitat use of kob antelopes (Kobus kob kob, Erxleben 1777) in the Comoé National Park, Ivory Coast as revealed by radio tracking. Afr. J. Ecol. 39, 249–256.
Fortin, D., Boyce, M.S., Merrill, E.H., Fryxell, J.M., 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos 107, 172–180.
Friis, I., Sebsebe, D., Breugel, P.v. (2010) Atlas of the potential vegetation of Ethiopia, Det Kongelige Danske Videnskabernes Selskab.
Gebre Kidan, W. (1996) The status of mountain nyala (Tragelaphus buxtoni) in Bale Mountains National Park 1986–1994. *Walia,* 17, 27–37.
Gelashe, B.M. (2017) Species Diversity and Distribution Patterns of Woody Plants in Adaba-Dodola Afromontane Forest, Oromia, Ethiopia. Seoul National University.
Girma, Z., Chuyong, G., Evangelista, P., Mamo, Y., 2018. Vascular Plant Species Composition, Relative Abundance, Distribution, and Threats in Arsi Mountains National Park, Ethiopia. Mt. Res. Dev. 38, 143–152.
Hart, J., Kingdon, J., Hoffmann, M., 2013. Mammals of Africa, Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. Bloomsbury Publishing, *London, United Kingdom*, p. *680*.
Hedberg, O., 1971. The high mountain flora of the Galama Mountain in Arussi Province, Ethiopia. Webbia 26, 101–128.
Hovick, T.J., Elmore, R.D., Dahlgren, D.K., Fuhlendorf, S.D., Engle, D.M., 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. J. Appl. Ecol. 51, 1680–1689.
IUCN (2016) Tragelaphus buxtoni. The IUCN Red List of Threatened Species 2016: e.T22046A115164345. ⟨https://doi.org/10.2305/IUCN.UK.2016–3.RLTS.T22046A50195483.en⟩.
Janse van Rensburg, J., McMillan, M., Giżejewska, A., Fattebert, J., 2018. Rainfall predicts seasonal home range size variation in nyala. Afr. J. Ecol. 56, 418–423.
Jayakody, S., Sibbald, A.M., Gordon, I.J., Lambin, X., 2008. Red deer Cervus elephus vigilance behaviour differs with habitat and type of human disturbance. Wildl. Biol. 14, 81–91.
Jeppesen, J.L., 1987. Impact of human disturbance on home range, movements and activity of red deer (Cervus elaphus) in a Danish environment. Danish Rev. Game Biol. 13, 1–38.

Kindu, M., Schneider, T., Teketay, D., Knoke, T., 2015. Drivers of land use/land cover changes in Munessa-Shashemene landscape of the south-central highlands of Ethiopia. Environ. Monit. Assess. 187, 452.
Knüsel, M.A., Lee, D.E., König, B., Bond, M.L., 2019. Correlates of home range sizes of giraffes, Giraffa camelopardalis. Anim. Behav. 149, 143–151.
Kostin, D.S., Kasso, M., Komarova, V.A., Martynov, A.A., Gromov, A.R., Alexandrov, D.Y., Bekele, A., Zewdie, C., Bryja, J., Lavrenchenko, L.A., 2019. Taxonomic and genetic diversity of rodents from the Arsi Mountains (Ethiopia). Mammalia 83, 237–247.
Kubsa, A., Tadesse, T. (2002) Granting exclusive user rights to the forest dwellers in the state-owned forest: the WAJIB approach in Ethiopia. In: Proceedings of the Second International Workshop on Participatory Forestry in Africa, Arusha, Tanzania pp. 18–22.
Malcolm, J., Evangelista, P., 2011. Observations of the status of the mountain nyala: 2000-2005. J. Ethiop. Wildl. Nat. Hist. Soc. 39–52.
Mamo, Y., Bekele, A., 2011. Human and livestock encroachments into the habitat of Mountain Nyala (Tragelaphus buxtoni) in the Bale Mountains National Park, Ethiopia. Trop. Ecol. 52, 265–273.
Mamo, Y., Pinard, M.A., Bekele, A., 2010. Demography and dynamics of mountain nyala Tragelaphus buxtoni in the Bale Mountains National Park, Ethiopia. Curr. Zool. 56, 660–669.
Mangiacotti, M., Scali, S., Sacchi, R., Bassu, L., Nulchis, V., Corti, C., 2013. Assessing the spatial scale effect of anthropogenic factors on species distribution. PLoS One 8, e67573.
Manor, R., Saltz, D., 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecol. Appl. 13, 1830–1834.
Manor, R., Saltz, D., 2005. Effects of human disturbance on use of space and flight distance of mountain gazelles. J. Wildl. Manag. 69, 1683–1690.
Mcloughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7, 123–130.
Miehe, S., Miehe, G. (1994) Ericaceous forests and heathlands in the Bale mountains of south Ethiopia. *Ecology and man's impact,* Stiftung Walderhaltung in Afrika, Hamburg.
Morris, D.W., Kotler, B.P., Brown, J.S., Sundararaj, V., Ale, S.B., 2009. Behavioral indicators for conserving mammal diversity. Ann. N. Y. Acad. Sci. 1162, 334–356.
Mueller, T., Fagan, W.F., 2008. Search and navigation in dynamic environments–from individual behaviors to population distributions. Oikos 117, 654–664.
Nega, M. (2014) *Carbon stock in Adaba-Dodola community forest of Danaba District,* West-Arsi zone of Oromia Region, Ethiopia: An implication for climate change mitigation. Addis Ababa University, Ethiopia.
Owen-Smith, N., 1979. Assessing the foraging effeciency of a large herbivore, the kudu. South Afr. J. Wildl. Res. 9, 102–110.
Plotz, R.D., Grecian, W.J., Kerley, G.I., Linklater, W.L., 2016. Standardising home range studies for improved management of the critically endangered black rhinoceros. PLoS One 11, e0150571.
R Development Core Team, R.C. (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 〈http://www.r-project.org/index.html〉.
Rivrud, I.M., Loe, L.E., Mysterud, A., 2010. How does local weather predict red deer home range size at different temporal scales? J. Anim. Ecol. 79, 1280–1295.
Setsaas, T., Hunninck, L., Jackson, C.R., May, R., Røskaft, E., 2018. The impacts of human disturbances on the behaviour and population structure of impala (Aepyceros melampus) in the Serengeti ecosystem, Tanzania. Glob. Ecol. Conserv. 16.
Shi, J., Dunbar, R.I., Buckland, D., Miller, D., 2003. Daytime activity budgets of feral goats (Capra hircus) on the Isle of Rum: influence of season, age, and sex. Can. J. Zool. 81, 803–815.
Smith, Y.C.E., Smith, D.A.E., Ramesh, T., Downs, C.T., 2019. Novel predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species. Behav. Process. 159, 9–22.
Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173.
Stephens, P.A., d'Sa, C.A., Sillero-Zubiri, C., Leader-Williams, N., 2001. Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. Biol. Conserv. 100, 307–322.
Tadesse, G., Zavaleta, E., Shennan, C., FitzSimmons, M., 2014. Policy and demographic factors shape deforestation patterns and socio-ecological processes in southwest Ethiopian coffee agroecosystems. Appl. Geogr. 54, 149–159.
Tadesse, S.A., Kotler, B.P., 2013. Effects of habitat, group-size, sex-age class and seasonal variation on the behavioural responses of the mountain nyala (Tragelaphus buxtoni) in Munessa, Ethiopia. J. Trop. Ecol. 30, 33–43.
Tang, X., Tang, S., Li, X., Menghe, D., Bao, W., Xiang, C., Gao, F., Bao, W., 2019. A study of population size and activity patterns and their relationship to the prey species of the eurasian lynx using a camera trapping approach. Animals 9, 864–3250.
Tefera, M., 2011. Wildlife in Ethiopia: endemic large mammals. World J. Zool. 6, 108–116.
Tessema, M.E., Lilieholm, R.J., Ashenafi, Z.T., Leader-Williams, N., 2010. Community attitudes toward wildlife and protected areas in Ethiopia. Soc. Nat. Resour. 23, 489–506.
Uhlig, S.K., 1988. Mountain forests and the upper tree limit on the southeastern plateau of Ethiopia. Mt. Res. Dev. 8, 227–234.
Vial, F., Macdonald, D.W., Haydon, D.T., 2011. Response of endemic afroalpine rodents to the removal of livestock grazing pressure. Curr. Zool. 57, 741–750.
Viana, D.S., Granados, J.E., Fandos, P., Pérez, J.M., Cano-Manuel, F.J., Burón, D., Fandos, G., Aguado, M.Á.P., Figuerola, J., Soriguer, R.C., 2018. Linking seasonal home range size with habitat selection and movement in a mountain ungulate. Mov. Ecol. 6, 1–11.
Wang, Z., Li, Z., Beauchamp, G., Jiang, Z., 2011. Flock size and human disturbance affect vigilance of endangered red-crowned cranes (Grus japonensis). Biol. Conserv. 144, 101–105.
Watson, C. (2013) Forest conservation for communities and carbon: the economics of community forest management in the Bale Mountains Eco-Region, Ethiopia. PhD thesis, The London School of Economics and Political Science (LSE), UK.
Wilder, M. (2016) An assessment of ecotourism as an effective tool for sustainable forest management: The case of Adaba-Dodola, Ethiopia. MSc Thesis, University of Washington, DC.
Wilson, M.W., Ridlon, A.D., Gaynor, K.M., Gaines, S.D., Stier, A.C., Halpern, B.S., 2020. Ecological impacts of human-induced animal behaviour change. Ecol. Lett. 23, 1522–1536.
Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.
Wronski, T., Bariyanga, J., Apio, A., Plath, M.J.T.R.J., 2015. Interactions between wildlife, humans and cattle: activity patterns of a remnant population of impala on the degraded Mutara Rangelands, Rwanda. Rangel J. 37, 357–365.
Young, J. (2012) Ethiopian Protected Areas: A "Snapshot". *A reference guide for future strategic planning and project funding,* pp46.
Young, N.E., Evangelista, P.H., Mengitsu, T., Leisz, S., 2020. Twenty-three years of forest cover change in protected areas under different governance strategies: a case study from Ethiopia's southern highlands. Land Use Policy 91, 104426.