



Full Length Research Article

DEMOGRAPHY AND POPULATION DYNAMICS OF MOUNTAIN NYALA (*Tragelaphus buxtoni*)
BEFORE ITS POPULATION CRASH IN 1991 IN THE BALE MOUNTAINS NATIONAL PARK,
ETHIOPIA

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ABSTRACT

This study was conducted to assess demography and dynamics of mountain nyala (*Tragelaphus buxtoni*) in relation to habitats/vegetation, slope, seasons, altitude. The data were collected in 1984 eight years before population crash of *T. buxtoni* in 1991 in Bale Mountains National Park. Sample total count method was used to survey the population in three sites where the species known to be abundant in the northern part of the Park. The sample total count of mountain nyala numbers were 10,862 (including 634 of unidentified individuals in to age and sex categories) of which 8,679, 1,349 and 834 were observed from Gaysay, Adelle/Amacho and Dinsho/Gojera study sites respectively. The total population estimate of the species including counts outside the three sites were 2400 individuals. The total number of observed among the sites were significantly different ($df = 2, F = 4.886, P < 0.01$), with the highest number of observation was made in Gaysay grassland site (8,679). The overall male to female sex ratio of the species was 1:2.7. Sex ratios among different habitats/vegetation types were significantly different ($df = 9, F = 2.112, P < 0.05$). Higher proportions of females per male were observed in montane grassland (15.0) followed by *Helichrysum* herb (13.0) habitat types; and the least was observed in *Hagenia* woodland (3.0) habitat. The overall mean group size or numbers of the species was 8.33, and mean group sizes among the sites were significantly different ($df = 2, F = 4.962, P < 0.001$). Thus, the grassland habitat had the biggest group sizes of mountain nyala than the forested habitats. Similarly, group size among different vegetation/habitat types were significantly different ($df = 9, F = 5.373, P > 0.001$), with higher group sizes were recorded in Open Grassland (11.52) followed by *Helichrysum* herb (10.37); while the lowest was recorded in *Juniperus* Woodland (5.00). The average age composition of the species was dominated by adults with a proportion of adults (41%), sub-adults (26%), juveniles (25%) and calves (8%). High proportion of adults in the present study could indicate higher degree of survival of sub-adults. Age compositions across the study sites were not significantly different except for calves ($df = 2, F = 2.191, P < 0.05$). But, the proportions for all age groups were significantly different across the vegetation/habitat types ($df = 9, P < 0.05$). Calves productivity was 0.16 calves per adult female (or 16 calves per 100 adult females); while juvenile mean productivity was 0.54 (or 54 juveniles per 100 adult females). Productivity of both calves and juveniles were significantly different across months (calves: $df = 11, F = 7.173, P > 0.001$; juveniles: $df = 11, F = 5.098, P > 0.001$), with the highest calves and juveniles productivities were recorded in the months of November and March respectively. Total number of mountain nyala observed among different altitudes showed no significance differences ($df = 26, F = 1.339, P > 0.05$). More than 95% of the species observed were within the narrow altitudinal ranges between 3100 and 3200 in their habitat. The species number showed significance difference among the slope categories ($df = 2, F = 13.312, P < 0.001$). Mountain nyala population reduced more than by half in the past three decades, and thus needs focused conservation attention to reverse the trend. Findings of this study could serve as yardsticks to make comparison against future research findings on the species.

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INTRODUCTION

The mountain nyala (*Tragelaphus buxtoni*) was brought to the attention of the scientific community in 1908 by Major Ivor Buxton (Lydekker, 1911), and its extensive range within the Bale Mountains was only confirmed in 1963 (Brown, 1969).

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The species belongs to the spiral-horned family of Bovidae (Genus *Tragelaphus*), and is endemic to Ethiopia and distributed in South-Eastern highlands of Ethiopia (Sillero-Zubiri, 2008). This species has no recognized subspecies or synonyms (Wilson and Reeder, 1993), and there are no records of the animals in captivity (Hillman, 1986a). The International Union for the Conservation of Nature (IUCN, 2002) designated the conservation status of the animal as endangered in 2002. The species is largely found in the Bale

Mountains, one of the few remaining forested landscapes in Ethiopia. The habitat range of mountain nyala (*T. buxtoni*) has become increasingly fragmented and used by the increasing human and livestock populations (Stephens *et al.*, 2001, and Yosef and Afework 2011). By the early 1970s, Bale Mountains National Park (BMNP) was established to protect the mountain nyala and the region's unusually high concentration of endemic fauna and flora (Waltermire 1975). The mountain nyala, is a relatively understudied (Shuker 1993; Hillman, 1993 and Bekele, 1982) antelope, unlike its closest relatives, such as the greater kudu (*Tragelaphus strepsiceros*) and nyala of SE Africa (*Tragelaphus angasii*). Only few demographic studies have been conducted on the mountain nyala for long period of time since its discovery by scientific community. The first formal survey on the species was done 45 years ago (Brown 1969), and after long pause, two relatively recent studies were made in small isolated sub-populations in BMNP (Refera and Bekele 2004, and Yosef *et al.*, 2010, and Yosef *et al.*, 2012). The first formal study of the mountain nyala, and arguably the most comprehensive, was conducted by Leslie Brown who explored the Bale Mountains in November, 1963, and February and March, 1966 (Brown 1969).

During these years, the Bale Mountains had considerably less number of people and livestock than today and from Brown's description, mountain nyala populations and available habitat were largely undisturbed by humans. His observations led him to believe that there was no immediate threat to the species (Brown 1969), and the mountain nyala was removed from the International Union's for Conservation of Nature (IUCN) List of Endangered Species from 1969 to 1975. However, these days habitat fragmentation caused by human settlement and agricultural cultivation has negatively affected the animals' potential to inhabit its suitable range (Stephens *et al.*, 2001, Yosef and Afework, 2011, and Evangelista *et al.*, 2012). Since 2000, some additional populations have been identified throughout the Bale Mountains (Evangelista *et al.*, 2007, 2008). Although new studies on the mountain nyala are emerging, there still remain large information gaps that restrict effective management and conservation of the species. In particular, recent demographic studies on mountain nyala by Yosef *et al.* (2010) occurred in northern part of the Park in relatively small area, but in terms of mountain nyala numbers, the area has highest concentration of the population as compared to rest of the species habitat ranges.

The area includes the Gaysay Valley and Adelay forests, and a fenced enclosure that surrounds the park headquarters. While these are important conservation area for the mountain nyala, the areas were surrounded by settlements and agriculture (Yosef and Afework 2011). A number of individuals were observed in relatively isolated areas of Dinsho Sanctuary, Gaysay/Adelay areas, Web Valley and the highlands in the central part of the Bale Mountains National Park. Together, on average they harbor about 900 mountain nyala (Yosef *et al.*, 2010, Atickem *et al.*, 2011), from world estimates of not more than 2000 (Yosef 2007). However, there is mounting concern that the carrying capacity these areas have reached a dangerous threshold and conditions that would have adverse effects on the local mountain nyala populations. Counts conducted by Yosef *et al.* (2010) found that mountain nyala average density in Gaysay and Adelay reached 21/km², while it reached a critical level of 129/km² at the park headquarters.

These numbers are alarmingly high when compared to Brown's (Brown, 1969) estimates (1.5/km² to 6.9/km²). High density of wild animals and their confinement to a small area poses a number of risks including loss of food resources, reduction in productivity and genetic diversity, and potential transmission of disease (Keller *et al.*, 2007). Small populations are more vulnerable to human interference than larger groups (Pullin 2002), so the future viability of these isolated individuals is bleak. As Primack (2002) noted, the long term persistence of small and isolated subpopulations of a given species is limited. The limitations of a species' potential for dispersal and colonization caused by habitat fragmentation have been widely reported (Kingdon, 1989; Rochelle *et al.*, 1999; Debinski and Holt 2000; Trombulak and Frisell, 2000; Primack, 2002, Pullin, 2002). To successfully manage and conserve any wildlife species, a basic understanding of the population's structure and group dynamics are required (Hebblewhite *et al.*, 2003; Taylor *et al.*, 2005; Bender 2006; Mech 2006). Gathering demographic information on mountain nyala in its preferred habitats can be a daunting task.

The elusiveness of the species is well documented by early trophy hunters and museum collectors (Sanford and LeGendre 1930; Baum 1935), and its partiality for rugged terrain and dense vegetation prohibits most standard observation methods. Mountain nyala have been recorded in all habitats in the park, except in the southern low lying Harena Forest, and northern part of the Park harbors the largest population of the species (Hillman 1986a). Therefore, this study is the first of its kind to analyze formally collected intensive data in 1980's. Population of mountain nyala had been crashed in 1991 due to widespread lowliness happened during the overthrow of the previous regime in Ethiopia (Woldegebriel 1996; Shibru 1995). Then in 1991 formerly abundant and widespread mountain nyala population in the Park abruptly declined to less than 200 individuals from an estimated number of more than 2,200 before 1991 incidence in the Park (Woldegebriel 1996). The dramatic drop in population at the end of 1990's was mainly due to mass killing, habitat disturbance by local people and then followed by emigration of the species (Woldegebriel 1996).

Moreover, increasing livestock and human population pressure have led to massive destruction of wildlife habitats as well as a drastic reduction in numbers of wildlife in the Protected Areas across Ethiopia (Shibru 1995). Therefore, this study tried to investigate mountain nyala's demographic parameters, abundance and dynamics before its population crash in 1991 in the BMNP by analyzing data collected in 1984. Specifically, the study tried to analyses how demographic parameters of mountain nyala in different locations, months, seasons, habits/vegetation, altitudes, terrain (slope) varies in the northern part of the Park. This study was the first of its kind with detailed formal investigation on demography and population dynamics of mountain nyala since any studies on the species begin.

MATERIALS AND METHODS

Study area and study animal

The Bale Mountains National Park (BMNP) is located 400 km southeast of Capital City in south-eastern Ethiopia. The park

area is encompassed within geographical coordinates of 6°29' – 7°10'N and 39°28' – 39°57'E. The Park encompasses approximately 2,200 km² of mountains and forest area and covers the largest area above 3000m *asl* in Africa. The park includes an afro alpine plateau over 3500m *asl* and a major section of moist tropical forest, the second largest in Ethiopia. The three main study sites that are located in the northern part of the Park named as: Dinsho/Gojera, Adelle/Amacho and Gaysay sites. Only male mountain nyala possess horns typical of the spiral-horned antelopes. The male horns are spectacular and can grow as long as 85cm, making 2 graceful twists. An adult male may weigh over 300 kg when mature at 4-5 years (often within the range of 180 - 300 kg). Each individual is uniquely patterned with spots and stripes. The female adult weighing 150 - 200 kg (Kingdon, 1997).

Methods of data collection

Survey of mountain nyala population following regular walking tracks and drive ways (lines) was made in 1984 in 19 different locations/sites of the park. Out of these areas, total sample counts were made only in three sites, where the species commonly known to be abundant in the Park, and the data from these sites were considered for analysis. The three sites were Dinsho/Gojera forested site, Adelle/Amacho forested site, and Gaysay montane grassland site. Each site was divided into a number of blocks of areas based on the abundance of mountain nyala and their distributions and major vegetation types in the area so as to avoid double counting of animals.

Dinsho/Gojera forested site was divided into three blocks; and Adelle/Amacho forested site and Gaysay montane grassland site into six blocks each. In each block maximum efforts were made to search and locate all mountain nyala as much as possible so as to have total count (Norton-Griffith 1978; Melton 1983; Caughley and Sinclair 1994; Sutherland 1996; and Wilson *et al.*, 1996) of mountain nyalas. In each block two observers and one recorder were assigned to search and count mountain nyala by walking from the north to the south direction of each block. Counting was carried out simultaneously in all blocks. The survey was conducted using vehicles, horseback and on foot along the walk way lines and forest roads that were established to monitor the Park.

The data were kept using excel spreadsheet, and latter imported to SPSS statistical software. They survey were carried out at every 1st and 15th day in each month, using the same techniques of data collection. During a given day, observations were made beginning from 6:00 am up to 18:00 pm. Data collection was carried out through direct observation of free-ranging animals using 7x35 magnification power binoculars. All sightings were made at a perpendicular angle from the walking and/or drive lines (Smith 1979; Burnham *et al.*, 1980; Southwell and Weaver 1993; Plumptre 2000). Perpendicular angles were determined using Silva Compass.

All mountain nyala observed during the census were sexed (male or female), and their age was assessed according to their coat color and body size, along with horn shape for males. Accordingly, they assigned to one of the following four age categories: Adult (animals of 2 years and older), Sub-adult (animals between 1 and 2 years), Juvenile (animals between 6 months and 1 year), and Calves (animals younger than

6 months). The assignment of age range based partly on literature cited for the species (Valden and Lergen 1992; Gebrekidan 1996; Kingdon 1997) and for closely related species of *Tragelaphus strepsiceros* (Annighofer and Schutz, 2011). Four social groupings were also assigned: Males only group (only male containing group), Females only group (Only female containing group), Calf containing group (group that has more than 2 individuals and containing calf or calves), and Ordinary or No calf group (groups with no calf or calves). All sightings of the animals were also noted against slope gradients, vegetation types, altitudes, where the observed animals were actually found. Three slope categories were assigned: Flat (ranges between 0-10%), Moderate (ranges between 11-30%), and Steep (ranges between 31-75%).

Data Analysis

From the 19 different sites/areas of the park where mountain nyala were counted, only counts in three sites were considered for analysis. In estimating total population and altitudinal distribution of the species, all the 19 sites counts were considered. In these three sites totally annual sample count made were 11,496 individuals, whereas in the rest of 16 sites only 338 individuals were counted. The three sites were Dinsho/Gojera forested site, Adelle/Amacho forested site, and Gaysay montane grassland site. The statistical software SPSS IBM version 19 was used to analyze the data. Descriptive statistics was used to calculate the mean and standard error. Selected demographic variables were compared across months of the year, vegetation types, time of the day and terrain type using one-way ANOVA to obtain *F* and *P* values.

RESULTS

Total numbers of mountain nyala

The total numbers of mountain nyala estimated in 1984 were 2,400 individuals considering all the 19 localities in the Park including the three study sites in the northern part of the Park (Gaysay, Adelle/Amacho and Dinsho/Gojera). The sample total count of mountain nyala numbers were 10,861 (including 634 of unidentified individuals in to age and sex categories) of which 8,679, 1,349 and 834 were observed in Gaysay, Adelle/Amacho and Dinsho/Gojera study sites respectively. In the rest of 16 localities across the Park only 338 individuals were counted. The total number of mountain nyala observed among the three study sites were significantly different ($df = 2$, $F = 4.886$, $P < 0.01$), with the highest number was observed in Gaysay grassland site (8,679). From the total sample count, greater proportions animal count were made from Open Grassland (36%) followed by *Artemesia* Grassland (30%), and the least count was from *Hygenia/Juniperus* Woodland (2%).

Sex relations (Sex-ratios) of mountain nyala

The overall female (♀) to male (♂) sex ratio of the species was 1:2.7. Sex ratios among different habitats/vegetation types were significantly different ($df = 9$, $F = 2.112$, $P < 0.01$). Higher proportion of females per male were observed in Open Grassland (♂3.0) followed by *Artemesia* Bush (♂2.9) habitat types; and the least was observed in *Hagenia/Juniperus* Woodland (1.4) habitat/vegetation type.

Diurnal and annual observed patterns in abundance of mountain nyala

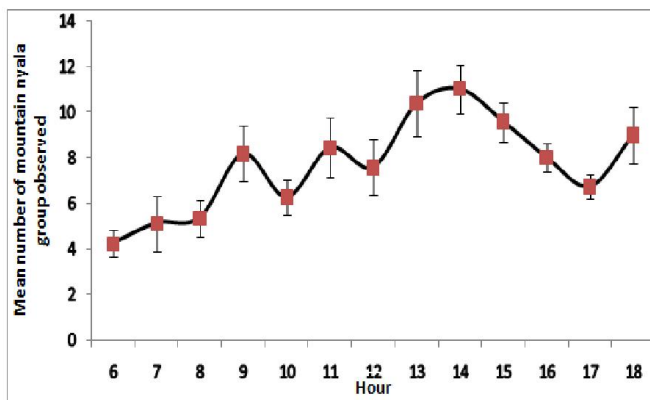


Figure 1. Diurnal changes of mean group sizes across hours of the day. Error bars are standard error values (n = 10,861)

Mean group sizes (±SE): [6: 4.26^a (0.59)], [7: 5.14^{ab} (1.22)], [8: 5.38^{ab} (0.80)], [9: 8.18^{ab} (1.22)], [10: 6.28^{ab} (0.79)], [11: 8.45^{ab} (1.31)], [12: 7.59^{ab} (1.22)], [13: 10.39^{ab} (1.45)], [14: 11.03^b (1.09)], [15: 9.6^{ab} (0.86)], [16: 8.03^{ab} (0.65)], [17: 6.75^{ab} (0.51)], [18: 9.01^{ab} (1.22)].

Mean values with different superscript letters were significantly different from each other (Fig. 1).

Mean group sizes (numbers) of mountain nyala observed among hours showed significance differences (df = 12, F = 2.628, P < 0.01), with the highest number of mountain nyala was observed in the afternoon around 14:00 O'clock or 2:00pm, while the lowest record was early in the morning at 6:00 O'clock (Fig. 1). The Pearson Correlation showed that mountain nyala abundance increases as time increases from early morning of 6:00 am towards late afternoon around 18:00 pm, the correlation was positive (r= 0.042) but not significant (P > 0.05).

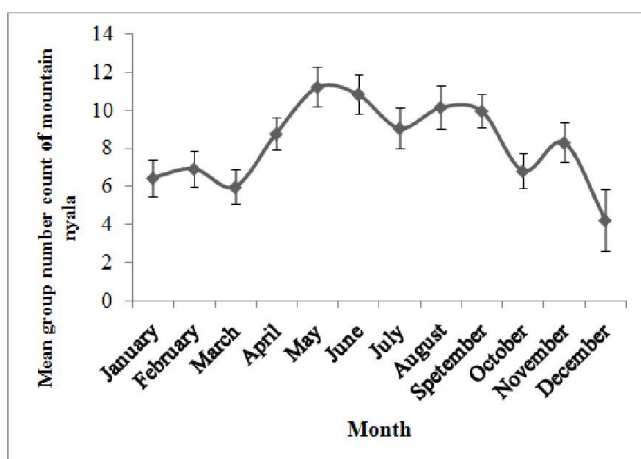


Figure 2. Annual changes of mean group sizes observed across months of the year with error bars at 95% CI of the mean (n = 10,861)

Mean group sizes (±SE): [Jan. 6.44^{abc} (0.98)], [Feb. 6.93^{abc} (0.96)], [Mar. 5.97^{ab} (0.92)], [Apr. 8.78^{abc} (0.85)], [May. 11.22^c (1.04)], [June. 10.85^{bc} (1.04)], [July. 9.06^{abc} (1.08)], [Aug. 10.16^{bc} (1.13)], [Sept. 9.97^{bc} (0.89)], [Oct. 6.82^{abc} (0.91)], [Nov. 8.30^{abc} (1.05)], [Dec. 4.23^a (1.62)].

Mean values with different superscript letters were significantly different from each other (Fig. 2).

Age class compositions and proportions of mountain nyala

The average age composition (proportion) of the species consisted of: adults (41%), sub-adults (26%), juveniles (25%) and calves (8%). The age-structured more or less appeared as inverted pyramidal shape having fewer proportion of calves at the bottom, nearly similar proportions of sub-adults and juvenile (young of a year) at the middle, and relatively larger proportion of adults at the top of the inverted pyramid. Age compositions across the study sites were not significantly different except for calves (df = 2, F=2.191, P<0.05). But, age compositions were significantly different across the vegetation/habitat types (df = 9, P<0.05) (Table 1).

Group sizes and social group types of mountain nyala

The overall mean group size or numbers of mountain nyala was 8.33, and mean group sizes among the study sites were significantly different (df= 2, F = 4.962, P < 0.001), with group sizes of 8.91, 7.33 and 6.50 were observed in Gaysay, Dinsho/Gojera and Adelle/Amacho sites respectively. Thus, the grassland habitat had biggest group sizes of mountain nyala than the other forested habitats. Similarly, group sizes among different vegetation/habitat types were significantly different (df = 9, F=5.373, P>0.001), with higher group sizes were recorded in Open Grassland (11.52) followed by *Helichrisum* Bush (10.37); while the lowest was recorded in *Juniperus* Woodland (5.00) (Table 2).

Herds containing largest number of mountain nyala were observed at *Hagenia* Woodland (96), followed by Open Grassland (83), while least herd size was recorded in *Hypericum* forest (22) habitat type (Table 2). Mean group numbers of mountain nyala among the different vegetation/habitat types showed significance differences (df = 9, F =2.566, P <0.05). Similarly, Group sizes among months of a year showed significance differences (df = 11, F = 3.810, P <0.001). Largest herd size was observed in the month of May (78), while the lowest in December (33) (Table 3). The group sizes tend to increase from March to September, which is mainly in the rainy season period, and decrease afterwards in most of the dry season (Fig. 2).

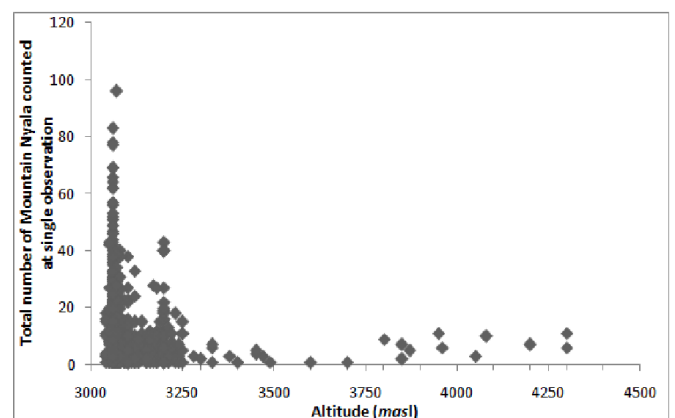


Figure 3. The distribution of Mountain Nyala across different altitudes of the study area (n = 11,834, including 16 localities)

Total number of mountain nyala observed among different altitudinal ranges showed no significance differences (df = 26, F = 1.339, P > 0.05).

Table 1. Age compositing and structure of mountain nyala in different vegetation/habitat types (n = 10,861)

Vegetation/habitat types	Adult	Sub adult	Juvenile	Calf	Sample size(n)
	n (%)	n (%)	n (%)	n (%)	
Open Grassland	1,850(47.5)	958(24.6)	829(21.3)	257(6.6)	3894
Artemesia Bush	1,560(47.3)	736(22.3)	802(24.3)	201(6.1)	3299
Hagenia Woodland	815(47.2)	422(24.4)	380(22.0)	111(6.4)	1728
Hypericum Bush	202(46.5)	92(21.2)	115(26.5)	26(5.8)	435
Swamp Grassland	211(48.1)	97(22.0)	93(21.3)	38(8.6)	439
Helichrysum Bush	148(47.5)	65(20.9)	82(26.3)	16(5.4)	311
Juniperus Woodland	148(51.1)	63(21.7)	68(23.5)	11(3.7)	290
Hypericum Forest	93(53.8)	40(23.4)	30(17.5)	9(5.3)	172
Montane Grassland	77(48.7)	38(24.1)	30(19.0)	13(8.2)	158
Hagenia/Juniper Woodland	77(56.7)	24(17.9)	24(17.9)	10(7.5)	135

All age categories were significantly different (df=9, P<0.05) across habitat types (Table 1).

Table 2. Mean group size or number (±SE) of the mountain nyala in different vegetation/habitat types (n = 10,861)

Vegetation/ Habitat types	Largest herd number	Mean group size	Mean group size across age categories of mountain nyala						
			Male adult	Female adult	Male sub- adult	Female sub- adult	Male Juvenile	Female Juvenile	calf
Open Grassland	83	11.52 ^f (0.79)	0.90 (0.10)	4.37 (0.30)	0.84 (0.08)	1.90 (0.16)	0.86 (0.08)	1.50 (0.14)	0.73 (0.07)
Helichrysum Bush	42	10.37 ^f (1.73)	0.43 (0.22)	3.97 (0.78)	0.47 (0.18)	1.47 (0.38)	0.80 (0.24)	1.63 (0.40)	0.50 (0.15)
Artemesia Bush	64	8.11 ^e (0.49)	0.60 (0.07)	2.71 (0.17)	0.51 (0.06)	1.05 (0.09)	0.54 (0.06)	1.16 (0.10)	0.43 (0.05)
Hagenia Woodland	96	7.03 ^d (0.6)	0.70 (0.09)	2.54 (0.22)	0.70 (0.08)	0.98 (0.12)	0.69 (0.10)	0.82 (0.08)	0.44 (0.07)
Hypericum Bush	43	7.02 ^d (1.06)	0.56 (0.12)	2.69 (0.37)	0.52 (0.09)	0.97 (0.21)	0.65 (0.14)	1.21 (0.26)	0.40 (0.11)
Montane Grassland	27	6.87 ^d (1.58)	0.30 (0.13)	3.04 (0.57)	0.48 (0.20)	1.17 (0.38)	0.39 (0.15)	0.91 (0.34)	0.57 (0.25)
Swampy Grassland	23	6.55 ^d (0.72)	0.31 (0.09)	2.79 (0.33)	0.31 (0.09)	1.10 (0.17)	0.36 (0.08)	1.01 (0.18)	0.55 (0.10)
Hagenia/Juniperus Woodland	27	5.40 ^c (1.13)	1.28 (0.40)	1.76 (0.29)	0.44 (0.21)	0.52 (0.15)	0.32 (0.14)	0.64 (0.16)	0.40 (0.20)
Hypericum Forest	22	5.09 ^c (0.86)	0.88 (0.29)	1.82 (0.33)	0.53 (0.18)	0.65 (0.16)	0.24 (0.09)	0.65 (0.17)	0.26 (0.10)
Juniperus Woodland	27	5.00 ^c (0.71)	0.66 (0.17)	1.74 (0.33)	0.38 (0.14)	0.64 (0.14)	0.26 (0.07)	0.84 (0.17)	0.17 (0.06)

Mean values within the same column given different superscript letters were significantly different from each other (Table 2).

Table 3. Mean group and largest herd sizes observed across months of the year (95%CI)

Months	No ind. observed	Mean group size	Std. Error	95% Confidence Interval for Mean		Max. herd size
				Lower Bound	Upper Bound	
January	117	6.44	0.680	5.10	7.79	40
February	123	6.93	0.817	5.31	8.54	66
March	134	5.97	0.501	4.98	6.96	36
April	158	8.78	0.788	7.22	10.33	69
May	105	11.22	1.355	8.53	13.91	78
June	104	10.85	1.493	7.89	13.81	96
July	96	9.06	1.134	6.81	11.31	62
August	88	10.16	1.264	7.65	12.67	69
September	141	9.96	1.118	7.75	12.17	83
October	135	6.81	0.713	5.41	8.22	49
November	102	8.30	1.052	6.22	10.39	57
December	43	4.23	0.796	2.63	5.84	33

Table 4. Mean (±SE) group sizes of different age groups of mountain nyala across slope gradients (out of the total 10,862 observed, 5,624, 3,828 and 1,410 mountain nyala were from Flat, Moderate and Steep slope categories respectively)

Age category of mountain nyala	Slope category					
	Flat		Moderate		Steep	
	Mean	SE	Mean	SE	Mean	SE
Total mean	9.32 ^b	0.50	8.83 ^b	0.49	5.36 ^a	0.37
Male adult	0.70	0.06	0.69	0.07	0.64	0.08
Female adult	3.42	0.19	3.13	0.17	1.99	0.15
Male sub-adult	0.63	0.05	0.71	0.06	0.40	0.05
Female sub-adult	1.43	0.10	1.23	0.09	0.70	0.08
Male juvenile	0.66	0.05	0.74	0.07	0.37	0.05
Female juvenile	1.32	0.09	1.13	0.08	0.74	0.07
Calf	0.54	0.05	0.58	0.05	0.28	0.05

Mean values in the same row given different superscript letters were significantly different from each other (Table 4).

group size average was 6.48. The average group sizes of mountain nyala were 9.32, 8.83 and 5.36 in Flat, Moderate and Steep slope categories respectively (Table 4); and the group size in Steep slope was significantly different from the rest of slope categories. The mean social group sizes of different age categories of mountain nyala observed were significantly different ($df = 2, F = 146.968, P < 001$) across the slope gradients (Table 4). From the four social group types considered, steep slope gradient had smaller, except larger males only group size, and significantly different group sizes from flat and moderate slope gradients

while dry season (November – December) average of calves and juveniles were 0.19 and 0.49 respectively.

DISCUSSION

Unlike the population of mountain nyala in Gaysay and the park headquarters, the mountain nyala in the other locations of the study area were much scattered. The population was abundant before its crash in 1991 but since then the population never recovered and gained the status before its crash. Rather, the population drastically reduced

Table 5. The distribution of social group types of mountain nyala in different locations habitats/vegetation types

Habitat/vegetation types	Social groups							
	Calf containing		Females only		Males only		Ordinary/ no calves	
	n	%	n	%	n	%	n	%
<i>Artemesia</i> Grassland	100	27.5 ^c	2	66.0 ^b	48	24.0 ^b	257	33.1 ^b
<i>Hypericum</i> Bush	15	4.1 ^a			8	4.0 ^a	39	5.0 ^a
<i>Hypericum</i> Forest	7	1.9 ^a			7	3.5 ^a	19	2.4 ^a
<i>Helichrysum</i> Bush	7	1.9 ^a	1	33.0 ^a	3	1.5 ^a	19	2.4 ^a
<i>Hagenia/Juniper</i> woodlands	5	1.4 ^a			3	1.5 ^a	17	2.2 ^a
<i>Hagenia</i> Woodland	62	17.0 ^b			61	30.5 ^b	123	15.9 ^b
<i>Juniperus</i> Woodland	9	2.5 ^a			15	7.5	34	4.4 ^a
Montane Grassland	6	1.6 ^a			4	2.0 ^a	13	1.7 ^a
Open Grassland	115	31.6 ^c			39	19.5 ^b	184	23.7 ^b
Swamp Grassland	27	7.4 ^a			3	1.5 ^a	37	4.8 ^a

Percentage values within the same column given different superscript were significantly different (Table 5)

Table 6. Mountain nyala mean productivity (number of calves or juveniles per adult female) for both calves and juveniles per surveyed months of the year

Months	Calves Productivity ¹		Juveniles Productivity ²	
	±SE(95% CI)	(0.11-0.23)	±SE(95% CI)	(0.29-0.44)
January	0.17±0.03	(0.11-0.23)	0.37±0.04	(0.29-0.44)
February	0.14±0.03	(0.08-0.19)	0.56±0.06	(0.45-0.67)
March	0.11±0.02	(0.10-0.15)	0.71±0.05	(0.60-0.81)
April	0.13±0.02	(0.10-0.18)	0.66±0.05	(0.56-0.76)
May	0.12±0.03	(0.10-0.17)	0.62±0.06	(0.49-0.75)
June	0.12±0.02	(0.07-0.17)	0.69±0.07	(0.54-0.83)
July	0.10±0.03	(0.04-0.15)	0.48±0.06	(0.36-0.61)
August	0.04±0.02	(0.01-0.07)	0.44±0.04	(0.35-0.52)
September	0.22±0.03	(0.15-0.28)	0.51±0.04	(0.43-0.59)
October	0.23±0.03	(0.16-0.30)	0.41±0.05	(0.31-0.51)
November	0.36±0.05	(0.27-0.45)	0.38±0.05	(0.29-0.47)
December	0.07±0.04	(0.00-0.16)	0.63±0.12	(0.38-0.88)
Total mean	0.16±0.01		0.54±0.02	

¹Total calves divided by adult female; ²Juveniles divided by adult female

Productivity of mountain nyala

Calves productivity was 0.16 calves per adult female (or 16 calves per 100 adult females); while juvenile mean productivity was 0.54 (or 54 juveniles per 100 adult females) (Table 6). Productivity of both calves and juveniles were significantly different across months (calves: $df = 11, F=7.173, P > 0.001$; juveniles: $df = 11, F=5.098, P>0.001$). The highest productivity of calves (0.36; varies between 0.27-0.45 at 95%CI) was recorded in November, while the lowest (0.04; varies between 0.01-0.07 at 95%CI) was in August (Table 6). Relatively higher productivity of calves were observed from September to November, which is in the period before the onset of dry season. In terms of Juvenile productivity, the highest was observed in March (0.71; varies between 0.60-0.81 at 95%CI); while the lowest was recorded in January (0.37; varies between 0.29-0.44 at 95%CI). Relatively higher productivity of juveniles were observed from March to June (Table 6). Mean productivity of calves and juveniles in wet season (March – October) were 0.13 and 0.57 respectively;

from 2400 individuals estimated in this study to between a range of 887 to 965 individuals as it was estimated by Yosef et al. (2010), which showed a reduction in number by 42% in the last three decades. Larger proportion of females than males, with average sex ratio of 2.7♀ to 1♂ was recorded before the population crash than that was reported of an average sex ratio of 2♀ to 1♂ after its population crash (Yosef et al., 2010; Refera and Bekele 2004). Although a skew in sex ratios toward females may increase the number of calves in the population, but this must be balanced against the negative effects of reduced calf condition (Holand, 2002). However, the result of the sex ratios reported in this study not greatly skewed towards females than necessary for reproduction in polygamous population like mountain nyala. Because in polygamous species with a fixed, narrow birth interval, effects of skewed sex ratios may impose limitations concerning a male's ability to fertilize many females within a short breeding season (Ginsberg and Milner-Gulland, 1994; White et al., 2001; Laurian et al., 2000). In addition to the relative proportions of females, what is also important is the spatial

distribution of females during rut may be an important factor influencing the reproductive success of individual males (Holand, 2002). Relatively higher proportion of adult female to male sex ratio of 4.06:1 (95% CI 2.72-6.10:1) were reported by Brown (1969) in the Bale Mountains during the rutting season from November to December in the dry season. In addition to seasonal differences, sex proportion can vary in age, varying levels of population density and stress (Clutton-Brock and Iason, 1986). For related species such as *Tragelaphus strepsiceros* (Annighofer, 2011) and *Tragelaphus scriptus* (Abebayehu, 2012), relatively lower proportion of female to male of 1:1.67 and 1:1.5 were reported respectively. For polygamous animals like mountain nyala larger number of females needed for increased reproduction, and hence pre-crash period, the population had better chance of increased reproduction than post population crash period. This may true because the proportion of calves from the total population number was higher before the crash than reported in different periods after its crash in (Yosef 2007; Yosef et al., 2010). Moreover, female ungulates usually produce and raise offspring alone, and they are therefore obvious the most important component with regard to population dynamics (Mysterud et al., 2002).

The majority of previous studies on mountain nyala reported that the sex ratios of females to males were nearer to 2:1 (Brown 1968; Referal and Bekele 2004; Yosef et al., 2010), these estimates were closer to those reported (1.67:1) for hunted populations of closely related kudu species (Annighofer and Schutz, 2011). The average group size observed in this study was 8.22 (varies between 6.29 and 10.16 at 95%CI). Estimates closer to this study were reported by Refera and Bekele (2004) and Yosef et al. (2010) which they estimated group size in Gaysay and the park headquarters between 7.9-10.2 individuals and 7.0-12 individuals respectively. Historical accounts of group size in Gaysay were estimated at an average of 5.62 individuals (Brown, 1968) and groups were rarely observed with more than 12 individuals with most group sizes between 4-12 individuals (Maydon, 1925). Wet and/or rainy season between March and October often supports larger group sizes of mountain nyala than dry season between November and February, although the group sizes between seasons were not significantly different (Refera and Bekele 2004; Yosef et al., 2010).

Similar findings were obtained by this study with larger group sizes of 7.82 were observed in wet season, while lower group sizes average of 6.48 was in dry season. This happen presumably because, during the dry season the Open Grassland habitat, which was the most utilized habitat type by the species (Yosef et al., 2012), naturally dries early in dry season and becomes less palatable, and accordingly supports fewer mountain nyala than it supports during the wet season. Larger herd sizes of mountain nyala that congregate, sometimes up to 96 individuals, were commonly observed before population crash of the species in 1991 than reported by studies that were made afterwards (Refera and Bekele, 2004; Yosef et al. 2010). The average age composition (proportion) of the species observed in this study consisted of: adults (41%), sub-adults (26%), juveniles (25%) and calves (8%). However, Yosef et al. (2010) reported highly reduced proportions of juveniles and calves, and increased proportion of adults, which showed 58% adults, 25% sub-adults,

9% juveniles and 5% of calves. From the 252 mountain nyala Brown were identified from both expeditions, 37 (14.7%) were males, 170 (67.8%) were females, and 44 (17.3%) were calves (Brown, 1969). Age structure is important since young and old individuals typically have lower survival rates than prime-aged individuals (Caughley, 1966; Gaillard et al., 1998, 2000), and for a given age, males frequently have lower survival rates than females (Coulson et al., 1997; Clutton-Brock et al., 1997). With regard to age composition, common perception is that, large proportion of young indicates an increasing in population (Abebayehu and Tilaye, 2012; Dereje, 2011). However, Romano (1991) argues that this may not be necessarily true. Lower proportion of adults compared to young could indicate low survival of adults, for example, as a result of selective hunting by people. Therefore, populations with such age structure could be declining in actual fact rather than increasing (Abebayehu and Tilaye, 2012). Accordingly, the high proportion of adults in the present study could indicate higher degree of survival of sub-adults.

Higher average productivity of calves (0.16) was observed in this study, which was double of the estimates made by similar studies on the species (Yosef et al., 2010). Yosef et al. (2010) reported productivity estimates for calves to be 0.08 and 0.09 for Gaysay/Adellay and the park headquarters respectively. For juveniles, this study observed about three times larger productivity than similar studies made on the species. Yosef et al. (2010) reported productivity of 0.19 and 0.17 for Gaysay/Adellay and the park headquarters respectively. However, the productivity reported by this study was closer to historical records from Brown (1968), who estimated productivity across the Bale Mountains between 0.25 - 0.33 calves/adult female. Brown (1968) also observed higher productivity during the calving season although the exact calving time period and duration of mountain nyala calving season is still uncertain and is likely to vary spatially (Evangelista, 2007, Yosef et al., 2010). Mean productivity of calves and juveniles in wet season were 0.13 and 0.57 respectively; while dry season average of calves and juveniles were 0.19 and 0.49 respectively.

Lower productivity of calves in wet season was presumably because calves born in wet season would not probably big enough to be observed in the wet season than dry season. The higher productivities of calves and juveniles reported by this study from the data collected before population crash of mountain nyala in 1991 could be the main causes for higher population numbers observed before its population crash. Because, variation in proportion of females breeding (Reimers, 1983, Gaillard et al., 1992), twinning rates (Andersen and Linnell, 1997; Keech et al., 2000), and calving dates (Festa-Bianchet, 1988) may have a considerable impact on population growth rates. More than 95% of the mountain nyala observed this study were with an altitudinal range between 3100 to 3200 m *asl*, which shows that the species had narrow altitudinal preference that make the species vulnerable if habitats or vegetation in this range would be affected by human disturbances and livestock grazing. Unsurprisingly due to anthropogenic pressures in the species habitat areas, many individuals of the species were pushed out of their preferred habitats. Divergent to the findings of this study, Kingdon (1997) has noted wider altitudinal ranges occupancy by the species from 3,000 up to 4,200m *asl* with

strugglers occur as low as 1,800m. Within the occupied altitudinal range, mountain nyala tend to dominate low and moderate slope unlike other endemic antelope of Ethiopia, which prefers steep slope enclave (Kefeyalew *et al.*, 2011). Observation of mountain nyala in higher proportions but in decreasing order from Open Grassland, *Artemesia* Bush to *Hagenia* Woodland habitats, could show that these habitat or vegetation types were commonly used by the species, and could be inferred as the most utilized by the mountain nyala (Yosef *et al.*, 2012). Similar results were noted by Kingdon (1997), high latitude valley-bottom grassland, woodlands (mostly *Juniper* and *Hagenia*), as heath and bush (dominated by sage brush, *Artemesia* and *Hypericum*) are greater choice for the species. Mountain nyala often tend to conceal and hide themselves in the forests and bushes around them in early hours of the day and their chance of being observed was low. But after noon around 2:00pm their activities reached its peak.

Conclusions

Mountain nyala population was abundant before its crash in 1991, since then the population never recovered and gained the higher abundance before its crash. High proportion of adults in the present study could indicate higher degree of survival of sub-adults. Moreover relatively higher productivity of calves observed in this study than similar recent studies on the species could indicate that higher productivity of mountain nyala before its population crash in 1991. In terms of sex ratios, particularly the proportion of female adults, which actually calves producing age group, were more abundant in the past three decades before the population crash in 1991. This could partly also contributed to the observed higher population numbers of mountain nyala before 1991. Large mammal conservation over large spatial extents is becoming more and more difficult as habitat fragmentation continues subsequent to human population growth. As the mountain nyala population continues to become fragmented, all populations within their geographic range need to be monitored and evaluated. Understanding and managing sub-populations can improve conservation at broad-scales. Future conservation and status evaluation efforts would greatly benefit from delineating and evaluating sub-populations of mountain nyala across its existing range. This study was the first of its kind with detailed formal investigation on demography and population dynamics of mountain nyala since any studies on the species begin. Hence, the findings could serve as yardsticks to make comparison against future research findings on the species.

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