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POPULATION SIZE AND STRUCTURE OF BEISA ORYX AND ITS HABITAT OVERLAP WITH SYMPATRIC SPECIES IN ALLEDEGHI WILDLIFE RESERVE, NE ETHIOPIA

Simeneh Admasu^{1,2*}, Afework Bekele² and Addisu Asefa¹

ABSTRACT: This study was undertaken in Alledoghi Wildlife Reserve, NE Ethiopia, to determine the current population size and structure of Beisa oryx [*Oryx beisa* (Linn. 1758)] and to examine its habitat overlap with two sympatric ungulate species: Soemmering's gazelle [*Gazella soemmeringi* (Cretzschmar 1828)] and gerenuk [*Litocranius walleri* (Brooke 1879)]. Wet and dry season wildlife surveys were undertaken in September 2015 and January 16 along 12 line transects in each of three major habitat types, grassland wooded grassland and bushland. The results showed that estimated population of Beisa oryx in the reserve was 1119 ± 7.8 , 58 ± 1 and 590 ± 7 during the wet season, dry season and pooled seasons, respectively. This population was female dominated during both seasons; males to females ratio remained 1:1.8. However, there was a marked seasonal variation in group sizes of the species: ranging from 1 to 5 and from 4 to 26 individuals in the dry and wet seasons, respectively. Considering habitat type, greater mean group size of oryx was recorded in the wooded grassland habitat than the other two habitat types. Beisa oryx showed stronger preference for wooded grassland habitat during wet season, but for bushland during dry season, possibly implying that, dependent on season, different habitats provide varying level of importance. The minimum habitat overlap among the ungulates was 35% during dry season between oryx and gazelle and maximum was 85% during wet season between oryx and gerenuk. The study has provided valuable information that would help conservation management efforts.

Key words/phrases: Conservation, Group size, Habitat overlap, *Oryx beisa*, Ungulates.

INTRODUCTION

Beisa oryx [*Oryx beisa* (Linn. 1758)] is a large antelope with compact and muscular body, long and patterned ears with a thick neck. Their horns are long, narrow and virtually parallel ridged on the lower half. Horns occur in both sexes and grow up to 75–120 cm long (Kingdon, 1997). Beisa oryx was previously considered as a sub-species of the gemsbok (*Oryx gazelle*),

¹ Ethiopian Wildlife Conservation Authority, P.O. Box 386, Addis Ababa, Ethiopia. E-mail: simeneh2009@yahoo.com; aa.mitiku@gmail.com

² Department of Zoological Sciences, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia. E-mail: afeworksimegn@gmail.com

*Author to whom all correspondence should be addressed

but, based on morphological and genetic analyses, Groves and Grubb (2011) recently classified it as a distinct species.

Historically, Beisa oryx was widely distributed across arid savanna, open scrub and in the semi-desert areas of northern Kenya, south-east Somalia, Ethiopia, Eritrea, Sudan, Djibouti and Uganda. However, the species is currently wiped out from the majority of its historic ranges, such as Sudan, Djibouti and Eritrea (Kingdon, 1997). Aerial survey conducted in 1990's revealed that at least 25,000 individuals of Beisa oryx were thought to exist throughout its entire range, with the largest population (~two-thirds) being recorded from Kenya (Woodfine and Parker, 2011).

In Ethiopia, Beisa oryx used to occur widely along the northeastern, eastern and southern lowlands with altitudes ranging from sea level to 1,700 m. a.s.l. (Yalden *et al.*, 1996; East, 1997). Its distribution in the country ranges from the Awash Valley from Awash National Park northwards to the Danakil region, and in the lower Rift Valley from Omo north and west including Mago and Omo National Parks, Murule and Borena controlled hunting areas (Thouless, 1995; Cherie Enawgaw, 1999; Conservation Development Centre, 2002; EWCO, 2002). It still occurs within most of its former range, but with a declining number because of overhunting and habitat loss (Thouless, 1995; Cherie Enawgaw, 1999). The estimated population of Beisa oryx in Ethiopia is reported to be between 4,000–5,000, with steadily declining population compared to the population size before four decades (East, 1997; Cherie Enawgaw, 2004; Woodfine and Parker, 2011). For instance, the Beisa oryx population in the Awash National Park, where it was considered as a flagship species, has been declining alarmingly; declined from 4,020 individuals in 1969 (Robertson, 1970) to ~450 in 2004 (Conservation Development Centre, 2002; Cherie Enawgaw, 2004). One of the protected areas of Ethiopia where viable population of the species exists at present is in Alledoghi Wildlife Reserve (Fanuel Kebede *et al.*, 2006).

Alledoghi Wildlife Reserve is one of the most important wildlife areas of Ethiopia. The Reserve was established primarily to serve as a buffer zone for neighbouring protected areas such as the Awash National Park (Hillman, 1993; Schloeder and Jacobs, 1993) and to conserve the remnant populations of Grevy's zebra (*Equus grevyi*) and other ungulates that occur in the area (Fanuel Kebede *et al.*, 2012). It represents one of the few places in Ethiopia where large populations of wild ungulates, such as Beisa oryx and Soemmering's gazelle [*Gazella soemmeringi* (Cretzschmar 1828)] are

occurring (Fanuel Kebede *et al.*, 2006). Recognizing the biological and ecological importance of the reserve, it is currently proposed to upgrade the protection status to a National Park. The boundary demarcation for the proposed park has almost been completed (Kassaye Wami and Arega Mekonnen, 2013). However, the area is also an important grazing land for the Afar and Ethiopian Somali pastoral communities (Almaz Tadesse, 2009; Fanuel Kebede *et al.*, 2012). Consequently, overgrazing and bush encroachment have been increasing in an unprecedented rate, becoming the most prominent threats to biodiversity conservation in the reserve (Almaz Tadesse, 2009).

The present study was aimed to provide basic ecological information on Beisa oryx population in the Alledoghi Wildlife Reserve. There are, at least, three main reasons why this study was so important. First, population of the species has been dramatically declining in Ethiopia across most of its historic ranges mainly due to modification of their natural habitat (i.e., deteriorating both in quality and quantity) due to human pressure (Cherie Enawgaw, 2004). Second, Alledoghi Wildlife Reserve is one of the sites where viable population of the species occurs at present and where the reserve itself has been threatened mainly due to anthropogenic activities (Fanuel Kebede, 2013; Kassaye Wami and Arega Mekonnen, 2013). Finally, unlike in other protected areas of Ethiopia, a series of ecological studies of species basis have not been documented in the Alledoghi wildlife reserve since the 1960's. As a result there is limited information on general ecology of oryx, including the degree of habitat use overlap between oryx and other co-occurring species in the area. Such information has paramount benefit as it enables managers to make effective conservation management decisions related to Beisa oryx. The specific objectives of present study were to determine the current population size and structure (age/sex composition and grouping pattern) of Beisa oryx in the Alledoghi Wildlife Reserve and to examine habitat use overlap between Beisa oryx and two other sympatric ungulates [Soemmering's gazelle and gerenuk [*Litocranius walleri* (Brooke 1879)]].

MATERIALS AND METHODS

The study area

Alledoghi Wildlife Reserve (39°30' to 40°30' E and 8°30' to 9°30' N) is located in the northeastern region of the Ethiopian Great Rift Valley at 280 km east of Addis Ababa (Fig. 1). It was established in the 1960's, and covers an area of 1,832 km² (Hillman, 1993) of which ~500 km² core

wildlife area is currently delineated to be designated as a National Park (Kassaye Wami and Arega Mekonnen, 2013). The landscape of the area is dominated by a large alluvial plain with mountains rising along the eastern border that ranges in altitude between 800 to 2,400 m a.s.l. (Almaz Tadesse, 2009). Several protected areas are found around Alledoghi Wildlife Reserve: Afdem Gewane Controlled Hunting Area occurs to the northeast, Blen Hartele Controlled Hunting Area to the northwest and Awash National Park to the southwest (Almaz Tadesse, 2009).

Alledoghi Wildlife Reserve is characterized by a semi-arid ecosystem with annual rainfall ranging between 400 and 700 mm (Daniel Gemechu, 1977). The area has a bimodal pattern of rainfall: the small rains usually occur between February and April while the big rains between July and September. The mean annual temperature ranges from 25 to 30°C (Daniel Gemechu, 1977). The major habitat types in the reserve are grasslands, bushland, shrubland, wooded grassland, shrubby grassland, gallery/riverine forest and highland forest (Almaz Tadesse, 2009). So far, more than 31 species of mammals and over ~213 avian species have been recorded (EWNHS, 1996).

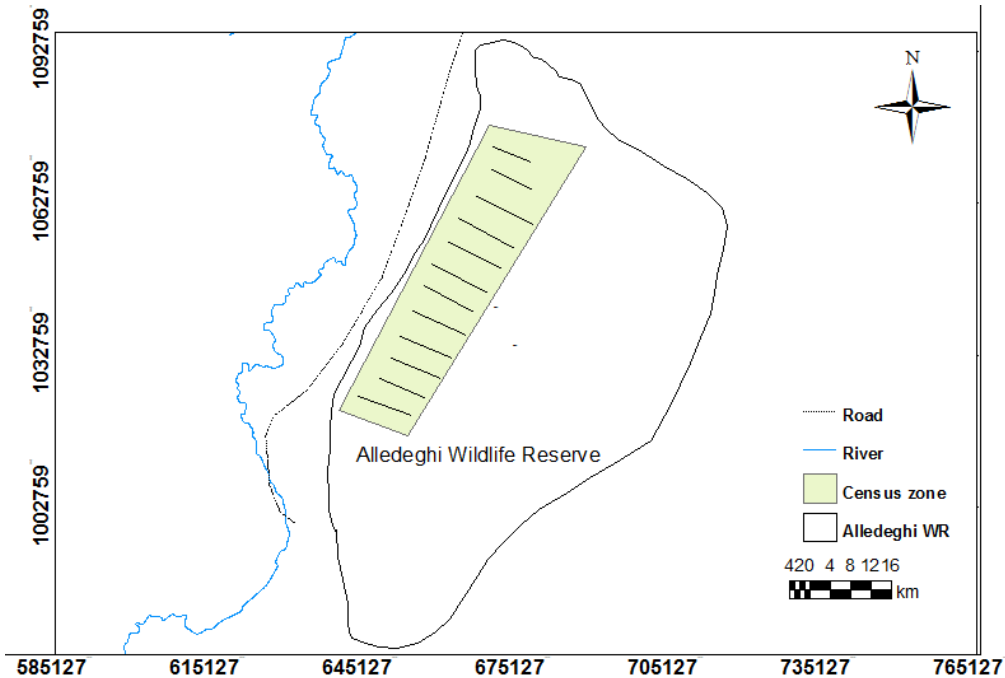


Fig. 1. The Alledoghi Wildlife Reserve study area and transect lines used for 2015/2016 survey.

Data collection

Data collection was conducted in September 2015, representing wet season, and in January 2016, representing dry season. Optimum suitable habitat map determined for Grevy's zebra by Fanuel Kebede (2013) in the Alledoghi Wildlife Reserve, as assumed for Beisa oryx and Soemmering's gazelle, was considered by this study as suitable habitat size. Accordingly, the extent of suitable habitat for Beisa oryx was estimated to be 480 km² and, based on our field observation during data collection, encompasses three contiguous habitats: grassland (area~82 km²; tree- and shrub-less habitat mainly covered by grasses), wooded grassland (53 km²; a grassland with some trees present) and bushland (29 km²; containing mainly dense dwarf tress). The extent of each vegetation type was estimated using the proportion of transect length that fell in each vegetation type to overall transect length (see below) as proxy to the proportion of available habitat of each vegetation type. These suitable habitats entirely fall within the boundary of the proposed Alledoghi National Park (Kassaye Wami and Arega Mekonnen, 2013). Given this information, data were collected on Beisa oryx population and the other two co-occurring species (Soemmering's gazelle and gerenuk) in all three of the habitat types.

Line transect counting method was used to collect data on Beisa oryx (detailed transect sampling method is available in Norton-Griffiths, 1978; Sutherland, 1996; Wilson *et al.*, 1996). The longer side of the census zone, lying south-north direction and measuring ~36 km, was used as a baseline to align sampling transects along. Twelve parallel line transects were systematically placed perpendicular to the baseline with a minimum distance of 2 km apart in an east-west orientation. Nearly 3 km distance was skipped at each ends of the baseline transect to avoid edge effects (Sutherland, 1996). Each transect covered the three major habitat types found in the census zone and transect length varied between 5 to 7 km, 2 to 5 km and 2 to 3 km in grassland, wooded grassland and bushland habitats, respectively. Animals were counted within a width of 0.6 km on both sides of each transect; this width was determined as effective detection width based on our preliminary observation conducted in the study area prior to the start of the actual data collection. With a total transect length of 138 km and widths of 0.6 km on each side of each transect, 167 km² (35% of the total suitable habitat of the species) area was sampled during the study period.

We used four-wheel vehicle to count animals while driving slowly at an average speed of 20 km per hour. The exception was that portions of some transects were found to be difficult to access by vehicle at all (e.g. in the bushland habitat) and during the wet season in all habitats, in which case, on foot survey was undertaken. Data recorded whenever a herd or individual animals of Beisa oryx was encountered were date and time of observation, total number of individuals, number of individuals of each sex and age category and habitat type (grassland, wooded grassland and bushland) where they were observed in. Similar procedures were used to collect data on populations of the two sympatric species (i.e., Soemmering's gazelle and gerenuk). Animals observed beyond the census width (i.e., 0.6 km) of each transect were not recorded. Age/sex composition of each herd was recorded in six categories, following Lewis and Wilson (1979) as: adult male, adult female, sub-adult male, sub-adult female, calves of both sexes and unidentified age/sex. To categorize individual animals into these age/sex types, relative body size, horn size, pelage, external genitalia and shape, fur color, the presence of scrotum in males or udder in females and other physical features were used as a clue (Lewis and Wilson, 1979; Kingdon, 1997). The operational definition of a "group" used in the present study was any number of animals of a species found together at any point in space, within a distance of less than 50 m between them, and time and apparently in sensory contact with one another (Hillman, 1987; Addisu Asefa, 2016). Lone animals of the species, whenever encountered, were recorded as a group by themselves, following Addisu Asefa (2016).

Each transect was surveyed twice in each season (wet and dry seasons), providing a total of four surveys in the course of the study period. Surveys were made early in the morning (06:30–10:30) and late in the afternoon (15:30–18:30) by same four experienced wildlife experts and game rangers of the reserve. On the average, four to five transects were covered on a single day while taking care to minimize the risk of double counting by noticing the movement of animals between adjacent transects. The start and end of geographical coordinates of each transects were saved in Garmin® GPS unit to ensure same transects were repeated during each counting session. Pairs of Navigator® binoculars 7 × 50 were used for counting the animals and for proper sex and age identification.

Data analysis

Population size and structure

As transects varied in length both within and between habitats, abundance values recorded along each transect were standardized by converting them to density (number of individuals per km²) (Burnhan *et al.*, 1980; Sutherland, 1996). Density of Beisa oryx along each transect in each vegetation type and in each season was calculated by dividing the average—from the two counting sessions in each season—number of individuals recorded per a given transect by the area of that transect. Areas of each transect were determined as a product of its length and width, by assuming that a width of 1.2 km (i.e., 0.6 km on each side of a given transect) was covered by the survey. These density values derived for each transect were used to compute mean density of Beisa oryx in each vegetation type during each season. Overall mean ($\pm$ 95% CI) density in the entire study area was estimated following the method suggested by Sutherland (1996) as a summation of the weighted mean density of oryx in each vegetation type. Total population of Beisa oryx in the study area was then estimated simply by multiplying the overall mean density by the total area of suitable habitat (i.e., the census zone; 480 km²) (Sutherland, 1996; Yosef Mamo *et al.*, 2014). Finally, the effect of habitat type and season on mean density of oryx was examined using two-way ANOVA in SPSS version 20 (IBM Corp., 2001).

Demographic characteristic of Beisa oryx was examined by calculating the ratio of age/sex categories as: adult male: adult female, sub-adult male: adult female, and male: female (by pooling adults and sub-adults). The presence of significant difference ratios between seasons was tested using Chi-square test in SPSS software.

Group structure

Three group types were identified from all group records: male (a group consisting of only adult males), female (consisting of adult females, and sub-adults and calves of both sexes) and mixed (group consisting of all age/sex categories). Adult male group type, for which only two records of solitary animals were made, was excluded from further analysis. Further, the female group type was either absent or recoded only fewer times in one or two habitat types in a given season. Thus group size was analyzed by pooling data on all group types. Following Bagchi *et al.* (2008) and Yosef Mamo *et al.* (2015a), group size was expressed in two ways as: mean group

size and group size frequency distributions. Mean values are more useful to compare different sets of data; whereas frequency distributions are better to illustrate the actual grouping patterns of a given species (Bagchi *et al.*, 2008). Accordingly, the effects of habitat type and season on mean group size were examined in SPSS version 20 using generalized linear model with log link function and poisson distribution (Quinn and Geough, 2002). To see pattern of group size distribution of the species, all groups recorded were classified into five group size categories, following Bagchi *et al.* (2008) and Yosef Mamo *et al.* (2015a)]: solitary (single individual), family unit (2-3 individuals), small groups (4-6), medium groups (7-10) and large groups (>10). Percent relative frequency of number of groups recorded in each group size category of each group type were graphically illustrated.

Habitat overlap of Beisa oryx with sympatric species

To examine habitat overlap among the sympatric ungulates, degree of habitat selection was determined first for each species. This was determined based on Manly's technique by calculating standardized resource selection ratios as a measure of habitat selection for species (Manly *et al.*, 2002; Yosef Mamo *et al.*, 2015b). Resource selection functions (B_{is}) were calculated as the proportion of available habitat units of habitat i that was selected by species s . B_{is} was estimated as:

$B_{is} = O_{is}/a_i$ where O_{is} is the proportion of abundance for species s that was found in units of habitat i , and a_i is the proportion of habitat i among all sampled habitat units. Then, the selection functions were standardized according to:

$$B^*_{is} = B_{is} / \sum_{i=1}^{i=3} B_{is}$$

Where B^*_{is} is the standardized selection ratio for species s (Cromsigt *et al.*, 2009). If the standardized selection ratio value for a particular habitat is equal to 1/m (where m is the total number of available habitat types, which in this case is 3), it shows no preference; if greater, preference; and if less than, avoidance (Cromsigt *et al.*, 2009; Yosef Mamo *et al.*, 2015b).

Then, overlaps between Beisa oryx with each of the other two species in respect to their habitat use were determined, separately for each season, using S18 Kulczynski similarity index in Primers software (Green, 1987; Clarke and Gorley, 2006).

RESULTS

Population size and structure

Overall, 824 individuals of *Beisa oryx* (732 and 92 during wet and dry seasons, respectively) were recorded in the Alledoghi Wildlife Reserve. Both habitat type (Wald Chi-square = 8.145, $df = 2$, $P < 0.05$) and season (Chi-square = 55.587, $df = 1$, $P < 0.05$), as well their interaction (Chi-square = 71.449, $df = 5$, $P < 0.05$) had significant effects on mean density of oryx in the study area. Mean density of *Beisa oryx* was significantly greater in the wooded grassland habitat than grassland and bushland habitats and greater during wet than during dry season. The difference among habitat types was revealed only during wet season (Fig. 2a).

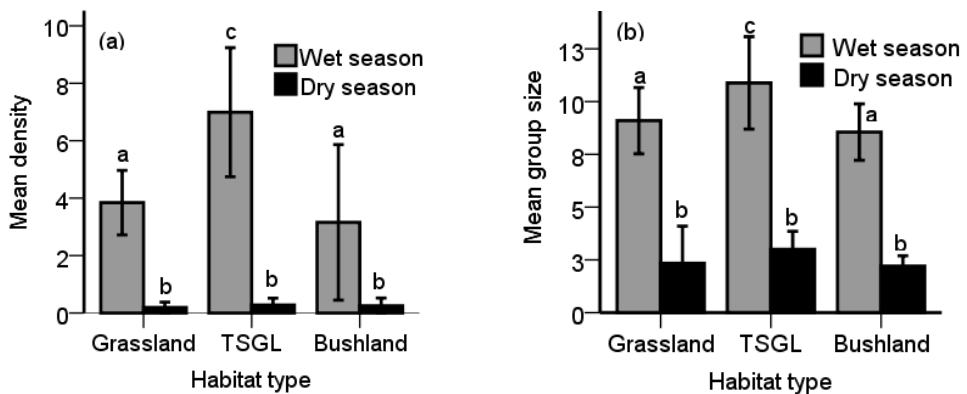


Fig. 2. Seasonal mean density (a) and group size (b) of *Beisa oryx* in the Alledoghi Wildlife Reserve. Means indicated by different letters in each figure are significantly different at $\alpha = 0.05$ (TSGL = wooded grassland).

Weighted mean ($\pm$ SD) population density of the species in the study area was estimated at 2.33 (± 0.25), 0.12 (± 0.01) and 1.23 (± 0.12) individuals per km^2 during the wet season, dry season and pooled seasons, respectively. Estimated total population size of *Beisa oryx* in the reserve was 1119 (± 8), 58 (± 1) and 590 (± 7) during the wet season, dry season and pooled seasons, respectively.

The ratio of adult male to adult female was 1.0:1.8 and 1.0: 1.7 and sub-adult male to sub-adult female was 1.0:1.9 and 1.0: 2.0 during wet and dry seasons, respectively. The difference in these ratio values were not statistically significant between seasons (in both cases, Chi-square = 0.003, $df = 1$, $P > 0.05$). Adult females contributed almost about half of the total population during both seasons, while calves were not encountered during the dry season (Fig. 3a).

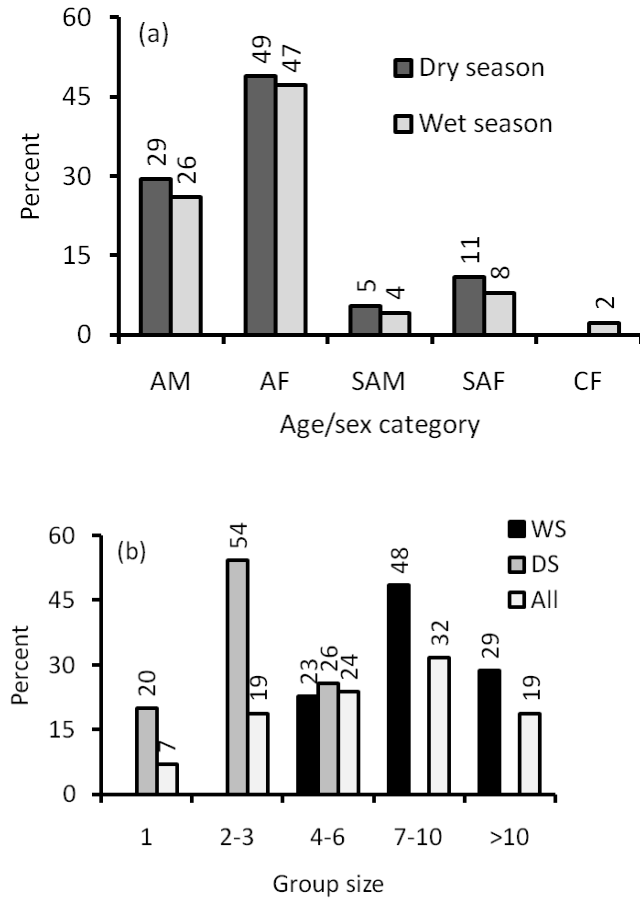


Fig. 3. Percentage contribution of each age/sex category to the total population (a) and group size frequency (b) of Beisa oryx in Alledoghi Wildlife Reserve during the wet and dry seasons. Sample size (N) for age/sex category, = 732 during wet season, and 92 during dry season; for group size, = 66 in wet season, = 35 in dry season, = 101 total. (Abbreviations, age/sex category: AM = adult male, AF = adult female, SAM = sub-adult male, SAF = sub-adult female, CF = calf).

Group size

Of the total 101 (66 groups during the wet season and 35 during the dry season) groups of Beisa oryx recorded during the entire study period, the minimum group size consisted of 1 and 4 individual/s and the maximum group size 5 and 26 individuals during the dry and wet seasons, respectively. Groups containing 7-10 individuals were the most frequently observed group sizes during wet season while those containing 2-3 individuals were the most frequently observed group sizes during dry season; in both cases these group sizes accounted for nearly half of all groups recorded in each

respective season (Fig. 3a). Lone animals were not recorded during the wet season, but they accounted for 20% of all group records during the dry season (Fig. 3b).

Season (Wald Chi-square = 146.232, $df = 1$, $P < 0.001$) and its interaction with habitat type (Wald Chi-square = 248.39, $df = 5$, $P < 0.001$) affected the group size of Beisa oryx, with greater differences occurring across habitat types during the wet season and greater group size occurring in the wooded grassland habitat than the other two habitat types (Fig. 2b). Mean group size was significantly greater during the wet season (mean $\pm$ SE = 9.46 ± 0.45) than the dry season (mean = 2.49 ± 0.37). Independent of season, the effect of habitat type on group size of Beisa oryx was not significant (mean size $\pm$ SE, grassland = 4.61 ± 0.88 ; wooded grassland = 5.71 ± 0.51 ; bushland = 4.34 ± 0.41 , Wald Chi-square = 4.56, $df = 2$, $P = 0.102$). However, wooded grassland habitat had significantly greater mean group size than the other two habitat types during the wet season (Fig. 2b).

Habitat association and overlap

Beisa oryx showed stronger association for wooded grassland habitat during the wet season (i.e., preference index of $>1/m$ [= 0.333]), but for the bushland during the dry season although this habitat type was avoided during the dry season (Table 1a). Gazelle showed preference for the grassland and wooded grassland during the wet season and the latter habitat during the dry season. In contrast, gerenuk preferred the bushland during both seasons (Table 1a).

Habitat overlap ranged between 52% (between Beisa oryx and gerenuk) 85% (between Beisa oryx and Soemmering's gazelle) during the wet season, and ranged between 35% and 75% during the dry season (Table 1b).

Table 1. Habitat association/selection index (a) and percent of overlap between each pair (b) of the three ungulates in the study area.

(a) Habitat selection							
Season	Habitat	Species					
		Oryx	Rank	Gazelle	Rank	Gerenuk	Rank
Wet season	GL	0.303	2	0.445	1	0.046	3
	TSGL	0.465	1	0.357	2	0.232	2
	BL	0.232	3	0.198	3	0.723	1
Dry season	GL	0.038	3	0.227	2	0.044	3
	TSGL	0.297	2	0.602	1	0.223	2
	BL	0.665	1	0.171	3	0.732	1
(b) Overlap							
Wet season				Dry season			
	Oryx	Gazelle		Oryx	Gazelle		
Gazelle	85			35			
Gerenuk	52	53		79	64		

GL = grassland, TSGL = wooded grassland, BL = bushland.

DISCUSSION

Population size and structure

Overall, our results suggest that there is a considerable population size of Beisa oryx in the Alledoghi Wildlife Reserve, but there is seasonal dynamics in population size of the species with disproportionately greater during the wet season than the dry season (1119 ± 7.8 vs 58.0 ± 1.0). Such huge seasonal population size difference could be attributed to seasonal changes in the quality and quantity of feeding resources that determines the decision of individual animals whether to stay or abandon a given habitat or area. Obviously, resources are less available during dry season compared to wet season; thus, such resource scarcity during the dry season might have caused the animals to emigrate to other surrounding areas in search of better foraging resources. Then, these animals might have then backed the reserve during the wet season when forage resources are in a better condition.

Although there have been some unpublished previous reports on population size of the species from the area (EWCA, unpublished data, 2012), they are found to be incomparable with our data as they lack information on the methodology used for counting and population estimation. Nonetheless, compared to population estimates of 810 individuals in 2010 (Fanuel Kebede, 2013), who used similar approach with us, the current estimated population size (= 590 individuals; based on average of the two seasons) of oryx reported here indicates a 27% decline in the population size of the species in the area since six years ago. The most probable reasons could be either true absence (mortality and/or emigration) and/or reduced natality.

Although we could not test the latter hypothesis due to lack of data on age structure for the previous studies, there are some evidences that could support the former (mortality and emigration) hypothesis. In the first place, there was unprecedented severe drought throughout most parts of Ethiopia including Alledoghi area during our study period, which leads to shortage of forage and water. This in turn might have led to emigration to other better sites such as to Blen Controlled Hunting Area in search of better feeding and watering resources. Further, increased rate of death of animals and/or decreased reproductive success in the last six years and/or during our study period could have caused the decline in the population of the species. Similar studies in African savannah ecosystems have demonstrated the deleterious effects of drought on populations of several herbivore species. For example, populations of several ungulate species in the Masai Mara Serengeti ecosystem have declined by 58% in the last 20 years due to drought related effects on vegetation (Ottichilo *et al.*, 2000) and the 2009 drought in the Amboseli ecosystem has reduced the wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) populations by 70–95% (Kenyan Wildlife Service, 2010). In addition to drought, expansion of exotic invasive species such as *Prosopis juliflora*, bush encroachment, livestock over-grazing, settlement encroachment and traffic killing could be the major factors for the current decline in population of the Beisa oryx in our study area (Almaz Tadesse, 2009; Fanuel Kebede, 2013).

Despite the declining population status of the species in the reserve, we still argue that the present population in the area is considerable and is of great conservation importance. This is particularly true given the dramatic declining rate and local disappearance of the species from its most of previous ranges due to habitat change and hunting (Cherie Enawgaw, 1999). For example, its population in the Awash National Park - a site nearby to our present study area and which was established to protect Beisa oryx - has declined from 4,020 in 1969 (Robertson, 1970) to below 446 individuals in 2004 (Conservation Development Centre, 2002). Therefore, Alledoghi Wildlife Reserve perhaps represents one of the most important sites which support viable population of the species.

The present study shows that, based on pooled data from adults and sub-adults across seasons, the ratio of male to female was 1.0:1.9. This ratio is slightly lower than what has been reported for some similar-sized ungulates. For instance, male to female ratio of 1.0: 2.3 has been reported both for greater Kudu (*Tragelaphus strepsiceros*) in Zimbabwe (Wilson, 1965) and mountain nyala (*Tragelaphus buxtoni*) in the Bale Mountains National Park

of Ethiopia (Befekadu Refera and Afework Bekele, 2004). In general, unequal sex ratio within a given species population can occur favoring either males or females and is often explained as a function of species-specific reproductive, foraging and defensive behavioral traits (Estes, 1974). In the present study, the high proportion of females in the population may indicate that there is an increased predation pressure on males (both by natural predators and humans), due to greater boldness, or the emigration of subordinate males to other habitats. Nonetheless, such large proportion of females could also indicate that the species has a high potential to increase in population size, if better conservation measures will be in place.

Group size

Our study showed that mean group size of Beisa oryx was generally greater during the wet season both within and across vegetation types compared to group size during the dry season, but, regardless of seasons, no such clear difference was found between sites. During the wet season, group size is greater in the wooded grassland habitat than both the grassland and bushland habitats. These findings are in agreement with many similar studies (e.g. Estes, 1974; Durant *et al.*, 1986; Yosef Mamo *et al.*, 2015a) that ungulates form large group size during the wet season and decline throughout the dry season. In general, there are several biological and ecological factors that determine the spatial and temporal group sizes of ungulates, such as seasonal variation in quality and quantity of feeding resources that lead to changes in intra- and inter-specific interactions such as food competition and predation (Yosef Mamo *et al.*, 2012; 2015a; 2015b; Addisu Asefa, 2016), and other behavioural activities including reproduction (Yosef Mamo *et al.*, 2015a). The greater group size reported in the present study during the wet season could therefore be attributed to increased availability of feeding resources that may lessen food competition might be existing in the area. However, lack of significant difference in group size between the habitat types may indicate the presence of different potential stimuli in similar proportions among the habitats.

Habitat overlap of Beisa oryx with sympatric species

The three ungulate species showed different level of seasonal habitat association. Beisa oryx showed strong association with the wooded grassland habitat during the wet season, but with the bushland during the dry season. Soemmering's gazelle also showed similar association with wooded grassland habitat during wet season, in addition to with grassland, but only with wooded grassland habitat during dry season. In contrast,

gerenuk had stronger preference for bushland during both seasons.

Habitat use overlap between each pair of species was greater during wet season (between 52% and 85%) than during dry season (35%–79%). Similar studies (Green, 1987; Fritz *et al.*, 1994; Yosef Mamo *et al.*, 2012) suggest that in addition to vegetation type other factors, such as vegetation height and habitat quality could have considerable influence on how ungulates select and use their habitats. The observed high habitat use overlap between each pair of species during the wet season is not surprising since there is no food shortage during this period compared to the dry season when feeding resources are scarcely available, leading them to occupy different habitats to avoid competition (Hirst, 1975; Green, 1987; Yosef Mamo *et al.*, 2015b). Further, in addition to competition other ecological factors such as predation and human disturbances also affect the distribution and habitat use of ungulates (Hirst, 1975; Barker, 2005; Stankowich, 2008). Thus, the reported habitat overlap among the ungulates might not necessarily be related only to food overlap among them.

CONCLUSION

This study has provided scientific information on population size and some ecological aspects of Beisa oryx in the Alledoghi Wildlife Reserve, Ethiopia. However, unless effective conservation measures are in place and the major determinant threats such as resource competition with livestock, bush encroachment (both by alien and indigenous invasive plant species) and traffic killing are reduced, survival of the species will fall under high risk of local extinction.

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