EFFECTS OF GRAZING BY HIPPOPOTAMUS (*HIPPOPOTAMUS AMPHIBIUS*) ON SYMPATRIC GRAZING UNGULATES IN THE LUANGWA VALLEY, ZAMBIA

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Effects of grazing by hippopotamus (*Hippopotamus amphibius*) on sympatric grazing ungulates in the Luangwa Valley, Zambia

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PREFACE

When a friend of mine, Kunda Changwe, suggested to me to consider doing my fieldwork on the problems of hippopotamus in the Luangwa Valley, I was immediately motivated to study interactions of hippopotamus with other grazing ungulates. I wanted to contribute by providing research-generated information to those concerned with the management of herbivore population in the Luangwa Valley. I also wanted to contribute to science by providing more evidence on facilitation and competition among different sized grazing ungulates when food resources are limiting in dry season.

The production of this Master's thesis would not have been possible without the financial support from the Zambia Wildlife Authority and the Department of Ecology and Natural Resources Management at the Norwegian University and Life Sciences. My project supervisor Dr. Stein R. Moe also offered advice and guidance from the time the project proposal was being developed to completion of thesis write-up. Thus, the research project enhanced my experience in the development of research proposal, mobilisation of resources for research, execution of research data collection, management and analysis of data and writing the thesis.

I hope this study will provide helpful information to wildlife managers in the South Luangwa National Park and that it will generate further research interests. Research in aspects beyond the scope of this study may provide further insights into the processes shaping interactions, distribution and abundance of ungulates in the Luangwa Valley.

Ås, 11th May 2007.

Paul Zyambo

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ABSTRACT

The effects of grazing by the common hippopotamus (*Hippopotamus amphibius*) have been assumed to impact some sympatric grazing ungulates in both adverse and positive ways in the Luangwa Valley, Zambia. Since no studies have confirmed these suspected impacts, I investigated the effects of hippopotamus (hippo) grazing on six grazing ungulates; buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), puku (*Kobus vardoni*), warthog (*Phacochoerus aethiopicus*), waterbuck (*K. ellipsiprymnus*), and plains zebra (*Equus burchelli*) in the South Luangwa National Park. I specifically assessed (1) whether hippo grazing facilitated grazing of other grazing ungulates, (2) the influence of hippo grazing on food availability for grazing ungulates and (3) the relationship between densities of hippo and abundances of other grazing ungulates. In two study sites having different hippo densities, I measured herbaceous layer cover and height in hippo-grazing lawns and ungrazed patches, assessed grazers' preferences for either hippo-grazing lawns or ungrazed patches, measured relative abundances of grazers and assessed their body condition. Finally, temporal population density data for hippo and grazing ungulates in the Luangwa Valley were correlated. Impala was the only species preferring hippo-grazing lawns. Buffalo, warthog and zebra avoided hippo-grazing lawns whereas puku and waterbuck did not respond to hippo-grazing lawns. The occurrence of medium and poor body conditions indicated food shortage among grazing ungulates in the area. The proportion of animals in good body condition class was lower for puku in the study site with higher hippo density. Species abundances between the two study sites were not different for impala, but were lower for puku, waterbuck and zebra in the study site with higher hippo density. Temporal data showed that densities of buffalo and zebra were significantly lower when hippo densities were high. The study shows that grazing by hippo facilitated feeding and access to favoured short grass for impala but facilitation by hippo at higher density did not result in higher spatial abundances of impala. At higher density hippo grazing appeared to result in higher food shortage for puku and less spatial cover of patches with tall grass for buffalo, waterbuck and zebra, and probably explains the lower spatial abundances of puku, waterbuck and zebra in Nsefu. The effects of hippo grazing on sympatric ungulates during the dry season appeared to depend on hippo density, forage quantity, body size and digestive strategies of grazing ungulates.

INTRODUCTION

Facilitative and competitive interactions among herbivores are regarded as important processes in structuring large herbivores (Bell 1971, Murray & Illius 2000, Arsenault & Owen-Smith 2002). Accordingly, coexistence and separation of herbivore assemblages in the African savannas have been attributed to facilitation and competition among herbivores (Bell 1971, Sinclair 1979, Sinclair & Norton-Griffith 1982, Prins & Olff 1998, Murray & Illius 2000). In facilitation, one species may benefit others by reducing grass biomass through its feeding and trampling activities and thus facilitating access to habitat or forage of suitable quality and height and ultimately promote coexistence among grazing herbivores (Vesey-Fitzgerald 1960, Bell 1971, McNaughton 1976, Verweij *et al.* 2006, Wegge *et al.* 2006). Competition occurs when one species reduces availability of shared resources that are in short supply to levels that cannot be used efficiently by other species (Illius & Gordon 1987, Caughley & Sinclair 1994). Herbivores respond to competition or food resource limitation by separating in types of habitat used (Lamprey 1963, Jarman 1972, Ferrar & Walker 1974, Murray & Illius 2000), in food types eaten (Jarman 1971, Field 1972, Dublin 1995) and in plant parts eaten or heights fed on (Gwynne & Bell 1968, Sinclair 1977, Woolnough & du Toit 2001). These responses by herbivores reduce the effects of competition and thus promote both separation and coexistence among herbivore assemblages (Sinclair 1977, Caughley & Sinclair 1994). Furthermore, because facilitation and competition processes affect the availability of resources in terms of quantity and quality to herbivores they may lead to increase or limitation of ungulate populations (Vesey-Fitzgerald 1960, Bell 1971, Sinclair 1977, Sinclair & Norton-Griffith 1982, Prins & Olff 1998).

Grazing activities by a megaherbivore (species weighing > 1000 kg as adults) can cause profound changes in the ecosystems (Owen-Smith 1989, Arsenault & Owen-Smith 2002, Fritz *et al.* 2002). As a megaherbivore, the common hippopotamus (*Hippopotamus amphibius* L.) (hereafter referred to as hippo) causes changes to vegetation and habitat structure, thereby affecting other ungulate species in either beneficial or detrimental way (Owen-Smith 1988, Arsenault & Owen-Smith 2002, Verweij *et al.* 2006). In the African savanna, grazing hippos have converted riparian grasslands with tall grass into extensive grazing lawns with short grass which has resulted in overgrazed areas in some cases

(Laws 1968, Olivier & Laurie 1974, O'Connor & Campbell 1986). Furthermore, hippo grazing changed population numbers of grazing ungulates utilising riparian habitats in Uganda (Eltringham 1974). The impacts of grazing by hippos on their habitats have raised concerns to wildlife managers in Africa, especially where hippopotamus population numbers have increased drastically (Attwell 1963, Lock 1972, Mackie 1976, O'Connor & Campbell 1986). As a result, measures to reduce hippo populations such as cropping and culling have been conducted in eastern and southern Africa (Bere 1959, Pienaar *et al.* 1966, Marshall & Sayer 1976).

In the central Luangwa Valley of Zambia, the population density of hippo is probably one of the highest in Africa (Tembo 1987, Jackmann 2000). The hippo is currently the only species among the megaherbivores in the central Luangwa Valley with a population that is considered overabundant because its population density has been fluctuating around the assumed carrying capacity of about 39 hippos per river km (ZAWA unpublished data). The problem of high hippo population density and its associated effects on the habitat in the Luangwa Valley have been documented from 1960s and the situation has persisted to date (Attwell 1963, Tembo 1987). One of the observed effects of high population density of hippopotamus in the Luangwa Valley is intensive grazing, commonly referred to as overgrazing (Jackmann 2000). The impacts of intensive grazing by hippos in the Luangwa Valley have been associated with three consequences. Firstly, the frequently observed mortalities of hippo during dry seasons are usually assumed to be a consequence of nutritional stress and diseases arising from food shortage (Siamudaala 2003). Secondly, the population decline of puku (*Kobus vardoni* S. & T.), common waterbuck (*K. ellipsiprymnus* O.), Cookson's wildebeest (*Connochaetes taurinus cooksoni* B.) and plains zebra (*Equus burchelli* G.) in Luangwa Valley has been linked to forage shortage arising from intensive grazing by hippo (Changwe & Child 1999, Jackmann 2000). Thirdly, it has been speculated that hippo grazing has benefited populations of impala (*Aepyceros melampus* L.) (Changwe & Child 1999) and possibly warthog (*Phacochoerus aethiopicus* P.).

Theoretically, the presumed impacts of hippo grazing on other sympatric grazers in the Luangwa Valley could be explained by facilitation and competition processes. Some evidence suggests that interspecific competition with hippo has limited the populations of the African buffalo (*Syncerus caffer* S.) and waterbuck in Uganda

(Eltringham 1974). Conversely, hippos have facilitated grazing of high quality grass and access to favoured habitats for other grazers by maintaining grazing lawns (Skarpe 1991, Arsenault & Owen-Smith 2002). Evidence suggests that facilitative habitat alterations by hippos and white rhinoceros (*Ceratotherium simum* B.) resulted in maintained or increased abundances of impala, warthog, wildebeest and zebra (Eltringham 1974, Owen-Smith 1988). Grazing on lawns stimulates regrowth of grass with higher quality, nutrient content and density of grass sward (McNaughton 1976 & 1984, Karki *et al.* 2000), thereby making grazing lawns more favoured by grazers. Even in dry season when grass is senescent and its quality declines, hippo-grazing lawns may still have higher forage quality than ungrazed patches (Verweij *et al.* 2006). Furthermore, grazing on lawns induces changes in habitat structure such as reduced grass height that might be favoured by other grazers (Eltringham 1974, Olivier & Laurie 1974).

However, suspected impacts of hippo grazing on other grazers have not been confirmed because no previous study has specifically focused on effects of hippo grazing on several species of different body sizes and digestive strategies. Therefore, I focused on assessing (1) whether hippo grazing facilitated grazing of other grazing ungulates, (2) the influence hippo grazing on food availability for grazing ungulates and (3) the relationship between densities of hippo and abundances of other grazing ungulates. Based on the Jarman-Bell principle (Bell 1971, Jarman 1974), I predicted that smaller/medium-sized grazers would prefer hippo-grazing lawns whereas larger-sized herbivores would avoid short grass swards.

METHODS

Study area

The study area is located in the South Luangwa National Park in the central Luangwa Valley of eastern Zambia (Fig. 1). It consists of riverine habitats along river segment of Luangwa River between 12º 50' 48" S, 32º 00' 00" E and 13º 05' 53" S, 31º 45' 00" E. The river runs in the southwest direction and separates the South Luangwa National Park in the west and the Lupande Game Management Area in the east. The study area covers habitats within a distance of about 3 km from the Luangwa River on the west riverbank.

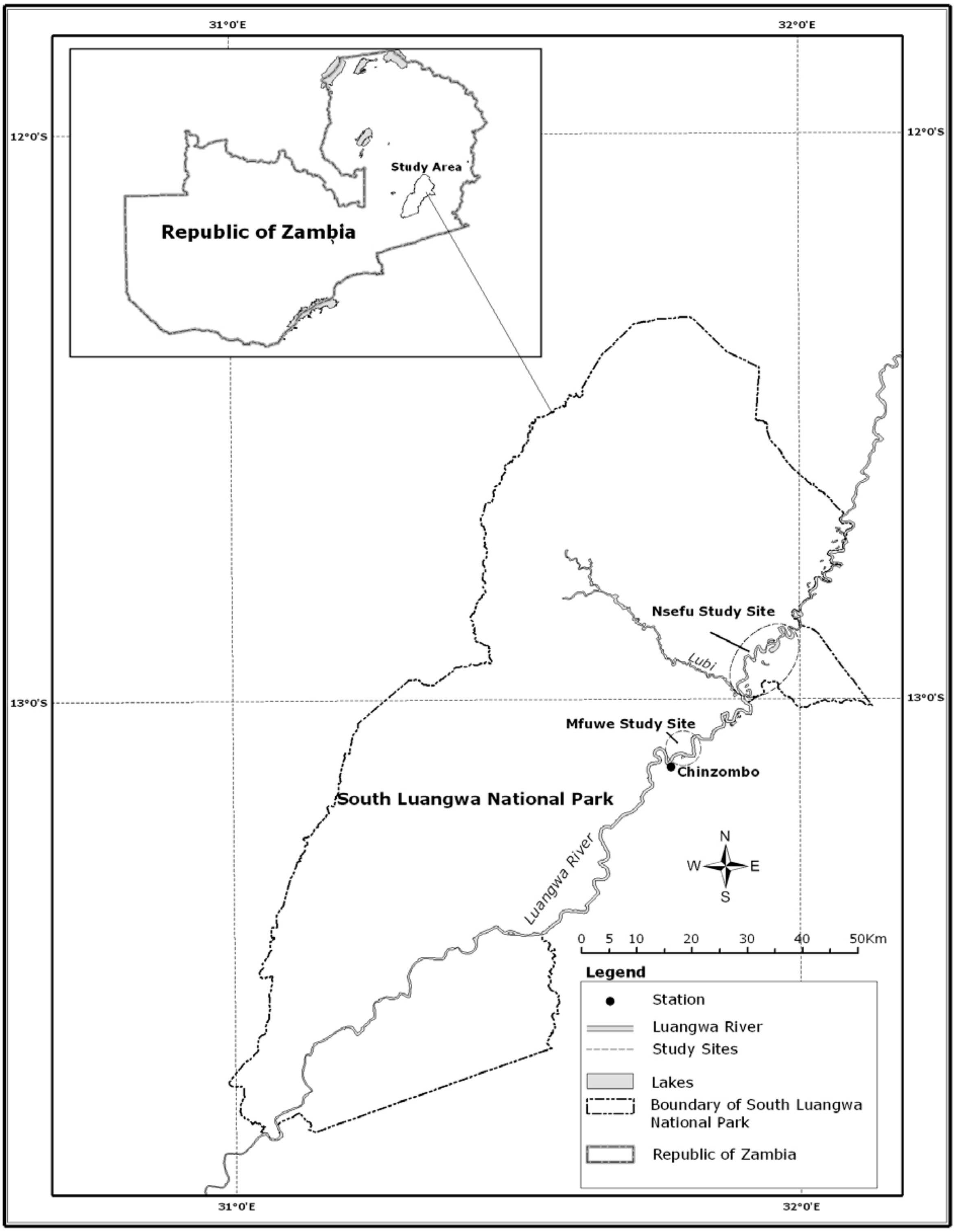

Fig. 1. Location of study sites in the South Luangwa National Park, Zambia

The mean annual rainfall is in a range of 400 - 800 mm (ZAWA 2002) and the mean temperature ranges from 10ºC in June-July to 38ºC in October (Ndhlovu & Balakrishnan 1991). The wet season is between November and April, but the dry season progresses from cool to hot between May and October. The landscape is characterised by recent alluvium with levees, point bar deposits, flood channels, abandoned channels, oxbow lakes and plains (Astle 1989). The habitats along the Luangwa River are a mosaic of flood plain and pan grassland, grassed dambos, riparian forest, mopane (*Colophospermum mopane*) woodland, *Combretum/Terminaria* woodland, and *Acacia/Combretum* woodland (Astle *et al.* 1969, Caughley & Goddard 1975).

Hippos and grazing ungulates

Hippo is a semi aquatic large mammal with average adult weights of about 1350 kg for females and 1500 kg for males (Owen-Smith 1988). They stay in water during the day and emerge at night to feed (Eltringham 1993) and prefer to graze short green grass close to rivers or lakes where they maintain extensive grazing lawns (Olivier & Laurie 1974). The diet consists of 95 – 99% grasses with sedges and forbs comprising the remaining proportion (Owen-Smith 1988). The foraging range is within a kilometre from a river or lake in the wet season, but increases depending on the availability of forage in dry season (Olivier & Laurie 1974, O'Connor & Campbell 1986) with average distances ranging between 1 to 5 km in eastern and southern Africa (Owen-Smith 1988).

Hippos are common along the Luangwa River and share the riparian habitats with other grazing ungulates. Buffalo, impala, puku, warthog, waterbuck and zebra prefer to graze in the riparian habitats and thereby overlap with hippos in habitat use and grass diet (Vesey-Fitzgerald 1960). Although impala is considered a mixed feeder, it is a preferential grazer that increases its browsing during dry season (Dunham 1980, Wronski 2003). Among the study species, impala, puku and warthog are in the small/medium body size range (50 - 150 kg) whereas those in large body size range (> 200 kg) are waterbuck, zebra and buffalo. Warthog and zebra are non-ruminants whereas buffalo, impala, puku and waterbuck are ruminants (Estes 1991). Wildebeest was omitted from the study because of the low population numbers and restricted distribution in the study area.

Data collection

The study was conducted from August to October during the dry season of 2006. The study area comprised Nsefu and Mfuwe study sites with the two extreme hippo densities along the Luangwa River. Nsefu study site (hereafter referred to as Nsefu) has had the highest hippo density with 51 hippos per river km and Mfuwe study site (hereafter referred to as Mfuwe) the lowest with mean density of 13 hippos per river km during the last 15 years (ZAWA unpublished data). The distance along the Luangwa River in Nsefu was 45.3 km whereas in Mfuwe it was 15.6 km. The study sites were about 15 km apart. The two study sites are comparable in that both the vegetation types and soils are similar (Astle 1989). A total of 21 transects (10 in Nsefu and 11 in Mfuwe) were randomly placed for sampling herbaceous layer and dung. The transects ran perpendicular to the Luangwa River and thus incorporated all animals distributed in the catena gradient. The transects were located within hippo grazing range on western riverbank of the Luangwa River. In Mfuwe, transects ranged from 0.6 km to 0.9 km with mean distance of 0.71 km whereas in Nsefu they ranged from 0.75 km to 1.2 km with 0.96 km as mean distance.

Herbaceous layer height and cover

To assess whether hippo density influenced food availability, I compared mean herbaceous layer heights and cover between the two study sites with different hippo densities. I estimated the herbaceous layer cover (in percentage) and measured height (in cm) in a rectangular 1-m^2 plot at every 150 m interval along each transect. The 1-m^2 rectangular plot (1.14 x 0.71 m) with sides in 1:2 ratio was used because rectangular plots are preferable in herbaceous layer measurements (Brower *et al.* 1990). Herbaceous layer cover was estimated according to ocular method described by Higgins *et al*. (1994). The wooden 1-m^2 plot was divided into 10 equal grids to improve the accuracy in estimating cover.

Patch utilisation by grazing ungulates

To evaluate whether hippo grazing facilitated grazing or access to favoured habitat for other grazing ungulates, I recorded the utilisation of hippo-grazing lawns and ungrazed patches by other grazing ungulates. Hippo-grazing lawns were easy to identify due to characteristic grazed lawn-like structure of short herbaceous layer height. Patches that had no characteristic grazed lawn-like structure of short herbaceous layer height were considered ungrazed by hippos. I used dung counts for other grazers as an indirect measure of patch utilisation and association (Riney 1982, Litvaitis *et al.* 1994, Jackmann 2001). I walked along the randomly placed transects in the two sampling sites with the help of four trained research assistants. Along each transect we placed a 25 x 25 m quadrat at every 150 m interval where pellet piles or dung groups for each grazing species were counted after being identified as described by Stuart & Stuart (1994). For buffalo individual droppings were counted. Impala may sometimes deposit droppings on a common latrine (Stuart & Stuart 1994). Where a common latrine was found in the quadrat, the number of dung groups per single impala was estimated at each latrine. To exclude dung groups that accumulated in wet season, I only counted the recent dung groups. Dung groups were considered recent if they were soft, slippery, sticky and showed no signs of disintegration or decay. The patch type was recorded accordingly as hippo-grazing lawn or ungrazed patch for each quadrat location.

Body condition assessments for grazing ungulates

To assess the influence of hippo grazing on food availability for grazers, I used animal body condition as an indirect indicator of food shortage and competition (Caughley & Sinclair 1994). I assessed body condition according to Riney (1960) were ungulates body conditions are classified as good, medium or poor. I sampled animals opportunistically using the road network in the study area. The complete road network was run only once to avoid double assessments on the same individual animals. The method by Riney (1960) could not be used on buffalo and zebra since it has no assessment description for body formation of these species (Riney 1982).

Dung and population densities of grazing ungulates

To evaluate the relationship between densities of hippo and abundances of other grazing ungulates I compared dung densities of grazing ungulates between the two study sites with different hippo densities. Dung counts for each species in 25 x 25 m quadrats along all transects were done as described above.

I also related available population density data of hippos and other grazing ungulates in the central Luangwa Valley. I used population density data sets for other grazing ungulates for the years 1979 and 1994 from Jackmann & Kalyocha (1994); 1996 from Jackmann (1996); 1993, 1998 and 1999 from Jackmann & Phiri (1999); 2001 from Simwanza (2002); 2002 from Dunham & Simwanza (2002) and 2006 from ZAWA unpublished data. The hippo population density data for corresponding years were from ZAWA unpublished data.

Data analyses

The herbaceous layer height and cover between study sites and between similar patches were compared and differences were tested using the Mann-Whitney *U*-test. The Mann-Whitney *U*-test was used because data on herbaceous vegetation height and cover were not normally distributed.

I tested the association between dung counts and hippo-grazing lawns or ungrazed patches using the χ^2-test. I calculated the expected values of dung counts for each species in the two study sites by multiplying the total number of dung counts by the proportion of the number of quadrats in hippo-grazing lawns or ungrazed patches.

The body condition classes for each species were compared between study sites using a Two-Proportions *Z*-test. In addition to the analyses on individual species, the observations for puku, warthog and waterbuck were pooled because total observations for each of these species in each study site were less than 100 observations and the pattern of change of good condition class proportions between sampling sites was the same for the three species.

I divided the total dung count for each species in a quadrat by the area of the quadrat expressed in km^2 to give me dung density per quadrat. I calculated the mean of dung density per quadrat for each species in each study site. I compared dung densities of each species between the two sampling sites using the Mann-Whitney *U*-test. This was used because dung density data were not normally distributed. Tests for correlations of population densities of hippo and other grazing ungulates were done using the Pearson product moment correlation coefficient *r*-test. I transformed population density data by taking logarithms of densities since population density data were not normally distributed.

All statistical tests were performed at 5% level of significance. Minitab statistical software version 14 (Minitab Inc. 2003) was used for statistical analysis.

RESULTS

Herbaceous layer height and cover

The spatial cover of hippo grazing lawns was higher in Nsefu (73%, n = 74) than in Mfuwe (49%, n = 63) (Z = 2.92, P < 0.01). However, Nsefu had significantly lower values of overall (combined hippo-grazing lawns and ungrazed patches) median herbal layer height and cover than Mfuwe (Mann-Whitney *U*-tests: P < 0.05) (Table 1). Conversely, there were no significant differences between study sites in herbal layer heights and cover for ungrazed patches (Mann-Whitney *U*-tests: P > 0.05) (Table 2).

Patch utilisation by grazing ungulates

Impala preferred hippo-grazing lawns in both Mfuwe and Nsefu study sites (P < 0.01 for both χ^2-tests) whereas buffalo and zebra preferred ungrazed patches (P < 0.01 for all χ^2-tests) (Table 3). Puku and waterbuck did not show preference for hippo-grazing lawns or ungrazed patches in any of the study sites (χ^2-tests P > 0.05). In Nsefu warthog preferred ungrazed patches (χ^2-test = 6.84, P < 0.01) but showed no preference for hippo-grazing lawns or ungrazed patches in Mfuwe (χ^2-test = 0.91, P > 0.05).

Body condition assessments for grazing ungulates

Irrespective of species and site most animals (over 60%) were in good body condition (Table 4). Puku had lower proportion of animals in good body condition class in Nsefu than in Mfuwe (Z = 2.20, P < 0.05). Furthermore, 3% of puku were in poor body condition in Nsefu (Table 4). The good body condition class for puku, warthog and waterbuck showed a similar pattern of being lower in Nsefu and pooled data for these species showed that there was a significant difference in proportions of good body condition class between the two study sites (Z = 2.42, P < 0.05).

Table 1: Comparison of overall (combined hippo-grazing lawns and ungrazed patches) mean height and cover of herbaceous vegetation between Mfuwe and Nsefu study sites in the Luangwa Valley, Zambia.

Herbaceous vegetation characteristic	Study site	Mean (±SE)	*P*-value
Height (cm)	Mfuwe (n=63)	24.41 (±2.50)	< 0.05
	Nsefu (n=74)	17.90 (±2.18)	
Cover (%)	Mfuwe (n=63)	58.38 (±3.87)	< 0.001
	Nsefu (n=74)	38.59 (±3.44)	

Table 2: Comparison of mean height and cover of herbaceous layer between similar patch types (hippo-grazing lawns or ungrazed patches) in Mfuwe and Nsefu study sites in the Luangwa Valley, Zambia.

Herbaceous vegetation characteristic	Study site	Patch type	Mean (±SE)	*P*-value
Height (cm)	Mfuwe (n=31)	Hippo lawns	12.14 (±1.90)	0.38
	Nsefu (n=54)	Hippo lawns	9.89 (±1.35)	
	Mfuwe (n=32)	Ungrazed	36.29 (±3.45)	0.41
	Nsefu (n=20)	Ungrazed	39.54 (±4.49)	
Cover (%)	Mfuwe (n=31)	Hippo lawns	46.45 (±5.25)	< 0.01
	Nsefu (n=54)	Hippo lawns	27.28 (±2.69)	
	Mfuwe (n=32)	Ungrazed	69.94 (±4.94)	0.78
	Nsefu (n=20)	Ungrazed	69.15 (±6.82)	

Table 3: Utilisation of hippo-grazing lawns and ungrazed patches by grazing ungulates indicated by dung counts in Mfuwe and Nsefu study sites in the Luangwa Valley, Zambia (values in parentheses are expected counts and χ^2 values are Yates values which are corrected for continuity).

Species	Study site	Total Counts of Dung in Quadrats		χ^2	*P*-value
		Hippo-grazing lawns	Ungrazed patches		
Buffalo	Mfuwe	81 (127)	178 (132)	16.27	< 0.0001
	Nsefu	111 (169)	121 (63)	29.26	< 0.0001
Impala	Mfuwe	260 (213)	173 (220)	9.86	0.002
	Nsefu	641 (539)	97 (199)	43.11	< 0.0001
Puku	Mfuwe	274 (274)	282 (282)	0.00	0.99
	Nsefu	250 (230)	65 (85)	3.16	0.08
Warthog	Mfuwe	23 (18)	13 (18)	0.91	0.34
	Nsefu	23 (37)	28 (14)	6.84	0.009
Waterbuck	Mfuwe	85 (76)	70 (79)	0.83	0.36
	Nsefu	33 (28)	5 (10)	1.33	0.25
Zebra	Mfuwe	141 (215)	296 (222)	25.26	< 0.0001
	Nsefu	21 (37)	30 (14)	8.99	0.003

Table 4: Number of observed grazing species with good, medium and poor body conditions in Mfuwe and Nsefu study sites in the Luangwa Valley, Zambia according to visual body condition assessment method (Riney 1960). Values in parentheses are proportions of the total expressed as percentages. Proportions with asterisks are significantly different between study sites.

Species	Study Site	Body Condition Classes			Total observation sample
		Good	Medium	Poor	
Impala	Mfuwe	127 (83.6%)	25 (16.4%)	0	152
	Nsefu	160 (88.4%)	21 (11.6%)	0	181
Puku	Mfuwe	75 (77.3%)*	22 (22.7%)	0	97
	Nsefu	41 (61.2%)*	24 (35.8%)	2 (3.0%)	67
Warthog	Mfuwe	19 (95.0%)	1 (5.0%)	0	20
	Nsefu	20 (83.3%)	4 (16.7%)	0	24
Waterbuck	Mfuwe	32 (82.1%)	7 (17.9%)	0	39
	Nsefu	14 (70.0%)	6 (30.0%)	0	20
Pooled Data (puku, warthog & waterbuck)	Mfuwe	126 (80.8%)*	30 (19.2%)	0	156
	Nsefu	75 (67.6%)*	34 (30.6%)	2 (1.8%)	111

Dung and population densities of grazing ungulates

Densities of impala, buffalo and warthog were not significantly different between Mfuwe and Nsefu (Mann-Whitney *U*-tests: $P > 0.05$) (Table 5). Puku, waterbuck and zebra densities were significantly lower in Nsefu than in Mfuwe (Mann-Whitney *U*-tests: $P < 0.001$).

During the period of high hippo population densities, the densities of other grazing ungulates were generally low (Fig. 2). However, only correlations with densities of buffalo ($r = -0.88$, n = 9, $P < 0.01$) and zebra ($r = -0.71$, n = 9, $P < 0.05$) were significant. Sample sizes in the correlations with densities of impala, puku and warthog are very low (n = 4).

Table 5: Comparison of species dung densities between Mfuwe and Nsefu study sites in the Luangwa Valley, Zambia. Dung densities for puku, waterbuck and zebra are significantly different between the two study sites.

Species	Study site	Mean dung density (±SE) (dung/km^2)	*P*-value
Buffalo	Mfuwe (n=63)	6,578 (±2,952)	0.65
	Nsefu (n=74)	5,016 (±1,496)	
Impala	Mfuwe (n=63)	10,995 (±1,451)	0.96
	Nsefu (n=74)	15,957 (±2,939)	
Puku	Mfuwe (n=63)	14,121 (±1,794)	< 0.001
	Nsefu (n=74)	6,810 (±996)	
Warthog	Mfuwe (n=63)	914 (±263)	0.81
	Nsefu (n=74)	1,102 (±305)	
Waterbuck	Mfuwe (n=63)	3,937 (±639)	< 0.0001
	Nsefu (n=74)	822 (±212)	
Zebra	Mfuwe (n=63)	11,098 (±1,615)	< 0.0001
	Nsefu (n=74)	1,103 (±250)	

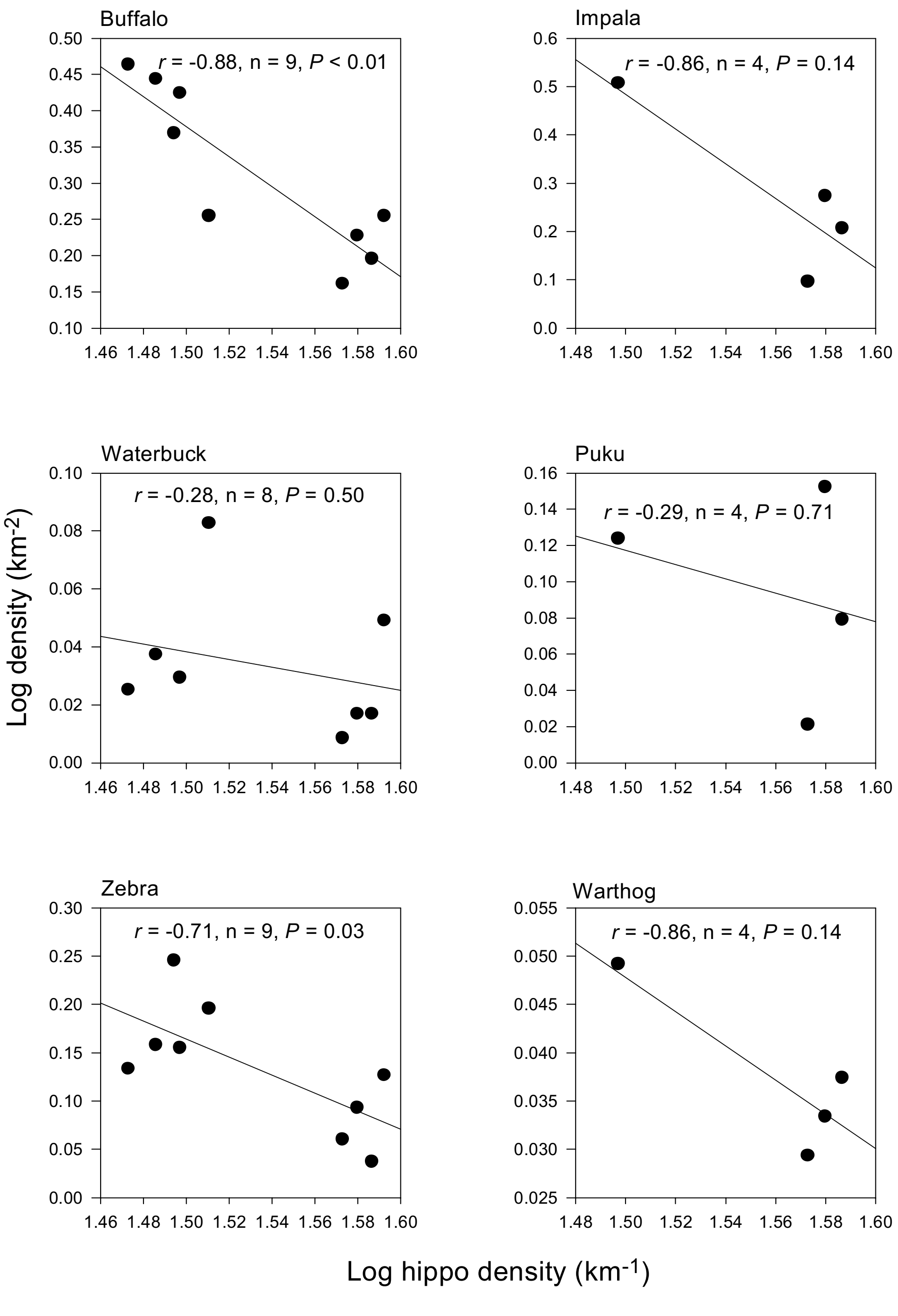

Fig. 2. The relationship (Pearson correlation coefficient) between hippo densities and those of buffalo, impala, waterbuck, puku, zebra and warthog in the Luangwa Valley, Zambia. Population density data were available for four to nine years in the period from 1979 to 2006. Hippo densities are expressed as numbers of hippos per river km.

DISCUSSION

Facilitation by hippo grazing

Impala preferred hippo-grazing lawns in the two study sites, thus suggesting that hippo grazing facilitates impala feeding and access to preferred short herbaceous layer even in dry season when food resources may be limiting. As predicted, the preference for short grass on hippo grazing lawns by impala supports the Jarman-Bell principle (Bell 1971, Jarman 1974). Since smaller herbivores are more selective for higher quality forage (Bell 1971, Jarman 1974, Gordon & Illius 1996), they prefer feeding on patches that have higher quality forage such as grazing lawns (McNaughton 1984, Fryxell 1991). Despite the fact that impala browse more when grass is senescent and its quality declines in dry season (Dunham 1980, Alden *et al.* 1995), impala preferred hippo-grazing lawns probably because hippo-grazing lawns maintain higher forage quality than ungrazed patches as shown by Verweij *et al.* (2006). Facilitation by hippo on impala feeding and access to preferred short herbaceous layer is supported by Prins & Olff (1998) who claimed that larger herbivores facilitate grazing for smaller animals by their grazing and trampling activities.

However, contrary to the Jarman-Bell principle, the small/medium sized ungulate warthog preferred ungrazed patches in Nsefu study site with lower herbage quantity. Furthermore, warthog usually prefer short grass patches (Kingdon 1979, O'Connor & Campbell 1986, Stuart & Stuart 1988, Cromsigt 2006). This is probably due to the fact that warthog is a non-ruminant ungulate with a digestive system that enables it to compensate for lower quality diet (Estes 1991, Cromsigt *et al.* 2006) and hence used ungrazed patches with more forage quantity but of lower quality. Similarly, although puku is similar in size with impala, it did not show preference for hippo-grazing lawns. However, Rosser (1992) found that puku shifted its strong selection for short grass to longer grass swards as dry season progressed in South Luangwa National Park. Thus, facilitative effects of hippo grazing on puku may have weakened during the study period in the mid dry season.

As predicted, the large body-sized buffalo and zebra preferred ungrazed patches. Due to their body sizes buffalo and zebra require large quantities of forage but can also tolerate lower quality (Demment & van Soest 1985, Illius & Gordon 1992). Although zebra can utilise both short and tall grasslands (Estes 1991), it prefers short grass (Smithers *et al.* 2000). As a non-ruminant hindgut fermenter which requires higher daily forage intake to compensate for its less efficient digestive system, zebra can sustain itself on lower quality grass (Bell 1971, Owen-Smith 1988, Duncan *et al*. 1990, Estes 1991). Thus, hippo-grazing lawns can probably not meet zebra's high forage intake requirements. Illius & Gordon (1992) and Voeten & Prins (1999) suggested that zebra selects lower quality tall grass swards when forage resources are limiting and forage intake is restricted as a result of the decline in quality and quantity of short grass swards.

Thus, despite the hypothesis that larger herbivores facilitate grazing for smaller animals by their grazing and trampling activities (Prins & Olff 1998), only one among the six grazing ungulates showed preference for hippo-grazing lawns. It suggests that grazing facilitation for smaller herbivores by a larger herbivore may not occur in some situations. Results in this study suggest that grazing facilitation by hippos on smaller herbivores may depend on available forage quantity, body size and digestive strategies of smaller sized ungulates. Thus, seasonal changes in the quantity and quality of forage may affect facilitative effects of hippos on smaller sized grazing ungulates.

Influence of hippo grazing on food availability

Although more than 60% of animals were in good body condition in both study sites, the observed occurrence of ungulates with medium and poor body condition classes were higher in Nsefu where hippo density was higher, and thereby indicating higher food shortage in this study site (Riney 1982, Caughley & Sinclair 1994, Ebedes 1996). Forage quantity was lower in Nsefu since herbaceous layer height and cover were significantly lower. The disparity in herbage quantity between the two study sites can probably be attributed to differential hippo grazing pressure. This is supported by the fact that there was no difference between the two study sites in herbaceous layer height and cover in ungrazed patches. Therefore, hippo grazing appeared to contribute to food shortage for grazing ungulates by reducing forage quantity.

Food shortage among grazing ungulates overlapping in habitat use and grass diet indicates the incidence of competition for food (Caughley & Sinclair 1994). Grazing ungulates that usually prefer short grass swards like puku, warthog and zebra did not show preference for hippo-grazing lawns with short grass probably as a response to competition for food. This suggests that hippo and/or impala might have competitively displaced warthog and zebra. For hippo to competitively displace smaller herbivores would not be consistent with the hypothesis that smaller herbivores are competitively superior because they have a higher foraging efficiency at low plant standing crop relative to that of larger herbivores (Illius & Gordon 1987, Prins & Olff 1998). However, Eltringham (1974, 1980) showed some evidence that suggests that hippos out-competed smaller grazers. Owen-Smith (1988, 2002) also suggested that hippos could compete successfully with smaller herbivore grazers due to their exceptionally wide mouths that enable them to feed effectively on short grass. Consistent with the hypothesis by Illius & Gordon (1987) and Prins & Olff (1998), impala is also able to competitively displace warthog and zebra from their preferred short grass swards since its body size is smaller.

Impala probably competed for food with hippo in the grazing lawns during the dry season because more than 11% of observed impalas were in medium body condition in both study sites. Since impala was not displaced from hippo-grazing lawns during the food shortage period and the fact that hippos expand their grazing range in dry season (Olivier & Laurie 1974, O'Connor & Campbell 1986, Owen-Smith 1988) suggest that impala may displace hippos from grazing lawns. Impala, as a smaller-sized herbivore and more selective feeder, may out-compete and displace hippo by removing the high quality parts of the vegetation and thereby reduces the quantity of quality grass for larger-sized hippo (Illius & Gordon 1987, Murray & Illius 2000). Thus, because hippos are restricted and dependent on the riparian habitat and water, they may be susceptible to food competition from selective feeders like impala and the effects of competition may ultimately affect population densities of hippos.

Hippo densities and abundances of grazing ungulates

On a spatial scale, the study site with higher hippo density (Nsefu) had significantly lower abundances of puku, waterbuck and zebra. The lower abundances in Nsefu can probably be attributed to higher food shortage for puku and less spatial cover of ungrazed patches with tall grass for waterbuck and zebra. Since waterbuck usually grazes in tall grass swards (Stuart & Stuart 1988, Smithers *et al.* 2000) and zebra preferred ungrazed patches with tall grass in dry season they probably had inadequate grazing areas in Nsefu. Furthermore, the vulnerability of waterbuck to predators might have increased because as Kingdon (1982) indicated, waterbuck uses long grass to hide from predators like the African lions (*Panthera leo* L.) and spotted hyenas (*Crocuta crocuta* E.), which are the most important factors in limiting waterbuck population. However, on the temporal scale only abundances of buffalo and zebra showed significant negative correlations with hippo densities in the central Luangwa Valley. Both buffalo and zebra preferred ungrazed patches, and thus their grazing patches in dry season were probably reduced in periods with high hippo densities which possibly affected their abundances.

Since hippo grazing facilitated feeding and access to favoured short grass swards for impala, it would be expected for the abundance of impala to be higher in the study site with higher hippo density and the correlation of hippo and impala densities to be significantly positive. However, comparison of impala abundances between the two study sites showed that there was no significance difference even though the two study sites had different hippo densities. Furthermore, the correlation of impala and hippo densities on a temporal scale showed no relationship although these data are small. Thus, the preference for hippo-grazing lawns does not seem to have resulted in increased impala abundance and it supports the suggestion by Arsenault & Owen-Smith (2002) and Owen-Smith (2002) that there is meagre empirical evidence where benefits of grazing facilitation actually resulted in population increase.

Movements of animals from the riverfront may affect spatial abundances of ungulates in the riparian habitats especially for buffalo and zebra which can cover over 10 km from nearest water sources (Sinclair 1977, Estes 1991). Thus, the effects of hippo grazing on overall populations of buffalo and zebra in the South Luangwa National Park may not be as high as on their spatial abundances in the riparian habitats. However, puku and waterbuck are restricted to riparian habitats due to their dependence on water and riparian habitats (Estes 1991) and thus are possibly the most affected by hippo grazing. Therefore, the effects of grazing by hippos on spatial abundances of grazing ungulates may depend on whether grazing ungulates are restricted to the riparian habitats or on their ability to move to and use habitats outside the grazing range of hippos.

Conclusion

The study shows that grazing by hippo facilitated feeding and access to favoured short grass for impala but facilitation by hippo at higher density did not result in higher spatial abundances of impala. However, at higher density hippo grazing contributed to higher food shortage for puku and less spatial cover of patches with tall grass for buffalo, waterbuck and zebra, and probably explains the lower spatial abundances of puku, waterbuck and zebra in Nsefu. Puku and waterbuck are probably the most affected since both species are restricted to the riparian habitats. The effects of hippo grazing on grazing facilitation and feeding patch selection by sympatric grazing ungulates in the riparian habitats appeared to depend on hippo density, forage quantity, body size and digestive strategies of grazing ungulates during the dry season. Thus, manipulation of hippo populations will lead to changes in facilitative and competitive effects on other grazing ungulates. Consequently, it may change some processes that are shaping the current abundance and distribution of grazing ungulates in the riparian habitats along the Luangwa River. Therefore, the objectives of conserving and managing herbivore populations should take into consideration the direct and indirect effects of hippo grazing on grazing herbivore assemblages in the Luangwa Valley.

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