International Journal of Biodiversity and Conservation Vol. 5(3), pp. 109-121, March 2013
Available online at http://www.academicjournals.org/IJBC
DOI: 10.5897/IJBC12.023
ISSN 2141-243X ©2013 Academic Journals

Full Length Research Paper

Factors affecting the Luangwa (Zambia) hippo population dynamics within its carrying capacity band – Insights for better management

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Accepted 18 May, 2012

This study assessed factors regulating the Luangwa (Zambia) hippo population within the carrying capacity band along the 165 km stretch of the Luangwa River, Eastern Zambia. Objectives of the study were to 1) establish whether the hippo population had reached and remained within the carrying capacity band in the last 32 years, and 2) determine the influence on population size and density distribution of grass biomass produced, mortality, non food resources (geomorphologic features) and levels of protection. Total river bank counts were made and global positioning system (GPS) locations of hippo schools recorded. Measurements from culled hippo carcasses were taken to determine sex and age classes. Kidney fat index (KFI) was used to determine body condition. Herbaceous growth was clipped and weighed to assess biomass. River geomorphologic features were taken by flying over the area in a light aircraft. Carrying capacity (*K*) was found to be 6,000 individuals at a density of 35 per km,oscillating within a carrying capacity band of 2,000 individuals in eight irregular cycles. At *K,* recruitment declined; calves and juveniles were 15% of the population and KFI was low at 40% by October. Grass biomass was high at 7, 850 kg/ha in 2008. Mortality did not disrupt population density. It was concluded that food was the main factor regulating hippo population size and density while geomorphologic features influenced the pattern of hippo population density distribution. Further research is required to establish primary production in 'lean' and 'fat' years and to monitor range trend condition as well as the impact of anthropogenic factors on the hippo population.

Key words: Carrying capacity, primary production, body condition, geomorphologic features.

INTRODUCTION

Over the last 32 years (1976 to 2008), the common hippo (*Hippopotamus amphibius*) population in the 165 km stretch of the Luangwa River, Zambia consistently recorded high densities of up to 42 hippos per kilometer of the river, with total numbers oscillating around 6,000 individuals (Chansa and Milanzi, 2010; Chomba, 2011). Culling and anthrax, such as the outbreak of 1987 to 1988, reduced the population to below 5,000, but the population rose above 6,000 by 1989 (Chansa and Milanzi, 2010; Chomba, 2011). To my knowledge, the factors that have maintained the Luangwa hippo population within this carrying capacity band of about 2,000 individuals have not been established. Knowing the carrying capacity band would help management in setting sustainable off-take quotas.

At the beginning of this study, Zambia Wildlife Authority (ZAWA) assumed that security and mortality were the main factors responsible for the oscillations of Luangwa hippo population. Based on that assumption and noting that population declines of the Luangwa hippo were quickly followed by increases, ZAWA conducted a number of hippo culling and cropping schemes since the 1960s. The current culling programme started in 2005 and will continue until 2013, during which time more than 1,500 hippos will be culled. Data on the number of specimens culled, age structure and sex ratios from previous culling exercises were not properly analyzed (Chomba, 2011; Chansa and Milanzi, 2010). The impact of previous culling schemes and other management interventions were also not properly assessed, and because of that, the main factors regulating hippo population within carrying capacity band were not known. It was assumed by this study that amount of grass produced, management interventions such as trophy hunting, culling and control, extent of poaching, disease infestation, influence of river geomorphology and security in form of anti poaching operations, and annual rainfall changes which influences primary production were potential environmental factors responsible for maintaining the hippo population within the carrying capacity band.

The aim of this study was to assess main factors regulating the Luangwa hippo population size between 5,000 and 7,000 individuals over the last 32 years (1976 to 2008). The following factors were investigated; (a) variations in population size, density and structure (b) primary production and grazing capacity, (c) impact of culling, cropping, problem animal control, disease, natural mortality and trophy hunting, (c) influence of annual rainfall and (d) influence of non food resources such as river geomorphologic features and security in form of anti poaching operations. This study also collated and analyzed data from the previous culling/cropping schemes and hippo counts that took place during the 2005 to 2008 culling programme.

MATERIALS AND METHODS

Location of study area

The present study was conducted in the Luangwa River and Valley in Eastern Province of Zambia (Figure 1). It covered the river and associated riverine habitat within 2 km on each side of the river bank and stretched the river length for 165 km, starting from the Chibembe pontoon (12° 48'S, 32° 03'E) to the Lusangazi-Luangwa confluence (13° 24'S, 31° 33'E). The study area was divided into study blocks A to H (Table 1). This subdivision was adopted in 1976 based on administrative arrangements and management of field logistics such as delivery of supplies to the study crew and convenience of sleeping during hippo counts. Administratively, the upper blocks (A-D) belong to Nsefu sector and the lower ones (E-H) to Lusangazi sector of the South Luangwa National Park. The total area covered by this study was approximately 660 km^2.

Total hippo counts along the Luangwa River

The river bank total foot count method involved six members of the research team walking along the bank of the river. Of the six, two were recorders, one recording on data sheets and the other on the map, two were observers using a pair of binoculars each, and the other two carried firearms to protect the team from dangerous animals. Up to 30 min were spent observing a spotted hippo school, which provided sufficient time to classify individuals into age groups and sex. The sizes of each school and associated river geomorphologic feature were also recorded and global positioning system (GPS) coordinates taken.

Assessing indices of carrying capacity

Parameters used to estimate carrying capacity were mean population size and density along the 165 km stretch of the river, population structure which is the composition of various age groups and sex, prevalence of pregnancy, incidence of pregnancy , exponential rate of increase and kidney fat index (KFI).

Population structure

To assess population structure, age and sex examination was carried out. Age classes were based on body size, while sex was based on external genitalia and body size for adults. This followed the method used by Marshall and Sayer (1976).

Sex was determined by observing external genitalia. In addition, sexual dimorphic features were also used, whereby males have broader fore heads than females. The sides of the male heads (around the ears) were darker; in females they were brownish (Skinner and Smithers, 1990). Males appeared to have a much bigger body size than females even when on the surface of the water (Skinner and Smithers, 1990). Also, most of the males stayed in isolation and on peripherals possibly to guard and defend the territory against intruders.

In live specimens, individuals were classified as calves, sub adults and adults. Calves mostly appeared on the sides of the adult females and their heads were smaller. Body length of a carcass was measured from the tip of the snout to the base of the tail. Lower jaws were also measured in cm from the rear end to the front, and skulls were examined for signs of tooth eruption and degree of wear of molar teeth, and these data were used to place animals into age groups I to XIX (Laws, 1967; Healy and Ludwig, 1965).

Prevalence of pregnancy

A qualified veterinary surgeon examined each female for presence of foetus or signs of lactation including inspection of the mammary glands for milk in the field and at the base camp. All pregnant and lactating females were recorded on a data sheet. The number of pregnant females divided by the total number of mature females was taken to be prevalence of pregnancy (*Pp*) (Sinclair and Grimsdell, 1982) as follows:

$$Pp = \frac{\text{Number of pregnant females}}{\text{Total number of mature females}}$$

Incidence of pregnancy

Incidence of preganacy (*Ip*) was used to measure birth rates in the population. The *Ip* was the number of pregnancies that an average female had each year, which is equivalent to the mean birth rate in animals that produce one young at a time like the hippo. The *Ip* was determined by calculating standard error (SE) for *Pp* as described by Sinclair and Grimsdell (1982):

$$\text{SE of } Pp = \sqrt{Pp\,(1-Pp)\,/\,N}$$

Where *N* is the total number of females in all samples and SE is the standard error of the prevalence of pregnancy, thus:

$$Ip = Pp.\ t\ /\ \text{Gestation time (days)}.$$

Where t = 365 days; and

$$\text{SE of } Ip = (\text{SE of } Pp).\ t\ /\ \text{Gestation time (days)}.$$

Exponential rate of increase

Exponential rate of increase was used to determine the rate at which the hippo population was increasing. Use of exponential rate

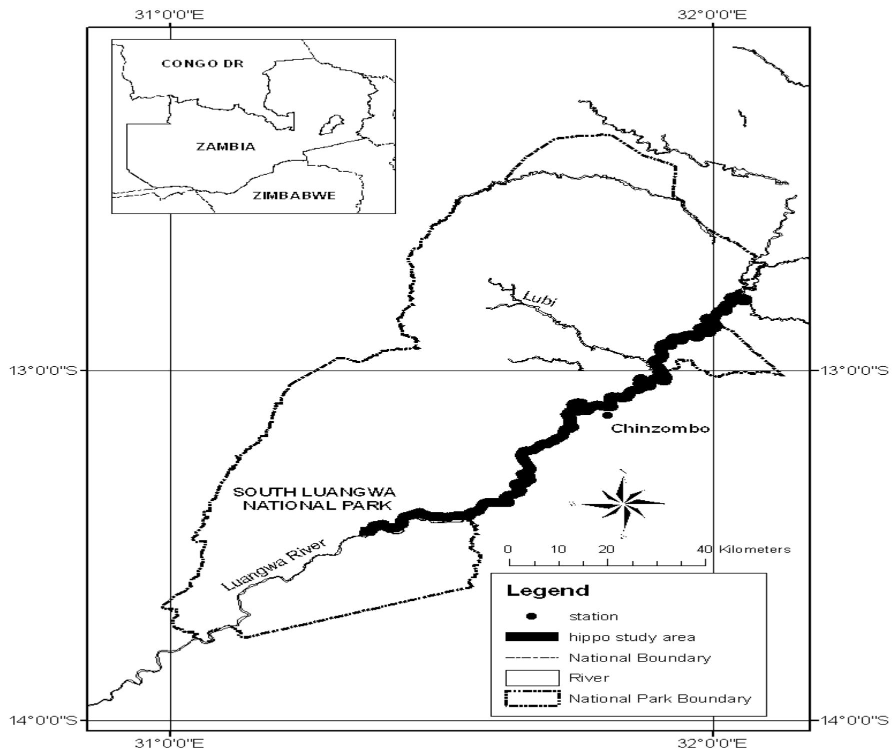

Figure 1. Location of study area along Luangwa River and South Luangwa National Park in Zambia.

Table 1. Details of the geographic location and coordinates of the study area blocks A – H, Luangwa Valley, Zambia.

Study block	GPS coordinates		Distance (km)
Upper study blocks			
A	E 12°46' 42";	S 032°02' 55"	16.1
B	E 12°50' 48";	S 032°00' 09"	45.3
C	E 12°59' 40";	S 031°54' 14"	14.2
D	E 13°03' 14";	S 031°52' 29"	15.6
Lower study blocks			
E	E 13°05' 53";	S 031°47' 10"	20.2
F	E 13°05' 45";	S 031°44' 09"	16.4
G	E 13°14' 39";	S 031°38' 54"	24.6
H	E 13°22' 35";	S 031°36' 41"	12.6
Total			**165**

of increase in the present study was found to be more useful than finite growth rate because it is easier to apply and numerically and logically simpler to understand by a reader. For instance, the value zero (0) means no growth in a population, a positive value means the population is increasing and a negative value means a decrease in the population, while in finite growth rate one (1) means no growth. The other advantage is that it gives an indication of the expected growth rate in the population at any given moment, while the finite growth rate considers only the first and last values of consecutive series of counts and gives the mean growth rate over the whole period of observation. In using *r*, it was assumed that a low exponential growth rate of less than $r = 1$ would imply a population at or above *K* and declining, while $r = 1$ would imply an increasing population. The value of *r* in exponential rate of increase was then calculated from consecutive hippo counts (1976 to 2008).
To determine the percentage growth, *r* (100) was used based on the equation described by Bothma (2010) and Caughley and Gunn (1996) as follows:

$$N_t = No\, e^{rt}$$

Where N_t=Population after time *t*; N_o=population at the beginning of time interval *t*; e= base of natural logarithm taking the value 2.71828 (constant) and *r*= exponential rate of increase or decrease.

Kidney fat index

KFI was used to determine body condition as an indication of available quantity and suitable food, quality and digestibility of that food and the general health of the hippo. In the present study, it was assumed that low KFI (≤40%) would imply poor body condition and low pregnancy rates and vice versa. Kidneys were extracted from 31 culled specimens which were 20% of the specimens culled during the year, 2008. The year was divided into four quarters of 3 months each. The specimens from which the kidneys were extracted were picked at random using random numbers obtained from a random table per quarter except for the first quarter (January to March) where the first and only specimen to be harvested in March was examined.

Specimens sampled at random were as follows; 10 specimens were sampled during the second quarter, 11 during the third quarter and 9 in the last quarter of 2008. Using a sharp knife, kidneys were removed together with the surrounding fat from the abdominal cavity and weighed in grammes using a solar powered digital weighing scale adjusted to the nearest 0.5 g. The fat deposited immediately around the kidney was removed and weighed separately. The kidney without fat was also weighed. All the data on weights for left and right kidneys were entered in separate columns on a data sheet. KFI was determined using the formula provided by Chapman and Reiss (2000) and Schemnitz (1980) as follows:

$$\text{Kidney fat index} = \frac{\text{Weight of kidney fat}}{\text{Weight of kidney}} \times 100$$

Grass biomass production

Line transects were used to sample herbs in study blocks A to H. A total of 100 transects were located in each study block A to H to determine biomass and match it with density along 165 km river stretch as described by Chansa et al. (2011).

Sampling of herbaceous plants was done once in March, 2008, just after the rains when the area was accessible and the grass was still fresh.

Hippo mortality

The number of hippos killed through trophy hunting, control, poaching and disease, and those dying from natural mortality for the period 1987 to 2004, were obtained from ZAWA records at regional headquarters in Mfuwe. The research team recorded numbers of hippo dying from the six mortality factors from 2005 to 2008 on data forms.

Influence of geomorphologic features and security on density distribution

River geomorphology

Information on river configuration and geomorphologic features such as lagoons, river confluences, river bends, and channel changes in the last half century was obtained by marking the coordinates in longitudes and latitudes for each geomorphologic feature on a map of the scale 1: 250,000 produced by the Government of the Republic of Zambia, Department of Surveys in 1994. Maps showing river course changes in the last half century were prepared using time-lapse aerial photographs collected from the University of Zambia, Department of Geography and Chinzombo Research Centre. The topographic map and aerial photographs were both more than 10 years old. To update information on these geomorphologic features, a Cessna 206 six seater fixed high wing aircraft fitted with Garmin 100 GPS, Radar Altimetre and two cameras one on each side of the aircraft was used to fly over the area during the months of March and October, 2008 as described by Chansa et al. (2010).

Location of Wildlife Police Officers (WPO) out posts and lodges as security features

The physical location of WPO out posts, lodges and Tourism Block Concession (TBCs) are considered to be important security features in deterring poaching incursions (Anonymous , 2007). GPS coordinates were taken for all lodges, WPO out posts and TBC along the 165 km river stretch, within 2 km of the river bank.

The number of patrol days conducted in the field for the period 2005 to 2008 was analyzed using Chi-square test (Ramos-Onsis and Rozas, 2002) to determine whether there was any significant increase in the number of days spent on patrol in the study area for the period 2005 to 2008. It was assumed that increase in the patrol effort would result into decrease in poaching of the hippo and vice versa. Data on patrol mandays, which show the intensity of patrols in the area, were collected from South Luangwa Area Management Unit headquarters at Mfuwe.

RESULTS

Mean population size and density

The mean hippo population size and density/km for the 165 km river stretch for the period 1976 to 2008 were 5,775 (rounded off to 6,000) and 35 per km, respectively. Plot of population size and time for the period 1976 to 2008 showed that 6,000 was the population's point of stability. I therefore, took the point of stability of 6,000 individuals to be the ecological carrying capacity *K* defined by Sinclair and Grimsdell (1982). From this point of stability, annual population changes for both population size and density were small and insignificant ($P > 0.05$). The correlation coefficient R^2= 0.12 obtained showed a weak positive correlation between population size as dependent variable and time as independent variable ($y = 314.73 \ln(n) + 4998$; $R^2 = 0.128$), suggesting a slow and insignificant population growth (Figure 2). The highest population size reached for the period 1976 to 2008 was 6,832 (rounded off to 7,000) and density of 42 per km in 1984; the lowest was 4,765 (rounded off to 5,000) and density of 29 per km in 1978. The population remained within the range of 5,000 to 7,000 in the last 32 years (1976 to 2008) (Figure 2).

Population oscillations within carrying capacity band

Annual variations in population size and density for the period 1976 to 2008 were insignificant ($P > 0.05$) (Figure 2). The population size and density fluctuated between 5,000 (density 29 per km) and 7,000 individuals (density 42 per km), respectively (Figure 2). I took this number of 2,000 individuals to be the carrying capacity band for the period 1976 to 2008.

Population oscillation cycles

The hippo population oscillated in four irregular cycles of about 8 years each, 4 years (range 2 to 7 years) above *K* of 6,000 and 3.5 years (range 2 to 5 years) below 6,000 before rising again to exceed it. The differences in the

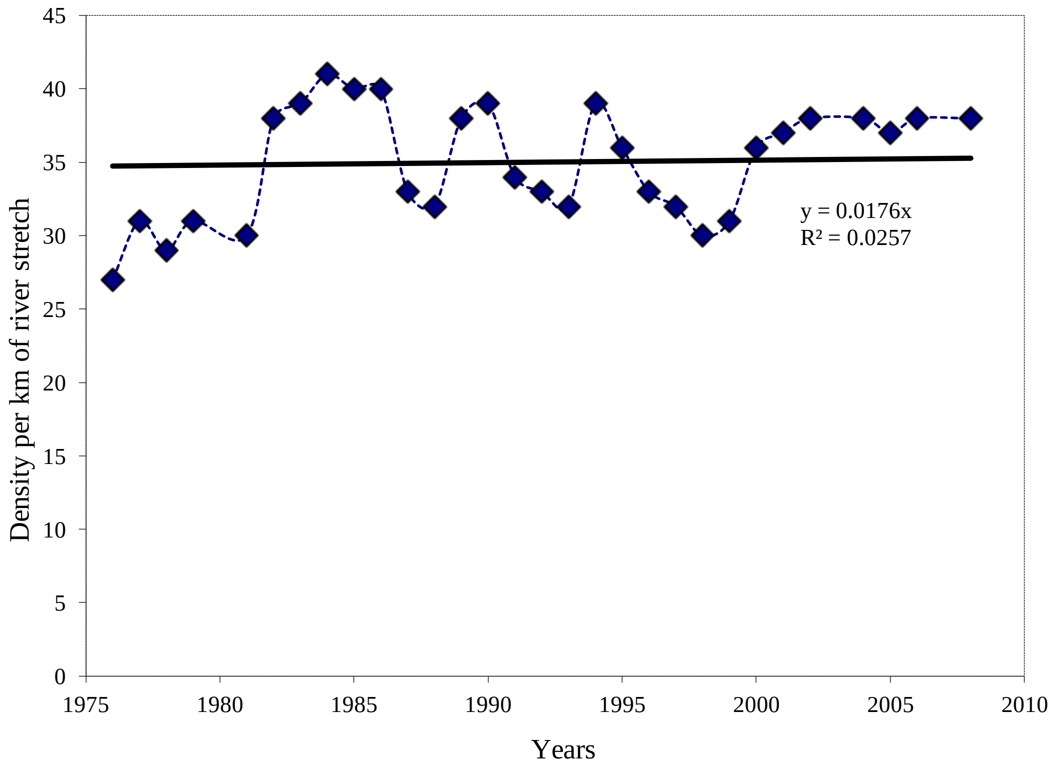

Figure 2. Plot of hippopotamus population density showing oscillations (1976 to 2008; Luangwa Valley, Zambia.

number of years when the population was above *K* and when it was below *K* varied significantly (P < 0.05), implying that cycles were irregular (Figure 2).

Population age structure

The age structure was biased towards older age groups. The propotion of calves, sub adults and adults in the population showed a significant difference (P< 0.001). Calves 1 year old and less were not recorded. Younger groups III and V comprised the minority with only 15% of the population (Table 2). The remaining 85% were older age groups VII to XIX comprising mature and senescent individuals of up to about 45 years old.

Exponential rate of increase

The exponential rate of increase for the period 1976 to 2008 was marginal $r = 0.04$ ($N_t = N_o e^{rt}$). This rate of increase was low as it was close to zero, when in fact an increasing population is expected to have $r = 1$. I took this to be one of the signs for a population at ecological carrying capacity *K* where growth stabilizes and population losses are quickly recovered, but the population hardly surpasses the point of stability and instead oscillates around it (Figure 2).

Body condition (KFI)

KFI of 40% was low with significant variations between months, being higher in the wet season months (≥80%) and lower in the dry season months, particularly the last quarter of the year (October to December) (P < 0.001). The month of July was the first one to show a drop in the KFI below 80%, which was taken to be the cut off point for good body condition (Figure 3).

Prevalence of pregnancy

The *Pp* values obtained during the present study for 2005, 2007 and 2008 were not significantly different (P > 0.05): The *Pp* obtained were, 28, 25 and 13%, respectively (Table 3). These *Pp* values were all below 30%, which is considered to be the bottom cutting point for high *Pp*.

Mean birth rates/Incidence of pregnancy

For the period 2005, 2007 and 2008, the mean birth rate of 0.22 was obtained. Annually, the mean birth rates were; 0.042 ± 0.080 (SE), 0.38 ± 0.328 and 0.20 ± 0.060 (SE), respectively. Such mean birth rates were low, suggesting a reduced recruitment rate which is also characteristic of a population at *K*.

Table 2. Hippopotamus age distribution based on the three culling programmes conducted so far in the Luangwa Valley, Zambia.

Age group	Estimated age (Year)	Year			Percentage composition of population 2005 - 2008
		1970	1971	2005-2008	
I	< 1	7	0	0	
III	1 - 2	5	4	2	2.2
V	3-5	16	16	13	13.26
VII	6 -11	67	69	31	31.63
IX	12 -17	82	34	25	25.51
XI	18 - 26	59	26	15	15.30
XV	27 - 34	125	54	9	9.18
XIX	36 - 41	15	7	3	3

(Data for 1970 and 1971 from Marshall and Sayer, 1976).

Table 3. Prevalence of pregnancy of the hippopotamus population, 2005 to 2008, Luangwa Valley, Zambia.

Year	Total culled (Male and Female)	Total mature females	Number pregnant	Prevalence of pregnancy (*Pp*)
2005	250	71	20	0.28
2007	12*	4	1	0.25
2008	157	69	9	0.13
Totals	419	144	30	Mean over the 3 sub samples = 0.22

Key * Fewer specimens were collected than in 2005 or 2008 because the culling started in the third quarter (July to September) of the year. This was too late for the company to cull a large number of hippopotami.

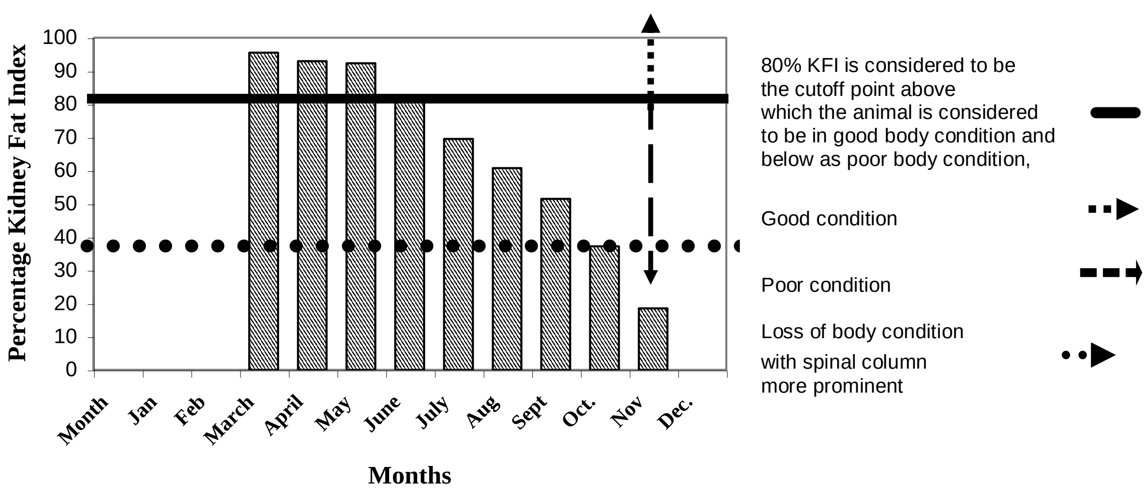

Figure 3. Monthly variations in hippopotamus KFI, Luangwa River, Zambia.

Primary production

Grazing capacity

The total primary production obtained during this study was 62, 800 kg with mean per study block of 7, 850 kg/ha^{-1} in 2008. At mean primary production of 7, 850 kg/ha^{-1}. I calculated that each hippo needed six hectares of pasture (6 ha/GU).

Influence of primary production on hippopotamus density distribution

The number and distribution of hippo schools followed the pattern of food distribution. The amount of grass biomass per study block A to H along the 165 km river stretch varied significantly, being higher in some study blocks and lower in others (P < 0.05). Study blocks with high grass biomass (46% of total primary production),

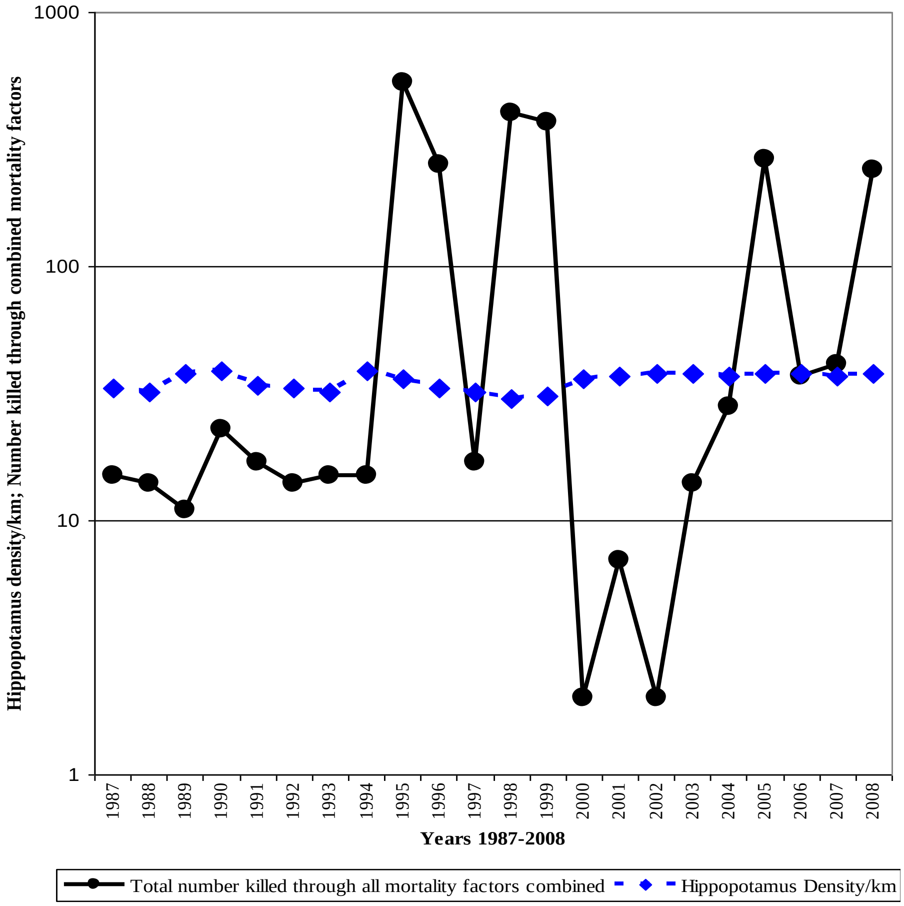

Figure 4. Number of hippopotami killed through six mortality factors combined and hippopotamus density. Luangwa Valley, Zambia.

had a higher number of hippo schools.

Mortality factors

All forms of mortality combined were not a major factor in population size and density and regulating the Luangwa hippo population within the carrying capacity band (Figure 4). The total number of hippos killed by all the six mortality factors combined for the period 1987 to 2008 was 2,674 (mean 122). The mean annual mortality of 122 individuals was found to be too low at 6% of carrying capacity band, and insufficient to reduce population density.

Single factor analysis of variance (ANOVA) showed that the number of hippos killed by six mortality factors (poaching, control, trophy hunting, natural mortality, disease and culling) varied significantly from year to year for the period 1987 to 2008 ($P < 0.05$) and between mortality factors (Table 4). Student NewMan's – Keuls Test (SNK) showed that culling and disease took more individuals (95% of total) than the other four mortality factors combined: culling took (63%), disease took (32%) and the remaining four took only 5% of total (Table 4).

Despite these recorded mortality incidences, hippo population density remained relatively stable over the period 1987 to 2008, varying only between 30 to 38 individuals per km, which was insignificant (χ^2,$P < 0.05$) (Figure 5). It was suggested that there were other factors acting with mortality to regulate population size and density.

Geomorphologic features

After food (grass biomass), geomorphologic features were the second most important factor in regulating hippo pattern of population density distribution between study blocks A to H. A total number of 64 geomorphologic features were recorded. The geomorphologic features considered were river bends, confluences and lagoons.

The number of geomorphologic features varied significantly along the 165 km stretch and between study blocks A to H, (χ^2, $P < 0.05$), being more abundant in some study blocks and fewer in others. Of the total num-

Table 4. Summary table of SNK test showing that disease and culling took a larger number of individuals than hunting, poaching, control and natural mortality combined. Luangwa Valley, Zambia.

Parameter	Mortality category					
	Hunting	**Poaching**	**Control**	**Natural mortality**	**Disease**	**Culling**
Total	197	52	48		2,540	
Mean	10.36	2.78	3.47	6.66	133.66	272
SE	2.3	2.2	1.9	4	5.3	160
Conclusion	Took the smallest number (5% of mortality factors)				Took the largest number (95% of all mortality factors)	

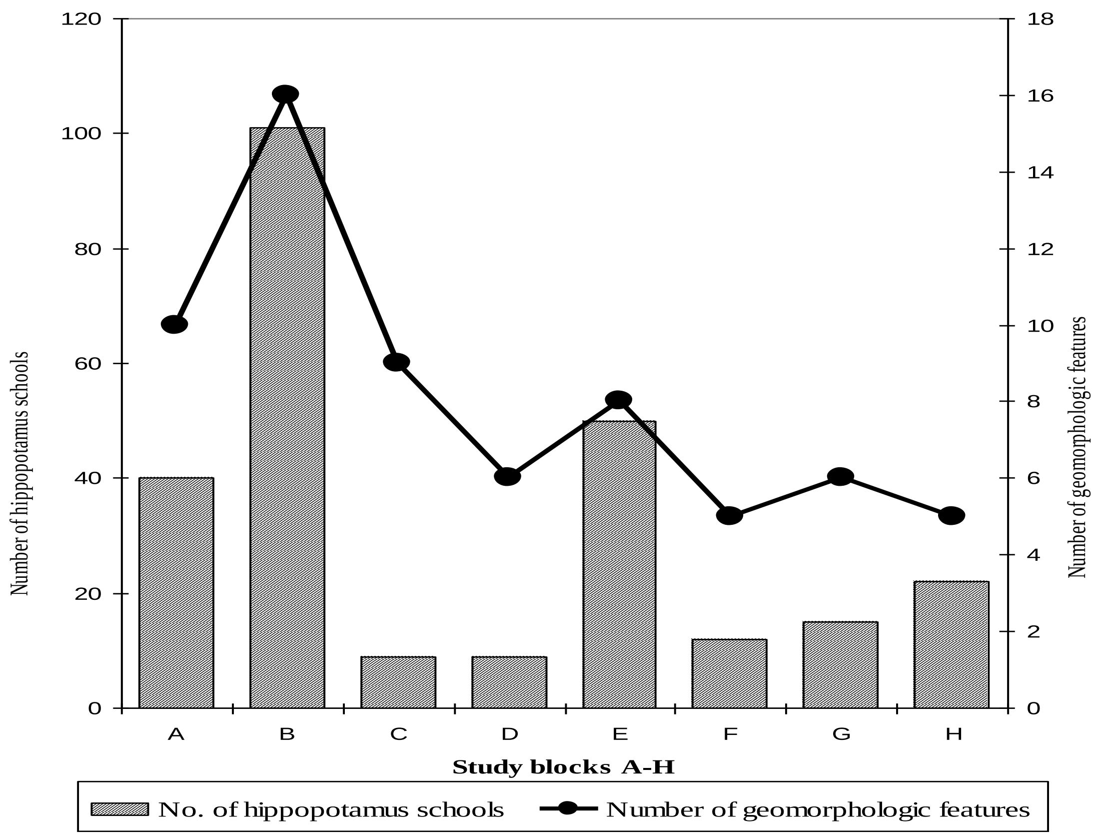

Figure 5. Plot of number of geomorphologic features and distribution of the number of hippopotamus schools, Luangwa Valley, Zambia.

ber of geomorphologic features recorded, 34 (53%) were river bends, 13 (20%) were lagoons and 17 (27%) were confluences. The length of river bends (km), width of river confluence (km) and length of lagoons (km) were found to be significantly different.

The hippo population was found to be significantly aggregated and higher in river segments with more and longer geomorphologic features and more sparse and less aggregated in river segments with fewer geomorphologic features (χ^2,P < 0.05). Plot of number of hippo of schools showed that population density declined with reduction in the number of geomorphologic features ($y = -1.131x + 13.214$; $R^2 = 0.5662$).

Among the geomorphologic features, it was found that population density was highest in river bends (75.48%), followed by confluences (9.18%), and lagoons (6.03%); all the other features put together had (9.38%). Study blocks and river segments with more river bends had the highest hippo density and the distribution of hippo schools was found to be biased towards river bends (Figure 5).

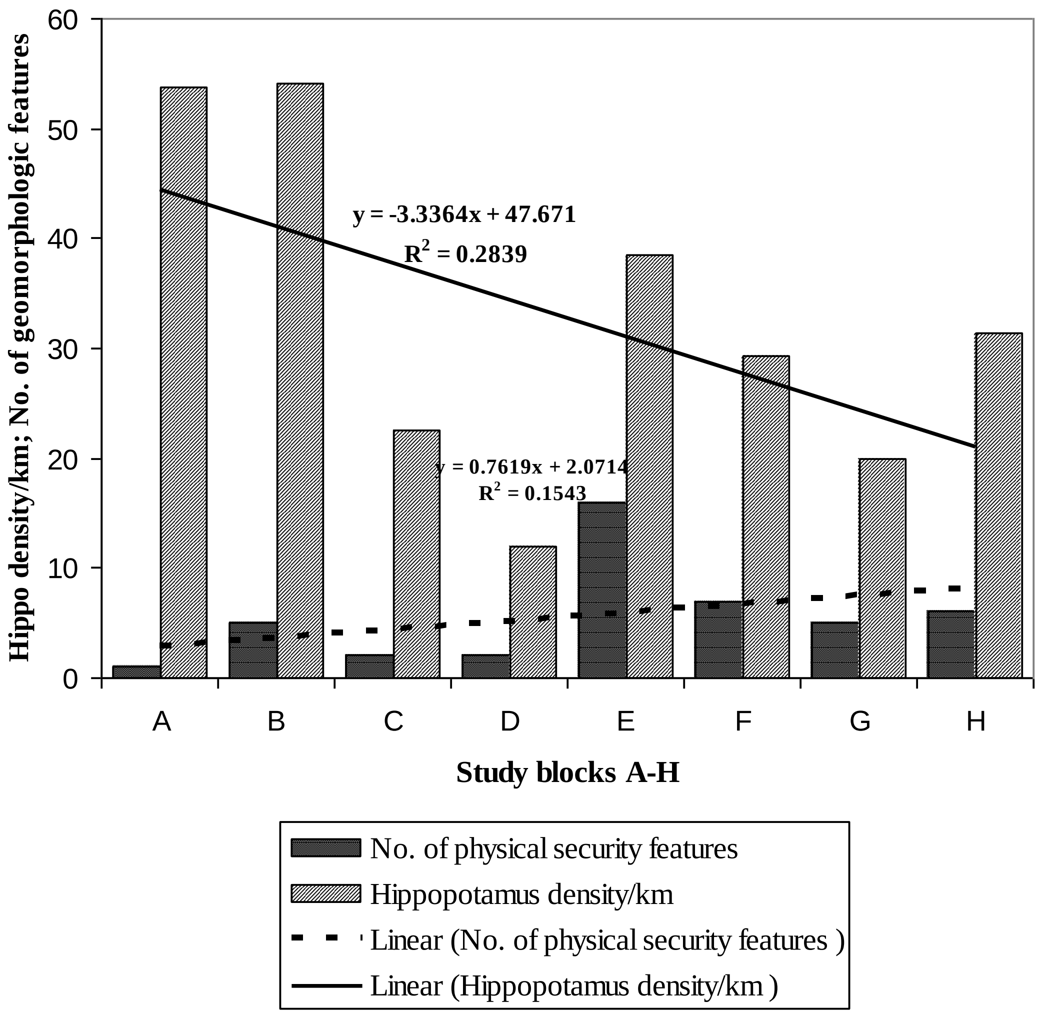

Figure 6. Plot of security features and population density for each study block. Luangwa Valley, Zambia, 2008.

Security

Wildlife Police Officers (WPO) out posts

The number of hippos killed by poachers as an indication of security was 3 per year, which was only 0.15% of carrying capacity band. It was suggested that Security was not an important factor in regulating the hippo population within the carrying capacity band. Results on the number and location of WPO out posts showed no direct influence on population size and density distribution along the 165 km stretch. The number and physical location of WPO outposts varied significantly in number between study blocks A to H ($P < 0.05$). These results showed that: as the number of security features increased ($y= 0.7619x + 2.0714$, $R^2 = 0.1543$), hippo population density declined ($y= -3.3364x + 47671$, $R^2 = 0.2839$).

The upper blocks (A to D) which had the highest population size and density had the least number of WPO outposts, only 10 (22.72% of total). The lower study blocks (E to H) despite having the largest number of WPO out posts (77.27%), had the lowest population size and density (Figure 6). Block E for instance, which had the highest number of security features,16 (36.36% of total), did not have the highest population density/km (Figure 6).

Patrol mandays

The number of patrol mandays and length of patrols did not influence population size and density distribution along the 165 km stretch. The total number of patrol mandays and length of patrols increased significantly between 2007 and 2008 (χ^2, $P < 0.05$), but conversely there was a slight decline in population size over the same period of time. Patrol mandays in 2007 were 7, 958 and actual time spent patrolling in the field for more than 1 day was 6,954 days. In 2008, patrol mandays were 10,001 and actual time spent patrolling in the field for more than 1 day was 8, 169 days. Conversely, in 2005 the population size was 6,500, declining by 131 individuals to 6,369 in 2006 and again declining by 51 individuals to 6,318 in 2008.

DISCUSSION

Population trends for the Luangwa hippo

The Luangwa hippo population size along the 165 km stretch had reached ecological carrying capacity, *K* at 6,000 individuals and had been oscillating within the carrying capacity band of 2,000 individuals. The population stability *K* was achieved after a period of more than 100 years, from the late 1890s, when the population was almost decimated (Attwell, 1963), to the current decade. Between 1952 and 1960, there was slow growth followed by a period of rapid or exponential growth from about 1962 to 1976 (Tembo, 1987; Chansa and Milanzi, 2010). Subsequently, the summation of direct environ-mental factors such as mortality and food availability and habitat welfare factors such as territories, basking and wallowing areas, together with indirect factors such as climate, fire, habitat changes and natural catastrophies, collectively formed environmental resistance or limitations. Such limitations coupled with social behaviour of hippos, gradually reduced birth and survival rates of the population (Botham, 2010), so that it prevented further growth of the population and ultimately determined the number at which the population leveled off and started to fluctuate (Chomba , 2011), as also noted by Watson and Moss (1970) and Bothma (2010). Bothma (2010) for instance noted that every animal species tolerates a certain degree of density, after which social behavioural factors prevent further crowding irrespective of whether there is sufficient food or not. Furthermore, since the environmental factors are not constant, but rather fluctuate from year to year, the population also followed the same pattern (Chomba, 2011).

This study found a vertical amplitude of the population oscillation around *K* to be 2,000 individuals which was caused by interactions between the hippo population and plant food supply. However, this relationship between population size and available food was not straight forward as noted by Sincliar and Grimsdell (1982) and Malpas (1977) and so the hippo population size could not fully stabilize at *K*. The amount of food (grass biomass) produced and the available space for basking, wallowing and establishment of territories and other habitat welfare factors together regulated the population size by influencing birth and survival rates.

These results on population oscillations are consistent with Mduma et al. (1999)'s 40-year study of the Serengeti wildebeest. According to Mduma et al. (1999), the wildebeest population estimates in the Serengeti reached its peak in the mid 1970s, after which it started to oscillate. He assumed that the wildebeest population oscillations were an indication of environmental resistance with regard to food supply. Similarly, Kirkpatrick et al. (1968) highlighted the role played by environmental resistance, particularly food, in regulating reindeer population size.

Kirkpatrick et al. (1968) showed that in 1957 a total number of 1,350 reindeer were introduced on St' Mathews Island. At the time of their introduction on the island, their body weight were found to exceed those of reindeer in domesticated herds by 24 to 53% among females and 46 to 61% among males. By 1963, the population had increased to 6,000 by which time average body weights had declined from the 1957 values by 38% for adult females and 48% for adult males. Kirkpatrick et al. (1968) assumed that reduced body growth was almost certainly related to qualitative and quantitative changes in food supply. A massive population crash followed soon after determination of 1963 values. Kirkpatrick et al. (1968) then concluded that food supply, through interaction with climatic factors, regulated reindeer population on the island.

Other examples of how food regulates population size have been provided by Finerty (1980) and McCullagh (1969). Examples included lemming (*Lemus*), fox (*Alopex* and *Vulpes*), Canadian lynx *(Lynx canadensis)* mice (Muridae), snowshore hare (*Lepus americanus*) and muskrat *(Ondatra zibethica).* The lemming population for example, increased rapidly from only 1 to 2 lemmings per hectare to about 30 or 40 lemmings per hectare. This increase as reported by Finerty (1980) occurred in only a few months. Shortly afterwards, the numbers declined to earlier low levels and remained low for few subsequent years. The lemmings on the other hand, followed a 4-year cycle. This pattern according to Finerty (1980) did not only occur in lemmings but also in mice (Muridae) and foxes. Other species such as the snowshoe hare, muskrat and some foxes and the Canadian lynx had 10 years population cycles. Finerty (1980) then concluded that the rise and fall in these mammal populations was probably due to some favourable factor, which resulted in an increase in birth rates in some years and decrease in others. The equally rapid fall in the population in the lemmings seemed to have resulted from a high death rate and lowering of birth rate due to environmental resistance. The population crash of these populations did not seem to be due to disease (Finerty, 1980). He finally established that food and other welfare factors were responsible for the rise and fall of populations. In this study therefore, amount of food was the limiting factor to Luangwa hippo population growth. In 2008 for instance, it was established that available food could only support 5,500, implying that the area was already overstocked by 818 hippos, such that by July signs of overgrazing were evident and body condition dropped below 80%, which was responsible for the low birth rates and incidence of pregnancy (<30%). In the Luangwa Valley, it has also been established that grass biomass influences conceptions and births which occur at a period of the year when food is most abundant. Births in particular take place between January to March, when there is green and nutritious grass which also supplies enough energy for milk production (Botham, 2010).

Indices of population carrying capacity

In the present study, indices of population carrying capacity (Sinclair and Grimsdell, 1982) were used to reinforce the findings on population size and density. Use of indices of population condition was based on the premis that although mammal populations have inherent high growth rate, maximum potential growth seldom occurs due to environmental resistance which includes food availability, predator pressure, famine, diseases, accidents, environmental disasters arising from extreme weather conditions, fire and others that influence birth rates (Botham, 2010). These environmental factors, collectively determine population size at which the population would stabilize (Bothma, 2010).

The exponential rate of increase obtained in the present study (r = 0.04) was low and indicative of a population at *K.* Reduced birthrates and incidences of pregnancy in mature females also showed that the population was about *K.* Accordingly, the proportion of young ones in the population was low. These low *Pp* values signaled that the population was at or above *K* as earlier noted by Sinclair and Grimsdell (1982).

Kidney fat index as indicator of body condition and pregnancy rates

The KFI of less than 40% indicated poor body condition which was taken to be a sign that the animals had mobilized fat reserves and muscle protein to generate energy for daily sustenance (Sinclair and Grimsdell, 1982; Youatt et al., 1965; Rees, 2001).

When animals have a high KFI (≥40%), it is assumed that the available food is suitable in quality and sufficient to provide adequate nutritional requirements and enable animals to store excess energy in form of fat reserves (Myers and Poole, 1962).

Studies on hippo and other large mammals have shown that KFI is a useful indicator of the potential of such animals to be resilient to nutritional related or sudden environmental stress, and to breed and increase in numbers (Sincliar and Grimsdell, 1982). Poor condition rating determined by KFI and its influence in reproduction has been demonstrated in species such as Himalayan thar *(Hemitragus jemlahicus)* (Caughley, 1970a; b), pronghorns (*Antilocarpa americana*) (Bear, 1971), mule deer *(Odocoileus hemionus)* (Anderson et al., 1972), and impala *(Aepyceros melampus)* (Hanks et al., 1976).

Animals with KFI below 40% were under constant stress and continued to exploit fat reserves in order to overcome the physical and emotional stress (Hanks et al*.,* 1976). Under such circumstances the kidney fat reserves were low and individuals were unable to breed (Hanks et al., 1976) (Figure 3) due to energy deficit.

For this reason, KFI is known to be highest in increasing populations which are below carrying capacity *K*, and lower in stable and declining populations where individuals have increased in number against limited food supply and would not derive adequate nutrition. Poor condition rating of the hippo in the Luangwa Valley was assumed to be responsible for the low recruitment rate.

Quantity of herbage produced

Study blocks with high biomass had more food available to support high density. Food availability enabled hippo to obtain adequate daily food requirements of 2.5% of body weight which was converted into protein, thus explaning why areas of high biomass such as study blocks with biomass > 7,000 kg/ha had hippo density exceeding 35 per km. Areas with grass biomass below 7,000 kg/ha could not provide adequate amount of food to keep hippos in good body condition. In such study blocks only low animal density of less than 35 per km could be sustained.

Influence of mortality factors on hippo population

This study has established that the current levels of mortality were not a significant factor in regulating population size and density as was originally contemplated by ZAWA. The mean number of hippos lost annually through mortality was only 6% of carrying capacity band of 2,000 hippos. When the number of hippos dying is less than 2,000 individuals, there would be no significant change in density as losses are quickly recovered.

Culling

Since the 1960's the hippo population in the Luangwa Valley has been considered to be thatt of over population (Tembo 1987). All culling programmes conducted in the Luangwa Valley since the 1960s have has the main objective of reducing population size. It was on the same premis that the current culling (2005 to 2013) was based. From 1987 to 2008 for instance, a mean number of 272 hippopotami were culled, and this number was thought to be large enough to lower the population size. However, this number was found to be far less (13.6%) than the carrying capacity band of 2,000, and therefore it could not significantly reduce the population below *K*. For as long as the number removed from the population was within the carrying capacity band of 2,000 hippos, the population easily recovered. Infact it has been documented that the act of culling removes excess males and frees resources for the remaining female individuals, leading to increased births and facilitating rather than suppressing population growth rate (Marshall and Sayer, 1976; Anonymous , 2008).

This evidence therefore suggested that culling regulates hippo population size by stimulating population growth. In this study, relatively lower levels of increase were obtained in the 2006 after the 2005 culling because the population was still above *K*. It is expected that at the end of the culling season in 2013, when the population is below *K,* relatively higher levels of increase in the hippo population size will be obtained in response to freed food resources.

Disease

The present study found that disease was not an important factor in regulating hippo population size within the carrying capacity band. Although it has been reported that mortality directly influences population density, in the Luangwa Valley where hippo densities are high (up to 42/km) it is the trampling of grass and over utilization of grazing areas that are known to cause soil erosion which reduces food resources for the hippo and in turn negatively impacting on the animal’s body condition and disease only comes in as a secondary factor (Child, 1999). Such conditions if left unchecked could lead to reduced food production (Child, 1999), and reduced food production, in turn, may lead to poor body condition, which makes the animals relatively more susceptible to disease (Plowright et al., 1964). Disease therefore, comes in as a secondary factor in causing hippo’s death, being related to the scarcity of food supply (Attwell, 1963; Marshall and Sayer, 1976; Tembo, 1987 and Child, 1999). Bere (1959) asserted that there was no known record of disease having influenced hippo populations in the Luangwa Valley or else where in Zambia or sub Saharan Africa. Anthrax, although recorded from hippo in Luangwa Valley and Uganda, has not apparently proved to be a significant controller of hippo population (Bere, 1959).

On that basis, it was suggested by the present study that causes other than disease, such as reduced amount of food or high levels of poaching like the one which occurred in the Luangwa Valley in the 1800s, are more important factors in regulating hippo population size than disease. Furthermore, the historical pattern of persecution described for Luangwa Valley in the 1800s and early 1900s also best describes the scenario for the Zambezi and Kafue Rivers and provides sufficient evidence to assume that disease is not an important factor in regulating hippo population.

River geomorphologic features

This study established that river geomorphologic features such as river bends and sand bars, confluences and lagoons are critical attributes influencing hippo density distribution patterns (Chansa et al., 2010). Sand bars for instance provide basking areas which conserves energy for the hippo, which is known to have low fat reserves relative to body size. Sand bars and shallow pools also act as mating and nusery areas, which increases calf survival. Areas with more geomorphologic features had higher densities and carrying capacity. This is probably because areas with many geomorphologic features favour smaller to medium sized hippo schools: smaller schools minimize aggressive behaviour, which conserves energy and enhances reproduction.

Security features along the Luangwa River

The pattern of distribution influenced by security levels was reported in elephant by Barnes (1983) and Barnes and Kapela (1991), but does not seem to apply to hippo. As already argued, the main factor responsible for population regulation was food. It was initially thought that security along the 165 km stretch, together with mortality, were the main factors responsible for regulating hippo population within the carrying capacity band. Results from the present study show that this is not the case. Security was a insignificant factor (Lewison, 2007), as indicated by the fact that hippo density/km declined as the number of security features increased.

The low number of hippos poached may be attributed to a number of factors; (a) hippo is not popular meat for Luangwa Valley residents who believe that it causes leprosy, a belief which is also shared with residents of Rukwa area in Tanzania, (b) a well developed Community Based Natural Resources Management (CBNRM) programme, in which local communities participate in managing wildlife, has improved and encouraged positive community attitudes towards wildlife, including hippo (Anonymous, 2007), (c) communities collect a 50% share from all hunting revenues, and also receive 50% of the meat from trophy hunting. Additionally, local communities in the Luangwa Valley avoid eating hippo meat as they traditionally believe that it causes leprosy. Therefore, hippos sold on safari is considered to be of more economic value, (d) hippo is classified in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Flora and Fauna) which requires a permit in order to export any hippo specimen, which makes it difficult for teeth from poached specimens to enter the international market, and (e) the area along the Luangwa River is the most patrolled area in South Luangwa National Park (Anonymous, 2008), which, when combined with community involvement in lawenforcement may be a deterrent to poaching incursions. Poaching is therefore discounted from being a key factor regulating the Luangwa hippo population.

Conclusion

This study has established that along the 165 km stretch of the Luangwa River, Zambia, the amount of food produced (grass biomass) regulated hippo population size within the carrying capacity band, while river geomorphologic features influenced patterns of density distribution. More specifically:

a) The hippo population reached carrying capacity *K* at 6,000 individuals and remained within the Carrying Capacity Band of 2,000 individuals for the period 1976-2008.
b) The amount of food (biomass) influenced the population size and density within the carrying capacity band.
c) Culling, trophy hunting, problem animal control, poaching, and disease, did not significantly affect population size and density.
d) River geomorphologic features influenced density distribution, with areas with more geomorphologic features having higher hippo densities and carrying capacity.
e) Security was not a significant factor influencing population density distribution.

ACKNOWLEDGEMENTS

I wish to thank the Regional Manager Mr. Mathews Mushimbalume, Mr. Jarton Shawa research technician, Mrs Priscilla Sichone Mukanga the area ecologist and all the research assistants at South Luangwa Area Management Unit in Mfuwe for their commitment and support throughout this study. Mr. George Muwowo of the WWF (World Wide Fund for Nature) country office facilitated acquisition of funds for this research from the Prince Bernard Scholarship. Mr.Chaka Harold Kaumba prepared all the maps and I am indebted to him.

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