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Group size dynamics of the endangered mountain nyala (*Tragelaphus buxtoni*) in protected areas of the Arsi and Ahmar Mountains, Ethiopia

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ABSTRACT

As an adaptive biological trait, group size may offer a useful metric for monitoring the welfare of wildlife species affected by their environmental surroundings. Here, we examine the drivers that cause variation in group size of the endangered mountain nyala (*Tragelaphus buxtoni*), including a range of natural ecological factors as well as the density of livestock. For this purpose, we collected data along transect lines during both wet and dry seasons focusing on the hitherto poorly studied populations in the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, which are managed for multiple use of a variety of natural resources. We found group sizes to be an average of 6.3, 4.4 and 4.1 individuals in the Arsi Mountains, Munessa-Kuke and Muktar Mountain study areas, respectively, and a combination of livestock density and habitat visibility explained as much as 74% of the variation in group size. We propose that whereas group size increases with forage availability (as measured by Normalized Difference Vegetation Index -NDVI) and in open habitats (probably due to a switch in antipredator strategy), the presence of livestock also has an independent, negative impact on group size because of the associated disturbance. The findings contribute to understanding the environmental drivers of variation in group size in social antelopes, particularly highlighting the need to improve livestock management to help conservation of species at risk.

1. Introduction

Group size is a key trait in the evolutionary dynamics of social wildlife species (Krause and Ruxton, 2003; Markham et al., 2015). A species' environmental surroundings, including the presence of predators and people, has the potential to affect group size directly (Valeix et al., 2009). This, in turn, may affect other biological and behavioral traits, including energy and nutritional budgets (Kie, 1999), mating system and sexual selection (Bowyer et al., 2020; Szemán et al., 2021), and predation risk and adaptive antipredator behavior (Bro-Jørgensen et al., 2019; Rudolph et al., 2019). Understanding the environmental drivers that influence group size among

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wildlife, particularly ungulates, can thus provide important information to support management and conservation (Buuveibaatar et al., 2013; Evangelista et al., 2012; Shi et al., 2019; Takada and Washida, 2020). Generally, the benefits and costs of living in groups often revolve around avoiding predators and foraging for food (Creel et al., 2014; Majolo and Huang, 2017; Valeix et al., 2009). Grouping is beneficial because it decreases predation risk through increased vigilance (Flølo et al., 2021; Jhala and Isvaran, 2016) and dilution benefits (Dehn, 1990). However, grouping also has disadvantages that individuals within the group may compete for the same resources (Averbeck et al., 2012; Barja and Rosellini, 2008) and increase disease transmission (Vander Wal et al., 2012).

In ungulates, group size is known to be influenced by natural factors, such as climate (Tadesse and Kotler, 2013; Underwood, 1982; Wronski et al., 2009), habitat structure and forage availability (Jhala and Isvaran, 2016; Marino and Baldi, 2014). Habitat structure can influence group size by promoting safety-in-numbers as a predator strategy in open habitats (Jhala and Isvaran, 2016). The forage availability can also affect group size, with group size increasing with forage availability (Isvaran, 2007). Seasonal changes is also known to affect group size in ungulates, with larger groups observed in the rainy seasons (Underwood, 1982); this may in fact be explained by better forage availability, or alternatively seasonal breeding. Compared to these natural ecological factors, less is known about the impact of anthropogenic activities, such as livestock grazing and human disturbance (Manor and Saltz, 2003).

Understanding how anthropogenic pressures affect wildlife behavior in protected areas is critical to management and conservation efforts (Setsaas et al., 2018). Anthropogenic activities can lead to habitat loss due to land use change, livestock grazing, and human settlement expansion (Fetene et al., 2019) and thereby negatively impact wildlife and their behaviors. One way to understand the impact of these pressures on wildlife is by investigating their behavior (Broekhuis et al., 2019).

Ethiopia has the largest number of livestock in Africa (Agricultural Sample Survey, 2008; Fashing et al., 2022). The Ethiopian highlands hosts over 85% of the national population and 75% of the country's livestock, making the area the most intensively cultivated part of the country (Amsalu and de Graaff, 2006; Leta and Mesele, 2014). Though human settlements, livestock grazing, and utilization of natural resources are not allowed in them, most protected areas are vulnerable to anthropogenic threats (Negarit Gazeta, 2007). The management effectiveness of many of Ethiopia's protected areas is low, as there is traditionally open access to natural resources, weak institutional capacity, lack of local community engagement, inadequate political support and few alternative livelihoods (Van Zyl, 2015). The rapid growth of human and livestock populations in and around protected areas are also primarily responsible for unsustainable use of natural resources and overgrazing. This has led to the conversion of natural habitat to agricultural land, and consequently habitat fragmentation affecting the conservation of endangered species (Girma, Chuyong, and Mamo, 2018; Stephens et al., 2001).

The mountain nyala (*Tragelaphus buxtoni*) is a large spiral-horned antelope endemic to the Ethiopian Highlands (Brown, 1969; Hillman, 1986; Yalden et al., 1996), where it inhabits the dense Afromontane forests, *Erica* heathlands and Afroalpine region of Bale, Arsi, and Ahmar Mountains in the southeast (Evangelista et al., 2008). The populations are highly fragmented and face multiple threats across its range, including habitat loss and degradation caused by human settlement, agricultural expansion, and livestock grazing (Atickem and Loe, 2014; Evangelista et al., 2008).

Mountain nyala form cohesive social groups of four - five individuals, with bachelor herds consisting of up to 13 individuals (Hillman and Hillman, 1987). For most of the year, mature males and females are segregated. Females will form family groups consisting of several mature females and their offspring from one or two previous years. Younger males will often accompany these family groups for around two years, while mature males will form bachelor groups that are similar in age-class (Evangelista et al., 2007; Sillero-Zubiri, 2013). Larger, more fluid groups often form during rest or feeding periods, when smaller social units temporarily merge (Hilman, 1988; Refera and Bekele, 2004), resulting in group size variation. During the breeding season, males compete for dominance over females and their family groups pushing young males out and keeping other mature bulls away (Evangelista et al., 2007; Sillero-Zubiri, 2013). It is clear from previous studies that significant variation exists in mountain nyala group sizes between different areas (Evangelista et al., 2015; Mamo et al., 2010; Tadesse and Kotler, 2013), but the causes of these differences remain unclear. Thus, the average group size in the Abasheba-Demaro Controlled Hunting Area, on the eastern flank of the Bale Mountains, was reported as 3.7 (range 3.3–4.1), with no significant differences when males were present (Evangelista et al., 2015), whereas in the Bale Mountains National Park, the mean group size has been reported as 10.2 (range 1–62) in the wet season and 7.9 (range 1–48) in the dry season (Refera and Bekele, 2004). Another study reported a mean of seven in the Gaysay area and 12 in Dinsho in the Bale Mountains National Park (Mamo et al., 2010). Still, it is worth noting that the mountain nyala populations at these sites occur within confined areas where they have adapted to human presence and high population density compared to other regions. Hence, we need a better understanding of the factors affecting variation in group size under a broader range of ecological conditions.

In this study, we examined how environmental factors influence the group size of mountain nyala in the Arsi and Ahmar Mountains, Ethiopia, where no previous studies have investigated the topic despite the severe conservation challenges of the region. We modeled the effects of topography (i.e., elevation and slope), ecological conditions (i.e., land cover type, food availability [Normalized Difference Vegetation Index -NDVI] and perceived predation risk [visibility]), anthropogenic impact (i.e., livestock density) and seasonality (i.e., wet and dry seasons) on group size. We specifically predict that group size will be larger (1) in open habitats due to higher benefits from relying on safety in numbers as an antipredator response, (2) during wet season and (3) in areas with high forage availability as measured by NDVI. We also predict that group size will be negatively influenced by the livestock density due to the associated disturbance. We will furthermore examine whether land cover type, elevation and slope have any detectable effect on grouping. By focusing on an important, but neglected conservation area for mountain nyala, we aim to provide insights into the ecology and social behavior of the species which will support decision-makers in the conservation of this endangered species.

2. Materials and methods

2.1. Study sites

We surveyed three study sites in the Arsi and Ahmar Mountains of Ethiopia: Arsi Mountains National Park (Arsi Mountains NP), Munessa-Kuke Controlled Hunting Area (Munessa-Kuke CHA) and Muktar Mountain Forest Reserve (Muktar Mountain FR) (Fig. 1).

2.1.1. Arsi Mountains National Park

Arsi Mountains NP is located in the southeast highlands of Ethiopia and was established in 2011. The park covers approximately 939 km^2 and is divided into four fragmented management blocks; Chilalo-Galama Mountain, Kaka, Hunkolo, and Dhera-Dilfaqar (Fig. 1). Our study focused on the Chilalo-Galama Mountains (7°31' to 8°01' N; 39°10' to 39°30' E), which covers about 793 km^2 and has the least anthropogenic disturbance. Mount Chilalo is isolated from the Galama Mountain range by a saddle known locally as Cheleleka. The elevation of Chilalo-Galama ranges from 2700 m to 4196 m asl, the average annual rainfall varies between 779 and 1090 mm, and the mean monthly temperature ranges from a minimum of 11 °C to a maximum of 22 °C (Girma, Chuyong, Evangelista et al., 2018).

The Chilalo-Galama Mountains is comprised of three vegetation zones; the Afroalpine at higher elevations (3276–4008 m asl), heathlands dominated by *Erica* spp. at mid elevations (3202–3985 m asl), and Afromontane forest (2843–3756 m asl) and mixed-species tree plantations at lower elevations (3181–3340 m asl) (Girma, Chuyong, Evangelista et al., 2018; Kostin et al., 2019). The Afroalpine vegetation is dominated by *Artimesia trimera*, *Alchemilla helichrysum*, and *Lobelia rhynchopetalum* (Hedberg, 1971). The heathlands, also known as the Ericaceous belt, is dominated by *Erica arborea* and *E. trimera*. The Afromontane forest has largely been cleared with only remnant trees of *Hagenia abyssinica* in the moist areas and *Juniperus procera* at relatively drier parts (Kasso et al., 2010). In addition, in the Afromontane forest zone, bushland habitat types are dominated by woody plant species intermixed with grasses and other herbaceous vegetation. The Chilalo–Galama mountain range has a diverse assemblage of mammals, including larger species such as mountain nyala, Ethiopian wolf (*Canis simensis*), Menelik's bushbuck (*Tragelapphus scriptus meneliki*), Bohor reedbuck (*Redunca redunca*), klipspringer (*Oreotragus oreotragus*), and spotted hyena (*Crocuta crocuta*) (Kasso et al., 2010). The mountain nyala population is currently estimated at 108 individuals (Ejigu Alemayehu Worku, unpublished result), following an estimate of 130

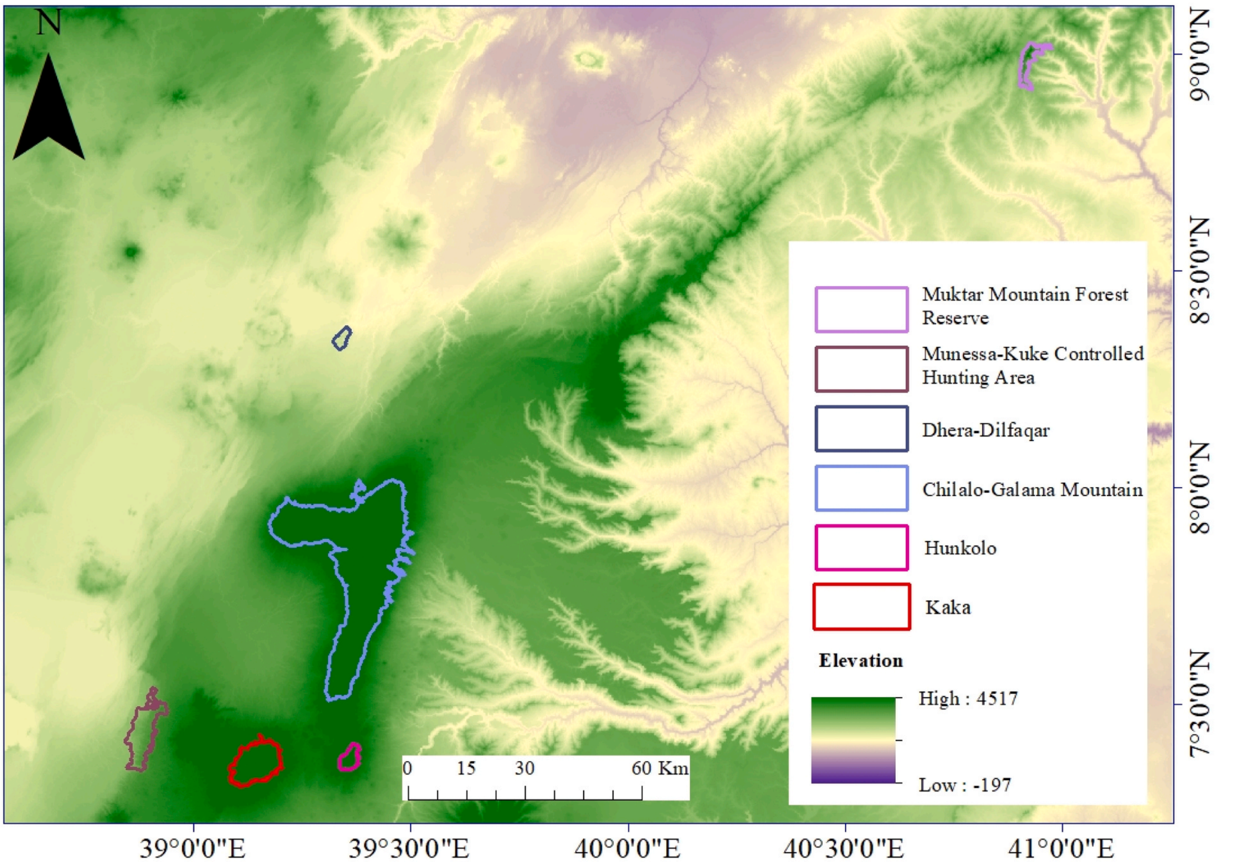

Fig. 1. Elevation map of the Arsi Mountains National Park (Chilalo-Galama Mountain, Kaka, Hunkolo, and Dhera-Dilfaqar blocks), Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia.

individuals between 2000 and 2003 (Malcolm and Evangelista, 2011).

The predominant land use in the region includes subsistence agriculture and human settlements (Evangelista et al., 2007). The anthropogenic impact from agricultural expansion, proliferating settlements, uncontrolled burning, and high livestock densities pose significant conservation challenges to the Arsi Mountains NP (Worku et al., 2021).

2.1.2. Munessa-Kuke Controlled Hunting Area

Munessa-Kuke CHA, situated west of Arsi Mountains NP, covers approximately 111 km^2 (Evangelista et al., 2007) and extends over an altitudinal range from 2000 to 2800 m asl (Tadesse and Kotler, 2013) (Fig. 1). The Munessa-Kuke CHA is located at 7°21' to 7°32' N latitude and 38°50' to 38°56' E longitude. The average rainfall is approximately 1250 mm annually, and the mean annual temperature varies from 15 °C to 20 °C (Tadesse and Kotler, 2013).

The vegetation type in the Munessa-Kuke CHA is primarily native Afromontane forest and mixed-species plantations. The Afromontane forest is dominated by tree species *Prunus africana*, *Afrocarpus falcatus, H. abyssinica, Croton macrostachyus*, *Maytenus added* and *Nuxia congesta*. Moreover, the plantation forests include *Pinus patula*, *Pinus radiate*, *Cupressus lusitanica* and *Eucalyptus spp.* (Kindu et al., 2013; Senbeta et al., 2002). The Munessa-Kuke CHA has a diverse set of mammalian species, including mountain nyala, Menelik's bushbuck, grey duiker (*Silvicapra grimmia*), black-and-white colobus monkey (*Colobus guereza*), anubis baboon (*Papio anubis*) and spotted hyena (Nino et al., 2017). The mountain nyala population is currently estimated at 220 individuals (Ejigu Alemayehu Worku, unpublished), following an estimate of 200 individuals between 2000 and 2003 (Malcolm and Evangelista, 2011).

The Munessa-Kuke CHA is intensively managed for sustainable use of natural resources and is open for trophy hunters to generate funds for wildlife conservation and forest management (Evangelista et al., 2007). The area has significant tourism potential (Nino et al., 2017), and the local community is generally supportive of mountain nyala conservation (Tadesse and Kotler, 2016). However, the demand for agricultural land and other resources, driven by a high human population growth rate and livestock populations, poses a conservation threat to the mountain nyala population.

2.1.3. Muktar Mountain Forest Reserve

The Muktar Mountain FR is located in the Ahmar Mountains and is the most northern range of the mountain nyala (Fig. 1). It was established in 1989 as part of Kuni–Muktar Mountain Nyala Sanctuary by the Ethiopian Wildlife Conservation Organization to safeguard the mountain nyala population (Evangelista et al., 2007). The forest area is located at 8°55' to 9°01' N latitude and 40°54' to 40°58' E longitude and covers an area of 36 km^2 and elevation ranges from 2196 to 2956 m asl. The average rainfall pattern ranges from 1025 to 1200 mm, and the average monthly minimum temperature ranges from 22.5° to 24.5°C.

The dominant vegetation type in the Muktar Mountain FR is classified as a Afromontane forest (Asefa, 2015) characterized by *J. procera* and *A. falcatus* at lower elevations (Evangelista et al., 2007). In addition, there are also patches of open grassland throughout the forest. The mountain nyala population in 2016 was estimated at 25 individuals (Ejigu Alemayehu Worku, unpublished). Human encroachment, tree cutting for construction and fuel, and livestock grazing are among the most important challenges to mountain nyala conservation in the forest (Evangelista et al., 2007).

2.2. Data collection

In total, 36 transect lines (129 km in total) were walked in the three study sites during wet (June 2016 to September 2016) and dry (November 2016 to February 2017) seasons. The transects were proportionally distributed accordingly to the size and topography of the respective study sites. As a result, a total of 16 (range 3.8–6.2 km), 12 (range 1.9–4.5 km), and 8 (range 1.4–3.4 km) transects were surveyed in Arsi Mountains NP, Munnessa-Kuke CHA and Muktar Mountain FR, respectively. A minimum distance of 1 km was set between transects to minimize the risk of double-counting of mountain nyala and livestock groups. We conducted our survey early in the morning between 06:30 and 10:00 and late in the afternoon between 16:00 and 18:00. Each transect was surveyed eight times, where we recorded the location with a handheld Garmin GPSMap 62 s global positioning system (GPS), group size and composition of all-mountain nyala groups encountered, and the number of livestock encountered, notably cattle and caprines. The study areas' dense vegetation reduced horizontal visibility to count mountain nyala and livestock numbers along transects. Therefore, we limited transect counts within a 50 m buffer of each transect line. We have also conducted a preliminary survey to gather all the available and relevant information including climatic conditions, topography, habitat characteristics and anthropogenic activities. We used the same transect to survey the group size as following the recommendations given by Plumptre (2000) to overcome sampling bias from potential gradients in environmental variables, eg., topographic and habitat characteristics. If animal groups were encountered away from the transect line, their locations were recorded once they had moved on. For mountain nyala, we divided social groups into five categories: female groups (FG; groups containing only adult females), male groups (MG; groups containing only adult males), female-juvenile groups (FJG: groups containing only adult females, as well as juveniles and/or calves), male-female groups (MFG; groups containing only adults but of both sexes), and male-female-juvenile groups (MFJG; groups containing adults of both sexes as well as juveniles and/or calves).

To understand which environmental and anthropogenic factors affected mountain nyala group size, we -collated data on 1) topography (i.e., elevation and slope), 2) ecological variables (i.e., land cover type, food availability [normalized difference vegetation index -NDVI] and perceived predation risk [visibility]), 3) livestock density, and 4) seasonality (i.e., wet and dry seasons).

Environmental variables data were collated from a combination of data collected in the field and remotely sensed data. Elevation was recorded during the fieldwork using a GPS. Slope (i.e., the steepness of a surface/angle of incline) for each group observed was derived from a digital elevation model (DEM) produced from NASA's Shuttle Radar Topography Mission (SRTM) (http://srtm.csi.

cgiar.org) at a resolution of 30 m x 30 m (Sappington et al., 2007).

The heterogeneity of the landscape were assessed using land cover type and the availability of forage (Bevanda et al., 2014). The dominant land cover types for each group location were collected during the field investigation and categorized as either: (i)

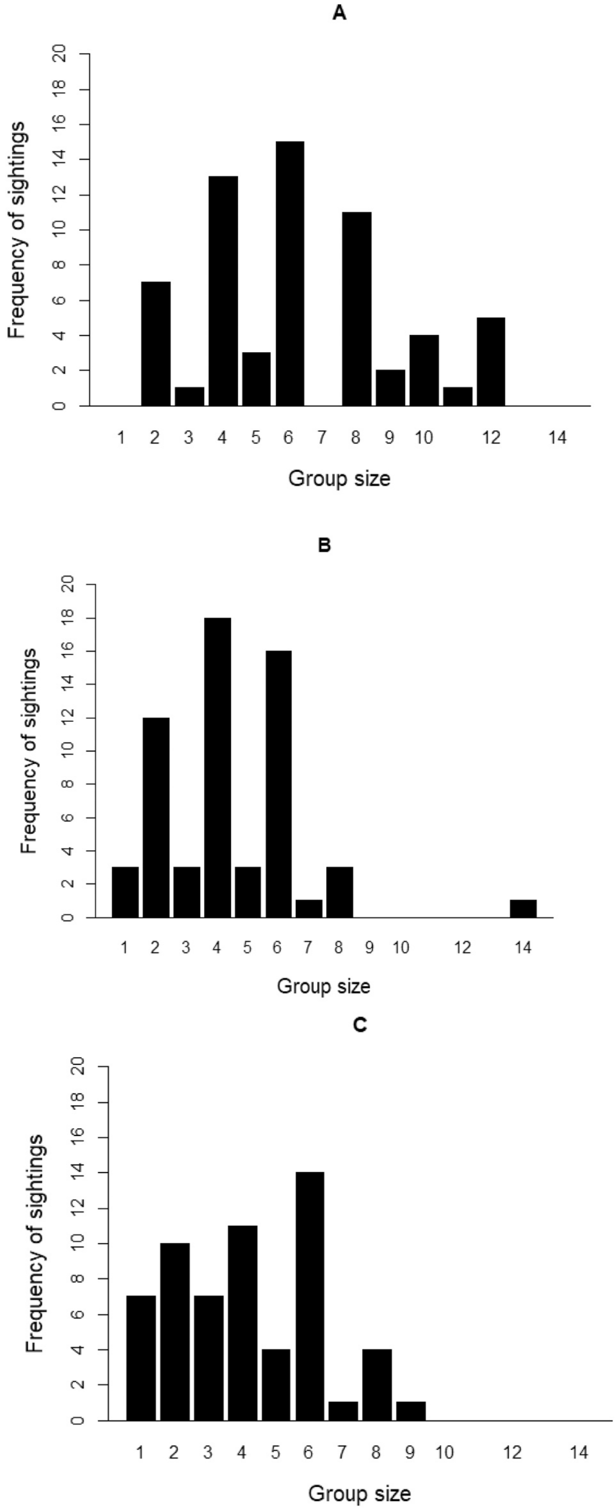

Fig. 2. Mountain nyala (*Tragelaphus buxtoni*) group-size distribution at **A**) Arsi Mountains National Park, (**B**) Munessa-Kuke Controlled Hunting Area, and **C**) Muktar Mountain Forest Reserve, Ethiopia (data pooled across seasons).

Afromontane forest, (ii) *Erica* shrub, (iii) bushland (dominated by woody shrubs of mixed species), (iv) grassland, or (v) plantation. To estimate forage availability of the mountain nyala group locations, we used remotely sensed normalized difference vegetation index (NDVI) produced from the Landsat 8 Operational Land Imager (OLI) downloaded from the United States Geological Survey (USGS) via https://earthexplorer.usgs.gov/. The NDVI is calculated as (NIR-RED)/(NIR + RED), where NIR and RED are spectral reflectance of near-infrared and red light, respectively (Pettorelli, 2013). NDVI is widely considered as a suitable proxy for forage quality and availability (Bradley and Fleishman, 2008; Buuveibaatar et al., 2013; Chirichella et al., 2015; Muposhi et al., 2016). With a spatial resolution of 30 m x 30 m, the NDVI values were extracted for all group locations using the Extraction tool in the Spatial Analyst extension of ArcGIS 10.8.1. The monthly NDVI values were used to measure the vegetation productivity of each group location. For each group of mountain nyala encountered in the field, we also recorded visibility to assess the perceived predation risk. We estimated visibility within a 50 m radius of the group observed based on terrain roughness and vegetation structure. Visibility was classified into two categories: high visibility (no visual restriction in any direction) and low visibility (reduced visibility in some or all directions) (Iranzo et al., 2021).

To account for the potential effect of livestock density on mountain nyala group size, we counted the total number of livestock observed within a 50 m-buffer along the length of each transect and divided this value by the length of the transect and buffer width (2×50 m) to provide a of measure of livestock density (individuals/km^2). In addition to livestock density, we wanted to examine the effects of season, which is characterized by a dry season (November to February) and bimodal rainfall pattern: long wet season (June to September) and short wet season (March to May).

2.3. Statistical analysis

The statistical analyses were conducted in R Statistical Analysis Software, 4.0.5 (R Development Core Team, 2021). Variance inflation factors (VIFs) were calculated using 'sdm' package to check that collinearity was not affecting the results (Zuur et al., 2010). We excluded the variable elevation because it was positively related to livestock density in our dataset. The predictors included in the model were slope, land cover type, NDVI, visibility, livestock density and season.

The mean group size was compared between the three study sites using Tukey Post Hoc tests. Moreover, we ran generalized linear mixed models to evaluate the relative effect of slope, land cover type, NDVI, visibility, livestock density and season on group size. We used separate linear mixed-effect models from package lme4 (Bates, 2010) to evaluate the relationship between group size as a response variable and (i) visibility (categorical), (ii) livestock density and (iii) NDVI; separate analyses were conducted for the wet and dry season for (ii) and (iii). Study sites and transects were included as random factors to account for variations among areas. The model with the smallest Akaike's Information Criterion (AICc) value was selected as the best model and any model within 2 AICc values were considered (Burnham & Anderson, 2002). P-values below 0.05 were considered statistically significant.

3. Results

A total of 181 mountain nyala group sightings and 899 individuals (349 in the dry season and 550 in the wet season) were recorded between June 2016 and February 2017. The group size ranged from a single individual to a maximum of 14 individuals (Fig. 2A, B and C).

The overall mean group size (MGS ± SE) of mountain nyala was 6.3 ± 0.37 (n = 62), 4.4 ± 0.29 (n = 59), and 4.1 ± 0.29 (n = 60) in Arsi Mountains NP, Munessa-Kuke CHA and Muktar Mountain FR respectively (Fig. 3). Post Hoc tests showed that group size in the Arsi Mountains NP significantly larger than both Munessa-Kuke CHA ($p < 0.01$) and Muktar Mountain FR ($p < 0.01$), with no difference between the latter two (Table S1).

The mean group size (mean ± SE) over the year was 5.1 ± 0.19 (range: 1–14). Of the 181 mountain nyala groups, 17.1% were FG, 22.6% were FJG, 13.3% were MFG, 22.1% were MFJG and 24.9% were MG. There was a significant difference in overall mean group

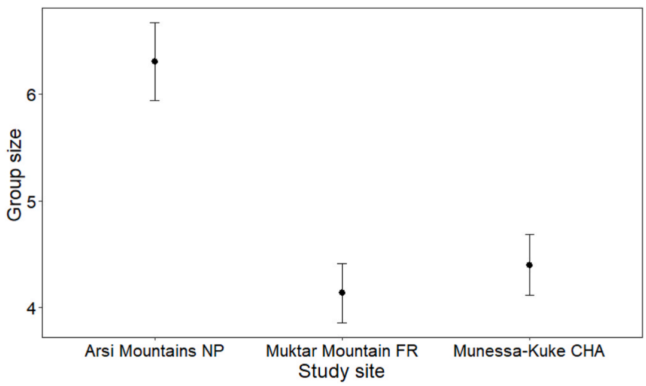

Fig. 3. Mountain nyala (*Tragelaphus buxtoni*) group size in Arsi Mountains National Park, Kuni Muktar Forest Reserve and Munessa-Kuke Controlled Hunting Area, Ethiopia.

size between wet (5.7 ± 0.28) and dry season (4.1 ± 0.24) ($p < 0.05$) (Fig. 4A) and between open (6.3 ± 0.33) and closed habitats (4.1 ± 0.20) (Fig. 4B).

Mountain nyala group size was negatively correlated with the livestock density with mountain nyala forming larger groups in areas with lower livestock density in both the wet and the dry season (Fig. 5 and Table 1).

The best model included livestock density and visibility as predictor variables and explained ~74% of the variation in group size (Table 2). This model accounted for 97% of the AICc weights among the two subset models we considered. Relative support was highest for livestock density (50.6%), followed by visibility (38.3%) and NDVI (11.1%). In the best model, group size correlated negatively with livestock density (Fig. 5 and Table 3) and positively with NDVI (Fig. 6).

4. Discussion

Our study shows that several environmental factors affect mountain nyala group size, notably livestock density, habitat visibility and forage availability (using NDVI as an index). As predicted, mountain nyala group sizes were negatively affected by livestock presence, an anthropogenic impact associated with increased disturbance. We also found strong support for the predictions that mountain nyala would aggregate into larger groups during wet season, in open habitats and in areas with high forage availability. An interaction term between livestock density and season suggests the negative impact of livestock presence on group size is most severe during the dry season, a finding that may be explained by intensified resource competition at this time. The mean group size of 5.1 individuals in the present study area is higher than that reported for Abasheba-Demaro CHA (mean group size 3.7) but lower than the Gaysay (mean group size 7) and Dinsho (mean group size 12) areas of Bale Mountains National Park (Mamo et al., 2010). We found that group size increased in the wet season, a trend reported also by Tadesse and Kotler (2013) for mountain nyala in the Afromontane forest of the Munessa-Kuke CHA (7.4 during the wet season and 6.3 during the dry season).

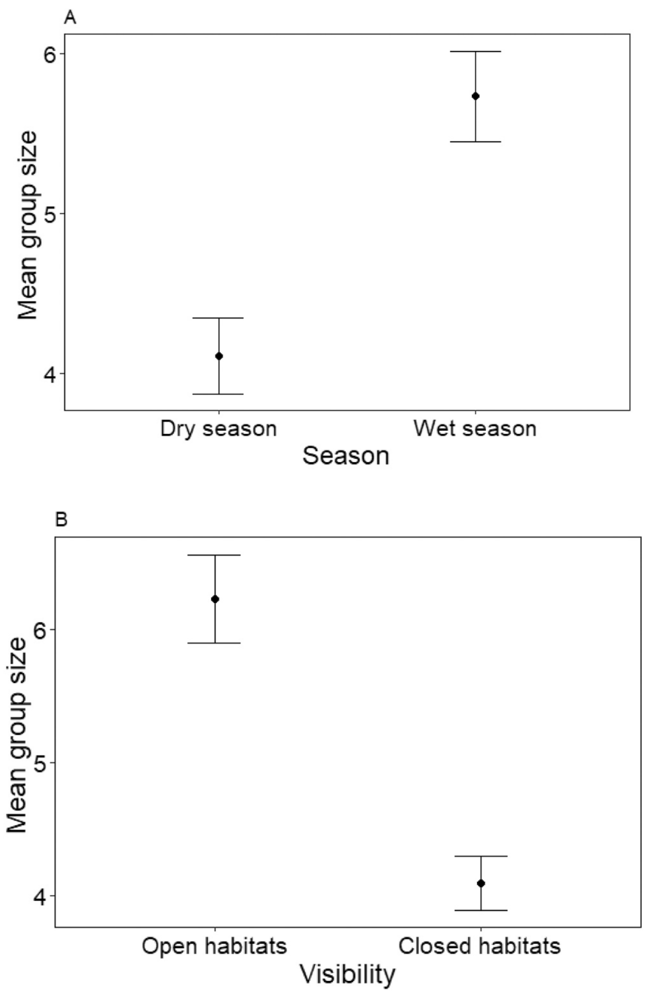

Fig. 4. Group mean size in mountain nyala (*Tragelaphus buxtoni*) (A) between dry and wet seasons, and (B) between open and closed habitat type in the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia.

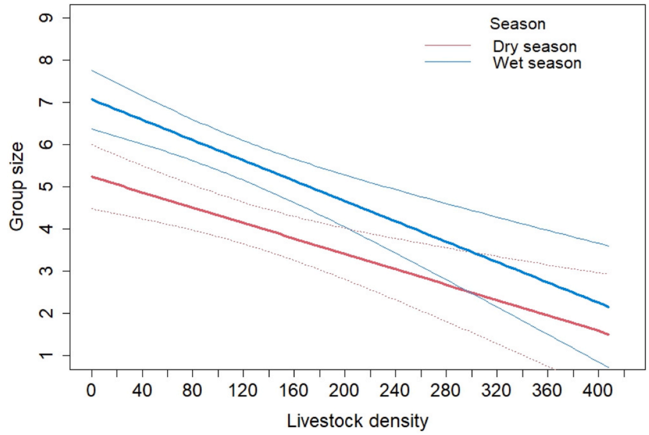

Fig. 5. Predicted mean group size (with 95% confidence intervals) of mountain nyala (*Tragelaphus buxtoni*) in dry (solid red line) and wet (dotted blue line) seasons in relation to the livestock density. Results obtained from a fixed effect model of data from the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia.

Table 1
Parameter estimates of mountain nyala group (*Tragelaphus buxtoni*) size in relation to season and livestock density analyzed using general linear mixed-effects model with 95% confidence interval (AIC = 829.7) in the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia.

Effects	Estimate	SE	t-value	P value
Intercept	5.24	0.38	13.5	< 0.01
Wet season	1.82	0.51	3.6	< 0.01
Livestock density	-0.10	0.02	-3.8	< 0.01
Wet season x livestock density	-0.02	0.03	-0.9	0.03

Dry season was used a reference level for categorical variable of season.

Table 2
Model selection results for estimation of factors affecting group size of mountain nyala (*Tragelaphus buxtoni*) in the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia. We present results of the top two ranked models that have AICcWt > 0.002, although 21 subset models were considered.

Model structure	AICc	Delta AICc	AICcWt	Deviance
Livestock density + visibility	811.74	0.00	0.98	0.74
Livestock density + NDVI	822.29	10.55	0.1	0.80

(AICc: Reported Akaike's Information Criterion, Delta AICc: difference between model AICc and the minimum AICc, and AICcWt: Akaike's model weight and Deviance: proportion of deviance explained by the model).

Table 3
Parameter estimates of the best model explaining mountain nyala (*Tragelaphus buxtoni*) group size in the in the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia (AIC = 782.85).

Effects	Estimate	SE	t-value	P value
Intercept	7.45	0.36	20.37	< 0.01
Livestock density	-0.40	0.08	-4.8	< 0.01
Closed habitats	-1.5	0.35	-4.9	< 0.01

Open habitat type was used as a reference level for visibility categorical variable

Livestock density was found to be strongly correlated with mountain nyala group sizes, with an observed negative relationship between the two. This is of conservation concern because small group size may negatively affect reproduction and survival and hence the species' population dynamics (Wilson et al., 2020). Livestock density currently exceeds mountain nyala density by 51:1 in the study sites (Ejigu Alemayehu Worku, unpublished. data), and the high livestock densities may threaten the mountain nyala population both by direct disturbance and by adversely affecting the habitat quality through overgrazing. The presence of livestock may also reduce access to shared resources to a level below what is required to sustain larger mountain nyala groups, and with increasing spatial overlap, the possibility for exploitative competition increases (Atickem and Loe, 2014). This is consistent with previous studies

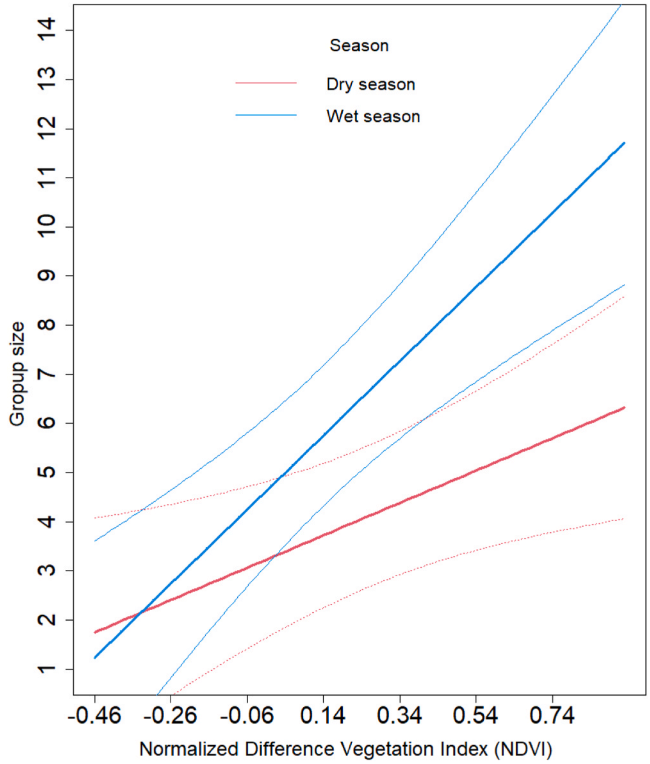

Fig. 6. Predicted mean group size (with 95% confidence interval) of mountain nyala (*Tragelaphus buxtoni*) in dry (solid red line) and wet (dotted blue line) seasons in relation to normalized difference vegetation index (NDVI). Results obtained from a fixed effect model of data from the Arsi Mountains National Park, Munessa-Kuke Controlled Hunting Area and Muktar Mountain Forest Reserve, Ethiopia.

showing that mountain nyala avoid areas with high livestock grazing pressure (Atickem and Loe, 2014; Gebre Kidan, 1996), and the presence of livestock may prevent the mountain nyala from using optimal habitats (Atickem and Loe, 2014; Atickem et al., 2011; Mamo and Bekele, 2011; Tadesse and Kotler, 2013).

The presence of livestock is also a common conservation threat in most other protected areas in Ethiopia (Aerts et al., 2004; Atickem and Loe, 2014; Mamo and Bekele, 2011; Stephens et al., 2001; Tessema et al., 2010; Wassie et al., 2009), and the threats to mountain nyala conservation are thus similar to those faced by wildlife in other parts of the country (Mamo and Bekele, 2011). The detrimental impact of livestock grazing on group size identified in our study, and the exploitive competition between mountain nyala and livestock reported by Atickem and Loe (2014), constitute evidence that if the current practices of livestock grazing are not managed, it will significantly impact the conservation of mountain nyalas and other wildlife in the long run. The seriousness of the concern is supported by previous studies, which have found that the presence of livestock negatively affects the vegetation structure and composition of the plant community for mountain nyala by reducing vegetation cover, height, and plant diversity and increasing the proportion of unpalatable plant species (Fial et al., 2011; Mamo and Bekele, 2011), ultimately affecting forage availability for the mountain nyala.

Our study found that group sizes in mountain nyala vary across the study sites, with larger groups in areas with high forage productivity, as measured by NDVI. The larger group sizes observed in areas with high NDVI suggest that enhanced food availability reduces resource competition between group members, and forage availability is known to limit the size of groups in many ungulates across different landscapes (Chiyo et al., 2014). Large group sizes were also more common during the wet season when food availability was high than in the dry season. We note that the negative effect of livestock density on mountain nyala group size was independent of the positive effect of forage productivity as measured by NDVI, suggesting that the impact of livestock is not purely due to its negative effect on food availability. We propose that disturbance associated with livestock grazing may also have a direct negative effect on gregariousness by breaking of larger groups. Studies on other ungulates reported similar trends that livestock presence and associated herd practices negatively affect group size as a result of competition for shared resources (Bagchi et al., 2004; Isvaran, 2007; Jhala and Isvaran, 2016) and associated disturbances (Namgail et al., 2007).

Moreover, group size increased with habitat openness: small groups are more common in closed habitats and larger groups in open habitats, where they have been observed avoiding areas of high livestock grazing intensity (Evangelista et al., 2007). Smaller group size in closed habitats agrees well with previous studies, e.g. Thaker et al. (2011) on African ungulates and Isvaran (2007) on the Indian blackbuck (*Antilope cervicapra*). Open habitats are well-known to be associated with a switch from concealment to safety-in-numbers antipredator strategies in ungulates (Caro et al., 2004; Jarman, 1974). This can be explained by the difficulty of hiding to avoid detection in open habitats, which favors joining groups where vigilance can be shared, thereby improving predator detection and/or increasing the time available for foraging (Creel et al., 2014; Pulliam, 1973).

In conclusion, our research identifies important predictor variables determining group size in mountain nyala and provides a baseline for monitoring and management of the species. Group size is reduced by livestock density and increased by habitat openness and forage productivity, hence increasing during the wet seasons. In particular, the negative impact of livestock presence on sociality in mountain nyala is a concern because of the likelihood that it may have adverse consequences for population fitness e.g. by affecting survival due to increased predation risk and reproductive success by interfering with the breeding system. Such possible fitness consequences and their impact on mountain nyala population performance would benefit from detailed investigation in future studies, as would the potential decline in fitness due to decreased foraging access (Namgail et al., 2007). Our study shows how studies of social behavior, by elucidating adaptive strategies, can provide helpful information for conservation management of ungulates by disentangling the effect of livestock presence. The livestock encroachment into the protected areas demonstrates a disregard for grazing laws, which is systemic throughout the community, and it has caused the mountain nyala habitat to shrink both in quality and quantity. The mountain nyala is an endangered flagship species, the conservation of which would promote the conservation of the entire ecosystem. The protected areas (i.e., national parks, Controlled Hunting Areas and forest reserves) should be protected from overgrazing, and we propose three recommendations for effective mountain nyala conservation:

1) Educational programs to promote effective enforcement of laws and regulations to control the high livestock grazing intensity.
2) Support for law enforcement to reduce the frequent incursions by the local people with their livestock which cause severe disturbance.
3) Long-term monitoring of mountain nyala population structure and dynamics to effectively conserve and manage the species.

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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.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02546.

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