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POPULATION STRUCTURE OF UNGULATES IN WATERBERG NATIONAL PARK, NAMIBIA

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Population Structure of Ungulates in Waterberg National Park, Namibia. Kasiringua, E., Procheş, Ş., Kopij, G. — A study on the seasonal variation in population structure of seven (7) ungulate species, African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), giraffe (*Giraffa camelopardalis*), oryx (*Oryx gazella*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*) and the greater kudu (*Tragelaphus strepsiceros*) was carried out using the field census approach during the wet (February–April) and dry (July–September) season, and a water hole census (September) at seven waterholes in the Waterberg National Park, Namibia. Male warthog, oryx and black rhino on average comprised about 40 % of the population, whereas male sable, roan antelope, eland and buffalo comprised 30 % of the population. Male kudu and male white rhino comprised 20 % of the sex structure of the population, whereas male giraffe comprised more than 50 % of population. Age structure was dominated by adults, with 60 % of the total population in warthog, sable, eland and the white rhino, and 70 % in kudu, roan, buffalo, giraffe and black rhino on average. Oryx had the highest number of adults, with only 10 % of the population comprised of juveniles. Larger herds were observed during the wet season and smaller herds during the dry season. Animals were observed more abundantly in three of the vegetation types (*Terminalia sericea* — *Melhania acuminata* vegetation, *Terminalia sericea* — *Thesium megalocarpum*, *Terminalia sericea* — *Blepharis integrifolia*), with lower abundances in the rock-inhabiting *Peltophorum africanum* during both seasons.

Key words: herd size, sex and age structure, African ungulates, wildlife management.

Introduction

Africa has ungulate communities of unique diversity (Sinclair, 1983), in which the composition and population structure of both small and large herbivores varies considerably (du Toit, 1995). Ecological studies have shown that variations in abundance, activity or the use of sites by ungulates is linked to the seasons, scale of human activity, other species, or the availability of resources (Keuroghlian et al., 2004; Di Bitetti et al., 2008; Pérez-Cortez et al., 2012; Reyna-Hurtado et al., 2012; Pérez-Irineo et al., 2016).

In large herbivores, habitat structure and population density are often reported as major determinants of group size variation within and between species (Marino et al., 2014). Hence, understanding the patterns of variation in abundance and community structure and the consequences for species diversity is a crucial point in ecology (Fritz et al., 2002; Hutchinson 1959; Gaillard et al., 1998).

Namibia is a semi-arid country, with several biomes (woodland, savanna, desert and Karoo) harbouring a vast variety of wildlife. The country has seven (7) national parks of which one is Waterberg National Park, which is the main source of rare and threatened species to all Namibia's national reserves and National parks. Unfortunately, in many species, populations are continuing to decrease within protected areas (Brashares et al., 2001; Newmark 2008; Tsindi et al., 2016; Gordon et al., 2004; Wilkie et al., 2011) often due to inconsistent rainfall, temperature increases, recurrent droughts, disease outbreaks, poaching and trophy hunting (Milner-Gulland & Bennett, 2003; Winterbach, 1998; Ogutu et al., 2009). It is therefore crucial to understand population dynamics and the sensitivity of a population to these factors in informing conservation policy decisions and recovery strategies (Tsindi et al., 2016; Butler et al., 2013).

Fritz et al. (2002) suggested that African herbivore abundance and community structure are primarily determined by rainfall (Owen-Smith, 1990; Mills et al., 1995; Mduma et al., 1999; Georgiadis et al., 2003; Mason & Ogutu, 2005) and the nutrient status of the soil, by their effects on the quantity and quality of the primary production, (Kennedy et al., 2003). The irregular availability of water in Namibia's semi-arid savannas affects the distribution, quantity and quality of food for large herbivores and hence, influences age and sex structure of herbivores with different dietary requirements across wet and dry seasons (McNaughton & Georgiadis, 1986; Davidson et al., 2013; Mduma et al., 1999). Herbivores in African savanna environments, and particularly in Namibia, depend strongly on rainfall received during the wet season for vegetation growth and hence food production (Rutherford, 1980). Coe et al. (1976) suggested a model describing the variation in biomass of the ungulate communities based on annual rainfall, a good predictor of primary production across the globe (Lieth, 1975; Lauenroth, 1979), and specifically in sub-Saharan Africa (Le Houérou & Hoste, 1977; Desmukh, 1984).

Wildlife populations are also determined by the relative rates of natality and immigration versus mortality and emigration, and reflect the interplay of numerous, often widely variable, environmental factors (Masen, 1990). The spatial distribution of organisms is often regarded as being driven by a need to maximize fitness (Jones et al., 2006), thus animals are expected to aggregate within the most favourable vegetation/habitat patches (Bailey et al., 1996; Cezilly & Benhamou 1996). Therefore, seasonal changes in the characteristics of the vegetation may affect spatial distribution over time (Illius & O'Connor, 2000). Seasonal changes are caused mainly by direct weather effects on plant primary production, in conjunction with variable grazing pressure resulting from changes in population density (Crawley et al., 2004). Many studies are now focusing on how sex and age structure affect the dynamic of ungulate populations (Coulson et al., 2001). Juveniles and older individuals within a population normally have lower survival rates than prime-aged individuals (Gaillard et al., 2000; Holland et al., 2002), and males frequently have lower survival rates than females (Clutton-Brock et al., 1997; Holland et al., 2002). According to Bianchet et al. (2003), large herbivores have strongly age-structured populations, and this is primarily because recruitment often decreases as population density increases in unexploited populations, where the proportion of older adults may increase with density.

Since survival senescence is common in ungulates (Gaillard et al., 2014; Bianchet et al., 2003), ignoring density-dependent changes in age structure could lead to apparent density-dependence in adult survival. The density of a population is associated with variation in age — and sex-specific vital rates and population dynamics (Nicholson, 1933; Gaillard et al., 1998; Gaillard et al., 2000; Mysterud, 2002). Therefore, it is important to know whether apparent changes in adult survival at high density (Fowler, 1987) are due to density dependence in survival, or to changes in age structure. If age structure was mostly responsible for changes in adult survival, increasing density may lower overall adult survival in naturally regulated populations, but not in harvested populations such as those in WNP (Langvatn & Loison, 1999).

Moreover, apparent trends in population numbers based on water point counts may be subject to counting variability between successive years. Field classification of sex and age classes also has limitations, particularly in that they do not provide information on adult mortality, which is necessary for interpreting age ratios (Masen, 1990). Hence, a combination of water hole and field surveys should facilitate more reliable assessment of population trends by providing complementary data on population size and structure.

The aim of the present study is to increase the understanding on how the population structure differs among species in the Waterberg National Park (WNP), Namibia. We specifically set off to determine 1) the relationship between species herd sizes and the four major vegetation types in WNP. We also investigated the 2) age and sex structure of species in WNP, and 3) the association between the field and water point census of herd sizes during wet and dry season of all species in order to find the most suitable sampling method.

Methodology

Study area

The study was conducted in Waterberg National Park, which is situated in the Otjozonzupa region in northern Namibia, 280 km N of Windhoek and 68 km SE of Otjiwarongo (20°25' S, 17°13' E; fig. 2). The WNP is 49 km long from SW to NE, and 8–16 km wide. It is 40,500 ha in size, with 40,000 ha on the plateau and 500 ha in foothills (Kasiringua et al., 2017).

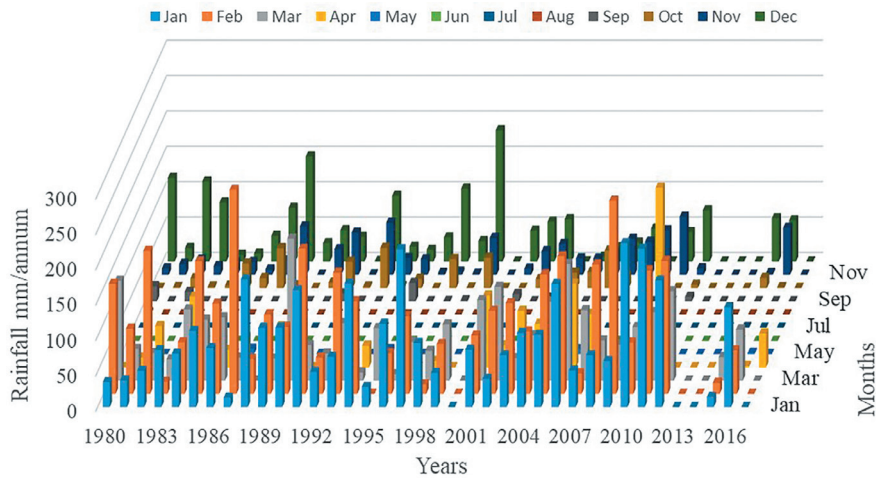


Fig. 1. Rainfall in the Waterberg N. P. for the years 1980 to 2017 (Sasscalweathernet.org/station_datasheet_we.php).

The plateau has an elevation of 1850 m above sea level and between 100 to 300 m above the surrounding plain. The periphery of the plateau forms almost vertical cliffs, up to 300m high. The top of the plateau is made up of aeolianite (lithified dunes) of the Etjo Formation, which is ca. 200 million years old. The sandstone is covered with Kalahari sand (W. Hegenberger, unpublished report). There are no permanent water courses or pans. The water is pumped from the canal which runs across north central parts of the country from the Berg Aukas and Kombat mines where it is then diverted to the seven water points holes in Waterberg N. P. (fig. 2, table 1) (Kasiringua et al., 2017).

The vegetation falls into the broad-leaf woodlands which are typical of the sandveld of eastern and north-eastern parts of Namibia (Mendelsohn et al., 2009). Three main vegetation communities within this park have

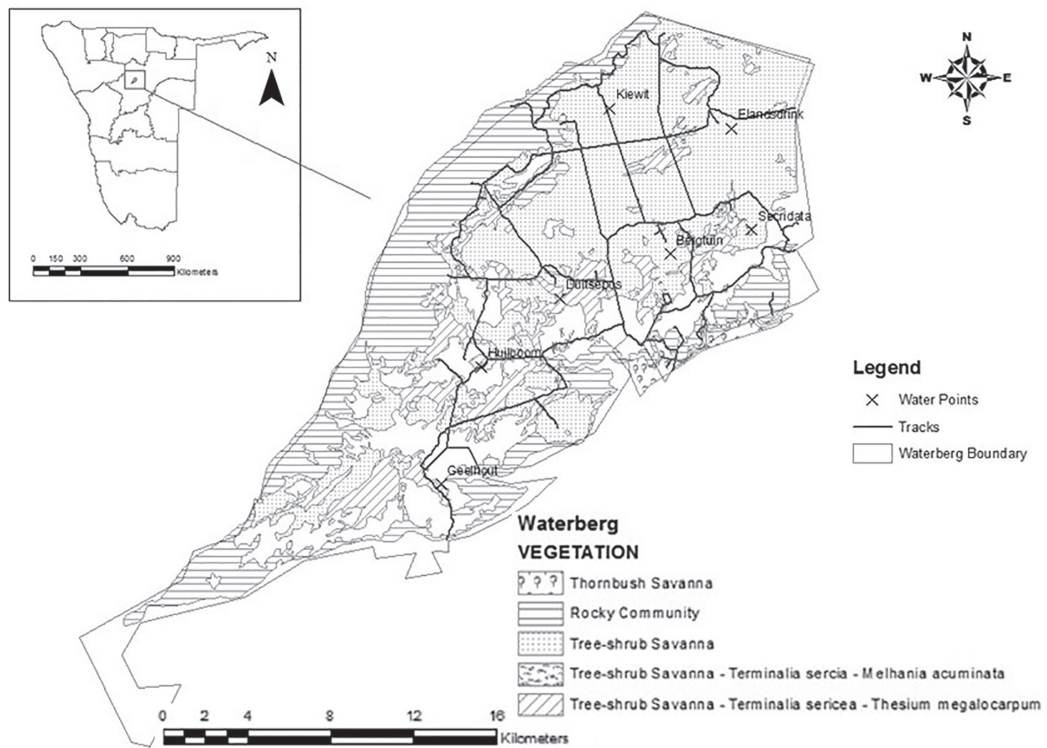


Fig. 2. Location of Waterberg N. P., the different vegetation types and the distribution of the seven (7) water holes in the park (Jankowitz, 1983).

Table 1. Location and elevation of the waterholes on the Waterberg National Park

Water-Holes	Coordinates longit.	Coordinates latit.	Elevation, m
Bergtuin	20°22'45" S	17°21'14" E	1621
Secridata	20°21'66" S	17°22'86" E	1598
Elandsdrink	20°19'22" S	17°22'54" E	1621
Kiewit	20°18'50" S	17°19'37" E	1647
Duitsepos	20°23'57" S	17°18'16" E	1624
Huilboom	20°25'47" S	17°15'69" E	1664
Geelhout	20°28'56" S	17°14'64" E	1655

been recognized, with a fourth one occurring on rocky substrates: *Terminalia sericea* — *Melhanian acuminata*, *Terminalia sericea* — *Blepharis integrifolia*, *Terminalia sericea* — *Thesium megalocarpum*, and the rock community *Peltophorum africanum* (Jankowitz, 1983).

More than 90 % of the rainfall occurs from October–March and has an average annual rainfall of 450.2 ± 75.4 mm (Mendelsohn et al., 2009) (fig. 1).

Data Collection

We studied only seven (African buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), giraffe (*Giraffa camelopardalis*), oryx (*Oryx gazella*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*) and the greater kudu (*Tragelaphus strepsiceros*)) of the species using field census data (collected along road transects), simply because the census sample size of all the other species was too small. Census data from these seven species were then compared to the same species with data collected using the waterhole counts of herd sizes and numbers of herds. The main aim of the comparison was to determine the best sampling method between the two and to see if they would yield the same results. The waterhole census included other species like black rhino (*Diceros bicornis*), white rhino (*Ceratotherium simum*), and warthog (*Phacochoerus africanus*) which were only represented by figures based on water point counts (fig. 4, 5 and 6). We specifically avoided presenting total number of white and black rhino in WPN due to the ongoing measures by the Namibian Ministry of Environment and Tourism to prevent rhino poaching in Namibia.

Field census

Data was collected using the distance sampling method during three months of Namibia's wet season (February to April) in both 2015 and 2016, while the data for the dry season were collected during June to August, of both years. A 4 x 4 truck was used to drive along the road transects, at a speed between 15–20 km/hour. Sampling was started at exactly 06h00 am on every sampling day, with the odometer set to 0 at the starting point. Observations were done from the vehicle by two to three observers aided by binoculars. A Global Positioning System (GPS) was then used to plot the coordinates of the observed animals, and distance was estimated between 0 and 100m for accuracy of identifying the sexes of the observed animals. All animal observations beyond 100m were not recorded (0 m was recorded as the distance when the animal was observed on the road). The total distance travelled per day varied between 50 and 70 km. We avoided recounting of the same animal by not returning along the same transects.

Water point census

Observations were conducted from specially constructed wooden shelter (hides) situated in a close proximity (ca. 50 m) to the seven water holes (table 1). Observations were carried out in the dry season (September), when the animals usually concentrate near water holes. The counts were organized around full moon nights, to achieve greater visibility of the game during the night. Observations were aided by binoculars. At each water point, there were 2–3 observers counting animals visiting the water points for 48 hours, i. e. from 10h00 am to 10h00 am of the last sampling day of the years 2008–2013.

Each animals coming for drinking was timed, counted and identified to species level. Whenever possible, each individual was also sexed and aged, and identified individually (especially rhinos and giraffe) as to avoid double counting of some individuals which come more than once to the water point. Animals were counted separately in each group. Animals were visually identified to sex and age classes using combinations of sexually dimorphic physical characteristics, such as morphological configuration, age-specific differences in body size, shape and size of horns (Ogutu et al., 2008). Body size, presence, length and shape of horns and coat colour were used to identify juveniles. Ages were not assigned to adult animals (Sinclair, 1995; Ogutu et al., 2008).

Statistical Analyses

Seasonal data for herd size was subjected to non-parametric Mann-Whitney U test because it satisfied the assumptions associated with the test (Zar, 1999), (table 3). Data for the number of individual species in a vegetation type was subjected to Kruskal-Wallis H-test using IBM SPSS package (v. 22), (table 5). The Kruskal-Wallis test (also referred to as the “one-way ANOVA on ranks”) is a rank-based nonparametric test that is used to determine if there are statistically significant differences between two or more groups of an independent variable on a continuous or ordinal dependent variable. Prior to running pair t-tests, the data was subjected to a Levene test for comparison of sample variances to satisfy the assumption of the t-test.

Results

Buffalo was characterised by the largest herd size compared to all other species, with 153 herds and a total of number of 824 individuals, followed by the giraffe that had 128 herds and 118 individuals. The herd size of eland was lower (49) compared to that of the giraffe but the eland had a higher number of individuals (517 individuals in total) within these herds (table 2). The Mann-Whitney U test on herd size in relation to seasonal variability in the WNP in 2015/2016 showed statistical differences ($P = 0.002$) between the dry and wet seasons, with 242 and 283 herds respectively.

The average means for individual species varied in between wet and dry seasons, with buffalo, eland, giraffe and kudu registering high averages in wet season (table 3). Eland had the highest average herd size, standard deviation and variation of 11.46, 21.93 and

Table 2. Herd sizes of all ungulate species found in Waterberg National Park

Ungulates	Average	SD	Variance	No of herds	No of individuals
Buffalo	5.71	8.70	4.48	153	824
Eland	8.92	17.33	35.38	49	517
Giraffe	3.01	3.39	0.08	123	118
Sable	3.32	4.25	0.43	33	104
Roan	3.47	3.03	0.09	49	167
Kudu	3.18	3.95	0.29	39	95
Oryx	2.21	1.99	0.02	38	84
Redhartebeest	6.92	6.80	0.01	13	90
Duiker	1.10	0.34	0.29	86	95
Steenbok	1.09	0.36	0.27	52	57
Klipspringer	2.13	0.83	0.83	8	17

Table 3. Herd sizes of different species in relation to season of year 2015–2016 in Waterberg National Park

tes	Season	Average of herd sizes	SD	Variance	No of Herds
Buffalo	Dry	5.49	9.26	7.10	78
	Wet	5.93	8.14	2.44	75
Eland	Dry	5.52	7.10	1.24	21
	Wet	11.46	21.93	54.77	28
Giraffe	Dry	2.93	3.25	0.05	57
	Wet	3.08	3.54	0.11	66
Sable	Dry	3.8	4.44	0.21	16
	Wet	2.88	4.16	0.83	17
Roan	Dry	3.85	3.41	0.10	20
	Wet	3.21	2.77	0.10	29
Kudu	Dry	2.63	2.24	0.08	19
	Wet	3.7	5.08	0.95	20
Oryx	Dry	2.85	2.51	0.06	13
	Wet	1.88	1.62	1.75	25

Table 4. Herd sizes of different species in relation to the four main vegetation types in Waterberg National Park

Ungulates	<i>Terminalia sericea</i> — <i>Melhania acuminata</i>		<i>Peltophorum afri-</i> <i>canum</i>		<i>Terminalia sericea</i> — <i>Blepharis integrifolia</i>		<i>Terminalia sericea</i> — <i>Thesium megalocarpum</i>	
	No. Herds	No. Individuals	No. Herds	No. Individuals	No. Herds	No. Individuals	No. Herds	No. Individuals
Buffalo	44	294	29	190	32	148	40	192
Eland	25	224	3	33	17	212	8	48
Giraffe	51	51	13	13	22	22	32	32
Sable	12	29	4	6	8	35	8	34
Roan	18	63	5	16	10	32	15	56
Kudu	15	44	6	4	6	28	8	19
Oryx	19	42	0	0	9	18	10	24
Mean rank		17.17		6.83		12.75		13.25

χ^2 (P-value = 0.088) 6.545

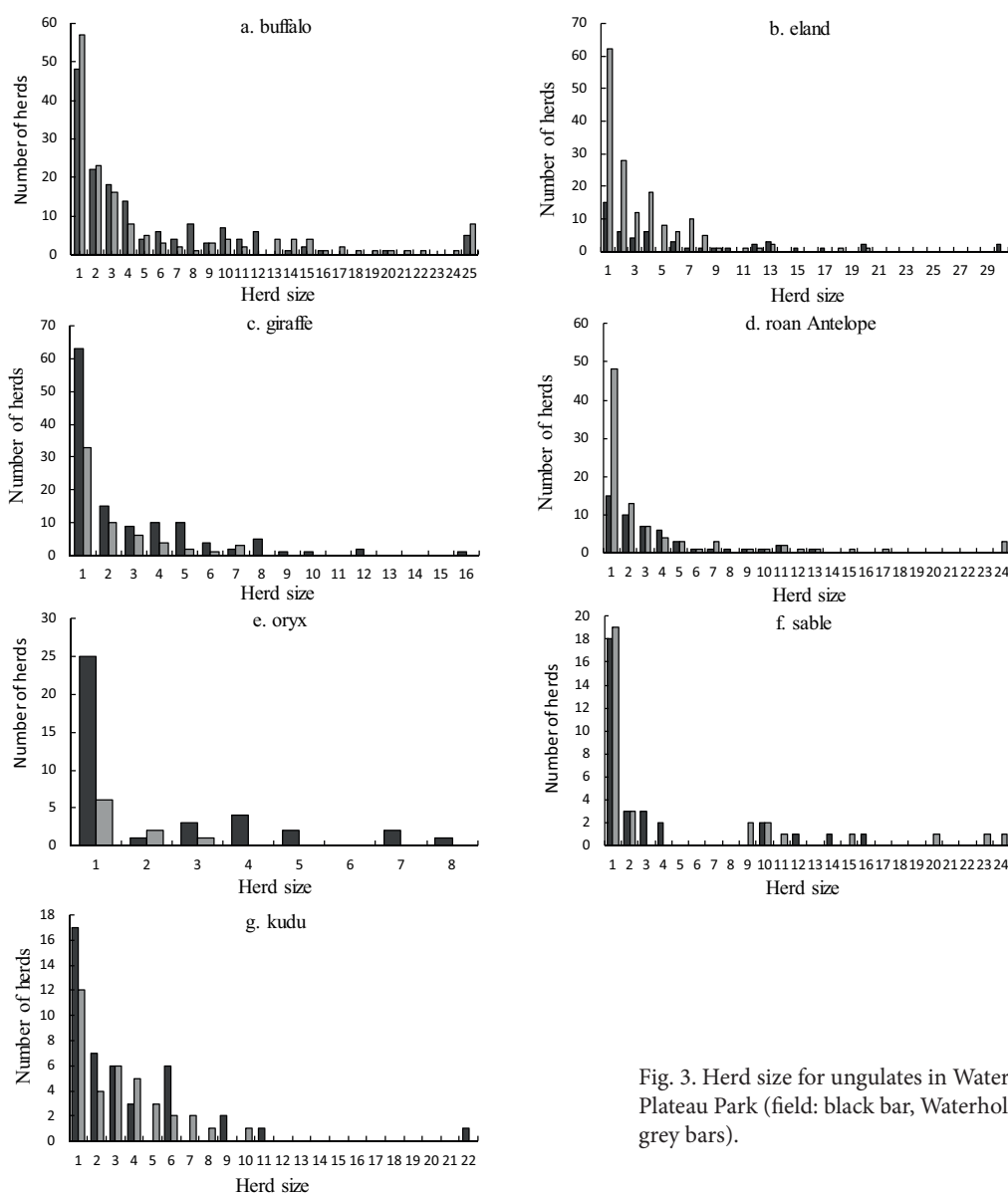


Fig. 3. Herd size for ungulates in Waterberg Plateau Park (field: black bar, Waterhole: grey bars).

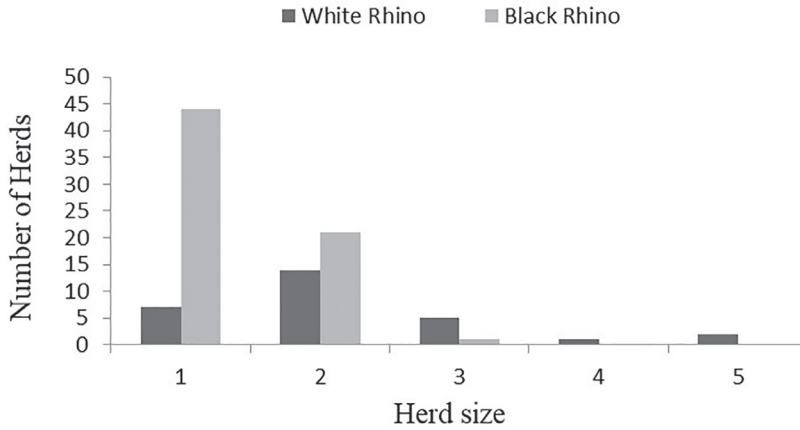


Fig. 4. Herd size and number of herds of White and Black Rhino based on water point census only in Waterberg Plateau Park.

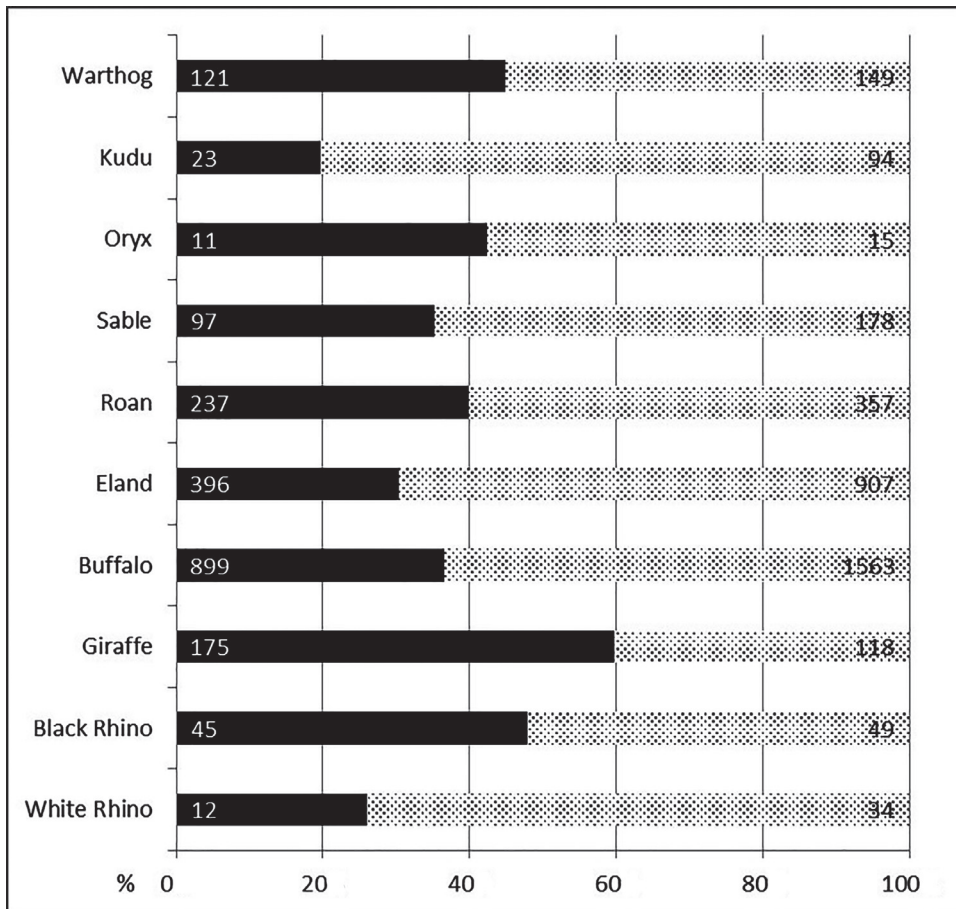


Fig. 5. Year to year changes in the proportion of sex (males: black bar, females: grey bars) in ungulates in the Waterberg Plateau Park in 2008–2013, based on water point census.

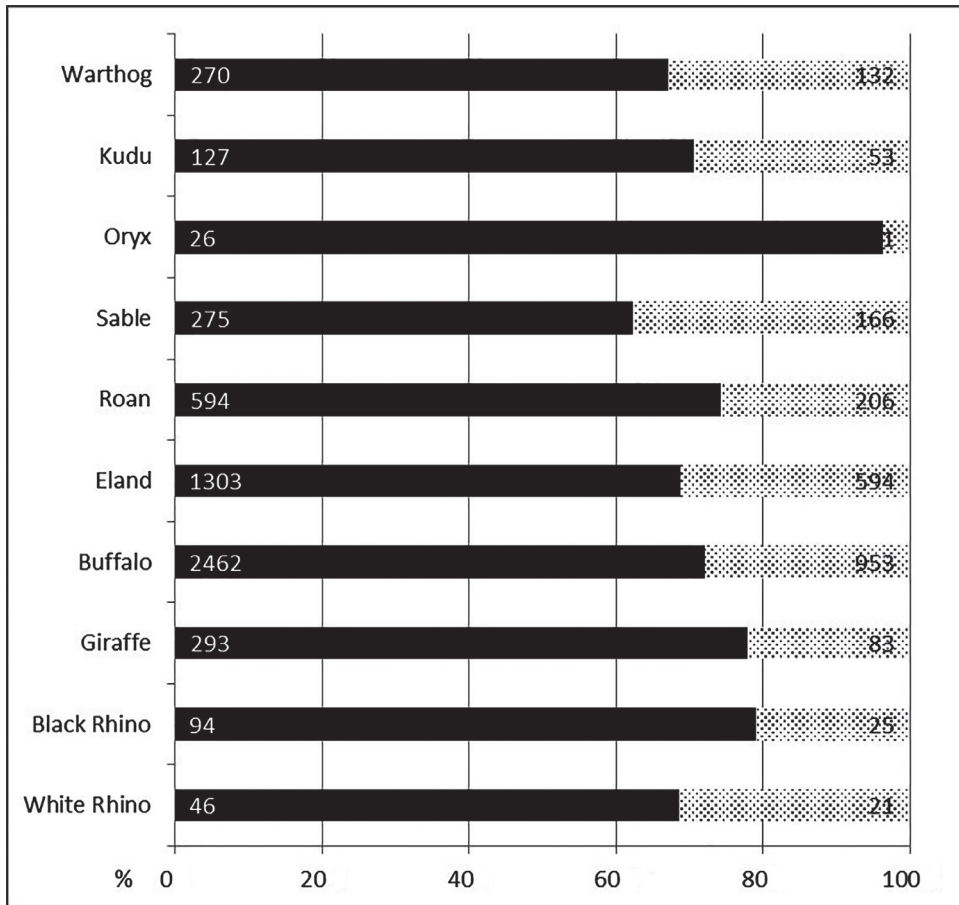


Fig. 6. Year to year changes in age structure (adults: black bar, Juveniles: grey bars) in ungulates in the Waterberg Plateau Park in 2008–2013, based on water point census.

54.77 respectively. A Kruskal Wallis H test showed that there was no statistically significant difference in number of individuals between different vegetation types. $\chi^2(2) = 6.545$, $P = 0.088$. Ungulates were abundant in three of the four vegetation types (*Terminalia sericea* — *Melhanian acuminata*, *Terminalia sericea* — *Thesium megalocarpum*, *Terminalia sericea* — *Blepharis integrifolia*), and less abundant in *Peltophorum africanum*, (table 4). Multiple pairwise comparisons of species using the Steel-Dwass-Critchlow-Fligner procedure were used. Chi-square test for the animal species, averaged over the four vegetation types, showed significant differences (table 4).

Results indicated a p value of 0.591 at 5 % significance between variance of field and water hole were similar. A comparison of the two sampling methods (field and water hole) was done to distinguish the best sampling method using herd sizes and number of herds observed (fig. 3, a–g). All number of herds decreased with increasing herd sizes in all species, and larger numbers of herds were observed using the water hole counts as compared to the field counts (fig. 3, a–g). The black rhino had larger number of herds in herd sizes 1–3, whereas in herd sizes 3–5 the white rhino had larger numbers of individuals than the white rhino (fig. 4).

All species seem to have had larger numbers of herds in the herd sizes of 1–4 animals. Proportionally, there were fewer males species observed than females in WNP during the years 2008–2013 with the exception of the giraffe that showed a higher proportion of males than females (fig. 5). All species showed a higher proportion of adults as compared to the juveniles, least so the sable and eland (fig. 6).

Discussion

The fluctuation in rainfall, especially between the year 2013–2015 in WNP (fig. 1), may have played a fundamental role in the ungulate population structure and should be evaluated and accounted for before the effects of other factors (such as predation, disease, fire, etc.) can be considered. Other studies have confirmed that rainfall has a significant influence on the abundance of species, which could confirm population dynamics of species in a given area (Ogutu and Owen-Smith, 2003; 2006; Owen-Smith, et al., 2005; Owen-Smith & Mills, 2006). All seven species showed an increase in number of herds and herd sizes in relation to the wet season of both years. Seasonal variation in rainfall effects were associated with seasonality in the number of recorded individuals, which contributed significantly to population fluctuation in all seven species.

The wet season census showed high herd sizes compared to the dry season herd sizes. This was primarily due to the better quality of fodder available during the wet season, because of the availability of growing grasses and bushes during the rainy season, which provides better fodder in the different vegetation as note by Megaze et al. (2018). Animals were more active during the wet season compared to the dry season, and this may be a result of the moderate temperature and cloudy weather conditions during the wet season as noted by Okello et al. (2015). The change in activity patterns of the different herd sizes during wet and dry seasons might be most likely due to changes in the availability of resources as observed by Ryan et al. (2006); Tshabalala et al. (2009); Ryan et al. (2012); Cornélis et al. (2014). Observations of smaller herd sizes in all the species during the dry season might reflect adaptations to a poor-quality environment, allowing the animals to better meet their energetic requirements (Megaze et al., 2018). In contrast, herd sizes of the buffalo, giraffe, sable antelope, roan antelope, kudu, oryx showed no major variation between wet and dry seasons (Melletti et al., 2007), but this was not the case for the eland which had an average herd size of 11.46 during the wet season and 5.52 during the dry season (table 3).

During both the wet and dry seasons, all the species formed larger aggregations in the *Terminalia sericea* — *Melhania acuminata* vegetation with scattered trees, than in the other vegetation types. This might be due to the abundance of food resources within the *Terminalia sericea* — *Melhania acuminata* vegetation, which can support large feeding herds or the fact that it covers an area twice the size of the other three vegetations. The *Peltophorum africanum* vegetation was least preferred by all the species mainly because the area has a scarcity of grass and is a mostly rocky community.

Buffalo in this study area were mostly sighted in herds of four or less individuals but occasionally bigger herds or about 70 individuals were also observed, especially at the water points. Herds of solitary buffalo were most commonly observed. Herd sizes of the African buffalo in WNP varied by season. The wet season census obtained high buffalo herds and number of individuals within these herds compared with the dry season census. This was primarily due to the better quality of vegetation available during the wet season in the study area. The availability of growing grasses, bushes and the moderate temperature and cloudy weather conditions caused the animals to be more active than in the dry season.

Higher numbers of juveniles were observed during this season, as buffalo mainly give birth during the wet season as noted in Vissher et al. (2004) and Turner et al. (2005). There was high proportion of females in the population. However, a low proportion of juveniles to adults (1 : 2.6) was observed during the present study. The male to female ratio of the buffaloes observed during the present study was 1 : 1.74 and agrees with the earlier observations in different parts of Africa (Prins, 1996; Vissher et al., 2004; Turner et al., 2005).

In WNP, buffaloes were seen in smaller herds during the dry season and in larger herds in the wet season, similar to observations of savanna buffaloes as noted by Sinclair (1977) and Taylor (1989). The variation in buffalo herd size during wet and dry seasons is a result of changes in the availability of resources as noted by Macandza et al. (2004) and Tshabalala et al. (2009). Melletti et al. (2007) and Korte (2008) reported that herd size of the forest buffalo showed no major variation between wet and dry seasons. African buffalo are said to congregate in large herds of 51–100 individuals as noted by several authors (Eltringham et al., 1973; Ryan et al., 2006; Bennitt et al., 2014), whilst Sinclair (Sinclair, 1977) reported that the average herd size in the Serengeti National Park was 350 individuals. In the present study area, the herd size of the buffalo was smaller. This may be justified in the context of patchiness and quantity of food resources in the different habitats. The pattern of herd size in the different habitat types of the study area was different and a scattered distribution of buffaloes was observed in the park.

The distribution of sable antelope within WNP was associated with the presence of particular land types, defined by vegetation features. Sable herds were more widely prevalent in the *Terminalia sericea* — *Blepharis integrifolia* vegetation, and less so in the *Peltophorum africanum* vegetation. Sable had more numbers of individuals in the *Terminalia sericea* — *Blepharis integrifolia* and *Terminalia sericea* — *Thesium megalocarpum* vegetation, although the latter generates more fertile soils and therefore more nutrient rich grasses. This pattern was also noted by Smit (2011). Highest sable average herd size occurred in the dry season.

Furthermore, sable herds were patchily distributed within landscape types and their presence seem to have been negatively dependent on the local abundance of two major grazers in the park (buffalo, roan). Roan and sable showed similar habitat preferences, with roan antelope concentrated especially in the *Terminalia sericea* — *Melhania acuminata* vegetation where sable herds were also recorded. The strongest negative effect on sable presence came from buffalo, which are grazers and widely distributed across the four habitats. Sable herds were unlikely to be present in the places where buffalo were concentrated at high density, whatever the habitat type. According to Cain et al. (2012), sable herds may inhabit areas further than 5 km from water and drink less frequently than daily, thereby avoiding the concentrations of other grazers that tend to develop near the water points. The proportion of adults to juveniles was 1:0.60 during the present study and male to female ratio of the sable observed during the present study was 1 : 1.84.

Other studies revealed that sable avoid close proximity to buffalo herds at a finer scale (Macandza et al., 2012). Hence competitive interactions did not explain the influence of these grazers, apart from the grass height favoured by both the sable and roan antelope. Joubert (1974) and Magome (1991) noted that the sable herds tend to be secluded from concentrations of other ungulates. This might impose more predation on the sable calves, which could influence the local occurrence of the sable herds. Hence, the restrictions on the distribution of sable herds because of avoiding competition may cause high predation risks for the sable and this is consistent with evidence implicating elevated predation as primarily responsible for the population declines shown by sable (Owen-Smith et al., 2012) and the roan (Harrington et al., 1999).

The roan antelope is the second largest African antelope, distributed throughout the continent in sub-Saharan savanna habitat. Many populations are isolated and occur in low densities, and are declining. By comparison, sable in WNP were mostly associated with the *Terminalia sericea* — *Melhania acuminata* vegetation, where they had the larger number of individuals within these herds and least so in the *Peltophorum africanum* vegetation (table 4). The vegetation preference of roan antelope appears to be influenced by topography, vegetation type, availability of water, and competitors as reported by Wilson et al. (1977) and Havemann, (2014). Heitkönig & Owen-Smith,

(1998) noted that roan antelope are most abundant in moist or dystrophic savanna and favour areas with few competitors or carnivores (Tyowua et al., 2012; Havemann, 2014). Their need to avoid extrinsic pressures such as competition and predation may be facilitated by their ability to tolerate low-quality food that other ruminants do not tolerate (Heitkönig & Owen-Smith, 1998). Roan herds usually roam less than 2–5 km from water (Grant et al., 2002; Martin, 2003; Kimanzi, 2011). In WNP roan antelope typically occurred in small herds, each with a dominant bull. The proportion of adults to juveniles was 1 : 0.35 during the present study and male to female ratio of the roan observed during the present study was 1 : 1.51.

Eland herd sizes and number of individuals within these herds varied from solitary animals to herds of 60 individuals in WNP (fig. 3, b). The largest herds always contained calves and juveniles, while the smaller herds comprised mostly of adult animals only. Herds were largest in wet seasons and smallest in dry seasons. Association preference in eland varied seasonally. In the dry season, females associations was mostly the basis of most herds, while female with juveniles were the nucleus of large rainy season aggregations. Such seasonal changes in herd sizes may be associated with food requirements. The proportion of adults to juveniles was 1 : 0.46 during the present study and male to female ratio of the eland observed during the present study was 1 : 2.29. In the present study, eland were associated more with the *Terminalia sericea* — *Melhania acuminata* and the *Terminalia sericea* — *Blepharis integrifolia* vegetation where the total number of individuals recorded was 224 and 212 individuals respectively (table 4). Eland have been classified as intermediate feeders preferring browse (Kerr et al., 1970; Jankowitz, 1982; Buys, 1990), while in others studies eland were found to be predominantly grazers (Lamprey, 1963; Underwood, 1975; Nge'the & Box, 1976). Some investigators have suggested that elands are not social animals, and they interact little with herd mates except for mating and mother to infant interactions (Kiley-Worthington, 1978; Hillman, 1987).

Interactions between individuals and family structure in giraffe have been described as temporary (Leuthold, 1979; Dagg & Foster, 1982; Pellew, 1984; Pratt & Anderson, 1985; Le Pendu et al., 2000). Loose relationships are thought to reflect weak herd structure in giraffe. Giraffe in this study area were mostly sighted in herds of five or less individuals, whereas in Hoanib River (Namibia) study area they were found in herd sizes of three and less individuals (Fennessy et al., 2003). Solitary giraffes were most commonly observed (fig. 3, c), as noted in other giraffe populations throughout Africa (Scheepers, 1992; Le Pendu et al., 2000; van der Jeugd & Prins, 2000; Fennessy et al., 2003). Giraffe in WNP showed a rather peculiar trend in herd sizes and number of individuals within these herds. For each of the four vegetation types the herd size and number of herds were the same (table 4). Giraffe associated more with the *Terminalia sericea* — *Melhania acuminata* and *Terminalia sericea* — *Thesium megalocarpum* vegetation but avoided to the *Peltophorum africanum* vegetation. The proportion of adults to juveniles was 1 : 0.28 during the present study and male to female ratio of the giraffe observed during the present study was 1 : 0.67, (fig. 5–6). The skewed ratio of males to females observed in the sex structure of giraffes could be the cause of conspicuousness by the males which could have made them easier to observe than the females.

The Oryx is an arid region mammal able to live indefinitely without free water (Taylor, 1969). Typically, oryx obtains water in waterless regions from their food by selecting food items with high water content (Taylor, 1969). We found that observations at water points were unsatisfactory for oryx (fig. 3, e), because the animals frequently fled and would not return. Most herds came and departed from water points as individuals or irregular herd. Individuals which arrived in herds at the water points often departed alone or with individuals already present at the water points. We conclude that the herds at water points were fortuitous collections of individuals, thus not necessarily of the same herd. A low proportion of adults to juveniles were observed (1 : 0.04), and this could be caused by the

type of landscape and the vegetation available in WNP, considering the fact that oryx are classified as rather arid to semi-arid mammals. Another explanation could be predation on the calves by the leopard (*Panthera pardus*), since the habitats in WNP are mostly dense making it an ideal hunting ground for the leopard. Male to female sex ratio was 1: 0.36, during the present study.

A total of 23 males and 94 females were observed based on water point census (fig. 5). The sex ratio of males to females in WNP was 1 : 4.09. This ratio expressed the number of females per one male (1 : 4.09). The adult sex ratio found in this study was similar to sex ratios found for other kudu populations (Owen-Smith, 1990, 1993; Perrin & Allen-Rowlandson, 1995). The skewed sex ratio towards females may be due to a higher mortality rate for male kudu with increasing age. According to Annighöfer & Schütz, (2011), male mortality accelerates sharply with age especially after reaching full weight at 6 years of age, as compared to females (Estes, 1997; Owen-Smith 1990, 1993). The proportion of adults to juveniles was (1 : 0.42). Kudu in WNP move in and out of the park, and are the only ungulates in the park known to do so. This is merely because of the topography of the park, which is partially fenced on the one side and governed by the steep slopes of rocks on the other where the kudu can climb down and up the mountain at their convenience, unlike most other species. Hence, the data presented here could be biased when it comes to reflecting the true picture of herd sizes of kudu in the park.

Conclusion

Age and sex structure requires constant monitoring in order to perceive changes in the demography of a population over time. Absence of adequate survey data on wildlife population structure and distribution prevents timely management and conservation decisions that could ultimately save many of the wildlife as suggested by Fynn & Bonyongo (2011). The sable and roan populations in WNP face a major decline in numbers because of their tendency to avoid habitats that are inhibited by other grazers or competitors like the buffalo. Hence, we suggest that the sable or roan antelope be relocated out of the park in order to reduce competition pressure by the buffalo. Relocation of the oryx to a more suitable environment might also be the best option considering that they are finding it difficult to adapt to the current environment. Therefore, it is expected that the present results will provide baseline ecological data, and motivation for conservation efforts focused on wildlife management strategies that will improve the conservation of these rare species in the WNP. The use of the field and water point counts yielded no major difference in sampling sizes of most of the species, except for the oryx. Thus, we conclude that both sampling methods were satisfactory and should continue to be used to complement one another.

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