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Long-term population dynamics of African ungulates in Waterberg Plateau National Park, Namibia

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ABSTRACT

The current study was undertaken to determine long-term population trends (33 years) of ungulate species in the Waterberg National Park (WNP), Namibia, using aerial and waterhole counts of ungulates during the years 1980−2013.We tried to establish how rainfall influences the multi-species population dynamics. During this period sixteen ungulates species were recorded. Among these, eight have shown an increase in numbers during the years 1984−2013, six other decreased, and populations of two other species remained stable. Roan and sable antelope, kudu and warthog were fairly common (with 5−12% of all ungulates recorded). White rhino, black rhino, giraffe, and gemsbok were classified as uncommon (together 11.9%), whilst the remaining eight species were rare (together 1.9%). The eland population showed a weak positive relationship with the annual average rainfall between the years 1981−2013, whereas population sizes of kudu, sable, gemsbok and roan showed a weak negative relationship with the amount of rain. No relationship was detected in giraffe, buffalo and hartebeest populations. We conclude that, irrespective of water supplementation, ungulate densities are to a large extent controlled by rainfall.

INTRODUCTION

From the point of view of wildlife conservation, some of the most important studies are those documenting population-level changes over medium to long-term time spans. Such knowledge can be used for the development and implementation of nature conservation strategies and for effective wildlife management, concurrently mitigating human-wildlife problems (Ranson *et al.* 2012). An absolute population estimate is often not a purpose of such studies. Relative estimate of population abundance may be sufficient, as long as the data are collected in a consistent manner (Sutherland 1998). More important, therefore, is the use of the same or similar method over a long period of time. In African savannas, a biome which occupies about half of the surface area of the Afrotropical Region, hoofed mammals (ungulates), beside termites, often represent the main component of the animal biomass, and play one of the most important roles in matter and energy fluxes.

Over the last few decades, many ungulate species declined in numbers and subsequently became threatened by extinction over larger areas the Afrotropical savanna (Craigie *et al.* 2010). For efficient conservation and rational utilization of such species, it is important to monitor their populations on a regular basis. Such monitoring studies are of utmost importance and relatively easy to conduct in small to medium conservation areas, especially where these represent key breeding grounds for the target species. Examples

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of such conservation areas in southern Africa are the Addo Elephant (N. P.), Mountain Zebra N. P., Pilansberg N. P., Sandveld Nature Reserve, Ndumo Game Reserve, and the Waterberg National Park (WNP) in Namibia. To date, however, long-term monitoring programs on the entire ungulate assemblages have been conducted only in a few larger areas in southern and East Africa: Ngorongoro Crater, Tanzania (Runyoro *et al.* 1995), Kruger N. P., South Africa (Mills *et al.* 1995, Ogutu and Owen-Smith 2003, 2005), Hwange N. P., Zimbabwe (Chamaille-Jammes *et al.* 2009), the Laikipia District, Kenya (Georgiadis *et al.* 2007), Hluhluwe-Mfolozi Park, South Africa (Grange *et al.* 2012), and Masai Mara National Reserve, Kenya (Bhola *et al.* 2012).

Ungulates in arid and semi-arid environments experience considerable seasonal, climatic and spatial variation in resources (Illius and O'Connor 2000), which affects the production of plant material and hence, indirectly, the carrying capacity of the ecosystem (Coe *et al.* 1976). Hence, environmental variability has a vital effect on the population dynamics of ungulates in arid and semi-arid grazing and browsing systems (Illius and O'Connor 2000). Spatial variation in grazing and browsing systems in semi-arid areas arises from variation in soil characteristics and topography, which causes variation in nutrient content and hydrology. In addition, spatial variation of habitat selection and accessibility of the different ungulate species during the wet and dry seasons can be regarded as having important influences on the dynamics of ungulate populations.

Rainfall, predation, disease, vegetation productivity, density-dependent forage competition and irregular climate have been shown to significantly affect vital rates of ungulates (Messier 1994, Patterson and Power 2002, Garrott *et al.* 2003). While numerous studies attempt to tease apart the effects of these factors, an ideal way to understand them is studying them in situations where some of them can already be assumed to have minimal influence.

One such example would be an area experiencing no predation or minimal predation. The movement of individuals is often limited by human-imposed barriers, but occasionally also by natural barriers such as mountainous ridges. The impact of rainfall on ungulates is twofold – direct, *via* water availability, and indirect, through vegetation productivity. A water-supplemented environment ensures that any effect of rainfall is in fact indirect. Despite the availability of systems where at least one of these conditions are met, not many studies have looked at population dynamics of multispecies ungulate assemblages in a high ridge mountainous area with little to minimal disease or large predators, or at the way in which rainfall indirectly affects water-supplemented populations.

In this study we investigate how rainfall indirectly influences the multispecies population dynamics in a water supplemented, disease free environment with little to no predators – the Waterberg National Park in Namibia. Specifically, the descriptive part of this study was aimed at: 1) determining population trends of all ungulate species in the WNP over the last 33 years using aerial and waterhole counts and 2) comparing the population trends with those documented in other regions of sub-Saharan Africa. The more advance part aimed at 3) testing the relationships between rainfall trends and the population dynamics of particular ungulate species; we assumed that, due to water supplementation of animals, these effects are primarily indirect, due to forage availability.

METHODOLOGY

Study area

The study was conducted in the Waterberg National Park (Fig. 1). It is situated in the Otjozondjupa region in northern Namibia, 280 km North of Windhoek (20°25′S, 17°13′E). The Waterberg National Park is 49 km long from south west to north east, 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). 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 300 m 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 (Hegenberger 1988). There are no

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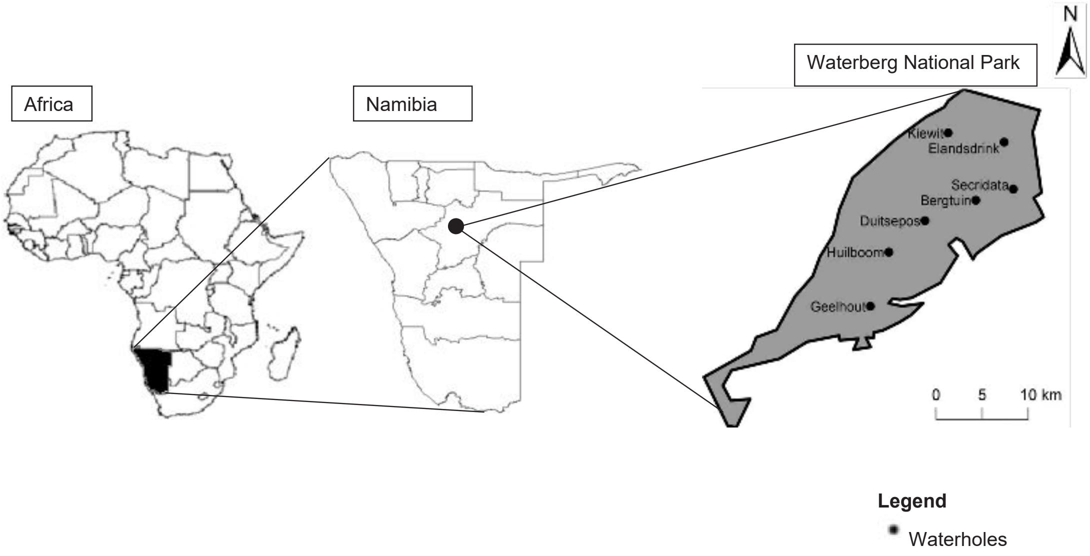

Fig. 1. Location of the study area and distribution of waterholes in the Waterberg National Park (Namibia). Source: Kasiringua *et al.* (2017).

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 seven waterholes in WNP (Fig. 1.)

The vegetation types fall into the broadleaf 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 been recognized, with the fourth one occurring on rocky substrates: *Terminalia sericea – Melhania acuminata*, *Terminalia sericea – Blepharis integrifolia*, *Terminalia sericea – Thesium megalocarpum*, and the rock community *Peltophorum africanum* (Fig. 1). Over 500 flowering plants and 140 lichen species are recorded from the Waterberg. Common trees include *Acacia ataxacantha, Burkea africana, Combretum collinum, C. psidioides, Dichrostachys cinerea, Grewia flavescens, G. retinervis, Lonchocarpus nelsii, Ochna pulchra, Peltophorum africanum, Terminalia sericea* and *Ziziphus mucronata*. Common grass species are *Andropogon schirensis, Brachiaria nigropedata, Digitaria seriata, Eragrostis jeffreysii, E. pallens, E rigidior* and *Panicum kalaharense* (Jankowitz and Venter 1987, Mendelsohn *et al*. 2009).

The area has a mean annual temperature of just over 18°C. More than 90% of the rainfall occurs from October to March, and the average annual rainfall is 450.2 ± 75.4 mm (Mendelsohn *et al.* 2009). The rainfall between the years 1980−2013 varied considerably. The period 2001−2013 had the highest rainfall of the 33 years considered here, especially during the early months (January-March) of the year. In 1980−2000 there seemingly was more rain later in the year (September-December) as compared to 2001−2014. The years 2000 and 2013 were both drought years with no rain from January to December (Fig. 2).

Game management of these species in WNP is in accordance with the national Species Management Plan document (M.E.T, Namibia). The main aim of the park is breeding rare species of large mammals without negatively affecting biodiversity. Therefore, the management objectives are to: 1) establish sustainable breeding populations of key species; 2) optimise population growth of key species by active management; 3) maintain biodiversity in the park. Key species for the WNP are the white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), roan (*Hippotragus equinus*), sable antelope (*Hippotragus niger*) and buffalo (*Syncerus caffer*). Here, these animals are free

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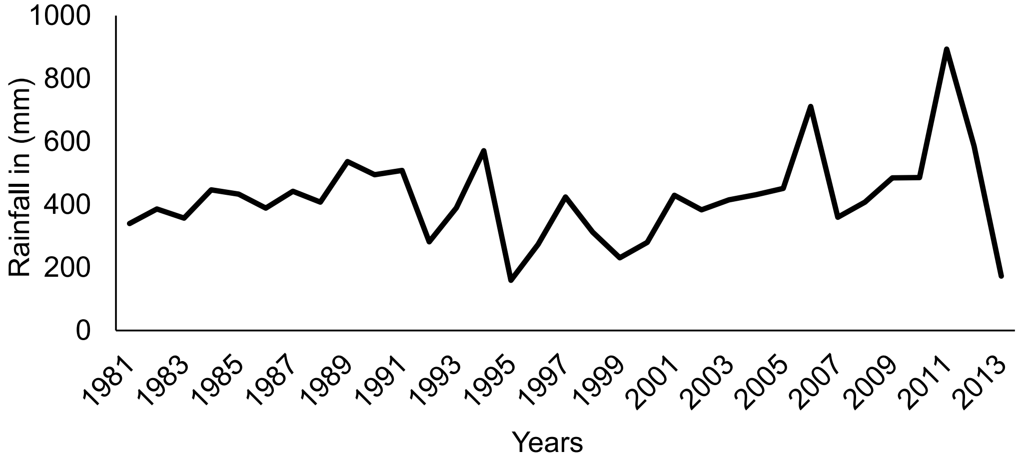

Fig. 2. Rainfall in Waterberg National Park. Year to year changes in rainfall during the years 1981–2013. Source: (Sasscalweathernet.org/station_datasheet_we.php).

of the foot and mouth disease virus (FMDV). The giraffe (*Giraffa camelopardalis*) and eland (*Taurotragus oryx*) serve as breeding stock for reintroduction to other parks. The introduction of ungulate species into the WNP was done mostly during the 1970s to the early 1980s. The following species were ranked as rare and endangered species in Namibia and were subsequently introduced to the Waterberg National Park: the white rhino was introduced in 1975 and 1976, black rhino in 1989 and 1994, giraffe in 1972, buffalo 1981, roan in 1975 and 1978, sable in 1978, hartebeest in 1974, tsessebe in 1984 (Du Preez 2001). Unfortunately, the harvesting of most of these species was not well documented from the year of introduction, except for giraffe, of which a total of 67 individuals were harvested between the years 1993–2009, buffalo (80 between the years 2006–2008) and eland (580 between 1989–2009) (Erb 1993). Some species, such as roan and sable, in which populations showed a decline, cannot be harvested at the current population size, and this was the case since introduction. Other species, *e.g.* hartebeest (*Alcephalus buselaphus*) and tsessebe (*Damaliscus lunatus*) were introduced into the park. However, comparatively less effort is spent on the breeding of these species. Hartebeest are viewed as less important due to their abundance on various game farms, and tsessebe have not bred successfully suggesting that the W.N.P is unsuitable for them as breeding habitat.

The park has seven water holes, namely: Duitsepos, Kiewit, Elandsdrink, Geelhout, Heilboom, Secridata, and Bergtuin, which are evenly distributed across the plateau. They serve as the main water supply for the animals throughout the year, with exception of a few natural pans that normally dry up soon after end of the rainy season. Water is pumped from the canal which runs across the north-central parts of the country from the Berg Aukas and Kombat, where it is then diverted to the seven waterholes in WNP (Fig. 1).

DATA COLLECTION

The aerial survey (total count)

The aerial survey was conducted firstly by the Nature Conservation Department (South West Africa) during 1983–1988 before Namibia's independence, and then by the Ministry of Environment and Tourism of Namibia, (Directorate of Scientific Services) during the years 1997, 2000, 2005 and 2009–2013 after Namibia's independence. The survey was carried out using a five-seater Bell Jet Ranger helicopter V5-HEM. During the years 1984–1988, the survey was conducted without GPS navigation system. The park was than divided into 25 sectors and each year, counts were conducted over two subsequent days, requiring in total *ca* 10 hours. The survey was conducted during the morning and early af-

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ternoon. The aerial census was held within the same week as ground waterhole counts, *i.e.* in August. An experienced pilot flew the helicopter together with two observers and one recorder. During a survey, each observer was allocated a 250 m strip width with the aid of the road, 250 m from the flight path of the helicopter and 80 m above the ground. The crew was connected by an intercom system. In order to improve visibility during the aerial survey, all four doors were removed, and the two observers wore ski-masked to protect their eyes from wind. Disturbance of animals during the census was kept to a minimum; animals were not followed. However, because of the altitude, it is not expected to obtain as accurate data on population structure (sex and age structure) as during the waterhole counts.

In the early 1990s, the surveys were conducted using GPS navigation systems (1997, 2000, 2005 and 2009–2013). Custom QBasic software was used to generate the transect lines, spaced 500 m apart over the entire park's surface area. The flight altitude was standardized at 100 m above ground as much as possible. Transects had north-south orientation, except for two areas with rocky gullies, which run predominately in the east-west direction. The beginning and the end point co-ordinates were recorded in ASCII file format. The areas laying below the plateau (Onjoka, Rodenstein) and the isolated Omuverumu Plateau were not surveyed. Transects generated by the software, were loaded into a Garmin 12 XL GPS using Ozi Explorer. One GPS was used for navigation purposes, while waypoints were recorded on a second GPS of the same model. The track plot flown was recorded on both GPS during the flight. During the survey, the observers systematically scanned their allocated strip widths. At each sighting made by the observer, the recorder would note down, waypoint number positioned in the GPS, ungulate species, their numbers and if possible sex and age of each animal.

To ensure the complete coverage of the ground, the pilot and the recorder assisted the observers by counting the animals directly beneath the helicopter. After each survey, the data recorded on the GPS were downloaded to an Ascii file format. Double counts were minimized by: not counting animals moving to the neighboring transects, circling and counting large herds, even slightly off the currently surveyed transect and while evaluating the data, highlighting rhinoceros sightings and attempting to individually identify them, maintaining transect lengths not longer than 10 km to ensure that the observer could remember animals moving to the neighboring transect. All ungulates were counted, with a special attention paid to rhinos and also buffalo, roan, sable or eland. Wherever herds of these species were encountered, the helicopter circled over the herds to obtain precise count and to sex and age the animals, especially rhino. Some bigger herds were photographed for subsequent count verification.

Waterhole counts

Since the Waterberg has a limited number of open waterholes, during the dry season, waterhole count were conducted as another alternative way to count ungulates. The counts were conducted during the years 2009–2013. To increase visibility, waterhole censuses were conducted biannually at the full-moon periods of dry season (June and/or July, and August). Specially constructed counting hides and public viewing hides were used at all seven waterholes. The game was accustomed to the permanent hides. Each counting site was manned by at least two people. The counting and recording of data were alternated between the two every four hours. Each count lasted 48 hours. The counting procedure was conducted simultaneously at all sites. Each data sheet had a serial number in order to facilitate filing. The location and name of the waterhole and observer(s) were recorded.

The following data were filled into standardised data sheets: 1) the time of arrival and departure of animals, as well as directions of arrival and departure; 2) the number, age and sex of the animals in each group, determined as accurately as possible. Regarding the age classes, animals were classified as adult, subadult or juvenile. Individuals that could not be assigned to any of these categories, were recorded under 'unknown'; 3) under the column 'comments' the observer(s) noted any particular observations that might help to recognize certain groups or individuals (*e.g.*

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details of markings, such as ear tags, collars/ neck bands or distinctive characteristics, such as broken or skew horns); 4) in case an animal or group is recognised as one that drank at a particular waterhole previously during the count, it was recorded in the prescribed way but with the addition of a mark next to the new observation.

Data analysis

Population dynamics for all ungulate species was elaborated using the total counts (aerial surveys), while the correlation between the amount of rainfall (measured from 1st July to 30th June of following year), and the number of individuals of particular ungulate species counted just after this season, *i.e*. in August/ September. In addition to the aerial surveys, water point counts were conducted during the years 2009−2013 to test the difference in the number of ungulates between the aerial counts and water point counts. The dominance of particular ungulate species was calculated as the percentage of the mean number of individuals belonging to this species to the total mean number of all ungulate individuals (except for the black rhino and white rhino) recorded in 11 years (during 1998−2013). The data for rhinos were omitted due to the current policy of a high confidentiality (poaching problems) enforced by the Ministry of Environment and Tourism of the Namibian Government. The regression analysis (regression coefficients, significance levels, relationship graphs and equations) were conducted using Microsoft Excel to generate the relationships between the number of individuals of particular ungulate species and the amount of rainfall.

RESULTS

During the years 1980−2013, 16 ungulates species were recorded in the this protected area. Two of them, the black rhino and white rhino belonged to the order Perrisodactyla, and the remaining 14 to Artiodactyla. Among the ungulates censused during the years 1998−2013, the most common were the African buffalo and eland, comprising together more than half of all ungulates recorded. Fairly common (each species with 5−12% of all ungulates recorded) were also the roan, sable antylope, kudu and warthog. Four other ungulates, namely the white rhino, black rhino, giraffe, and gemsbok have been classified as uncommon (together 11.9%). The remaining eight species were rare in the WNP (together 1.9%). Among these 16 ungulate species, eight have shown an increase in numbers during the years 1980−2013, six others a decrease, and the populations of two other species remained stable.

The population of the buffalo has shown the most dramatic increase over these years, from a dozen or so individuals in the 1980s to more than 500 in the early 2010s. A similar increase rate was also recorded for the giraffe from a few individuals in the early 1980s to about 200 in the early 2010s. It was difficult to determine population trends for the small antelopes, as they can be easily overlooked during surveys. Collected data suggest a slight increase for the common duiker (*Sylvicapra gimmia*) and steenbok (*Raphicerus camperstris*), and a stable population of the klipspringer (*Oreotragus oreotragus*). While the roan has decreased, the sable antelope have slightly increased in numbers during the years 1980−2013. The eland population remained faily stable, but the related kudu *Strepsiceros strepsiceros* and gemsbok (*Oryx gazella*) have declined. Similarly, the tsessebe population remained stable, but that of related hartebeest dramatically declined. The warthog has dramatically declined in the 1980s but in subsequent years its numbers stabilized on a low level. The decline of the blue wildebeest (*Connochaetes taurinus*) and impala (*Aepyceros melampus*) was so drastic that both species eventually became locally extinct (Table 1).

During the years 1998−2013, males of the white rhino, black rhino, gemsbok and warthog have increased in numbers faster than females, while the reverse situation was recorded for species such as the giraffe, African buffalo, eland, and roan. In African buffalo and eland, the numbers of observed juveniles increased faster that adults (suggesting increasing population), while the reverse trend (suggesting decreasing population) was recorded for the roan and gemsbok. In other species such differences were minimal (Table 2).

The comparision between aerial counts and waterhole counts of observed animals be-

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Table 1. Ungulate community in the Waterberg Plateau National Park during the years 1998–2013.

Species	x	Var	D(%)	SD	Min.	Max.
Giraffe (*Giraffa*)	63.8	127935.4	4.7	32.9	5	103
Buffalo (*Syncerus caffer)*	415.4	5026807.4	30.4	248.1	169	1029
Eland (*Taurotragus oryx*)	386.4	4812139.7	28.3	128.6	154	537
Roan (*Hippotragus equinus*)	174.5	997028	12.8	31.7	131	227
Sable antelope (*Hippotragus niger*)	102.9	364294.5	7.5	29.3	59	145
Gemsbok (*Oryx gazella*)	29.6	30051	2.2	21.2	5	68
Kudu (*Tragelaphus strepsiceros*)	82.3	240256.1	6.0	46.3	24	165
Hartebeest (*Alcelaphus buselaphus caama*)	12	4501.3	0.9	7.8	5	25
Wildebeest (*Connochaetes*)	1.5	77.3	0.1	0.4	2	3
Tsessebe (*Damaliscus lunatus*)	4.5	992.1	0.3	8	1	23
Impala (*Aepyceros melampus*)	4.4	952.1	0.3		48	48
Warthog (*Phacochoeru safricanus*)	83.3	235174.6	6.1	32.3	19	124
Klipspringer (*Oreotragus reotragus*)	0.7	26.4	0.1		8	8
Duiker (*Cephalophinae*)	3.9	451.7	0.3	10.2	1	26
Steenbok (*Raphicerus campestris*)	1.6	133.9	0.1	4.5	1	11

n = 11 years. x – average number of individuals per year, Var. – variance, D% – dominance (the percentage of individuals of a given species related to the total number of all ungulates recorded), SD – standard deviation (based on dominance), Min. – minimum number of individuals per year, Max. – maximum number of individuals per year. The data for rhinos were omitted due to the current policy of a high confidentiality (as an anti-poaching measure) imposed by the Ministry of Environment and Tourism of the Namibian Government

tween 2009–2013 varried among the different species (Fig. 3). In giraffe, sable, gemsbok and hartbeest more numbers were observed at the waterpoints than those in aerial counts. However for the eland, buffalo, roan the aerial counts generated more numbers as compared to waterpoint counts. Kudu trents where not consistant across the years regarless of the method used to sample them (Fig. 3).

For some ungulate species relationships were detected between their population sizes and precipitation. The population of eland ($R^2 = 0.005$) was positively but weakly linked with the annual average rainfall between the years 1981–2013, whereas the population of kudu ($R^2 = 0.0456$), sable ($R^2 = 0.1697$), gemsbok ($R^2 = 0.0275$) and roan ($R^2 = 0.0501$) were negatively but weakly linked with the amount of rain (Figs 4C, D and G). On the other hand, the populations of giraffe ($R^2 = 0.0039$), buffalo ($R^2 = 0.1506$) and hartebeest ($R^2 = 0.5083$) were not significantly related to rainfall (Figs 4A, B and H). The breaking point of all species densities was in the year 1995, when all species densities decreased dramatically except for buffalo which was only slightly affected. The year 1995 had the lowest rainfall (159 mm) during the period 1980–2013 (Figs 2 and 4). The year 2011 had the highest rainfall (893mm) of the period, but most species densities decreased, whilst all species densities except for hartebeest gradually recovered in the year 2012 onwards (Figs 2 and 4).

DISCUSSION

Historically, vast populations of large herbivores roamed the plains of Africa (Gordon *et al*. 2004, Owen-Smith *et al*. 2005a), controlled to a large extent by predators, water and forage availability. Currently, many of the species

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Table 2. Trends in population growth between males and females, and between adults and juveniles during the years 2008–2013 in Waterberg Plateau Park.

Species	Males		Females		Adults		Juveniles	
	Equation	R^2-value	Equation	R^2-value	Equation	R^2-value	Equation	R^2-value
White rhino	1.4x - 0.6	0.8448	6x - 7.4	0.6777	7.4x - 8	0.7392	3.1x - 3.3	0.6768
Black rhino	5.9x - 4.1	0.8187	7.2x - 6.8	0.7355	13.1x - 10.9	0.7803	3.5x - 3.1	0.7996
Giraffe	5.5x + 9.1	0.3795	6.4x + 0.4	0.5995	11.9x + 9.5	0.5186	4.3x - 0.3	0.4609
Buffalo	37.9x + 28.1	0.4979	73.2x + 37.2	0.5953	111.1x + 65.3	0.5690	56.3x + 1.9	0.7119
Eland	13.3x + 16.5	0.2928	26.8x + 57.8	0.4189	40.1x + 74.5	0.3764	41.3x - 27.9	0.7286
Roan	5.9x + 14.3	0.2780	14.8x + 8.2	0.5772	20.7x + 22.5	0.5164	4.8x + 16.6	0.1381
Sable antelope	0.6x + 10.4	0.0183	-1.1x + 32.05	0.0122	-0.5x + 36.7	0.0009	1.1x + 27.45	0.0047
Oryx	1.1x – 1.1	0.8176	1.1x + 0.3	0.4449	2.2x - 0.8	0.6142	0.077x + 0.46	0.0769
Kudu	-0.6x + 6.55	0.1036	-3.8x + 26.8	0.1933	-4.4x + 32.4	0.1629	1.7x + 7.15	0.1917
Warthog	3x + 11	0.2064	-0.1x + 23.7	0.0001	2.9x + 34.7	0.0406	0.6x + 20.2	0.0037

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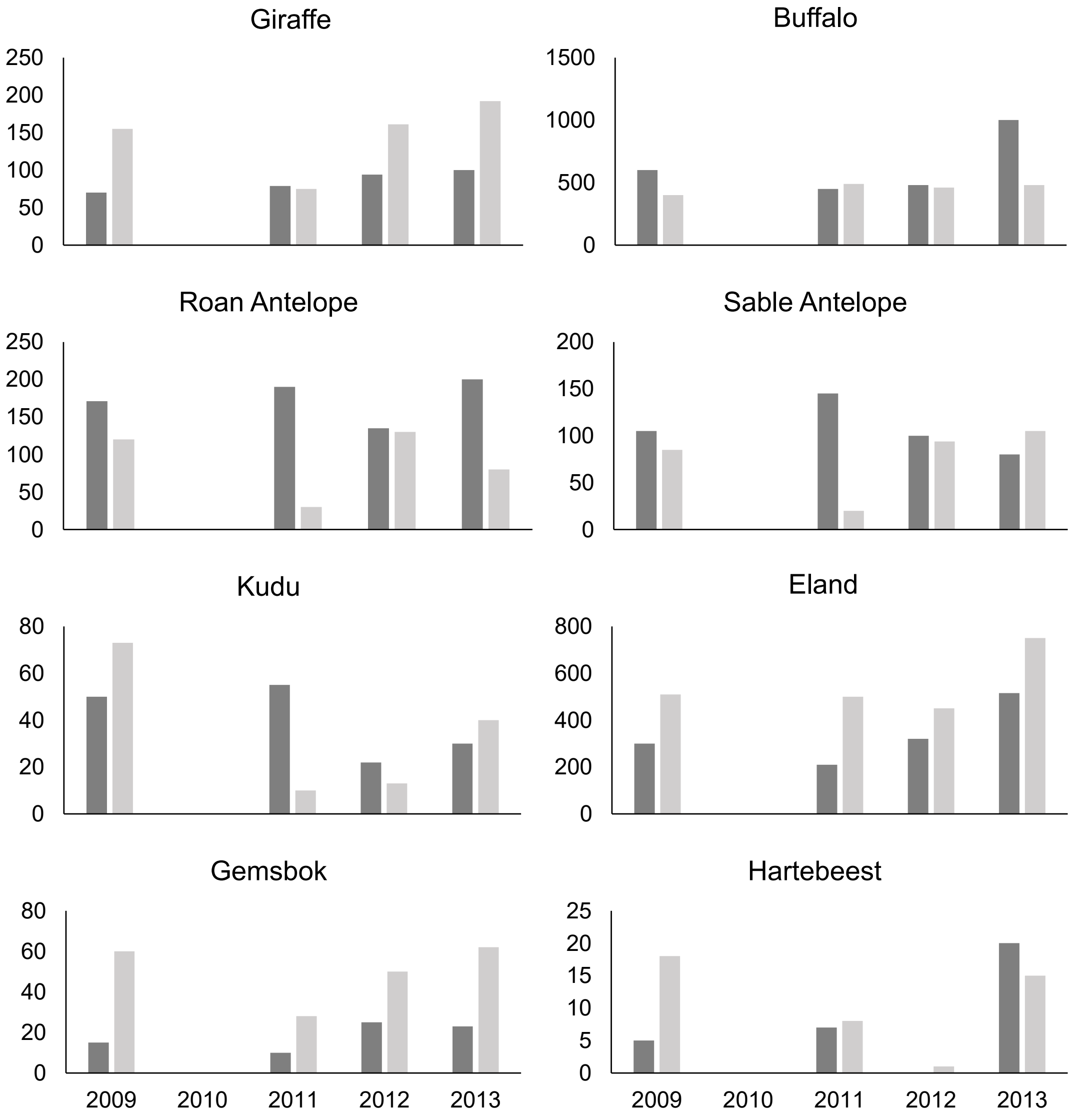

Fig. 3. Differences in the number of ungulates between the aerial counts (grey columns) and water point counts (dark columns) in Waterberg Plateau Park during the years 2009–2013 (note the different scales).

have to be actively conserved in an environment substantially impacted by anthropogenic activities (Gordon *et al.* 2004). Often this modified environment has fewer predators and is water-supplemented. While it is important to understand ungulate population dynamics in a pristine setting, contemporary conservation also requires an understanding that specifically targets these modified settings. In both pristine and modified environments, long-term ecological studies of population dynamics in large ungulates provide a detailed understanding of the intrinsic and extrinsic factors that determine population size and population structure (Gaillard *et al.* 2000). These studies concentrate on the relationships between population density, climate and individual survival rates of different sex/age classes (Gaillard *et al.* 2000).

Coe *et al.* (1976) noted that there is a direct relationship between annual rainfall and abundance of large African herbivores. Large ungulate populations are known to be limited by their food supply (Coe *et al.* 1976). This suggests that the relationship between rainfall and herbivore abundance operates through

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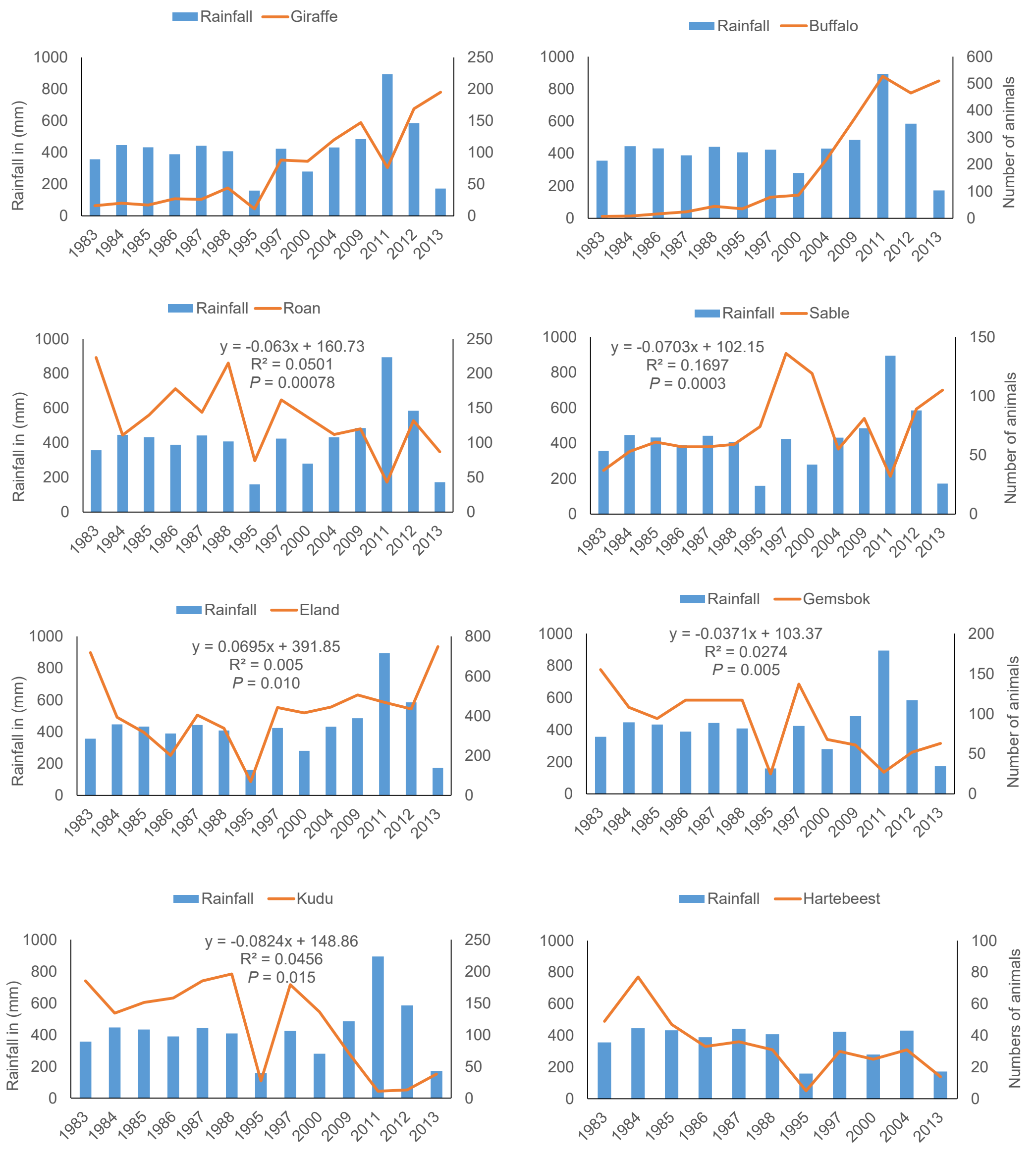

Fig. 4. Trends in rainfall (vertical axis to the left) and the number of animals (vertical axis to the right) during the years 1983–2013 in Waterberg Plateau Park: the results of regression analyses are given above the bars (note the different scales).

the effects of precipitation on primary production. Irregular rainfall and the availability of water in semi-arid environments affects the spatial distribution, quantity and quality of food for large herbivores (Tsindi *et al.* 2016). As illustrated elsewhere, the larger herbivore species, the more tolerant it is to low quality diet (Bhola *et al.* 2012). Species found in the WNP, such as the white rhino, giraffe, eland, gemsbok and other grazers may benefit from open areas, as long as these areas provide cover and shade, although they differ in their specific dietary needs and preferences. Availability of specific food plants may limit their reproductive success and population growth. Important is both the composition of grass species as well as plant height. The main habitat in the WNP (*Terminalia sericea* – *Melhania acuminata* – tree-shrub savanna) is dominated by relatively coarse and unpalatable species, particularly (*Eragrostis pallens*). With low amount of such preferred palatable species as the black-footed

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grass (*Brachiaria nigropedata*), bottle brush grass (*Anthephora pubescens*), or crab grass (*Digitaria seriata*), this habitat should be regarded as sub-optimal for the grazers.

The most successful species in the WNP: giraffe, eland and buffalo have a relatively wide dietary spectrum. The buffalo is the only grazer that can cope with denser bush by pushing it aside in order to access the grass (Estes 1997). On the other hand, the sable and roan antelope are highly selective grazers. They depend on medium to tall climax grass species. Roan feed a wider range of grass species on the plateau than the sable, but both grazers may feed also on a number of same grass species, thus they might compete with each other (Erb 1993). Those two antelopes may also compete with the buffalo, as it may easily switch to graze on grass species preferred by the roan and sable. Both antelope species appear to avoid competition with the largest grazer, the white rhino. Their preferred foraging habitats (taller grass) are of lower dietary value for the white rhino.

The number of ungulate species in a given area is related mainly to the diversity of habitats, and this, in turn, is often the outcome of the area's size. For example in the Kruger National Park, South Africa (19.6 thousands km^2) there are 16 habitat types and 37 ungulate species; in Kafue NP (24.0 thousands km^2) – 11 habitat types and 30 ungulate species, in Hwange NP (14.6 thousands km^2) – 9 habitat types and 27 ungulates species, while in Etosha NP (23.2 thousands km^2) – 7 habitat types and 24 ungulates species (Grange *et al.* 2012). In the much smaller WNP (405 km^2), with only five habitat types, 17 species were recorded. Elsewhere, the presence of larger water bodies may further increase this diversity, as some ungulate species are strictly water-dependent, *e.g.* hippopotamus (*Hippopotamus amphibious)*, waterbuck (*Kobus ellipsiprimnus)*, red lechwe (*Kobus leche)*, sitatunga (*Tragelaphus selousi)*, or bush pig (*Potamochoerus larvatus*) (Sinibaldi *et al.* 2004). This was, however, not the case in WNP, as there is a lack of permanent water bodies in this area.

In African savanna, rainfall and predation (especially by lions) are widely regarded as the main factor controlling population density of large ungulates (Coe *et al.* 1976, Owen-Smith 1990, Mills *et al.* 1995, Ogutu and Owen-Smith 2003). These factors are in some areas interlinked (Mills *et al.* 1995). Rainfall determines vegetation growth and therefore food resources for ungulates (Coe *et al.* 1976). Since grasses respond more steadily to annual rainfall variability, grazers are more directly affected by this variability than browsers (Ogutu and Owen-Smith 2003). The strong relationships between species densities and rainfall in WNP suggest that rainfall does infect control the dynamics of some ungulates, and that changes in rainfall indirectly altered the abundance of these animals (Mills *et al.* 1995, Mduma *et al.* 1999, Georgiadis *et al.* 2003, Owen-Smith *et al.* 2005a, Ogutu *et al.* 2008). The amount of rain in WNP between the years 1980–2013 varied considerably more so between the years 1980–1999, where WNP received most of its rains only during the early months of the year (January-March). The WNP experienced three years of drought (1995, 2000 and 2013), and received its highest rainfall between the years 2009–2012. While populations of the giraffe and buffalo increased across the years 1980–2013, those of the kudu, sable antelope, roan and gemsbok decreased. Differences in rainfall responses of the grazers to those of the browser and mixed feeders suggests that the influence of rainfall on abundance was not substantially altered by the dietary guild of these herbivores as noted in Ogutu *et al.* (2008).

In the Kruger National Park, the survival of ungulates was subject to past prey availability to main predators and to the effect of preceding rainfall. However, juvenile survival differed from adult survival in most species investigated (Owen-Smith *et al.* 2005b). Six ungulate species declined substantially in abundance over the years 1982–1994: kudu, sable, roan, warthog, tsessebe and waterbuck, while populations of zebra (numbers significantly influenced by movements), giraffe, wildebeest and impala were stable (Owen-Smith *et al.* 2005a*)*. Those ungulate species with stable populations were not affected by the amount of rainfall, but the decline in kudu numbers was attributed to the outbreak of anthrax and decline in the amount of rainfall. Similarly, the declining population density of the sable and warthog was also attributed to the declining amount of rainfall over the years 1982–1994. Historically, lion predation

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in Kruger National Park was the main factor responsible for the decline of the roan, sable and warthog. The sable was in addition negatively influenced by dry season rainfall.

In the Hluhluwe-iMfolozi Park, South Africa, population growth rates of seven large ungulate species (giraffe, kudu, impala, nyala (*Tragelaphus angasii*), wildebeest, zebra (*Equus quagga*) and warthog) were in 1986–2010 little affected by both rainfall variation and changes in lion numbers. Only wildebeest numbers were affected by rainfall, and zebra numbers by lion predation (Grange *et al.* 2012). However, in the Kruger National Park, South Africa, buffalo, kudu, roan, waterbuck, and tsessebe populations increased with raising prior rainfall; and populations of the zebra, wildebeest, and giraffe were negatively affected by prior rainfall. The warthog, sable, eland and impala were most abundant in intermediate level of preceding rainfall (Owen-Smith 1990, Mills *et al.* 1995, Ogutu and Owen-Smith 2005). While the wildebeest, and to lesser extent zebra, were more vulnerable to lion predation in wetter compared to drier years, the reverse was true in the case of the buffalo and waterbuck, and no effect was recorded in the case giraffe and kudu (Mills *et al.* 1995). In Hwange N. P., Zimbabwe, the relationship between large ungulate densities in the late dry season and the rainfall of the previous rain season, were all negative. However, due to low sample size the correlation was not statistically significant. Possibly, changes in the population dynamics of the elephants affected the numbers more than variation in the rainfall (Chamaille-Jammes *et al.* 2009).

In the Masai Mara National Reserve, and adjoining Koyiaki pastoral ranches in Kenya, the declining pattern of ungulate populations during the years 1977–2008 was consistent with a general declining trends in other protected areas in East Africa (Bhola *et al.* 2012). This was caused by increasing human settlement and associated poaching, conversion of natural vegetation into arable grounds and competition with livestock and displacement of wild ungulates by livestock incursions into protected areas. The year-to-year changes in the ungulate population densities in the Masai Mara National Reserve differed from those in the neighbouring pastoral ranches. These differences were also related to the body size, feeding guilds and nutritional value of the forage, predation risk and competition with livestock. Small ungulate species were more common on the pastoral ranches than in the reserve (reduced predation risk). Medium-sized herbivores, preferring short grasses, such as zebra, wildebeest and topi (*Damaliscus korrigum*) moved seasonally between the two areas (depending on water and food availability), but medium-sized species preferring long grasses (hartebeest and waterbuck) remained in the reserve. Large-sized herbivores were more common in the reserve than in the pastoral ranches (no need to avoid predators). Although the authors do not discuss the year-to-year variation in the abundance of particular ungulate species in the Masai Mara National Reserve, some pattern are apparent from the presented graphs. Giraffe, buffalo, impala, topi, hartebeest and Thomson's gazelle (*Gazelle thomsoni*) declined, while eland, Grant's gazelle (*Gazella granti*), wildebeest, and warthog populations were stable over the years 1977–2008. Elephant (*Loxodonta africana*), wildebeest and zebra population greatly fluctuated from year to year, with a long-term stable tendency. The annual rainfall averaged 1010 mm, but the authors failed to provide data on year-to-year changes in the amount of rainfall. The long-term declines could be linked to increasing human-induced factors (increased number of people, and livestock) rather than to the amount of rainfall. However, similar tendencies were shown in the reserve and ranch. Larger ungulates are usually more vulnerable to human pressure, but this is also not apparent in this study. This suggests that the main factor responsible for these changes was the amount of rainfall changing from year to year.

In non-protected areas of the Laikipia District, Kenya, changes in the type and intensity of land use were the most important factors controlling population densities of wild ungulates. Rainfall limited densities of only dominant grazing species (*i.e.* zebra) and other ungulate species which reached high population densities (Georgiadis *et al.* 2007). The breeding success of African ungulates, and therefore population density, can be further limited by amount of rainfall. For example, the roan and sable antelope do not occur in areas that re-

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ceive less than an average of 400 mm rainfall per annum (Martin 2003), while the buffalo does not occur in areas that experience less than 250 mm rain per annum (Apps 2000). The WNP falls within the 500–600mm rainfall isohyet (Du Preez 2001), and with the mean annual rainfall of 424.5 mm during the years 1981–2001, provide good environmental conditions for these species (Du Preez 2001). The majority of the key species which reside in the WNP depend on permanent access to water. There are seven artificial waterholes widely distributed over the WNP, which provide good quality water throughout the year. The WNP therefore, fulfils the requirements of all ungulate species which reside there. Nevertheless, rainfall affects ungulates *via* the availability of food, and *via* food quality.

To summarise, the population dynamics of ungulates is driven by variations in climatic conditions which affects the growth, development, fecundity, and demographic trends of the population (Gedir *et al.* 2016).Variations in precipitation affect the production of plant material and indirectly the carrying capacity of the ecosystem in which these animals occur (Coe *et al.* 1976). Thus, low rainfall restricts plant growth and hence reduces the nutritional value of available plants, whilst excessive rainfall could also be detrimental by favourably promoting the growth of more competitive grasses, higher in fibre content (Ogutu *et al.* 2015). It was evident in this study that population dynamics trends of ungulates in a water supplemented environment, are in fact regulated by rainfall, which promotes vegetation growth and hence food production (Rutherford 1980). The population trends were inconsistent across the different ungulate species mainly due to the fluctuating rainfall but other factors such as competition amongst the grazers may also have influenced the population trends. The temporal pattern of population declines of gemsbok, redhartebeest, roan and sable was consistent with a lagged effect from years of drought or competition for food in addition to the effects of seasonal rainfall. Species that maintained high abundance like the giraffe and buffalo responded mainly to an immediate or lagged density feedback (as in Owen-Smith *et al.* 2005a).The population trends of ungulates in WNP were comparable to those documented in other regions of sub-Saharan Africa, while keeping in mind that here the effects of predation were limited to leopards only. Harvesting of game is necessary in the absence of predators as a means of controlling population densities of species that show population growth beyond (or approaching) the maximum ecological capacity of a given park. Thus, we recommend that numbers of harvested animals in WNP should be based on accurate and updated data on population sizes, including demographic profiles (age classes and sex ratio). These data are necessary to allow objective assessment of harvesting rates. In addition, simulation modelling to project population development over time should be applied (Erb 1993), including however new rainfall data, and possibly the development of local predator population.

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