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Effect of human nuisance on the social organisation of large mammals: group sizes and compositions of seven ungulate species in Lake Mburo National Park and the adjacent Ankole Ranching Scheme

Christiane Averbeck, Martin Plath, Torsten Wronski & Ann Apio

Most ungulates in East African savannahs experience some form of human disturbance, such as direct pursuit (e.g. hunting and poaching), habitat degradation and competition with livestock. In many studies, the impact of human activities on wildlife is assessed through census counts, i.e. by estimating population sizes or densities, but also the social organisation of gregarious species can be affected. Using seven species of ungulates occurring in the Akagera Ecosystem, we compared grouping patterns (i.e. group sizes and compositions) of different group types (e.g. bachelor, all-female and mixed-sex groups) between sites situated inside a protected area, i.e. Lake Mburo National Park in Uganda and the adjacent Ankole Ranching Scheme (ARS), an unprotected area with intense human pursuit. Differences in group sizes were detectable in only a few cases, e.g. bachelor group size in common eland *Tragelaphus oryx pattersonianus* increased in the ARS, which may be advantageous due to increased vigilance. However, we found pronounced differences in group compositions in numerous species and for different group types, for example, in eland and waterbuck *Kobus ellipsiprymnus defassa* (i.e. in all group types), and topi *Damaliscus lunatus jimela*, oribi *Ourebia ourebi* and warthog *Phacochoerus aetiopicus* (all-female and mixed-sex groups). We discuss that continuous monitoring of grouping patterns of these (and other) species may be a valuable approach to detect 'subtle' effects of human nuisance even before an overall population decline can be observed.

Key words: African ungulates, domestic livestock, game ranching, poaching, social organisation, Akagera Ecosystem

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The 'Unified Classification of Direct Threats' of the IUCN lists a number of threats to wildlife across natural habitats in Africa and other parts of the world (CMP 2005, CMP-IUCN 2007). Under the category 'Livestock Farming and Ranching', Salafsky et al. (2008) list raising of domestic or semi-domesticated animals which are allowed to roam in the wild and are supported by natural habitats (i.e. game ranching; Nuding 1996). In many regions

throughout the African continent, wild ungulate species encounter exactly this form of anthropogenic nuisance, which includes competition between domestic livestock and game (Prins 1992, Treydte et al. 2005) and regular burning of the vegetation (Glover 1968, Sodeinde 1992). Killing or trapping of wild animals for commercial purposes or subsistence (e.g. Newby 1990, Fischer & Linsenmair 2007, Setsaas et

al. 2007) naturally represents another severe threat listed in Salafsky's et al. (2008) compilation.

These forms of human activities are known to affect population sizes or densities of wild ungulates negatively (Norton-Griffiths 1979, Newby 1990, Sodeinde 1992, Prins 1992, 2000, Treydte et al. 2005, Holmern et al. 2006, Fischer & Linsenmair 2007, Hassan 2007). Still, where protected areas with a self-sustaining population of a given species exist in close proximity to areas that are affected by human activities, source-sink dynamics may occur, whereby an apparently stable population in the disturbed area depends on continuous immigration from the protected (source) habitat (Watkinson & Sutherland 1995, Gundersen et al. 2001, Awerbeck et al. 2009). This confounding effect can complicate efforts to determine whether anthropogenic effects indeed affect a given (meta) population negatively as the adverse effects of hunting and competition on the population size or density of a resident population can be masked.

A situation as outlined above is found in some ungulate species inhabiting Lake Mbuho National Park (LMNP) and the adjacent unprotected ranchland of the Ankole Ranching Scheme (ARS) in Uganda, which are part of the Akagera Ecosystem (Awerbeck et al. 2009, 2010). Livestock keeping and burning of the vegetation in areas subjected to pastoralism are often accompanied by shifts in landscape structuring and habitat modifications, which can be followed by pronounced changes in the communities of ungulates (de Boer & Prins 1990, Prins 2000, Treydte et al. 2005, Lamprey & Mugisha 2009). Although landscape structures in the ARS have been modified to a relatively small extent (Hoag & Clements 1993), some vegetation types have clearly changed; e.g. the proportion of mixed *Bracharia*-woodlands declined in the ARS (Hoag & Clements 1993, Awerbeck et al. 2009).

Population sizes of some species such as topi *Damalicus lunatus* (Rannestad et al. 2006, Awerbeck et al. 2009) and African buffalo *Synceros caffer* (our study) are obviously declining in the ARS. Still, Awerbeck et al. (2009) reported on other species such as impala *Aepyceros melampus* being even slightly more abundant in the ARS than inside LMNP even though impala experience strong hunting and poaching in the ARS (Awerbeck 2001, 2002, Lamprey & Mugisha 2009). Awerbeck et al. (2009), therefore, suggested that source-sink dynamics may be operating, with dispersing animals from inside the park constantly replenishing the hunted population in the

ARS. For other species, we have previously argued that relaxed competition by species that became less abundant outside LMNP may actually provide benefits, thus trading off some of the costs (through direct pursuit, stress and competition with livestock) associated with life in the unprotected ARS. Such a mechanism was proposed for the competitive interaction between common duiker *Sylvicapra grimmia*, which is a species that became more abundant in the ARS and bushbuck *Tragelaphus sylvaticus*, which is a species that became less abundant in the ARS. Common duiker showed a significant change in habitat use in the ARS; they tended to use the vegetation type otherwise used by the bushbuck (Awerbeck et al. 2009).

We argue that even if no direct (negative) effects of human activities can be seen at the level of overall population densities in some ungulate species, it may still be possible to determine other, more subtle, effects of human nuisance in the ARS as compared to areas inside LMNP. Human activities can lead to changes at the level of behaviour, and ultimately group structure or composition, or more generally speaking, the social organisation of a species (Caro 1999, Fischer & Linsenmeier 2007). Thus, examining the behaviour and/or group structure of social mammals can be an important tool in conservation biology (McLean 1997, Sutherland 1998, Reed 2002). For example, direct human pursuit (i.e. hunting and poaching) can lead to increased vigilance, so individuals may form larger groups, which provide anti-predator benefits through a 'many-eyes-effect' (Quenette 1990, Hunter & Skinner 1998, Burger et al. 2000), numerical dilution or predator confusion (Roberts 1996, Krause & Ruxton 2002). This effect should be especially pronounced in species that naturally form very small groups (i.e. in our study, this would be oribi *Ourebia ourebi*, warthog *Phacochoerus aetiopicus* and reedbuck *Redunca redunca*). Hence, an increase in group size may be seen only for the smallest type of social groups within a species; e.g. in impala, only the very small bachelor groups increased in size in the ARS (Awerbeck et al. 2010). On the other hand, habitat degradation (leading to increased competition for resources), as well as direct competition with livestock for shared resources, may favour the formation of smaller groups, as competition is a function of group size (Pulliam & Caraco 1984, Ranta et al. 1993, Krause & Ruxton 2002). Accordingly, the largest group type in impala (mixed-sex groups) decreased in the ARS (Awerbeck et al. 2010). A similar pattern would be predicted for

several of the species considered here, as bachelor groups in ungulates are typically by far smaller than all-female and especially mixed-sex groups (Estes 1974, Leuthold 1977, Rodgers 1977; see also results in our study).

Specifically, we compared group structures and compositions of wild ungulates in and outside LMNP. Data on the most common antelope in the study area, the impala, are presented elsewhere (Averbeck et al. 2010). Also, data on the crepuscular, mostly solitary bushbuck *Tragelaphus sylvaticus* (previously believed to be synonymous with *T. scriptus*; Moodley et al. 2009) have been discussed within the framework of a comparison of grouping patterns of different bushbuck ecotypes throughout sub-Saharan Africa, where no differences were found between LMNP and the ARS (Wronski et al. 2009). We considered three types of social groups, i.e. mixed groups (composed of several females and their offspring as well as one or few dominant males), bachelor groups (comprising males of different age classes), and all-female groups (comprising females of different age classes and their most recent offspring). We asked if group sizes would be affected by human activities as shown for impala (Averbeck et al. 2010). Specifically, the smallest group type (i.e. bachelor groups) might become larger in the ARS, as larger groups may provide benefits due to increased vigilance (Quenette 1990, Roberts 1996, Li et al. 2009), whereas larger groups (all-female or mixed-sex groups) should either not respond to the same extent, or even become smaller (Averbeck et al. 2010).

Besides that, human nuisance may affect group compositions; e.g. selective hunting on certain age classes or preferential hunting of one sex will affect group compositions (Averbeck et al. 2010). In impala, for example, the chance of being injured is considerably higher for poachers when using nets compared to using snares or firearms, so poachers prefer hornless females (and their calves) over horned males. Differences in group compositions may also be indicative of site-specific differences in the dispersal behaviour of different age classes: for example, if feeding competition in large groups (i.e. especially mixed-sex groups) becomes increasingly important in the ARS, then yearlings and subadult individuals should be disproportionately affected by this, and might leave mixed-sex groups more frequently so as to join smaller bachelor groups (in the case of young males) or all-female groups (i.e. young females).

Methods

Study area and period

We carried out our study from July 1997 to December 1999 in Lake Mburo National Park (LMNP) and the adjacent Ankole Ranching Scheme (ARS), Nyabushozi County in southwestern Uganda. The average altitude of our study area is about 1,200 m a.s.l. The area is characterised by low undulating hills and an extensive system of permanent lakes and swamps and is part of the Akagera ecosystem extending from Rwanda and northwestern Tanzania into southwestern Uganda. LMNP is dominated by *Acacia* savannahs with open grasslands and flooded plains in the valley bottoms (Menault 1983, Vande weghe 1990). The mean annual rainfall (during 1975–1997) in the study area reaches 887 mm with a minimum of 480 mm and a maximum of 1,270 mm; the mean monthly temperature is 20.2°C with a maximum of 27.5°C and a minimum of 15.0°C (Kamugisha et al. 1997). In 1998, the area experienced an 'El Nino' event and the annual rainfall reached 1,110 mm, whereas the following year was distinctly drier with an annual rainfall of 748 mm.

In 1935, the area around Lake Mburo was declared 'Controlled Hunting Area', i.e. both regulated game hunting and traditional human activities were permitted (Averbeck 2006). In the 1940s, a severe outbreak of the Nagana disease forced pastoralists out of the area and severely reduced the game population (Herne 1979). By the early 1960s, vectors of the Nagana disease (tsetse flies) had been eradicated, once again opening up the area to pastoralism (Kreuzer 1979). To protect the remaining wildlife, the 'Lake Mburo Game Reserve' was gazetted, even though resident pastoralists were still permitted to retain their livestock. In 1983, 'Lake Mburo National Park' was established comprising an area of 650 km² while strictly excluding the herdsmen. In order to solve the ongoing conflict between pastoralism and wildlife conservation, the park area was reduced in 1986 by 60% to 260 km² (Snelson & Wilson 1994). Since then, law enforcement activities of Uganda Wildlife Authority have further improved (i.e. regular patrols of the park boundary to prevent cattle from entering the park, driving cattle out of the protected area and severe fines for violating the ban; Averbeck 2001). In 1963 the implementation of 50 ranches adjacent to the Lake Mburo Controlled Hunting Area (the predecessor of the first LMNP) was planned and designed, the 'Ankole Ranching Scheme', which totals an area of about 647 km²

(Hoag & Clements 1993). The LMNP of today has no buffer zone and is bordered by farmland and the ARS (Fig. 1). Resident pastoralists live around the periphery of the park, in an area that is too small to support the number of cattle they require. Infield (1993) reported on an actual stocking rate of 1 cow/1.5 ha, whereas the recommended stocking rate was 1 cow/2 ha. Severe overstocking has resulted in changes in vegetation types (Hoag & Clements 1993, Averbeck et al. 2009). The prevalent approach of the conservation authorities towards local communities was simply to keep them out of the protected area. In the late 1980s and early 1990s, this policy changed. A project on Community Conservation was established (Averbeck 2006), while emphasising formal environmental education, capacity building and support of community development. However, this approach did not stop the local communities from using wildlife in an unsustainable manner. Finally, in 1996, a participatory research project laid the foundation for a community-based wildlife utilisation project (Averbeck 2002, 2006).

Study species

In our study, we considered seven ungulate species including two highly gregarious, non-selective roughage feeders of > 300 kg body weight (African buffalo *Syncerus caffer* and common eland *Tauro-*

tragus oryx pattersonianus). The topi *Damaliscus lunatus jimela*, a medium sized (i.e. 130 kg) savannah dweller, is a migrating species and a pure grazer; the defassa waterbuck *Kobus ellipsiprymnus defassa* (weighing up to 250 kg) is a mixed feeder and also highly gregarious (Dorst & Dandelot 1970). Two grazing antelope species < 80 kg inhabiting the grasslands of our study area were included, i.e. bohor reedbuck *Redunca redunca wardi* and oribi *Ourebia ourebi cottoni*. Apart from these bovids, we included a diurnal suid species, the warthog *Phacochoerus africanus*.

Strictly nocturnal species such as hippopotamus *Hippopotamus amphibius* and bushpig *Potamochoerus larvatus* and species either confined to rocky outcrops (i.e. klipspringer *Oreotragus oreotragus*) or living more or less solitarily in dense habitats, such as common duiker *Sylvicapra grimmia campbelliae* were excluded from our analysis. The only equid in the area, plains zebra *Equus burchelli böhmi*, had to be omitted from our analysis as sex and age classes could not be determined unambiguously in the field. Mammalian predator species encountered during our study in LMNP were leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta*, black-backed jackal *Canis mesomelas schmidtii* and side-striped jackal *Canis adustus lateralis*.

Data collection

From July 1997 to December 1999, we carried out road counts. Road counts enabled us to cover a large area, comprising most parts of the park (except the hilly part in the west), as well as the ARS including the northern and eastern ranches. We established four tracks, each with a total track length of 150 km (Averbeck et al. 2009). Two road transects were situated inside LMNP, one on the northern ranches and one on the eastern ranches of the ARS (see Fig. 1). Apart from the woodland along the western hills of LMNP, the road transects covered all vegetation types. To account for seasonal differences in the distribution of ungulates, counts were conducted approximately twice a month for each transect. In total, we recorded 2,532 sightings of ungulate groups or 7,852 individual altogether (for details and estimates of mean group-sizes across group-types; Table 1). Three persons participated in the road counts, namely a driver and two people counting wildlife on either side of the road. We recorded all visible animals whenever encountered, and group sizes and compositions were noted. We determined age classes following criteria such as horn length and

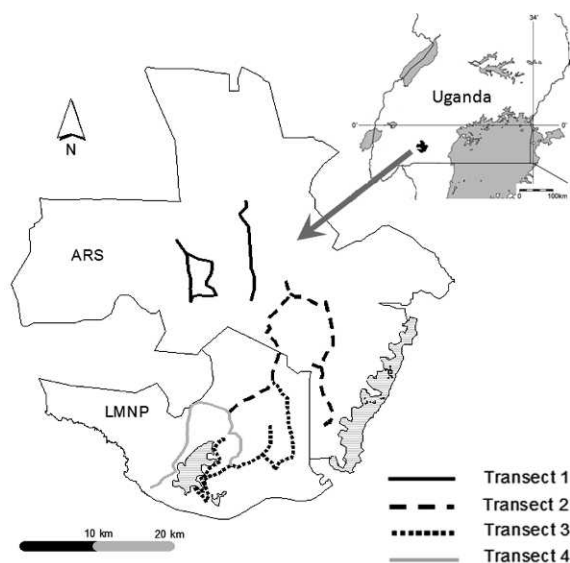


Figure 1. Lake Mbuho National Park (LMNP), the adjacent Ankole Ranching Scheme (ARS) and the location of the four roads transects. Inlet indicates location of study area in southwestern Uganda.

Table 1. Grouping patterns of seven species of ungulates in Lake Mburu National Park (LMNP) and the adjacent Ankolet Ranching Scheme (ARS). Data for the eighth species included here (impala) were published elsewhere. Depicted are numbers of sightings of three group types (bachelor, mixed-sex and nursery (all-female) groups), along with total numbers of individuals encountered within each category during our survey. Mean group sizes across group types (MGS) are given as means $\pm$ SE.

Species	Park (LMNP)						Ranch (ARS)						Reference
	# Sightings			# Individuals			# Sightings			# Individuals			
	Bachelor	Mixed	All-female	Bachelor	Mixed	All-female	Bachelor	Mixed	All-female	Bachelor	Mixed	All-female	
Buffalo	122	18	9	178	480	25	-	-	-	-	-	-	Our study
Eland	20	21	56	31	267	370	10	3	7	26	27	46	Our study
Topi	259	220	114	349	1155	372	15	10	8	21	52	28	Our study
Waterbuck	161	97	54	378	547	170	25	1	30	82	7	82	Our study
Reedbuck	28	27	58	35	68	74	3	7	23	6	14	24	Our study
Oribi	32	69	60	34	165	106	25	89	17	27	207	23	Our study
Warthog	301	180	316	363	868	1059	19	6	12	23	25	38	Our study
Impala	937	736	206	3057	13344	1088	645	432	150	2385	6250	693	7.77 ± 0.28 Averbeck et al. (2009)

shape and body proportions established by Anthony & Lightfoot (1984) for topi, Jeffery & Hanks (1981) for eland, Spinage (1967) for waterbuck, Manson (1985) for warthog, Viljoen (1982) for oribi and Spinage & Brown (1988) for African buffalo.

Statistical analysis

We distinguished between mixed groups (i.e. groups consisting of females and some associated males including pairs), pure bachelor groups (i.e. groups consisting of only male individuals including single males) and all-female groups (i.e. groups consisting of only female individuals and their offspring including single females). In our first analysis, we tested for general differences in group-sizes between the protected area (LMNP) and the adjacent ranchlands (ARS). We subjected mean group sizes for each species and group type to General Linear Models (GLM, using SPSS 12.0), in which we used the location (inside LMNP or in the ARS) as well as season (wet or dry) as independent variables (fixed factors). Specifically, this analysis tested for a potential decrease in group sizes on the unprotected ranchlands in the case of all-female and mixed-sex groups, and a potential increase in bachelor group size. We initially conducted all analyses while including the factor 'year', but removed it from the final analyses, as no statistically significant effects were uncovered.

Our second analysis considered the question of whether group compositions of bachelor, all-female and mixed groups (i.e. numbers of different sex and age classes present in the herds) would differ between LMNP and the ARS. We compared group compositions (i.e. the percentage proportion of different sex/age categories; see Fig. 3) between sites (inside and outside LMNP) for each group type using χ^2 -tests.

Results

Differences in group size between LMNP and the ARS

In none of the examined species, we detected seasonal variation in group sizes (see factor 'Season' and interaction effect of 'Season by Ranch/Park' in Table 2).

We did, however, find statistically significant differences in mean group sizes in two cases (see factor 'Park/Ranch' in Table 2): First, group sizes of eland bachelor groups increased from 1.55 ± 0.18 (mean $\pm$

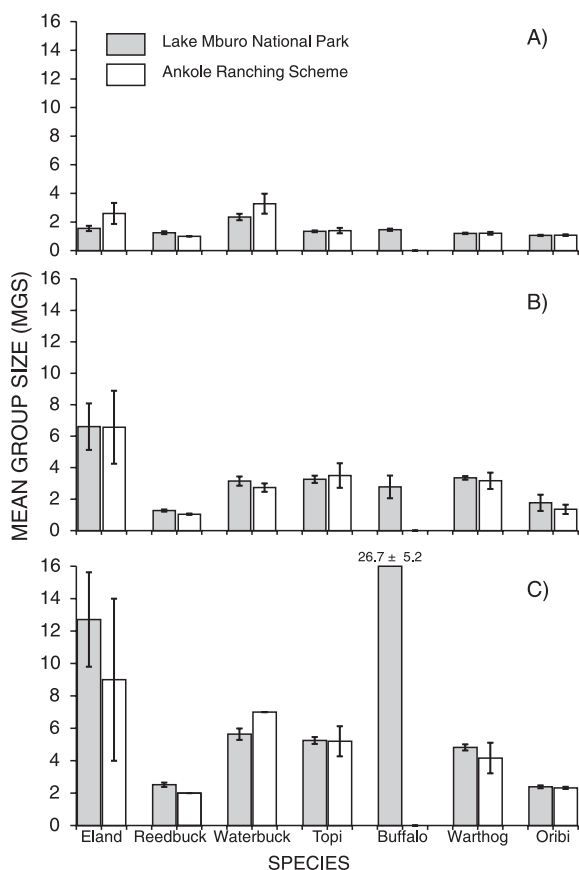


Figure 2. Mean group sizes (MGS) of the three group types A) bachelor, B) all-female and C) mixed-sex groups in seven ungulate species occurring in Lake Mburo National Park and the adjacent Ankole Ranching Scheme. Note that no buffalo were sighted in the Ankole Ranching Scheme (ARS).

SE) inside LMNP to 2.60 ± 0.73 in the ARS ($P = 0.024$; see Table 2). We saw a similar, albeit non-significant trend in the case of waterbuck bachelor groups (Fig. 2). In all other species, bachelor males were almost invariably organised in very small 'groups', i.e. exhibited mean groups sizes around one (see Fig. 2).

Second, reedbuck all-female groups decreased significantly from 1.28 ± 0.07 in LMNP to 1.04 ± 0.04 in the ARS ($P = 0.027$; see Table 2 and Fig. 2); in other words: reedbuck females were more likely to be solitary in the ARS. Waterbuck, warthog and oribi showed a similar trend, but the decrease in group sizes in the ARS was not statistically significant (see Table 2).

Differences in group compositions

Bachelor group compositions differed significantly between LMNP and the ARS in the case of eland and

waterbuck (Table 3), and in both cases, this effect was driven by bachelor groups being composed of relatively more young males ('M1', 'M2') but fewer males of the oldest age class ('M3') in the ARS than inside LMNP (Fig. 3).

All-female group composition differed significantly between LMNP and the ARS in all species except reedbuck (see Table 3). In the case of topi and waterbuck, this effect was driven by relatively more juveniles and fewer or no young females ('F1', 'F2') in the ARS compared to group compositions inside LMNP (see Fig. 3), whereas in the case of eland and oribi, it was driven by fewer juveniles in the ARS (see Fig. 3). In eland and warthog the difference among sites was also due to relatively more yearling and subadult females ('F1', 'F2') on the ranches (see Fig. 2).

Also, mixed-sex group compositions differed significantly between LMNP and ARS in all species except reedbuck (see Table 3). In eland and warthog, this effect was driven by no or fewer juveniles in the ARS (see Fig. 3). In both cases, the number of yearlings and subadult individuals was largely reduced in the ARS, in the case of eland even to such an extent that exclusively adults were observed on the ranches (see Fig. 3). In case of waterbuck, topi and oribi, the effect was driven by fewer or no adult males, but distinctly more adult females in the ARS (see Fig. 3). Furthermore, no waterbuck calves were observed on the ranches (see Fig. 3).

Discussion

Bachelor groups

Overall, eland bachelor groups were significantly larger in the ARS than inside LMNP. The same pattern was described for impala (Averbeck et al. 2010), and in our study, also waterbuck bachelor groups showed a similar (but non-significant) trend towards larger groups. According to the 'many-eyes-theory', larger groups provide increased vigilance for the individual group members even though each group member can decrease its individual vigilance, but also 'safety in numbers' plays a role (Elgar 1989, Dehn 1990, Roberts 1996, Krause & Ruxton 2002). Animals in larger groups automatically benefit from the 'dilution effect', as the individual predation risk per attack is reduced as a function of group size. Negative effects of large group size, such as increased competition (i.e. reduced foraging success) and risk of disease transmission, can act against the formation

Table 2. Results from General Linear Models (GLM) using mean group sizes of bachelor, all-female and mixed-sex groups as dependent variables, and location (park/ranch) and season (wet or dry) as fixed factors. Removing non-significant interaction terms qualitatively did not alter the direction of the statistical tests (results not shown). Statistically significant effects are in italic typeface.

Species ¹⁾	Group type	Effect	df	Mean square	F	P
Eland	<i>Bachelor</i>	<i>Park/ranch</i>	<i>1</i>	<i>12.42</i>	<i>5.76</i>	<i>0.024</i>
		Season	1	2.40	1.12	0.30
		Park/ranch*season	1	4.91	2.28	0.14
		Error	26	2.16		
	All-female	Park/ranch	1	0.79	0.01	0.93
		Season	1	100.12	0.89	0.35
		Park/ranch*season	1	3.12	0.03	0.87
		Error	59	111.98		
	Mixed-sex	N/a ²⁾				
Reedbuck	Bachelor	Park/ranch	1	0.29	1.25	0.27
		Season	1	0.04	0.17	0.68
		Park/ranch*season	1	0.04	0.17	0.68
		Error	30	0.23		
	<i>All-female</i>	<i>Park/ranch</i>	<i>1</i>	<i>1.03</i>	<i>5.06</i>	<i>0.027</i>
		Season	1	0.00	0.16	0.90
		Park/ranch*season	1	0.00	0.16	0.90
		Error	77	0.20		
	Mixed-sex	Park/ranch	1	0.77	1.97	0.17
		Season	1	0.25	0.65	0.43
		Park/ranch*season	1	0.26	0.65	0.43
		Error	30	0.39		
Waterbuck	Bachelor	Park/ranch	1	6.81	0.79	0.38
		Season	1	17.61	2.04	0.16
		Park/ranch*season	1	16.14	1.87	0.17
		Error	182	8.65		
	All-female	Park/ranch	1	23.82	2.51	0.11
		Season	1	3.80	0.40	0.53
		Park/ranch*season	1	0.03	0.00	0.96
		Error	331	9.48		
	Mixed-sex	N/a ²⁾				
Topi	Bachelor	Park/ranch	1	0.02	0.02	0.90
		Season	1	0.26	0.27	0.60
		Park/ranch*season	1	0.26	0.27	0.60
		Error	270	0.97		
	All-female	Park/ranch	1	0.00	0.00	0.98
		Season	1	1.41	0.24	0.63
		Park/ranch*season	1	0.02	0.00	0.96
		Error	118	5.96		
	Mixed-sex	Park/ranch	1	0.04	0.00	0.95
		Season	1	1.28	0.13	0.72
		Park/ranch*season	1	0.06	0.01	0.94
		Error	233	10.05		

Table 2. Continued.

Species ¹⁾	Group type	Effect	df	Mean square	F	P
Oribi	Bachelor	Park/ranch	1	0.00	0.06	0.80
		Season	1	0.05	0.73	0.40
		Park/ranch*season	1	0.06	0.89	0.35
		Error	53	0.07		
	All-female	Park/ranch	1	1.18	0.09	0.77
		Season	1	4.71	0.36	0.55
		Park/ranch*season	1	1.36	0.10	0.75
		Error	73	13.09		
	Mixed-sex	Park/ranch	1	0.41	0.88	0.35
		Season	1	0.17	0.38	0.54
		Park/ranch*season	1	0.63	1.37	0.24
		Error	154	0.46		
Warthog	Bachelor	Park/ranch	1	0.15	0.20	0.66
		Season	1	0.18	0.24	0.63
		Park/ranch*season	1	1.54	2.03	0.16
		Error	316	0.76		
	All-female	Park/ranch	1	0.03	0.01	0.93
		Season	1	7.84	1.96	0.16
		Park/ranch*season	1	0.71	0.18	0.67
		Error	324	4.00		
	Mixed-sex	Park/ranch	1	7.52	1.18	0.28
		Season	1	12.82	2.01	0.16
		Park/ranch*season	1	14.55	2.28	0.13
		Error	182	6.37		

¹⁾ No sightings of African buffalo on ranchland.

²⁾ No sightings of mixed-sex groups in eland and waterbuck on ranchland during the dry season. Recalculating GLM while lumping data from both seasons and leaving out the factor 'season' from the analysis did not yield significant results in either case (not shown).

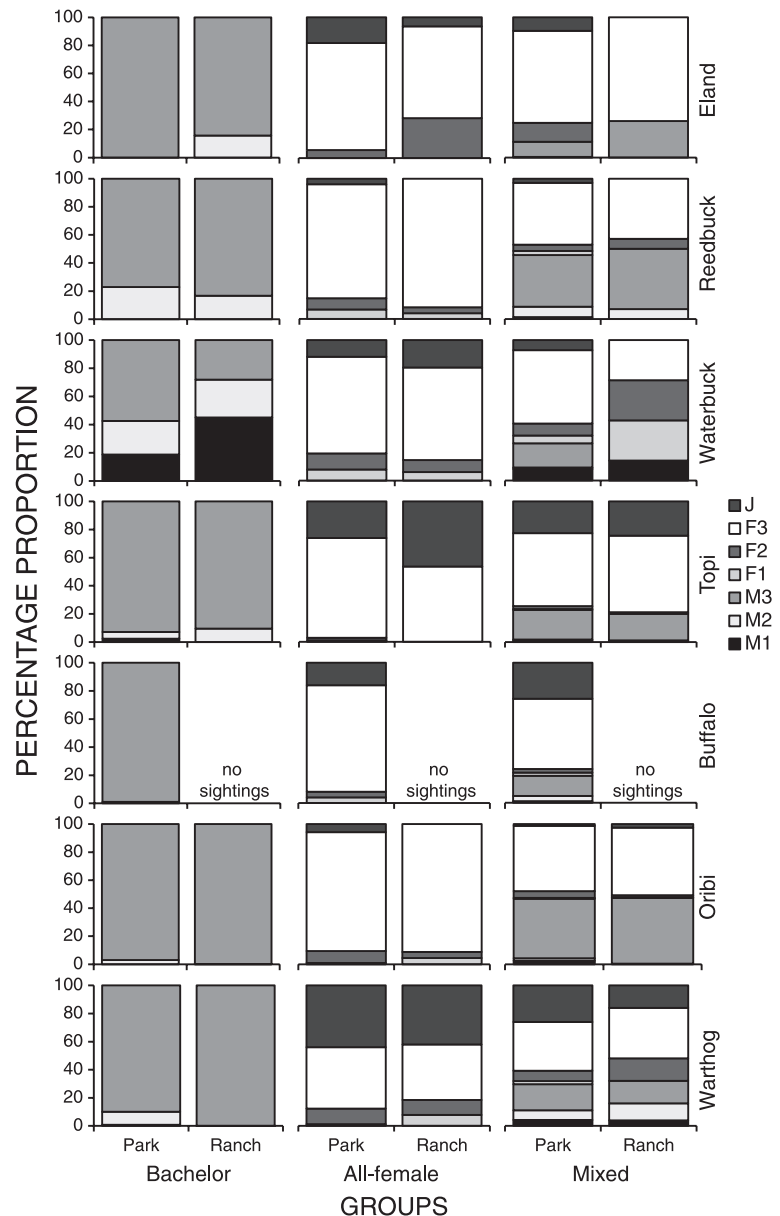
of larger groups but are outweighed by the aforementioned advantages (increased vigilance and dilution) under higher predation risk. We argue that increased vigilance may be of particular importance in the ARS, where human pursuit is strong. Bachelor groups are relatively small compared to all-female or mixed-sex groups (see Fig. 2), so benefits from increasing group sizes (in terms of increased vigilance

or dilution) may be particularly strong for this group type (Averbeck et al. 2010). However, habitat types inside and outside the park are different (Hoag & Clements 1993), so it is also possible that bachelors are being excluded from the better habitats inside the park by more dominant breeding males. This factor may contribute to the observed difference in bachelor-group size of the large-bodied wide-ranging

Table 3. Results of χ^2 -tests comparing group compositions (according to age classes) of all three group types considered in our study between Lake Mbuo National Park and the adjacent Ankole Ranching Scheme.

	Bachelor			All-female			Mixed-sex		
	χ^2	df	P	χ^2	df	P	χ^2	df	P
Eland	3110	2	< 0.01	2963	3	< 0.001	1119	6	< 0.001
Reedbuck	11	2	n.s.	1.79	3	n.s.	1.33	6	n.s.
Waterbuck	3131	2	< 0.01	443	3	< 0.05	1248	6	< 0.001
Topi	177	2	n.s.	11.08	3	< 0.01	259	6	< 0.05
Buffalo				not applicable					
Oribi	83	2	n.s.	3.24	3	< 0.05	1141	6	< 0.001
Warthog	256	2	n.s.	11.46	3	< 0.01	502	6	< 0.01

Figure 3. Group compositions (fractions of different age classes) of the three group types in seven ungulate species occurring in Lake Mburu National Park (Park) and the adjacent Ankole Ranching Scheme (Ranch). Age classes considered were juveniles (J), and males (M) or females (F) of three age categories (1: yearlings, 2: subadults and 3: adults).



species and could also account for why this change in group size does not occur in females.

The pattern of increased bachelor group sizes, however, does not necessarily apply to other regions (i.e. is not a generalisable pattern): For instance, in impala from Nairobi National Park (Kenya), only all-female groups, but not bachelor groups, showed a shift towards larger groups in areas subjected to human disturbance (Shorrocks & Cokayne 2005). Also in stark contrast to our findings, a study on grouping patterns in Buffon's kob *Kobus kob kob* in Comoé National Park (Ivory Coast) suggested that

being alone or in small groups might be advantageous to avoid human pursuit, as poachers are less likely to detect singletons or small groups (Fischer & Linsenmaier 2007). Still, the formation of large groups may be beneficial in the face of predation by natural predators (Fischer & Linsenmaier 2007, Gude et al. 2006).

In summary, it appears as if 1) only some ungulate species considered in our study show the predicted increase in bachelor group sizes (Averbeck et al. 2010, our study), and 2) even within the same species, different responses can be seen in different regions

(e.g. Shorrocks & Cokayne 2005, Averbeck et al. 2010). We tentatively suggest that the trade-off between costs (like increased competition and/or aggressive combat within groups; Krause & Ruxton 2002) and the benefits of increasing group sizes vary across species and regions (as exemplified by the aforementioned study by Fischer and Linsenmaier 2007). This could be due, e.g. to regional differences in forms of hunting and poaching (see below). Also, some large-bodied species like eland offensively defend themselves against predators (Hillman 1974), rendering the formation of larger groups a more profitable option, whereas other (small) species like oribi, reedbuck and warthog rely on concealment and flight (Jungius 1971, Montfort & Montfort 1974, Cumming 1975).

Differences among study sites (when comparing this to the various aforementioned studies) may affect this trade-off, as landscape and habitat structures can affect the behaviour of predators (and hunters/poachers), the possibility to detect ambushing predators and escape abilities of their prey (Gros & Rejmanek 1999, Hopcraft et al. 2005, Heithaus et al. 2009). Some predators simply hunt where prey is most abundant (as described for numerous carnivores e.g. Litvaitis et al. 1986, Murray et al. 1994, Thom et al. 1998, Pike et al. 1999, Palomares et al. 2001, Spong 2002), whereas others hunt in areas where prey is locally scarce but cover enables sit-and-wait predators to take advantage of the camouflage (Pienaar 1974, Sinclair 1985, Prins & Iason 1989, FitzGibbon & Lazarus 1995, Sinclair & Arcese 1995, Bouskila 2001). Due to intense cattle grazing and frequent human-induced burning of the vegetation, grass height in the ARS is lower compared to areas inside LMNP (Muhuku 1993), a trend which holds until the present day (A. Apio & T. Wronski, pers. obs. in 2011). This benefits chasing predators like hyenas, rather than leopards *Panthera pardus* or lions *P. leo*. On the other hand, regular burning and heavy grazing leads to bush encroachment in the ARS (Muhuku 1993), which, in turn, benefits ambushing predators. This aspect of predator-prey ecology clearly warrants further investigation in and around LMNP.

All-female and mixed-sex groups

Reedbuck all-female groups were significantly smaller in the ARS. This pattern was visible (at least qualitatively) in all species considered in our study (see Fig. 2) except topi and eland (even though at least mixed-sex groups tended to show the same

pattern in eland; see Fig. 2). Also mixed-sex groups of impala in the same study area decreased in size in the ARS (Averbeck et al. 2010). Manor & Saltz (2003) attributed the decrease in group size in mountain gazelle *Gazella gazella gazella* in the Negev desert to anthropogenic nuisance. In that case, it was demonstrated that 1) vigilance is a function of group size and larger groups are more able to detect predators, but 2) the increase in vigilance with increasing group size becomes insignificant in areas with very high anthropogenic nuisance. The relationship between group size and vigilance still needs to be determined for all-female groups of the ungulate species examined here; however, based on our present study (i.e. based on the observation of larger bachelor groups in the ARS in impala (Averbeck et al. 2010) and eland (our study)), we are inclined to argue that vigilance indeed increases with increasing group size also in disturbed areas.

As we have discussed above (see Introduction), competition among the members of a herd generally favours the formation of smaller groups (leading to a trade-off between costs and benefits of increased group size), and this effect could be aggravated in areas where habitat degradation or competition with livestock play a role. In reedbuck, however, such a scenario is highly unlikely, as all-female groups were generally very small. Indeed, resource competition within the very small reedbuck groups is unlikely to account for the decrease from 1.28 ± 0.07 (in LMNP) to 1.04 ± 0.04 females per group (in ARS). Interviews with poachers, however, revealed that reedbuck ranks among the preferred prey species (6.6% of bush-meat), with impala (35%), warthog (8.4%) and waterbuck (2.8%) being other commonly hunted species (Averbeck 2001, 2002). Also bushpig *Potamochoerus larvatus* (25.3%), bushbuck (9.4%) and the common duiker (9.4%) are preferred prey species. We established the relative population densities of these species during the study period as 0.04 reedbuck/km², 24.4 impala/km², 0.33 warthog/km², 0.68 waterbuck/km², 0.01 bushpig/km², 0.21 bushbuck/km² and 1.2 common duiker/km² (Averbeck 2000). Relating the poaching preferences to relative population densities, it appears that bushpig is by far the most preferred species, followed by bushbuck and common duiker as well as warthog and reedbuck, while impala is proportionally less preferred. In the ARS, these species are usually hunted using nets and spears (Averbeck 2001, 2002), which requires careful choice of the appropriate age and sex class. The chance of being injured is considerably

higher for the hunter when using nets compared to snares or firearms. Poachers, therefore, tend to prefer the hornless females and their calves, as it is less dangerous to handle net-caught calves and females than males (C. Awerbeck, pers. obs.). Hence, this bias in prey choice may be responsible for the observed patterns of fewer juveniles in impala (Awerbeck et al. 2010) and warthog (our study), as well as for smaller all-female groups in reedbuck in the ARS.

While we predicted that increased competition in the ARS may cause the younger age classes (yearlings and subadults) to leave mixed-sex groups more frequently so as to join bachelor or all-female groups, we argue that at least a part of the observed differences in group compositions between LMNP and the ARS are also caused by selective hunting on different age classes. Adult oribi are not hunted, but still juveniles and yearlings did not occur in the ARS, neither in mixed nor in all-female groups. Instead adult females take a larger proportion in both mixed and all-female groups, so selective hunting on oribi juveniles will need to be examined in more detail in the future.

As outlined before, eland has substituted size and cooperative maternal defense for speed to protect itself and its offspring against predation. Eland fear only humans and have the longest flight distances (300-500 m) of all large ungulates in Africa (Estes 1991, Hillman 1974). Increased human nuisance and disturbance in the ARS may therefore affect eland herds disproportionately, and females may be too stressed to conceive, and thus, prefer the safer areas within LMNP.

The occurrence of topi in the ARS has declined considerably during the last two decades (Monday 1993, Awerbeck 2000, 2002), even though poachers virtually neglect this species (Awerbeck 2001, 2002). Increased stress and reduced reproduction due to direct persecution are therefore unlikely. Decreasing topi numbers in the ARS may be explained by competition with cattle, as cattle stocks have increased constantly since 1997 (Monday 1993, Awerbeck 2000), or by the infestation of pasture (grass) with pasture weeds (Schwartz et al. 1996). Pasture weeds are unpalatable or poor quality herbs infesting overgrazed pastures, and reduce forage (grass) availability and accessibility for grazing game species such as the topi. The infestation of grassland with pasture weeds in the ARS is distinctly higher than in LMNP (Schwartz et al. 1996), causing topi to avoid these areas or use them only during the wet season (when topi give birth) when grass availability is im-

proved (Kingdon 1982, Monday 1993, Rannestad et al. 2006). It is an interesting fact that buffalo seem to avoid the ARS entirely, indicating high competition with cattle and low pasture quality as outlined for topi (Schwartz et al. 1996).

In summary, our study provides evidence for multiple, species-specific responses of large ungulates to anthropogenic nuisance on the levels of group sizes and compositions. Several effects observed here (such as the increase in bachelor group size) were specific to only some of the seven species considered in our study, and also, may not necessarily apply to other areas. Still, our study highlights that monitoring grouping patterns (by analysing sizes and compositions of different group types) can be a powerful tool to detect negative effects of human activities on gregarious species that may go undetected when focusing exclusively on mean population densities in a given area. We encourage further long-term studies on grouping patterns to monitor temporal variation in social organisation in areas with different degrees of human disturbance. This, in turn, will contribute to monitoring the effects of recreational hunting in the area and will benefit the conservation of wildlife in LMNP and the adjacent ARS (Lamprey & Mugisha 2009).

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