Poultry, Fisheries & Wildlife Sciences
ISSN: 2375-446X
Tsindi et al., Poult Fish Wildl Sci 2016, 4:1
DOI: 10.4172/2375-446X.1000154
Review Article Open Access

Seasonal Variation in Population Structure and Status of Selected Herbivores in the Mana Pools National Park Flood Plain, Zimbabwe

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Abstract

A study on the seasonal variation in population structure and status of the African buffalo (*Syncerus caffer*), the greater kudu (*Tragelaphus strepsiceros*) and the common impala (*Aepyceros melampus*) was carried out in the Mana Pools National Park floodplain, Zimbabwe. Data was collected during the wet (February) and dry (September) seasons of 2012. The simple random sampling method was employed in transect placement. A total of 10 transects were sampled. The line transect method was used to estimate dry and wet season populations of buffalo, kudu and impala. Results from the two tailed t-test showed no significant variation for the populations of kudu (P>0.05) and buffalo (P>0.05) with season. However, impala population varied significantly with season (P<0.05). Female biased sex ratios were observed in all the species. The sex ratio of adult male to adult female for buffalo, kudu and impala was 1:1.78, 1:2.75 and 1:1.48 respectively. Age composition for buffalo comprised 53.13% (n=102) adult, 35.94% (n=69) sub adults and 10.94% (n=21) juveniles. For kudu, 47.37% (n=44) were adults 42.11% (n=38) were sub-adults and 10.53% (n=11) were juveniles. Impala age composition comprised of 46.27% (n=689) adults, 45.53% (n=679) sub-adults and 8.2% (n=121) juveniles. Group size for impala significantly changed with season (P<0.05) and no significant variation in group sizes for buffalo and kudu were observed (P>0.05). Dry season mean group sizes for buffalo, kudu and impala were 9.8, 3.6 and 14.1 respectively. The population of buffalo declined from 446 in 1995 to 174 in 2012. The populations of kudu and impala showed an increasing trend between 1995 and 2012. Results from this study suggest that seasonal variation in forage availability could be the primary factor influencing the status of herbivores in the MPNP floodplain. There is an urgent need for management to revise staff and ration quotas for herbivores and increase law enforcement efforts to assure the sustainable management of herbivores in MPNP.

Keywords: Age composition; Line transect method; Population status; Population structure; Sex ratio

Introduction

Background of study

Populations of wildlife species are declining in most parts of the world [1-3]. Contributory causes include disease outbreaks, erratic rainfall and temperature increases, illegal hunting, human encroachment into prime wildlife habitats as well as recurrent droughts [4-15]. Understanding population dynamics and a population's sensitivity to these factors is therefore of great help in informing conservation policy decisions, planning, recovery strategy and management triggers, especially when management actions are risky or expensive [16-18].

The African buffalo, kudu and impala have all been classified by the International Union for Conservation of Nature and Natural Resources (IUCN) as species of Least Concern [19]. The common impala (*Aepyceros melampus melampus*) is widespread, common and abundant in most savannah protected areas. However, it has been eliminated in some parts of their range such as Burundi [20]. It is therefore of paramount importance to closely monitor impala populations locally to avoid further local extinctions like its close relative, the black-faced impala (*Aepyceros melampus petersii*) which is now vulnerable and endemic to Uganda (IUCN, 2013). Similarly, the greater kudu and the African buffalo must be closely monitored as local declines have been recorded elsewhere [7,21].

Irregular availability of water in semi-arid savannahs 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 seasons [22-24]. In Mana Pools National Park (MPNP), the Zambezi river floodplains form an important dry season concentration area for numerous large mammals of a wide variety of species, from warthog (*Phacochoerus aethiopicus*) to elephant [25]. The *Faidherbia albida* is a dominant trees species in the floodplain and it has reverse phenology which makes it shed its leaves during the wet season and grow new ones towards the end of the rains [26]. It bears leaves and fruits in the dry season and these form high quality foods for domestic and wild herbivores [26].

Previous studies by Dunham and duToit, Dunham and Jarman on large herbivores in Mana Pools have been largely biased towards short term changes herbivore densities in the floodplain [25,27,28]. The demographics of buffalo, kudu and impala have also not been studied. By using the line transect method, this study seeks to examine the influence of seasonality on group size and age and sex structures of three herbivores (buffalo, kudu and impala) which are highly susceptible to anthrax and have different dietary requirements.

Problem statement

Populations of wild large herbivores are declining through much of the world due to several environmental stressors [2,3].

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Received May 05, 2016; **Accepted** June 09, 2016; **Published** June 21, 2016

Citation: Tsindi MF, Kupika OL, Moses M, Simbarashe M (2016) Seasonal Variation in Population Structure and Status of Selected Herbivores in the Mana Pools National Park Flood Plain, Zimbabwe. Poult Fish Wildl Sci 4: 154. doi:10.4172/2375-446X.1000154

Drought and increasing temperatures as well as other environmental stressors within the Zambezi Valley might have caused changes in the population structure and status of selected herbivores in MPNP. Yearly variations on rainfall received might also have an effect on vegetation and food availability which is a primary driver of population change [29]. Landmark events such as the 2001/2 and 2011/2 drought and associated anthrax outbreak might also have caused massive changes in selected herbivore status and structure. For example, an anthrax outbreak led to a local decline among Grevy's zebra population in southern Samburu, Kenya [6]. The purpose of this study is to examine the seasonal variations of age and sex structures of selected herbivores in MPNP.

Objectives of the study

1. To compare the populations of selected herbivores during the wet and dry seasons in the MPNP floodplain.

2. To compare age and sex structure of selected herbivores during the wet and dry season in MPNP floodplain.

3. To determine the population trends of buffalo, kudu and impala between 1995 and 2012 in MPNP floodplain

Research questions

1. Does the populations of selected herbivores differ during the dry and wet seasons in the MPNP floodplain?

2. Does the age and sex structure of selected herbivores differ during the wet and dry season in MPNP floodplain?

3. What are the population trends of buffalo, kudu and impala between 1995 and 2012 in MPNP floodplain?

Research hypotheses

1. H_0: There is no significant difference in the populations of selected herbivores in the wet and dry seasons in MPNP floodplain.

2. H_0: There is no significant difference in the age and sex structure of selected herbivores in the dry and wet seasons in MPNP floodplain.

3. H_0: There is no significant change in the population trends of buffalo, kudu and impala in MPNP floodplain.

Significance of study

The knowledge of sex ratio and age distribution of individual herbivores is vital for evaluating the viability of a species since these variables reflect the structure and the dynamics of a population [30]. Knowing the status of a given species at a given time is also of great help in planning, policy formulation and developing recovery strategies. Moreover, this study is expected to provide information on seasonal variation in abundance of selected herbivores in MPNP and give base line information on age and sex structure for further study on these species. Most importantly, it is anticipated that the outcome of this research project shall contribute towards adaptive and sustainable management of herbivores in MPNP.

Literature Review

Large herbivore dynamics

Monitoring the dynamics of herbivore populations over time is critical for effective conservation [29]. Most species of wildlife have declined in most parts of Africa in both protected and unprotected areas [7,29]. Wildlife populations in the Mara region declined progressively after 1977, with the exception of a few [31]. Populations of almost all wildlife species declined to a third or less of their former abundance in both the protected Masai Mara National Reserve and in the adjoining pastoral ranches [31]. In contrast, Valeix analysed long-term water hole census data and noted that large herbivore populations were fluctuating in Hwange National Park (HNP) [32].

A study on population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997 showed that non-migratory wildlife species declined by 58%. Declines of over 70% were recorded in buffalo, giraffe, eland and waterbuck. No significant decline or increase was recorded for elephant, impala and ostrich. A similar study also investigated population trends of resident wildebeest and factors influencing them in Masai Mara ecosystem between 1977 and 1997. The results showed that resident wildebeest population had a massive 81% decline from about 119,000 in 1977 to about 22,000 in 1997 [21].

Stoner examined changes in large herbivore populations across large areas of Tanzania using aerial census data collected during the late 1980s to early 2000s. Results showed that the Thomson's gazelle, Grant's gazelle, hartebeest, reedbuck, roan antelope, sable antelope, warthog and zebra declined in over 50% of the zones where they were surveyed [29]. However, a few populations increased significantly. The population dynamics of 11 ungulate species within Kenya's Nairobi National Park were compared to those in the adjoining Athi-Kaputiei Plains, where human settlements and other developments had expanded. Results showed that migratory wildebeest decreased from almost 30,000 animals in 1978 to approximately 5,000 in 2011 but there was a small change in the migratory zebra population in the region. Hartebeest, impala, eland, Thomson's gazelle, Grant's gazelle, waterbuck, warthog and giraffe numbers declined regionally, whereas buffalo numbers boosted. Among the non-migratory species, only giraffe showed a substantially greater decline outside the park than within it. Their findings also emphasized on the interdependency between the park and the plains for seasonal wildlife movements, especially in exceptionally dry or wet years [33].

Gandiwa also carried out a study on large herbivore dynamics in northern Gonarezhou National Park, comparing densities and distribution of wild ungulates and domestic livestock based on aerial surveys conducted during 1991-2010. No significant differences in the densities of buffalo, eland, elephant, giraffe, impala, kudu, waterbuck and zebra were observed between 1991-1998 and 2001-2009. However, there was a slight no significant decline on the populations of zebra and giraffe [34,35]. Several authors suggested that the interaction of domestic livestock and wild ungulate that have similar body size and niche would lead to the competitive exclusion of the wild ungulates [36-38].

Surprisingly, none of the eight wild herbivores showed decline in densities following the human and livestock encroachments into the northern GNP in 2000. Strict antipoaching measures and restriction of human activities within 4 % of the park was attributed for the stabilization of herbivore populations [35].

Similarly, niche segregation between wild (guanaco) and domestic (sheep) herbivores was studied in Chilean Patagonia. Guanaco and sheep showed significantly different habitat preferences through all seasons, in spite of their spatial overlap at landscape scale. Additionally, the habitat used by guanaco was similar regardless of the presence or absence of livestock, which further indicated that sheep were not displacing guanaco where they lived together [39]. These results suggested that the interaction between livestock and wildlife will not automatically lead to the displacement of wildlife which is consistent with the findings by Gandiwa [34]. Bhola also concluded that the interaction between livestock and wildlife is of advantage to wildlife as livestock maintain grassland in short, nutritive growth stage and hence, promoting their abundance. Studies in Europe and America indicate that large herbivore populations have increased their range and density substantially [40]. For instance, Gill and Andersen recorded increase in the density of roe deer in Europe whilst Warren recorded increase for the white-tailed deer population in North America [41-43].

Factors influencing herbivore dynamics

An understanding of what factors cause wild herbivore populations to increase, decrease or remain stable is fundamental to the provision of advice on how to manage [1]. A combination of density dependence factors and stochastic environmental variations such as food resources, habitat quality, inter-specific competition, disease and parasites, weather, predation, human activities and population density can account for the demographic variation observed among years within large herbivore populations [44].

Disease outbreaks can cause sudden and unexpected local declines in abundance of wild animals [5,45]. For instance, at least 53 Grevy's zebra died from anthrax infection in southern Samburu, Kenya, between December 2005 and March 2006. The abundance of Grevy's zebra was lower in the region during the outbreak as compared to similar periods in 2003, 2004 and 2005. However, the outbreak did not affect the population structure as it affected both mature and immature individuals equally [6]. It should also be noted that not all diseases outbreak cause population declines. For example, the foot and mouth disease (FMD) which is a viral infection which mostly affect cloven-hoofed animals can reach a 100% morbidity rate without causing high mortality. Impala that are found in sub-Saharan Africa are sometimes referred to as indicator species due to their high susceptibility to infection and probably explains their huge and persistent population [46].

Forage production in savannahs is primarily limited by rainfall, which varies considerably in space and time, producing patchiness in green forage and seasonal water availability [47]. Increased temperatures also increases evaporative water loses and thereby elevating dry season aridity and reducing moisture available to support vegetation growth [7]. A study on the effect of drought on large mammals in MPNP, indicated that the densities of most herbivores declined during or after the 1983/4 drought with grazers being the most affected as compared to browsers [28]. Ogutu and Owen-Smith also recorded severe population declines by seven herbivores in Kruger National Park between 1977 and 1996 owing to erratic rainfall and elevated temperatures [7]. However, African herbivores have adapted to the seasonal variability in forage and water by performing regular seasonal migrations and unpredictable dispersal movements between water and forage resources [48,49]. A study on the dynamics of an insularised and compressed impala population also showed that high rainfall depressed reproductive success in impalas [40].

Relationships between rainfall and changes in age and sex structured abundances of seven ungulate species were examined monthly over a period of 15 years using vehicle ground counts in the Masai Mara National Reserve, Kenya. Species abundance showed strong and curvilinear relationships with current and cumulative rainfall. Monthly rainfall exerted both negative and positive effects on the abundances of impala, waterbuck and zebra. Strong relationships between abundance and rainfall suggest that rainfall underpins the dynamics of African savannah ungulates and that changes in rainfall due to global warming may markedly alter the abundance and diversity of these mammals [14].

Human population growth and associated activities is one of the major causes of habitat deterioration, fragmentation and loss which will consequently lead to herbivore population decline. For instance, Ogutu noted that decline of five ungulate species in Mara-Serengeti was significantly correlated with increasing number of settlements and people in the pastoral ranches [14]. Ochittilo also demonstrated a clear association between the decline in resident wildebeest populations and the expansion of agriculture into prime and original wildebeest wet season ranges in the Masai Mara ecosystem. A recent study on the impact of land-use change on large herbivore populations in some Masai Mara adjacent group ranches indicated that population dynamics of large herbivores have drastically reduced and human-wildlife conflicts increased [12]. Contrary to this, wild herbivores showed no decline in density following human and livestock encroachments into the northern Gonarezhou National Park in 2000 [50]. Populations may also decline in line with management objectives. For instance, in MPNP, the density of elephants declined after a cull and rhinoceros density decreased because of translocation [28].

Predation plays a key role in the top-down control of large herbivore populations in tropical ecosystems, especially the non-migratory species [51]. For instance, based on data and information in 42 published studies from over a 50-year time span, Ripple and Beschta analysed the composition of large predator guilds and prey densities across a productivity gradient in boreal and temperate forests of North America and Eurasia. Results showed that predation by carnivores such as sympatric gray wolves (*Canis lupus*) and bears (*Ursus species.*) limited densities of large mammalian herbivores [52]. Humans as super predators also exert top-down control on large wild herbivore abundances through hunting and exert bottom-up controls through fires and livestock grazing which affects wild herbivore abundances through altering resource availability [34].

Herbivore population status and structure

Most large herbivore populations have female biased sex ratios. For instance, a study on the population status and structure of the mountain nyala in Ethiopia showed that the male to female ratio was unequal, which was 1:2.3 [53], Doku, Regassa and Yirga also confirmed that sex ratios are biased in favour of females among zebras in Ethiopia [54,55]. Megaze also observed that female constituted 58, 8% and males constituted 35% of the population in a study of the population ecology and structure of the African buffalo in Chebera Churchura National Park and the results were similar to those observed in different parts of Africa [56-58]. The male to female sex ratio was 1:1.51. The difference in sex ratios among buffalos can be as a result of predation given that lions frequently prey on male buffalos [24].

Annighöfer and Schütz also compared the population structures of kudu in two differently managed areas in Namibia. The population structure on both study sites was similar despite different management strategies and sex ratios were clearly female-biased in all sites, even though at birth they are close to parity, indicating sex- and age-specific mortality. A total of 112 males and 187 females were observed in the whole study area, giving a male to female ratio of 1:1.67 [59].

Group sizes of herbivores tend to vary from season to season. Megaze observed larger buffalo herds of up to 27 individuals during the wet season and smaller herds of 8 in the dry season. The mean herd size during the wet and dry seasons was 24, 81 and 7, 77, respectively [56]. For the mountain nyala, The most frequently observed group size was 12 animals in the wet season and 7 animals in the dry season. The average group size was 10, 2 and 7, 9 for the wet and dry season respectively [53]. Yirga and Reggassa also noted that group sizes, composition and structure for Grevy's zebra varied with the season. The average number of wet season counts (1224) was grouped in 56 herds (groups) and the mean group size was 14.6. During dry season, the total count (1536) was grouped into 59 groups and the mean group size was 10.4 [55].

A study on the variation of group size among African buffalo herds in a forest-savannah mosaic landscape over two years in Lope National Park indicated that the mean group size was stable with little variation in group size between marsh and savannah habitats or throughout the day, but there was evidence of some variation across seasons. There was a tendency for larger group sizes during wet seasons than during dry seasons and group size was larger during dry than wet seasons in a few cases [60].

Many studies have been carried on the seasonal variation of age and sex structures of herbivores in different protected and unprotected areas [53-56]. However, in MPNP literature is only restricted to information on large herbivore densities. Using the line transect method, this study seeks to examine the influence of seasonality on group size and age and sex structures of three herbivores (buffalo, kudu and impala) which are highly susceptible to anthrax and have different dietary requirements.

Materials and Methods

Study area

MPNP is located 15°40′-16°20′S and 29°08′-29°45′E in a semi-arid region in northern Zimbabwe [61]. It covers an area of 2 196 square km.

The park is situated adjacent to Sapi, Chewore and Hurungwe Safari Areas as well as the Mukwichi Communal Land on the south of the park. MPNP is part of more than 10 000 km² of wildlife land which is mostly used for sport hunting [27].

Climate: MPNP experiences a single rainy season from November to April and the long-term (1967-2012) annual average rainfall is 708 mm (Figure 1). The hottest month is November and the coldest month is July [61]. Temperatures in MPNP are high with monthly means approaching 40°C prior to the rains. Mean minimum temperatures remain above 10°C [84].

Geology and soils: The greater part of the Valley floor within the park is covered by Pebbly Arkoses and Forest Sandstone fluvial and Aeolian sequences of the Upper Karoo Group of Triassic to Jurassic age overlain by post-Karoo Red Beds close to the Escarpment foot. The soil types in the alluvial floodplain are very variable, consisting of deep, poorly Consolidated, stratified deposits [61]. One widely occurring feature is a poorly structured and relatively heavy textured surface which reduces rainfall infiltration causing surface wetness. Sodic soils which are highly saline occur above the southern edge of the floodplain. Away from the Zambezi, the Kalahari-type Jesse Sands exhibit deep, well-drained, poorly consolidated red sandy loams, formed in strongly pre-weathered material, which are very acidic and are in marked contrast to the immediately adjacent upper Karoo soils [62].

Flora: *Colophospermum mopane* woodland, *F. albida* woodland, *Brachystegia - Julbernardia* woodland and *Commiphora - Combretum* thicket are the four main types of vegetation types in MPNP as classified as classified by Guy [62]. *F. albida* woodland is found only on recently deposited alluvial soils, hence its close association with the rivers. Trees that are found in the alluvial deposits include *F. albida* (usually the dominant species), *Kigelia africana, Lonchocarpus capassa, Trichelia emetica, Tamarindus indica, Ficus zambesiaca, Garcinia livingstonei* and *Cordyla africana*. The understorey is less well developed and includes species such as *Combretum mossambicense, Combretum obovatum, Diospyros senensis, Gardenia spatulifolia, Grewia flavescens* and *Cardiogyne africana.* The herb layer consists mainly of annual grass species, in particular *Panicum maximum, Rottboellia exaltata, Echinochloa colonum* and *Urochloa trichopus*, and various annual forbs. Perennial grass species usually line the watercourses which drain the floodplain, with V*etiveria nigritana* and *Setaria shacelata* especially well represented. Dunham and du Toit further subdivided the vegetation in the alluvial floodplain as young *F. albida* woodland, established *F. albida* woodland, *F. albida* dominated mixed woodland, mixed riverine woodland and the mopane ecotone [27].

Fauna: During the dry season, there is aggregation of large mammals in the alluvial floodplain with concentration increasing as the dry season progresses [25,28]. Availability of water from the Zambezi River and a few pools in the alluvial floodplain, green grass near Zambezi and fallen fruits from *F. albida* trees attracts these herbivores [26]. MPNP is rich in wild ungulates, notably African buffalo (*Syncerus caffer*), African elephant *(Loxodonta africana*), eland (*Taurotragus oryx*), hippopotamus (*Hippopotamus amphibius*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), plains zebra (*Equus quagga*), sable antelope (*Hippotragus niger*), nyala (*Tragelaphus angasaii*) and waterbuck (*Kobus ellipsiprymnus*). The large carnivores in the park include cheetah (*Acinonyx jubatus*), lion (*Panthera leo*), wild dog (*Lyacon pictus*) and spotted hyena (*Crocuta crocuta*).

The park has been listed as an Important Bird Area (IBA) as it is an important staging post for migratory birds. More than 400 bird species have been recorded [84]. The mid-Zambezi valley is the only known locality in Zimbabwe for Shelley's Sunbird (*Nectarinia shelleyi).* Other notable species in the park include the Rock Pratincole (*Glareola nuchalis*), the African Skimmer (*Rynchops flavirostris*), the Racket-tailed Roller (*Coracias spatulatus*), Meves's Glossy-starling (*Lamprotornis mevesii*), the White-headed Black-chat (*Myrmecocichla arnoti*), the White-breasted Sunbird (*Nectarinia talatala*) and the Broad-tailed Paradise-whydah (*Vidua obtuse)*. MPNP is also a host of raptors such as Fish Eagles (*Haliaeetus vocifer*) and the Pel's Fishing Owl (*Scotopelia peli).*

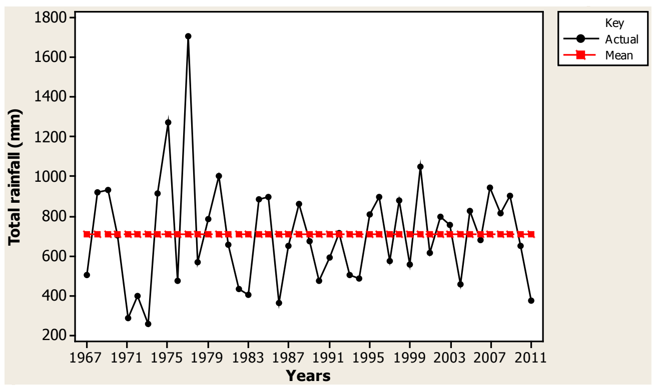

Figure 1: Long term annual rainfall in MPNP.

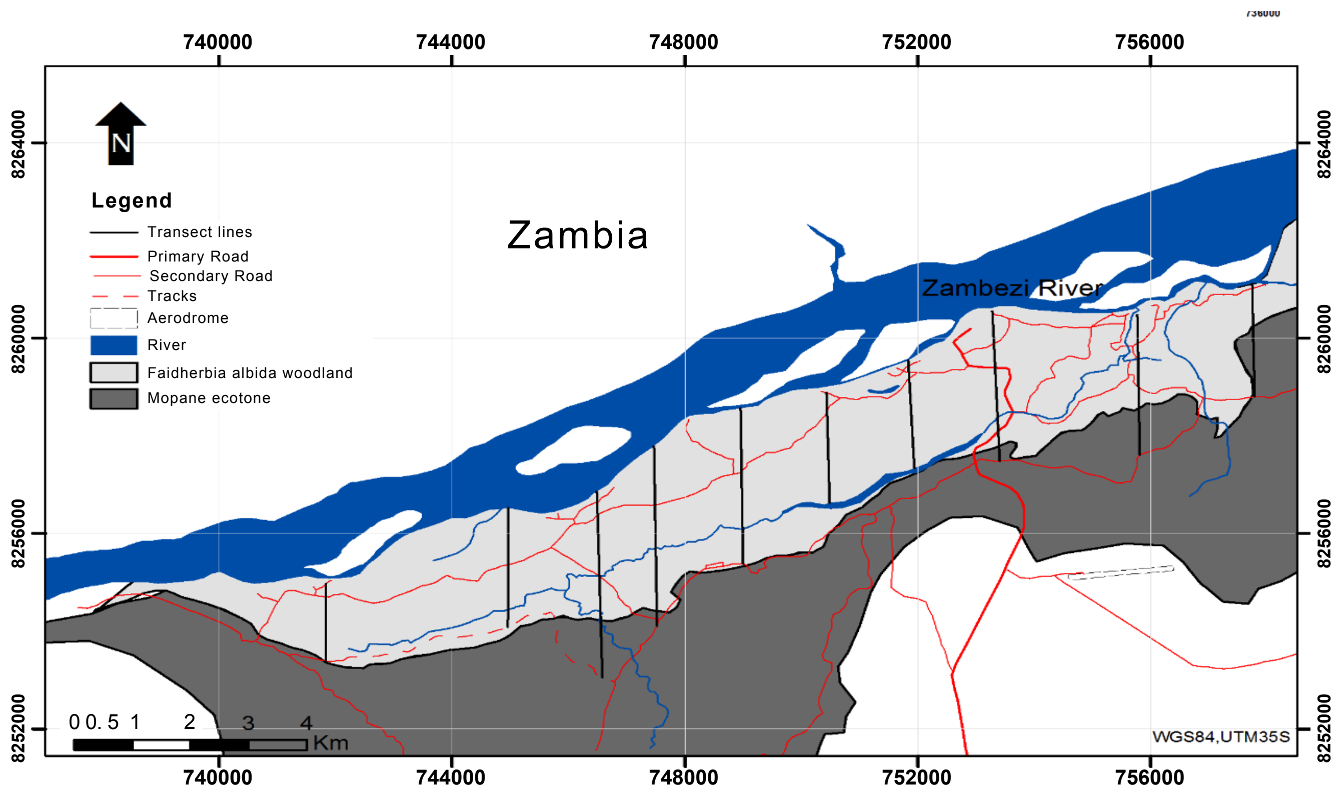

Figure 2: Vegetation types and location of sampled transects in the MPNP floodplain.

Water sources: The Zambezi River is the main water source in MPNP. The Long pool and the Mana pools in the floodplain are also capable of retaining water throughout the dry season. The Chitake spring is the permanent water source in the Zambezi Valley escarpment. There are also a number of seasonal water pans such as Zhanjane and Sapi number one pans.

Research design and data collection

Data collection was carried in the months of February 2012 and September 2012 in the MPNP floodplain which covers approximately 55 km^2. Reconnaissance observations were made in January 2012 before the actual data collection to have information on accessibility, vegetation cover, topography and distribution of the selected herbivores. Since the vegetation types were not easily distinguished, the simple random sampling method was applied in transect placement. Adjacent transects were roughly parallel and at least 1000m a part [55]. A total of 10 transects were sampled (Figure 2). Data collection was carried out in February and September 2012 so as to accommodate both the wet season and the dry season. Separation of dry and wet seasons was based on the change of rainfall pattern and vegetation cover. Seasonal differences in the population size, age categories and group sizes of selected herbivores were compared. Quantitative data of each species which were collected include group/herd size, age and sex categories.

Population estimate

A line-transect census was employed to assess the number and structure of the African buffalo, kudu and impala using methods adopted by Brennan and Block for different mammals and Regassa and Yirga for zebra. Counts were conducted from 07:30 to 10:30 hours in the morning and from 15:00 to 18:00 hours in the afternoon where visibility was good and animals were most active [53,55,63]. The length of transects varied from 2.3 to 3.8 km and an average of 2.5 km. Transects were surveyed with the help of well experienced rangers who assisted in species and sex identification [56,64]. A Global positioning system (GPS) was used to walk along transects as the starting and ending GPS co-ordinates were determined prior to the census [55]. Upon spotting animal group or an individual, the silent detection method was practiced so as to minimize disturbances [30]. During transect walking; the observers recorded the start and end time, animal species, group size, group spread and age and sex structures.

Age structure and sex ratio

During the counts, the three species were each grouped into their age and sex classes. The categories used were adult male and female, sub-adult male and female and juvenile male and female and unidentified using the methods of Boyer and Hillman [65,66]. However, as it was difficult to confirm sexes of juveniles in the field, data on them were pooled together [54,56,59]. Identification of age and sex was carried out using morphological characteristics such as horn length and shape, body size, pelage (fur), external genitalia and mammary glands [40,67]. Sex ratios for the groups were obtained from direct count of the animals as adopted by Doku, Yirga and Regassa [54,55].

Group size

The size of the group was recorded first before the allocation of age and sex structures during the count [53]. Where the distance between individuals was less than 50m, they were considered as the same group following the methods of Hillman and Hillman, Borkowski and Furubayashi for the study of different animals [68,69]. For the purposes of analysis single animals were considered as a group [70]. To avoid double counting of the same group, recognizable features such as group composition, cluster size, and individuals with distinct body deformations such as cut tail and ear as well as broken horns were used [30,60]. Determining group size was also aided by binoculars were necessary.

Historical data

Historical data on the populations of buffalo, impala and kudu were obtained from the Parks and Wildlife Management Authority (PWMA) records. Data from National Wildlife Society annual game counts which have collected since 1993 using line transects were used [27,82]. Data on the amount of rainfall received in MPNP has been recorded at the Nyamepi weather station since 1967. For the purpose of this study, herbivore population trends since 1995 were analysed.

Data analysis

The data were analysed using Minitab version 16 computer software program. Data were first tested for normality using the Ryan-Joiner test which is similar to the Shapiro-Wilk test because all are correlation based tests. Wet and dry season populations of selected herbivore and rainfall data were normal. Age structure, sex and group composition data did not satisfy the normality assumptions. Consequently, population estimates for the African buffalo, kudu and impala for wet and dry seasons were compared using two tailed t-test for independent samples (P=0.05). Mann-Whitney U test was used to analyse age structure, sex ratio and group sizes. Group compositions were analysed by working out the proportions of different animal categories and then expressed in percentages.

Results

Population estimate

Dry season counts (September 2012) for buffalo, kudu and impala were 137, 36 and 959 respectively. Wet season (February 2012) counts were 55, 57, and 530 for buffalo, kudu and impala respectively. The most abundant species was impala, followed by buffalo and kudu respectively. The results of counts for each species in the wet and dry seasons are given in Table 1. The dry season count for impala was significantly higher as compared to the wet season count (t=-2.28, P=0.038, C.I 95%). Even though there was a small increase in the number of buffalos recorded in the dry season, the two tailed t-test indicated that there was no significant difference between wet and dry seasons (t=-1.56, P=0.293, C.I 95%). Similarly, there was no significant difference in kudu counts (t=1.09, P=0.293, C.I 95%) between the two seasons even though wet season counts were slightly higher than dry season counts.

Age and sex structure

Buffalo: The population structure and the proportion of various age-sex categories of buffalo, kudu and impala in MPNP are provided in Table 2. Out of the total 192 buffalos observed during the present study period, 39.06 % (n=75) were males and 50% (n=96) were females. Male to female sex ratio was 1:1.28. Among the observed individuals, 53.13% (n=102) were adults, 35.94% (n=69) were sub-adults and only 10.94 % (n=21) were young individuals. The average ratio of adult male to adult female was 1:1.78 and young to others was 1:7.81. No significant difference between dry and wet seasons were observed in the proportions of adult female (Mann Whitney test, U'=45, P=0.6511) and adult male (Mann Whitney test, U'=65, P=0.4755). The age structure was also stable across seasons with no significant variation in the proportions of adults (Mann Whitney test, U'=89, P=0.8645) and sub-adults (Mann Whitney test, U'=84, P=0.5772). Individual buffalo encountered during the study period were grouped as adult male: 75.7% (n=28) and 24.3% (n=9), adult female: 70.8% (n=46) and 29.2% (n=19) and juvenile: 42.9% (n=9) and 57.1% (n=12) during dry and wet seasons respectively (Figure 3).

Kudu: A total of 93 individuals of kudu were sighted during the observation period. Among them, females constituted 53.76% (n=50) and males constituted 35.48% (n=35). The ratio of males to females in the dry and wet season was 1:1.34 and 1:1.58 respectively. Averagely, 48.39% were adults, 47.31% sub-adults and only 10.75% young individuals. Individual kudu encountered during the study period were grouped as adult male: 41.7% (n=5) and 58.3% (n=7), adult female: 36.36% (n=12) and 63.64% (n=21) and juvenile: 20% (n=2) and 80% (n=8) during dry and wet seasons respectively (Figure 4). The adult

Number of individuals (Mean ± SE)					
Species	Wet season	Dry season	Mean	t-value	p-value
Buffalo	5.50 ± 2.00	13.70 ± 4.90	9.60 ± 3.45	-1.56	0.147
Kudu	5.70 ± 1.70	3.60 ± 0.98	4.65 ± 1.34	1.09	0.293
Impala	53.0 ±10.0	95.9 ± 16.0	74.45 ± 13.0	-2.28	0.038*
Superscript * represents significant difference (P<0.05)					

Table 1: Wet and dry season comparisons of abundance of each species using t-test.

Species	Categories	Wet season	Dry season	Mean
Buffalo	Young:Others	1:3.58	1:14.22	1:7.81
	Sub-adult:Others	1:2.67	1:1.54	1:1.78
	Male:Female	1:1.34	1:1.25	1:1.28
	Adult Male:Adult Female	1:2.11	1:1.04	1:1.78
Kudu	Young:Others	1:6.13	1:18	1:8.5
	Sub-adult:Others	1:1.71	1:0.89	1:1.33
	Male:Female	1:1.58	1:1.34	1:1.43
	Adult Male:Adult Female	1:3	1:2.11	1:2.75
Impala	Young:Others	1:6.07	1:19.4	1:11.12
	Sub-adult:Others	1:1.01	1:1.31	1:1.2
	Male:Female	1:1.51	1:1.5	1:1.5
	Adult Male:Adult Female	1:1.05	1:1.7	1:1.48

Table 2: Age and sex ratios of buffalo, kudu and impala observed in the dry and wet seasons.

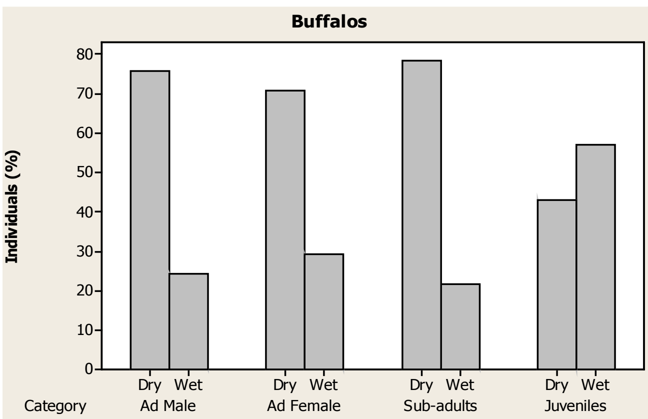

Figure 3: Percentages of age and sex categories of buffalo during the dry and wet seasons.

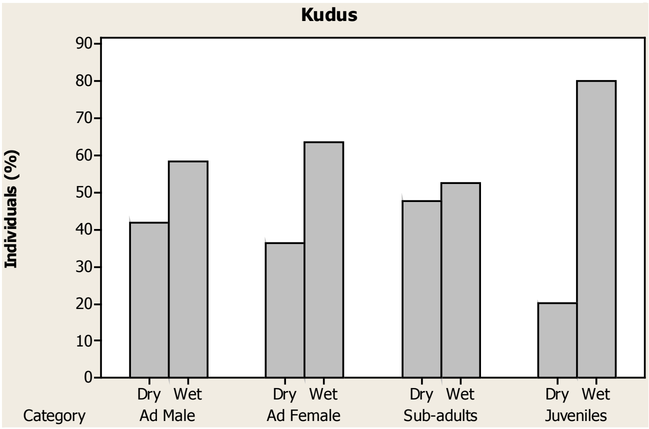

Figure 4: Percentages of age and sex categories of kudu during the dry and wet seasons.

male to adult female sex ratio was 1:3 and 1:2.11, sub-adult to others sex was 1:1.71 and 1:0.89 during wet and dry seasons, respectively. There was no significant difference in the proportions of adult male (Mann Whitney test, U'=97, P=1.0000) and adult females (Mann Whitney test, U'=87, P=0.3874) between the dry and wet seasons. Age structures for adults (Mann Whitney test, U'=169, P=0.4131) and sub-adults (Mann Whitney test, U'=141, P=0.3480) showed no significant difference between the seasons.

Impala: A total of 1 489 individuals were observed during the study period. Among them, 36.67% (n=546) were males and 55.14% (n=821) were females. Male to female sex ratio was 1:1.51 in the wet season and 1:1.5 in the dry season. Of the observed individuals, 46.27% (n=689) were adults, 46.6% (n=679) were sub-adults and only 8.12% (n=121) were juveniles. The mean ratio of sub-adult to others was 1:1.2 and young to others was 1:11.12. Age structures for adults (Mann Whitney test, U'=3637, P=0.0001) and sub-adults (Mann Whitney test, U'=4037, P=0.0251) varied significantly between the dry and wet season. The sex structure was also unstable across seasons with significant variation in the proportions of adult males (Mann Whitney test, U'=3920, P=0.0041) and adult females (Mann Whitney test, U'=3596.5, P=0.0000). Individual impala encountered during the study period were grouped as adult male: 66.2% (n=184) and 33.8% (n=94), adult female: 76.4% (n=312) and 23.6% (n=99) and juvenile: 38.5% (n=47) and 61.5% (n=75) during dry and wet seasons respectively (Figure 5).

Group/Herd size

Impala: The average group size for impala, buffalo and kudu for each season are given in Table 3. Wet season count (n=530) was grouped into 67 groups and the mean group size was 7.9. During the dry season, the total count (n=959) was grouped into 68 groups and the mean group size was 14.1. The most frequently seen group was 15 animals in the dry season and 7 animals in the wet season. Mann-Whitney U test showed that impala groups observed in the dry season were significantly larger as compared to those observed in the wet season (Mann Whitney test, U'=3836, P=0.0015).

Buffalo: The herd size of buffalo ranged from 1-16 individuals in the wet season and from 1-33 in the wet season. Mean herd sizes during wet and dry seasons were 6.9 and 9.8 respectively. The total number (n=55) of buffalos observed in the wet season constituted 8 herds and total count (n=137) in the dry season was composed of 14 herds. Solitary bulls were frequently observed in the wet season and herds of 7 individuals were common in the dry season. Herds of greater than 16 were rarely encountered in both seasons. Herd size over the two seasons showed no significant difference (Mann Whitney test, U'=88, P=0.8112).

Kudu: Kudu groups ranged from 1-6 in both seasons. Groups of more than 6 individuals were not observed during the study period. Wet season count (n=57) was grouped was grouped into 13 groups with a mean group size of 4.4. The dry season count (n=36) was grouped into 10 groups forming the mean group size of 3.6. The most frequently observed group sizes in the wet and dry seasons were 6 and 5 respectively. Kudu group sizes over the two seasons showed no significant difference (Mann Whitney test, U'=174.5, P=0.2643).

Population trends

The population trend of the selected herbivores has been fluctuating between 1995 and 2012. The population of the three species showed a sharp decline between 2000 and 2001. The populations of kudu and buffalo also declined also declined between 2011 and 2012. However, impala population increased during the same period.

Impala: Impala population increased from 2 464 in 1995 to 5 813 in 2012 at an annual rate of 13.8%. Figure 6 shows the population trend of impala in the MPNP floodplain between 1995 and 2012. The population increased from 2 464 in 1995 to 5 813 in 2012 at an annual rate of 13.8%.

Buffalo: The population of buffalo in the MPNP floodplain declined by 39% from 446 in 1995 to 174 in 2012 (Figure 7).

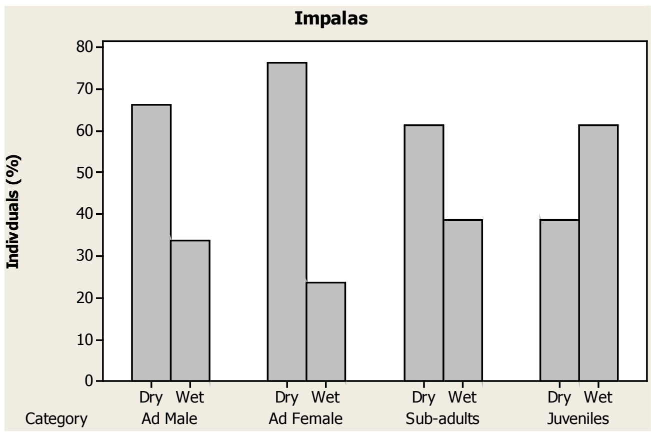

Figure 5: Percentages of age and sex categories of impala during dry and wet seasons.

Species	Season	Observed number	Groups	Range of group size	Mean group size
Impala	Wet	530	67	1-44	7.9
	Dry	959	68	1-77	14.1
Buffalo	Wet	55	8	1-16	6.9
	Dry	137	14	1-33	9.8
Kudu	Wet	57	13	2-6	4.4
	Dry	36	10	1-6	3.6

Table 3: Group sizes of impala, buffalo and kudu during wet and dry seasons.

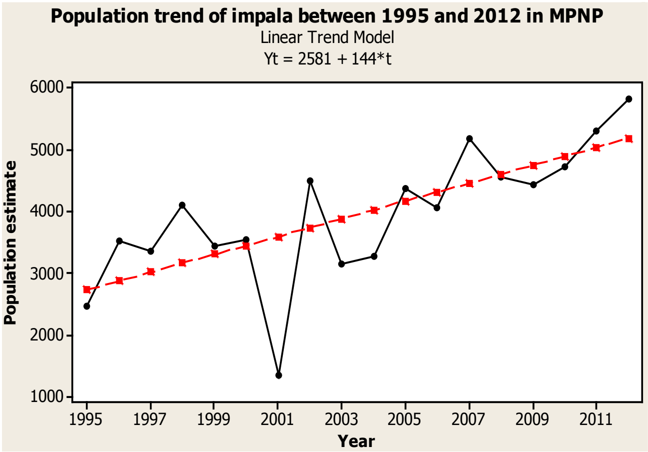

Figure 6: Population trend of impala in the MPNP floodplain between 1995 and 2012.

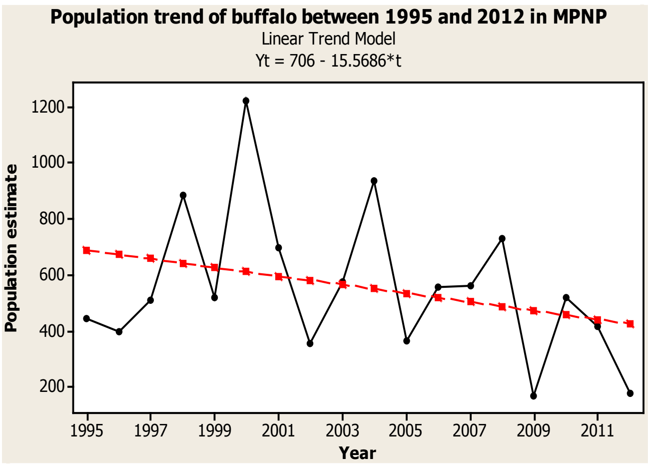

Figure 7: Population trend of buffalo in the MPNP floodplain between 1995 and 2012.

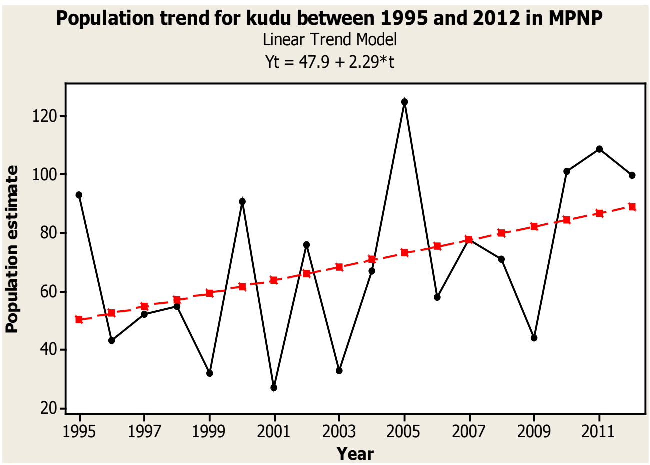

Figure 8: Population trend of kudu in the MPNP floodplain between 1995 and 2012.

Kudu: The population trend of kudu shows a steady increase 93 in 1995 to 100 in 2012 at an annual rate of 6.3% (Figure 8).

Discussion

Population Estimate

Buffalo: The slight increase in the number of buffalo counted in the dry season was primarily due to the drying up of seasonal inland water bodies which forced the animals to move towards the permanent water pools in the floodplain and the Zambezi River. The results are consistent with findings of Macandza and Ryan who noted that savannah buffalos moved into riverine habitats during the dry season [71,72]. The provision of feed supplementation in the floodplain during the dry season could also be attributed to the increase in buffalo numbers.

Kudu: Kudu population recorded in the wet season were also slightly higher as compared to the dry season count despite the fact that it was statistically of no significant difference. More young animals were recorded in the wet season as compared to the dry season during this study. Kudu give birth mainly in the wet season which explains the results of the present study showing an increase in number during the wet season [73,74].

Impala: The population of impala recorded in the dry season was significantly higher as compared to the wet season population. This could be attributed to the availability of water and pods from the *F. albida* trees in the floodplain. This supports the findings of Regassa and Yirga who noted that animals tend to aggregate in areas with strategic and scarce resources such as water and pasture in the dry season meanwhile in the wet season these resources are well distributed in the range, and therefore are evenly distributed [55].

Group sizes

Buffalo: No major variation of group sizes of buffalo in MPNP were observed similarly to observations of forest buffaloes [60]. In contrast, Megaze observed smaller herds in the dry season and larger herds in the wet season. Wet and dry season variation in herd size is as a result of changes in the availability of resources [71,75]. In MPNP, changes in resource availability appear to have been affected by provision of supplementary feed to buffalos in the dry season which explains insignificant herd size variation between the seasons.

Kudu: Group sizes recorded in this study show much the same distribution as given by Simpson. Herds ranged in size from a maximum of 7 in the dry season to 12 in the wet season [73]. The mean group size found in this study agrees with results of other studies in different parts of the world [76]. The average group size observed during this study was 4.4 and 3.6 in the wet and dry seasons respectively. Larger group sizes were observed in the wet season because male groups tend to break up before the rut to attach themselves to female groups [73].

Impala: Impala groups observed in the dry season were significantly larger as compared to those observed in the wet season. Averbeck also noted that group sizes among impala varied with season in the Lake Mburo National Park, Uganda [77]. This variation can be explained variation in the numbers of juveniles in relation to the number of reproductive females per group.

Age and sex structure

Buffalo: Sex and age structure of a population at any given point of time is an indicator of the status of the population [78]. The sex ratio of the buffalos observed in this study agrees with the observation of Megaze [56]. The difference in sex ratios among the buffalos can be as a result of predation given that lions frequently prey on male buffalos [24].

Kudu: The present study shows that male to female sex ratio for kudu is female biased, which is 1:1.43. Annighöfer and Schütz, Owen-Smith and Mason also witnessed a similar sex ratio in Namibia and South Africa respectively [59,79]. In contrast, Simpson witnessed a male biased sex ratio in Zimbabwe [73]. Differences in sex ratio are often attributed to disparity at birth [59]. However, the foetal sex ratio in kudu does not seem to differ significantly from parity [73,76]. In comparison to female mortality, male mortality increases with age especially after reaching full weight at 6 years of age Estes which explains the results of the current study [74].

Impala: The present female biased sex ratio is similar with the observations of Bothma in Lake Mburo National Park [80]. Males are prone to predation from leopards and wild dogs since they spent most of their time solitary. More males are also allocated in the staff ration and training quota which explains the present study findings.

Population trends of herbivores

Buffalo: The population trend of buffalo shows that major population declines coincided with periods of drought and outbreak of anthrax. Sharp declines in population were recorded in the years 2001/2 and 2011/2. Between September 2011 and October 2011, 32 buffalo carcasses showing symptoms of anthrax were recorded in MPNP (Unpublished data) supporting the view that buffalos are highly susceptible to anthrax. Buffalo declines have also been noted in other parts of Africa and at global level [19,21]. In contrast, Ogutu observed that buffalo population is expanding in Kenya's Nairobi National Park [33]. Fluctuations in rainfall may have further contributed to the decline of buffalo population in MPNP. Since there is a well-established relationship between rainfall and primary production of grass in semi-arid savannah it is assumed that during the years 2002 and 2012 when MPNP experienced droughts, primary production was low and limiting [22,24]. Therefore, it is possible that the buffalo population experienced food shortages and could have suffered drought-induced mortality and reduced rate of natural increase. Dunham has indicated that the drought that occurred in MPNP in 1984 resulted in the decline of the buffalo population [28].

Kudu: There is a stable increase in the population trend of kudu in MPNP. In the late 1960s, thousands of kudu were killed each year in the Zambezi valley in an attempt to control the spread of trypanosomes, carried by tsetse flies [73]. Between 2001 and 2002 the kudu population dropped from 91 to 27 presumably because of nutritional stress associated with drought periods. The current female biased sex ratio (1:1.43), a high proportion of sub-adults to other age groups (1:0.89) and the fairly high proportion of young (10.53%) in the population indicates a healthy and increasing population status of kudu in MPNP. The current trend shows that the kudu population appear to be recovering due to the implementation of strict wildlife management regulations such as the absence of kudu on the staff training and ration quota as well as regular patrolling of MPNP rangers.

Impala: The population of impalas has increased from about 2 400 in 1995 to 5 800 in 2012. In contrast, Averbeck observed a decreasing population of impala in Lake Mburo National Park, Kenya [77]. During the dry season, observations of individuals with mange were made. Mange is a highly contagious skin disease caused by one or a combination of several species of mites [81]. The status of impalas in MPNP can therefore be attributed to their ability to absorb and recover from environmental stressors such as diseases and feed shortage since no carcases were observed in the present study. There was high proportion of females in the population, indicating that the impalas have potential to increase in number. However, only low proportion of young to that of other age groups (1:11.12) was observed during the present investigation.

Conclusion

Results from this study show that population status of impala and kudu have increased whilst that of buffalo has declined drastically over the past 17 years. The population structure and group composition of the selected herbivores were female biased. The high percentages of females and fairly high young population of buffalo and kudu populations showed that they have a potential to increase. Impala also had a high proportion of females as compared to females. However, the proportion of juveniles to other was very low. Only the group sizes of impala varied with season. The abundance of herbivores in the MPNP floodplain varied with season. There was a dry season aggregation of herbivores in the MPNP floodplain. The availability of forage and permanent water sources in the floodplain were the major attractions of herbivores in the dry season. Therefore there is need for measures from a conservation perspective such as staff training, effective quota and proper human wildlife conflict resolution to be implemented for sustainable survival of buffalo and other wildlife species in MPNP.

References

1. Gordon IJ, Hester JA, Festa-Bianchet M (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41: 1021-1031.
2. Collen B, Loh J, Whitmee S, McRae L (2009) Monitoring changes in vertebrate abundance: the Living Planet Index. Conservation Biology 23: 317-327.
3. Wilkie DS, Bennett EL, Peres CA, Cunningham AA (2011) The empty forest revisited. Annals of the New York Academy of Sciences 1223: 120-128.
4. Winterbach HEK (1998) Research Review: The status and distribution of Cape buffalo Syncerus caffer in Southern Africa. South African Journal of Wildlife Resources 28: 82-88.
5. Cleaveland S, Hess GR, Dobson AP, Laurenson MK, McCallum HI, et al. (2002) The role of pathogens in biological conservation. In: The Ecology of Wildlife Diseases (Eds Hudson PJ, Rizzoli A, Grifenfell BT, Heesterbeek H, Dobson AP). Oxford University Press Inc. New York.
6. Muoria PK, Muruthi P, Kariuki WK, Hassan BA, Mijele D, et al. (2007) Anthrax outbreak among Grevy's zebra (Equus grevyi) in Samburu. African journal of ecology 45: 483-489.
7. Ogutu JO, Owen-Smith N (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates 6: 412-419.
8. Mduma SAR, Hilborn R, Sinclair ARE (1998) Limits to exploitation of Serengeti wildebeest and implications for its management 243-265.
9. Loibooki M, Hofer H, Campbell KLI, East ML (2002) Bushmeat hunting by communities adjacent to the Serengeti National Park. Tanzania: the importance of livestock ownership and alternative source of proteins and income. Environ. Conserv 29: 391-398.
10. Foguekem D, Tchamba MN, Omondi P (2010) Aerial survey of Elephants (Loxodonta Africana Africana), other mammals and human activities in Waza National Park. Afr J Environ Sci and Tech 4: 401-411.
11. Ottichilo WK, de Leeuw J, Prins HHT (2001) Population trends of resident wildebeest [Connochaetes taurinus hecki (Neumann)] and factors influencing them in the Masai Mara ecosystem. Biological Conservation 97: 271-282.
12. Wasilwa SN (2013) The impact of land-use change on large herbivore populations in some Masai Mara adjacent group ranches. Kenya.
13. Ogutu OJ, Piepho H, Dublin HT, Bhola N, Reid RS (2007) ENSO, rainfall and temperature fluctuations in the Mara-Serengeti ecosystem. Afr J Ecol 46: 132-143.

14. Ogutu JO, Piepho H, Dublin HT, Bhola N, Reid RS (2008) Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. J Anim Ecol 77: 814-829.

15. Ogutu JO, Piepho H, Dublin HT, Bhola N, Reid RS (2009) Dynamics of Mara-Serengeti ungulates in relation to land use changes. J Zool 278: 1-14.

16. Norton-Griffith M (1978) Counting Animals. (2ndedn) Africa Wildlife Leadership. Nairobi.

17. Hafner H, Fasola M (1997) Long-term monitoring and conservation of herons in France and Italy. Colon. Waterbirds 20: 298-305.

18. Butler MJ, Harris G, Strobel BN (2013) Influence of whooping crane population dynamics on its recovery and management. Biological conservation 162: 89-99.

19. IUCN (2013) IUCN Red List of Threatened Species.

20. IUCN SSC Antelope Specialist Group 2008. Aepyceros melampus. In: IUCN 2013. N IUCN Red List of Threatened Species.

21. Ottichilo WK, de Leeuw J, Skidmore AK, Prins HHT, Said MY (2000) Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. East African WildLife Society Afr J Ecol 38: 202-216.

22. McNaughton SJ, Georgiadis NJ (1986) Ecology of African grazing and browsing mammals. Annu Rev Ecol Syst 17: 39-65.

23. Skarpe C, Bergstrome R (1986) Nutrient content and digestibility of forage plants in relation to plant phenology and rainfall in the Kalahari. Botswana. J Arid Environ 11: 147-164.

24. Davidson Z, Valeix M, Van Kesteren F, Loveridge AJ, Hunt JE, et al. (2013) Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna.

25. Jarman PJ (1972) Seasonal distribution of large mammal populations in the unflooded Middle Zambezi Valley. J Appl Ecol 9: 283-299.

26. Dunham KM (1990) Biomass dynamics of herbaceous vegetation in Zambezi riverine woodlands. Afr J Ecol 28: 200-212.

27. Dunham KM, du Toit AJ (2012) Using citizen-based survey data to determine densities of large mammals: a case study from Mana Pools National Park. Afr. J. Ecol.

28. Dunham KM (1994) The effect of drought on the large mammal populations of Zambezi riverine woodlands. J Zool 234: 489-526.

29. Stoner C, Caro T, Mduma S, Mlingwa C, Sabuni G, et al. (2006) Changes in large herbivore populations across large areas of Tanzania. Afr J Ecol 45: 202-215.

30. Wilson DE, Cole FR, Nichols JD, Rudran R, Foster M (1996) Measuring and Monitoring Biological Diversity. Standard Methods for Mammals. Smithsonian Institution Press.

31. Ogutu OJ, Owen-Smith N, Piepho H, Said MY (2011) Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. Journal of Zoology 41: 1-11.

32. Valeix M, Fritz H, Chamaille-Jammes S, Bourgarel M, Murindagomo F (2008) Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-term data. Animal Conservation 11: 391-400.

33. Ogutu JO, Owen-Smith N, Piepho H, Said MY, Kifugo SC, et al. (2013) Changing Wildlife Populations in Nairobi National Park and Adjoining Athi-Kaputiei Plains: Collapse of the Migratory Wildebeest. The Open Conservation Biology Journal 7: 11-26.

34. Gandiwa E (2013) Top-down and bottom-up control of large herbivore populations: a review of natural and human-induced influences. Tropical Conservation Science 6: 493-505.

35. Gandiwa E, Heitkönig IMA, Gandiwa P, Matsvayi W, Westhuizen H, et al. (2013). Large herbivore dynamics in northern Gonarezhou National Park, Zimbabwe. Tropical Ecology 54(3): 345-354.

36. Voeten MM, Prins HHT (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120: 287-294.

37. Mishra C, Van Wieren SE, Ketner P, Heitkönig IMA, Prins HHT (2004) Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. Journal of Applied Ecology 41: 344-354.

38. Acebes PJ, Traba, Malo JE (2012) Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. Journal of Arid Environments 77: 39-44.

39. Iranzo EC, Traba J, Acebes P, Gonzalez BA, Mata C, et al. (2013) Niche Segregation between Wild and Domestic Herbivores in Chilean Patagonia 8: e59326.

40. Bhola N, Ogutu JO, Piepho H, Said MY, Reid RS, et al. (2012) Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. Biodiversity and Conservation.

41. Gill RB (1990) Monitoring the Status of European and North American Cervids. GEMS Information Series Global Environment Monitoring System. United Nations Environment Programme. Kenya.

42. Andersen R, Duncan P, Linnell JDC (1998) The European roe deer: the biology of success. Oslo: Scandinavian University Press. pp 376-385.

43. Warren RJ (1997) The challenge of deer over abundance in the 21st century. Wildlife Society Bulletin 25: 213-214.

44. Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58-63.

45. Woodroffe R, Ginsberg JR (1999) Conserving the African wild dog (Lycaon pictus). I. Diagnosing and treating causes of decline 33: 132-142.

46. Vosloo W (2013) Foot and mouth disease: a persistent threat. Microbiology Australia.

47. Boutton TW, Tieszen LL, Imbamba SK (1988) Biomass dynamics of grassland vegetation in Kenya. Afr J Ecol 26: 89-101.

48. Fryxell JM, Greever J, Sinclair ARE (1988) Why are migratory ungulates so abundant? American Naturalist 131: 781-798.

49. Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. Trends in ecology and evolution 9: 237-241.

50. Ogutu JO, Piepho H, Kanga E (2012) Dynamics of an Insularized and Compressed Impala Population: Rainfall, Temperature and Density Influences. Ecology Journal.

51. Sinclair ARE, Krebs CJ (2002) Complex numerical responses to top-down and bottom–up processes in vertebrate populations. Biological Sciences 357: 1221-1231.

52. Ripple WJ, Beschta RL (2012) Large predators limit herbivore densities in northern forest ecosystems. Eur J Wildl Res.

53. Refera B, Bekele A (2004) Population status and structure of Mountain nyala in the Bale Mountains National Park. Afr J Ecol 42: 1-7.

54. Doku Y, Bekele A and Balakrishnan M (2007) Population status of plains zebra (Equus quagga) in Nechisar plains. Tropical Ecology 48: 79-86.

55. Regassa R, Yirga S (2013) Distribution, abundance and population status of Burchell's zebra (Equus quagga) in Yabello Wildlife Sanctuary. Journal of Ecology and the Natural Environment 5: 40-49.

56. Megaze A, Belay G, Balakrishnan M (2012) Population structure and ecology of the African buffalo (Syncerus caffer Sparrman, 1779) in Chebere Churchura National Park. Blackwell Publishing Ltd. African journal of ecology.

57. Grimsdell JJR (1978) Ecological Monitoring. African Wildlife Foundation. Nairobi.

58. Turner WC, Jolles AE, Owen-Smith N (2005) Alternating sexual segregation during the mating season by male African buffalo (Syncerus caffer). J Zool Lond 267: 291-299.

59. Annighöfer P, Schütz S (2011) Observations on the population structure and behaviour of two differently managed populations of the greater kudu (Tragelaphus strepsiceros). Eur J Wildl Res 57: 895-907.

60. Korte LM (2008) Variation of group size among African buffalo herds in a forest-savanna mosaic landscape. Journal of Zoology 275: 229-236.

61. Dunham KM (1989) Vegetation-environment relations of a Middle Zambezi floodplain. Vegetation 82: 13-24.

62. Guy PR (1977) Notes on the vegetation types of the Zambezi Valley. Rhodesia, between the Kariba and Mpata Gorges 10: 543-557.

63. Brennan LA, Block WM (1996) Line transects estimates of mountain quail density. J Wildl Managt 50: 373-377.

64. Walker C (1996) Signs of the Wild, a Field Guide to the Spoor and Signs of the Mammals of Southern Africa. Struik Publishers. CapeTown.

65. Boyer RT (1984) Sexual segregation in southern mule deer. J Mann 65: 414-417.

66. Hillman JC (1986) Bale Mountains National Park Management Plan. Report to Ethiopian Wildlife Conservation Organization.

67. Ndhlovu DE, Balakrishnan M (1991) Large herbivores in Upper Lupande Game Management Area. Afr J Ecol 29: 93-104.

68. Hillman JC, Hillman SM (1987) The mountain nyala (Tragelaphus buxtoni) and the Simien Fox (Canis simensis) in the Bale Mountains National Park. Walla 3-6

69. Borkowski J, Furubayashi K (1998) Seasonal and diet variation in group size among Japanese Sika deer in different habitats. J Zool London 245: 29-34.

70. Arcese P, Jongejan G, Sinclair ARE (1995) Behavioural flexibility in a small African antelope: group size and composition in the oribi (Ourebia ourebi, Bovidae). Ethol 99: 1-23.

71. Macandza VA, Owen-Smith N, Cross PC (2004) Forage selection by African buffalo in the late dry season in two landscapes. S. Afr. J Wildl Res 3: 113-121.

72. Ryan SJ (2006) Spatial Ecology of African Buffalo (Syncerus caffer) and Their Resources in a Savanna Landscape. Berkeley.

73. Simpson D (1968) Reproduction and Population Structure in Greater Kudu in Rhodesia. The Journal of Wildlife Management 32: 149-161.

74. Estes RD (1999) The Safari Companion: A guide to watching African animals. Tutorial Press. Zimbabwe.

75. Tshabalala T, Dube S, Lent PC (2009) 0Seasonal variation in forages utilized by the African buffalo (Syncerus caffer) in the succulent thicket of South Africa. Afr J Ecol 48: 438-445.

76. Perrin MR, Allen-Rowlandson TS (1995) The reproductive biology of the greater kudu, Tragelaphus strepsiceros. Z Säugetierkunde 60: 65-72.

77. Averbeck C, Apio A, Plath M, Wronski T (2009) Hunting differentially affects mixed-sex and bachelor- herds in a gregarious ungulate, the impala (Aepyceros melampus: Bovidae). Blackwell Publishing Ltd. Afr J Ecol 48: 255-264.

78. Woolf A, Harder D (1979) Population dynamics of a captive white tailed deer herd with emphasis on reproduction and mortality. Wildl Monograph 67: 1-53.

79. Owen-Smith N, Mason DR (2005) Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. Journal of Animal Ecology 74: 762-774.

80. Bothma J, du P (1996) Game ranch management. J. L. van Schaik Publishers. Pretoria.

81. Gakuya F, Ombui J, Heukelbach J, Maingi N, Muchemi G, et al. (2012) Knowledge of Mange among Masai Pastoralists in Kenya 7: e43342.

82. Anon (1995) Triple count at Mana Pools. Zimbabwe Wildlife 79: 24-25.

83. Bergstrome R, Skarpe C (1999) The abundance of wild large herbivores in a semi-arid savannah in relation to seasons, pans and livestock. Afr J Ecol 37: 12-26.

84. Mana Pools National Park (2009) General Management Plan.

85. Muposhi VK, Muvengwi J, Utete B, Kupika O, Chiutsi S, et al. (2013) Activity Budgets of Impala (Aepyceros melampus) in Closed Environments: The Mukuvisi Woodland Experience. International Journal of Biodiversity.

86. Wilson VJ (1965) Observations on the greater kudu from a tsetse control hunting scheme in Northern Rhodesia. E African Wildl J 3: 27-37.