

# **Interspecific Association in Ungulates of the Bale Mountains National Park, Ethiopia**

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## **Abstract**

The aim of the study was to determine the frequencies of interspecific association formation and species preferences among five ungulates [bohor reedbuck (*Redunca redunca*), common warthog (*Phacochoerus africanus*), grey duiker (*Sylvicapra grimmia*), Menelick's bushbuck (*Tragelaphus scriptus meneliki*) and mountain nyala (*Tragelaphus buxtoni*)] in the northern Bale Mountains National Park, Ethiopia. Data were collected in three forest patches and in open grassland using total count technique in 2009 and 2011. The total number of ungulate groups found in interspecific associations was 444, comprising 26.8% of the total 1657 groups recorded. For the five study species, the relative frequency with which a given species occurred in interspecific association deviated significantly from the expected mean relative frequency (i.e., 26.8%). Each study species showed preferences to form interspecific associations with one or two other species. Interspecific association formation increased mean group sizes for bohor reedbuck and mountain nyala. And, most of the species had greater overall mean group sizes in the open habitat compared to forest habitat. In general, the association pattern reported here could be attributed to anti-predator response and/or mutual grazing facilitation, which might be beneficial to one or all of the species involved.

**Keywords:** Bale Mountains National Park; group size; interspecific association; social organization; species preferences; ungulates.

## **Introduction**

The Bale Mountains National Park (BMNP) is recognized as the single most important conservation area in the Ethiopian Highlands; it is a centre of diversity and endemism and the most important area for a number of threatened Ethiopian endemics across all taxa (NH, 2004; Williams *et al.*, 2004; OBARD, 2007; Asefa, 2011). The northern section of the park, where this study was conducted, is particularly identified as the top priority conservation zone in the National Park (OBARD, 2007); it holds over two-thirds (1500-700 individuals) of the total global population of the endangered Ethiopian endemic antelope, the mountain nyala (*Tragelaphus buxtoni*), and a considerable population numbers of other ungulates (Hillman, 1986; Stephens *et al.*, 2001; Refera & Bekele, 2004; OBARD, 2007; Asefa, 2008). However, the ever-increasing livestock grazing, unsustainable forest exploitation, domestic dog predation and unregulated human movement in the area are threatening wildlife species here (Stephens *et al.*, 2001; Asefa, 2008; Mamo & Bekele, 2011). One of the impacts of such human-induced threats to wild ungulates is a change in their social organization patterns (Stankowich, 2008), which is a determinant factor to their reproduction and survival (Leuthold & Leuthold, 1975; Gerard & Loisel, 1995; Stankowich, 2008).

Social organization, be it intraspecific (groupings between individuals of same species) or interspecific (between individuals of two or more species), in ungulates is often considered to be the adaptive outcome of selective pressures arising from predation and intraspecific and/or interspecific competition (Leuthold & Leuthold, 1975; Gerard & Loisel, 1995; Desbiez, Rocha & Keuroghlian, 2010). Interspecific associations in ungulates are usually restricted to social species that normally live together in groups (Stensland, Angerbjörn & Berggren, 2003). Studies indicate that such associations are affected by several factors, including changes in the

environment/habitat due to disturbance, season and the presence of other species (Gerard & Loisel, 1995; Fischer & Linsenmair, 2007; Stankowich, 2008). Thus, data collected on patterns of social grouping in ungulates in protected areas such as the BMNP is of paramount importance for conservation managers to detect changes in response to the ever-increasing anthropogenic environmental and/or habitat changes and to make appropriate management decisions.

Only five ungulate species occur in the northern section of the BMNP: bohor reedbuck (*Redunca redunca*), common warthog (*Phacochoerus africanus*), grey duiker (*Sylvicapra grimmia*), Menelick's bushbuck (*Tragelaphus scriptus meneliki*) and mountain nyala (*Tragelaphus buxtoni*). Except Menelick's bushbuck which is restricted to the forest habitat, all of them inhabit both habitat types (Hillman, 1986; Asefa, 2011). Although limited information on patterns of intraspecific association of these ungulates in the BMNP is available (Hillman, 1986; Refera & Bekele, 2004; Afework, Bekele & Krishnan, 2009), to my knowledge, data on their interspecific association is lacking. The aim of the present study was to determine the frequencies of and species preferences for interspecific association formations for these five ungulate species in the northern section of the BMNP, and to examine the effects of this association and habitat type on the group sizes of these species.

## **Materials and Methods**

### *Study area*

The BMNP was established in 1971. It is located between 6° 29' and 7° 10' north, and 39°28'-39° 58' east. The current extent of the national park is 2200 km<sup>2</sup>, ranging in altitude from 1500 to 4377 m a.s.l. (Hillman, 1986; OBARD, 2007). The BMNP contains five vegetation zones: the northern montane grasslands, the northern dry Afromontane forest, ericaceous forest, the Afro-

alpine moorland and grassland, and the southern Haremma forest (Hillman, 1986; NH, 2004). Seventy-eight mammal and 278 bird species have been recorded from the BMNP; of which 17 mammal and 6 bird species are endemic to Ethiopia (Asefa, 2007, 2011). Two of these endemics, Menelick's bushbuck and mountain nyala, are among the five ungulate species occurring in the present study site and considered for the study. The Bale Mountains area is characterized by eight months (March-October) of rainy season and four months of dry season (Hillman, 1986).

The present study was carried out in the northern section of the BMNP (6° 48' - 7°10' north, and 39° 31'- 39° 36' east), which spans an area of ~20 km<sup>2</sup> and includes two of the vegetation zones (the northern woodlands and the Montane grasslands) found in the National Park. The landscape in this particular part of the National Park is characterized by mountainous ranges with a central broad flat valley and an altitude range of 3000 and 3550m a.s.l. The mountainous areas are covered by three patches of forest (hereafter referred to as forest habitat): Adellay (central location, 6°50' N & 39°33' E), Boditti (6°57' N & 39°33' E) and Dinsho hill (6°50' N & 39°36' E). This forest habitat is dominated by *Hagenia abyssinica-Juniperus procera* tree species. The central flat valley is generally classified as a montane grassland ecosystem (hereafter referred to as open habitat; 6°53' N, 94 & 39°33' E). The vegetation of this grassland is dominated by swamp grasses and sedges of *Cyperus* and *Scirpus* genera and shrub species of *Artemesia afra* and *Helichrysum splendidum* (OBARD, 2007; Afework *et al.*, 2009). All the five ungulate species occurring in the study area were included in this study.

#### *Data collection*

Three of the forest patches and the open habitat (i.e. Gaysay grasslands) were delineated as separate blocks. Blocks were surveyed on different days using total count technique, but within similar time of the day and under similar weather conditions by same two people between

August - October each year for two years (2009 & 2011). Each block was visited four times in each year, and observations were made early in the morning (from 07h30-10h30) and late in the afternoon (from 14h30 to 17h30) when the animals are more active (Refera & Bekele, 2004; Afework *et al.*, 2009). Observations were aided by 8 × 40 Bushnell® binoculars.

Data were collected on all of the five ungulate species occurring in the area. The following information was recorded whenever an animal or group of animals of the same species or multi-species was encountered: date, time, habitat type and group composition (i.e. species identity and total number of individuals of each species). A ‘group’ was defined following Leuthold & Leuthold (1975) and Hillman (1987) as: ‘any number of animals of one or more 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’. Lone animals of any species, whenever encountered alone, were recorded as a group by themselves.

#### *Data analysis*

Observations obtained from each block during each counting session were insufficient to make valid comparisons between counting sessions or between years. Therefore, data from the three forest patches across the two years were pooled and used for further analyses. For each species: (1) deviations of observed relative frequencies of interspecific association formations from theoretically expected frequencies (i.e. if each species occurred in interspecific associations with equal probability); (2) a species preferences of one to another species to form interspecific associations with (i.e. if each species associate with the others with equal probability); and, (3) differences in relative frequencies of interspecific association formations between the two habitats (i.e. if each species occurs in interspecific association in the forest and open habitat with

equal probability) were calculated and tested using chi-square tests. For this analysis (analysis 3) data from the three forest blocks were pooled and compared with open grassland habitat.

To determine species preferences, association indexes between each possible pairs of species were first calculated using the following simple formula:

$AI_{ij} = N_{ij}/(N_i + N_j + N_{ij})$ ; where,  $AI_{ij}$  = association index between species  $i$  and  $j$ ;  $N_{ij}$  = number of group records containing both species  $i$  and  $j$ ;  $N_i$  = number of group records containing of species  $i$  alone (i.e. not associating with species  $j$ ); and,  $N_j$  = number of group records containing of species  $j$  alone (i.e. not associating with species  $i$ ). These indexes were then used to calculate relative preferences as follows:

$RP_{i,j} = (AI_{ij}/(\sum AI_{ij})) * 100$ , where,  $RP_{i,j}$  = relative preference of species  $i$  for species  $j$  where  $j \neq i = 1, 2, \dots, 5$ ;  $AI_{ij}$  = as defined above; and, 100 = a constant multiplier to express the values in percentages. If the relative preference values of specie  $i$  for species  $j$  was equal to the expected value (i.e. 25% expected if it associates with equal probability, or equal preferences, with the four associating species), it was subjectively considered to indicate no preference; if greater, preference; and if less than, avoidance. Chi Square procedure was used to test if the relative preference of species  $i$  for species  $j$  was significantly greater than the expected value.

To determine the effect of habitat type on the relative frequencies of interspecific association formation of each species, relative frequencies (i.e. number of groups of species in interspecific association in a given habitat, divided by total number of group records of that species in that habitat) were calculated, and means of these relative frequencies from the two habitats was used as the expected relative frequencies of each respective species in each habitat to derive Chi Square values and test for differences.

General Linear Model was used to analyze the effect of association status (i.e., in interspecific association vs not in interspecific association), habitat type (forest vs openland) and their interaction on group size of each species. Mean comparisons were done on  $\log_{10}$  transformed group size data to meet the assumptions of normality of mean and homogeneity of variance and Tukey's post hoc tests were used to compare multiple means from the interaction of association and habitat type. All analyses were conducted using SPSS version 20.

## Results

The total number of groups found in interspecific association was 444, comprising 26.8% of the 1657 groups recorded. For all species, the observed relative frequencies of interspecific association formations were significantly higher than the overall mean (26.8% expected if each species occurred in mixed associations with equal probability (for all species,  $\chi^2 = 9.59 - 23.93$ ,  $P < 0.05$ ; Table 1). The association index values between each pair of three species (bohor reedbuck, common warthog and mountain nyala) were relatively larger than the values for any other species pair, suggesting that there is a relatively stronger association propensity existing among them (Table 2). Analysis of species preferences also indicated that all the species demonstrated preferences for one or two species to form interspecific associations with (Table 3). However, statistically significant preferences were found in the cases of: 1) common warthog and bohor reedbuck for mountain nyala, which in turn significantly preferred both species (in all cases,  $\chi^2 = 5.20 - 13.84$ ,  $P < 0.05$ ; Table 3); and, 2) Menelick's bushbuck for common warthog ( $\chi^2 = 172.625$ ,  $P < 0.05$ ; Table 3). On the other hand, in addition to the lack of preferences between grey duiker and bushbuck for each other, all the other three species also showed avoidances to associate with both of them (Table 3). A significant effect of habitat type on the relative

**Table 1.** Frequencies of inter-specific associations in ungulates of the BMNP.

Species	bohor reedbuck	common warthog	grey duiker	Menelik's bushbuck	mountain nyala
Number of groups associated with other species	249	282	90	188	293
Total number of groups recorded	563	701	159	295	545
Percentage in inter-specific associations	44	41	41	45	54
Significance <sup>a</sup>	15.49*	9.59*	10.11*	16.43*	23.93*

\* Statistically significant at  $P < 0.05$

**Table 2.** Interspecific association indexes between each pair of the five ungulates species in the BMNP

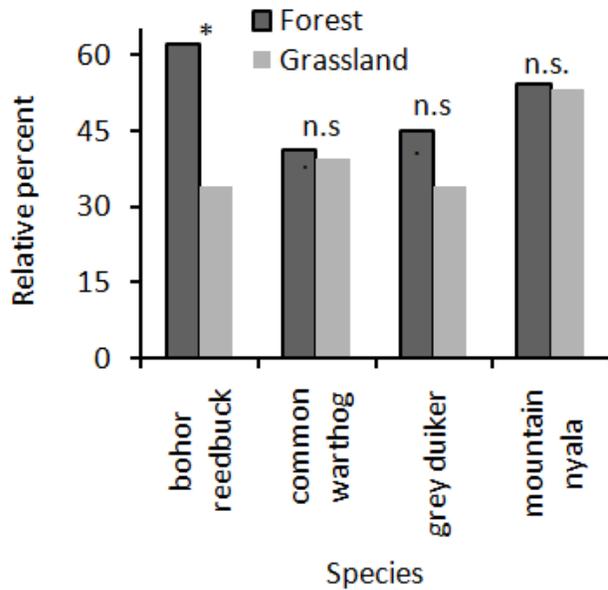
Species	bohor reedbuck	common warthog	grey duiker	Menelik's bushbuck
common warthog	0.13			
grey duiker	0.04	0.03		
Menelik's bushbuck	0.05	0.09	0.03	
mountain nyala	0.17	0.16	0.04	0.07

**Table 3.** Species preferences for interspecific association formation in five ungulate species in the BMNP. Row values under each species column are its relative preferences (expressed in %) for each corresponding species in the rows. Figures in parenthesis are chi square values [only provided for relative preferences values that are greater than the expected value (i.e. 25% expected if a species associates with equal preferences with all the four associating species)].

Species	bohor	common	grey duiker	Menelik's	mountain
	reedbuck	warthog		bushbuck	nyala
bohor reedbuck		32 (1.80)	29 (0.52)	21	39 (7.40)*
common warthog	33 (2.76)		21	38 (6.25)*	36 (5.20)*
grey duiker	10	7		13	9
Menelik's bushbuck	13	22	21		16
mountain nyala	44 (13.84)*	39 (7.84)*	29 (0.52)	29 (0.71)	

\* Statistically significant at  $P < 0.05$

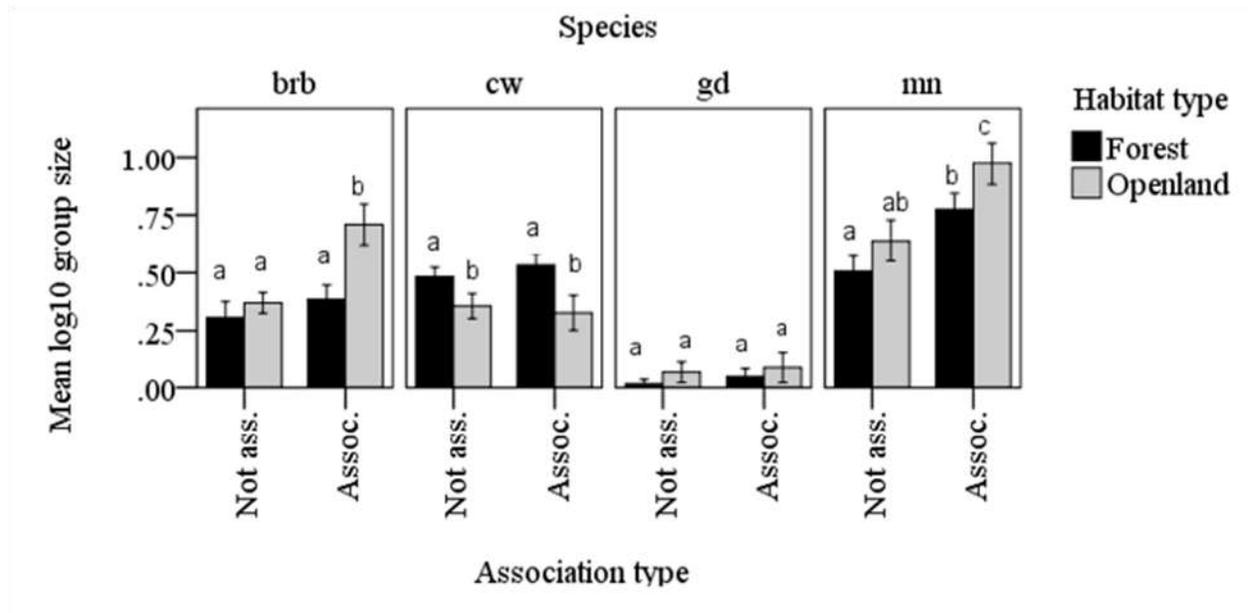
frequencies of interspecific association formation was revealed only for bohor reedbuck, which was higher in the forest habitat than in the open habitat ( $\chi^2$  – value = 8.17,  $P < 0.05$ ; Fig. 1).



**Figure 1.** The effect of habitat type on relative frequencies (expressed in %) of interspecific association formations of four ungulate species in the BMNP (for each species: relative frequency in a given habitat was expressed as percentage of number of records of interspecific associated groups to total records containing at least that species; and, the mean of the relative frequencies from the two habitats was used as expected relative frequency).

\*Significantly different at  $P < 0.05$ ; n.s. = non-significant difference.

The interaction effect of association type and habitat type on group size was revealed only for bohor reedbuck ( $F_{1,56} = 14.61$ ,  $P < 0.05$ ), with groups in interspecific association in the open land habitat showing significantly greater mean group size (Fig. 2). Both habitat type and association type had also independently affected mean group size of bohor reedbuck (mean  $\pm$  S.D.  $\log_{10}$  group size, habitat type: open land =  $0.49 \pm 0.43$  and forest habitat =  $0.36 \pm 0.33$ ,  $F_{1,559} = 32.185$ ,  $P < 0.05$ ; association type: in interspecific association =  $0.55 \pm 0.45$  and not in interspecific association =  $0.35 \pm 0.34$ ,  $F_{1,559} = 37.64$ ,  $P < 0.05$ ). For mountain nyala, although the effect of their interaction was non-significant, both habitat type ( $F_{1,541} = 16.66$ ,  $P < 0.05$ ) and association type ( $F_{1,541} = 54.98$ ,  $P < 0.05$ ) had independently affected its group size, with greater size in open land compared to forest habitat (mean [ $\pm$  S.D.]  $\log_{10}$  group size =  $0.82 \pm 0.47$  vs



**Figure 2.** The effect of habitat type and association type (i.e. in interspecific association [assoc.] and not associated with other species [Not ass.]) on mean Log10 group sizes of four ungulate species in the BMNP. Error bars represent  $\pm$  95% confidence interval. Significantly different means (at  $P < 0.05$  level) for each species is indicated by different letters (Abbreviations for species names: brb = bohor reedbuck; cw = common warthog; gd = grey duiker; and mn = mountain nyala).

0.65  $\pm$  0.47) and in those groups in interspecific association than not associated (0.84  $\pm$  0.48 vs 0.63  $\pm$  0.43). In the case of Menelick's bushbuck, which is restricted to the forest habitat, although mean group size of associated groups was greater than that of the lone groups, this difference was statistically non-significant [mean ( $\pm$  S.D.) log<sub>10</sub> group size = 0.12  $\pm$  0.17 vs 0.09  $\pm$  0.15,  $F_{1,289} = 1.596$ ,  $P > 0.05$ ). For the other two species, neither interspecific association formation nor its interaction with habitat type had significant effect on their mean group sizes (Fig. 2). However, habitat type had affected group size of common warthog ( $F_{1,697} = 32.21$ ,  $P < 0.05$ ) and grey duiker ( $F_{1,155} = 5.62$ ,  $P < 0.05$ ), for warthog mean group size was significantly greater in the forest compared to the open land habitat and vice-versa for duiker (mean [ $\pm$  S.D.]

$\log_{10}$  group size, warthog =  $0.50 \pm 0.36$  vs  $0.35 \pm 0.32$ ; duiker =  $0.70 \pm 0.14$  vs  $0.03 \pm 0.09$ ; see also Fig. 2).

## **Discussion**

This study showed that there is a high frequency of interspecific association formation among the ungulate species at BMNP. Each species showed significant preferences for one or two species, and such association formations resulted in greater mean group sizes. The high frequency of interspecific association formation observed for three of the species (mountain nyala, common warthog and bohor reedbuck) known to form large intraspecific groups (see Hillman, 1986; Refera & Bekele, 2004; Afework *et al.*, 2009) supports the hypothesis that the tendency for an ungulate species to form interspecific associations is a reflection of its intraspecific sociability (Leuthod & Leuthold, 1975; Stensland *et al.*, 2003). However, the result found for the other two species (i.e. grey duiker and Menelick's bushbuck) contradicts this hypothesis. These species have relatively small home ranges (Kingdon, 1997) and are often solitary (mean group size in the BMNP, grey duiker: = 1.1; and Menelick's bushbuck: = 1.3; Hillman, 1986). The present findings may therefore suggest that animals of these species may prefer individuals of other co-occurring species than individuals of their conspecifics to form associations with. Alternatively, these findings could be a result of the movement of the other associating species to them, leading to frequent group mixing (Schaefer, Steens & Messier, 1996).

Predation pressure and resource availability often vary between habitats, so may act simultaneously to regulate the distribution and organization of sympatric populations of species communities (Sinclair, 1985; Sinclair & Arcese, 1995). The stronger interspecific association indexes and the existence of significant species preferences demonstrated by most of the

ungulate species studied may therefore indicate that there is a non-random tendency for the formation of the association and there is some sort of beneficial symbiotic relationships among them (Leuthod & Leuthold, 1975; Schaefer *et al.*, 1996; Stensland *et al.*, 2003; Fischer & Linsenmair, 2007). Schaefer *et al.* (1996) suggested that species that differ in their feeding requirements more often overlap spatially than potential competing species, leading to more frequent group mixing of species with differing feeding requirements. This supposition could primarily work for the preferences reported for the association of mountain nyala with common warthog or bohor reedbuck, and vice-versa, of Menelick's bushbuck with common warthog, and grey duiker with bohor reedbuck. This is because the feeding requirements of mountain nyala, grey duiker and bushbuck (being browsers) greatly differ from that of common warthog and bohor which are generally known to be grazers (Hillman, 1986; Kingdon, 1997; Afework *et al.*, 2009). Thus the reason (a stimulating factor) for the formation of such interspecific associations between such browser and grazer species pairs could be an anti-predator response (for better detection and escape; Jarman, 1974; Hillman, 1987; Fischer & Linsenmair, 2007).

Common diurnal wild predators in the study area that could pose pressure on the ungulates and may have caused such behavioural responses to occur include small-sized carnivores that hunt on ungulate juveniles, such as common jackal (*Canis aureus*) and serval cat (*Felis serval*) (Hillman, 1986; Asefa, 2008). However, predation by domestic and semi-feral dogs (*Canis canis*) on juveniles of nyala and reedbuck (Hillman, 1986; Asefa, 2008) and anthropogenic disturbance due to unrestricted human and domestic animal movement in the area (Mamo & Bekele, 2011; see also review of Stankowich, 2008) could also play an important role similar to that of wild predators, probably contributing to the formation of such multi-species associations.

Mutual grazing facilitation is considered to be another possible reason for the formation of interspecific associations in ungulate species, particularly between species that differently exploit similar food resources (e.g., feeding on different parts of same plant species; Leuthold & Leuthold, 1975). This may support the strong association index and preferences, although statistically not significant, found between common warthog and bohor reedbuck. These species are generally known to be grazers, but slightly differ in their feeding habits; warthogs prefer to graze on short grasses while reedbuck on relatively taller grasses (Hillman, 1986; Kingdon, 1997; Afework *et al.*, 2009). This slight difference in their feeding habits may therefore explain the high association tendency observed between them, which may function as grazing facilitation for either or both of them. However, despite the role of predator and/or mutual grazing facilitation as possible causes for the observed interspecific association formations in these ungulates, these findings should be interpreted cautiously. Because these findings can also be the result of a coincidence, rather than true symbiotic relationships, as gathering of these species at their preferred similar resources such as habitats or sites used for hiding, feeding and resting (Stensland *et al.*, 2003) could also lead to the formation of such frequent interspecific groups.

The greater mean group sizes reported for mountain nyala, grey duiker and bohor reedbuck in the open land than the forest habitats in this study agrees with the findings of previous similar studies (Leuthold & Leuthold, 1975; Gerard & Loisel, 1995; Fischer & Linsenmair, 2007). These authors suggested that African ungulates are generally known to form larger group sizes in open habitats than forested habitats although the evolutionary functions and advantages could vary from place to place depending on the local stimuli. However, the reason for the observation of increased group sizes of these two species when in interspecific state than when seen lone (when not associated with other species) is unclear. Nonetheless, female-juvenile

group type of these species has been reported to form larger intraspecific group sizes than the other age/sex group types [see Refera & Bekele (2004) for nyala; Afework *et al.* (2009) for reedbuck)]. Therefore, there might be a greater tendency for this group type to form interspecific association, accounting for the observed larger group sizes of the associated groups of these species. However, this requires further investigations to examine which age-sex categories more frequently associated with other species.

In conclusion, if the reasons for the formation of multi-species groupings observed in ungulates of the BMNP is attributed to one or more of the factors discussed above, it is beneficial to one or all of the species involved. However, the present findings should be interpreted cautiously as the duration (stability) and function of these multi-species associations are not clearly understood, and the observations could thus be an artefact of coincidence rather than true symbiotic relationships. Further research is therefore necessary to understand the stability/duration of the interspecific associations observed in the present study, which age/sex categories show more tendencies to form such associations, and the functions and activity patterns of the association.

### **Acknowledgements**

Jemal Kassim and Usman Abdella are duly acknowledged for their help during the data collection. These data were collected during a bird study conducted in the study area, a project funded by the Fitzpatrick Institute of Ornithology Centre of Excellence/University of Pretoria and Frankfurt Zoological Society-Bale Mountains Conservation Project.

## References

- AFEWORK, B., BEKELE, A. & BALAKRISHNAN, M. (2009) Population status, structure and activity patterns of the Bohor reedbuck *Redunca redunca* in the north of the Bale Mountains National Park, Ethiopia. *Afr. J. Ecol.* **48**, 502–510.
- ASEFA, A. (2007) Birds of Bale Mountains National Park, Southeast Ethiopia. *Walia* **25**, 22-33.
- ASEFA, A. (2008) Mountain Nyala and Ethiopian Wolf Mortalities in the northern side of Bale Mountains National Park, Ethiopia. *Ethiop. J. Biol. Sci.* **7**, 179-184.
- ASEFA, A. (2011) Mammals of the Bale Mountains National Park, Ethiopia: compiled and annotated checklist. *Walia-Special Edition on the Bale Mountains*, 3-14.
- DESBIEZ, A.L.J., ROCHA, F.L., & KEUROGHLIAN, A. (2010) Inter-specific association between an ungulate and a carnivore or a primate. *acta ethol* **13**, 137-139.
- FISCHER, F. & LINSENMAYER, K. E. (2007) Changing social organization in an ungulate population subject to poaching and predation – the kob antelope (*Kobus kob kob*) in the Comoé National Park, Côte d'Ivoire. *Afr. J. Ecol.* **45**, 285-292.
- GERARD, J. & LOISEL, P. (1995) Spontaneous emergence of a relationship between habitat openness and mean group size and its possible evolutionary consequences in large herbivores. *J. Theor. Biol.* **176**, 511-522.
- HILLMAN, J.C. (1986) *Management plan of Bale Mountains National park*. Ethiopian Wildlife Conservation Organization, Addis Ababa.
- HILLMAN, J.C. (1987) Group size and association patterns of the common eland (*Tragelaphus oryx*). *J. Zool. Lond.* **213**, 641-663.
- JARMAN, P.J. (1974) The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215-267.

- KINGDON, J. (1997) *The Kingdon Field Guide to African Mammals*. Academic Press, London.
- LEUTHOLD, W. & LEUTHOLD, B. (1975) Patterns of social grouping in ungulates of Tsavo National Park, Kenya. *J. Zool. Lond.* **175**, 405-420.
- MAMO, Y. & BEKELE, A. (2011) Human and livestock encroachments on habitat of mountain nyala (*Tragelaphus buxtoni*) in Bale Mountains National Park, Ethiopia. *Trop. Ecol.* **52**, 265-273.
- NH (The National Herbarium) (2004) *Biodiversity assessment of the Bale Mountains National Park and surrounding areas*. The National Herbarium, Addis Ababa University, Addis Ababa.
- OBARD (OROMIA BUREAU OF AGRICULTURE AND RURAL DEVELOPMENT) (2007) *General Management Plan of the Bale Mountains National park (BMNP), Ethiopia*. OBARD, Addis Ababa.
- REFERA, B. & BEKELE, A. (2004) Population status and structure of mountain nyala in the Bale Mountains National Park, Ethiopia. *Afr. J. Ecol.* **42**, 1-7.
- SCHAEFER, J.A., STEVENS, S.D. & MESSIER, S. (1996) comparative winter habitat use and associations among herbivores in the High Arctic. *Arctic* **49**, 387-391.
- SINCLAIR, A.R.E. 1985. Does inter-specific competition or predation shape the African ungulate community? *J. Anim. Ecol.* **54**, 899-918.
- SINCLAIR, A.R.E. & ARCESE, P. (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* **76**, 882-891.
- STANKOWICH, A. (2008) Ungulate flight responses to human disturbance: A review and meta-analysis. *Biol. Conserv.* **141**, 2159-2173.

- STENSLAND, E., ANGERBJÖRN, A. & BERGGREN, P. (2003) Mixed species groups in mammals. *Mammal Rev.* **33(3)**, 205-223.
- STEPHENS, P.A., D'SA, C.A., SILLERO-ZUBIRI, C. & WILLIAMS, N.L. (2001) Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, Southern Ethiopia. *Biol. Conserv.* **100**, 307-322.
- WILLIAMS, S., VIVERO POL, J.L., SPAWLS, S., SHIMELIS, A. & KKELBESSA, E. (2004) Ethiopian Highlands. In: *Hotspots revisited* (EDS. R.A. MITTERMEIER, P.R. GILL, M. HOFFMANN, J. PILGRIM, T. BROOKS, C.G. MITTERMEIER, J. LAMOREUX AND & G.A.B. DA FONSECA). CEMEX Publisher, Mexico City.