

GLOBAL JOURNAL OF BIOLOGY, AGRICULTURE & HEALTH SCIENCES

(Published By: Global Institute for Research & Education)

www.gifre.org

Does Mortality Impact Negatively on Hippopotamus (*Hippopotamus amphibius*) Population Size and Density in Luangwa River, Zambia? A Historic Perspective

Chansa Chomba

School of Agriculture and Natural Resources, Disaster Management Training Centre, Mulungushi University, P. O. Box 80415, Kabwe, Zambia. chansachomba@rocketmail.com

Abstract

Influence of mortality on hippopotamus (*Hippopotamus amphibius*) population size and density in the Luangwa River, Zambia was assessed. Mortality factors considered were culling, trophy hunting, control, disease (anthrax), poaching and natural mortality. Number of hippos killed were collected from Zambia Wildlife Authority (ZAWA) records, Department of Veterinary and Livestock Services (DVLD) and field observations during this study. Analysis of data showed that hippos killed through different forms of mortality were 2,674 (mean 429) varying significantly from year to year, being higher in some years and lower in others. Hippos killed by each of the six mortality factors also varied significantly, with some mortality factors killing more hippos than others. Student New Man's – Keuls Test (SNK) showed that a combination of culling and disease killed more hippos (95%) than the other four mortality factors combined. Culling killed (63 percent), disease (32 percent) and the remaining four (4) mortality factors killed only 5 percent. However, the number of hippos killed through all six mortality factors combined was still too low and insignificant to negatively impact on hippopotamus population density over the same period. Population density appeared not to be negatively affected by mortality as density did not fluctuate significantly in response to the number of animals dying. It was concluded that mortality was not an important factor in reducing the Luangwa hippopotamus population density. More studies are required to identify key factors affecting population density.

Keywords: Mortality, culling, disease, density, poaching, assessment

1. Introduction

The impact of mortality on the hippopotamus density in the Luangwa valley has not been assessed. Jackmann (1994), for instance acknowledged the large number of hippopotamus that were killed by anthrax in 1987 which he related to drought and nutritional stress. He noted that during the dry season particularly in very dry years, hippos died as a consequence of nutritional stress due to forage shortage. Anthrax outbreaks were also recorded during very dry years when hippos over grazed and in the process pulling out grass roots which exposed anthrax spores that were subsequently inhaled by the hippos (Kajuni pers. comm. 2007). As a consequence of the large number of hippos killed by anthrax in 1987, it was assumed that mortality had a negative impact on hippopotamus density although no comprehensive analysis of such impact had been made to evaluate the effect of mortality on hippopotamus population density in the Luangwa Valley.

Historical data on the Luangwa hippopotamus population including that by Marshall and Sayer (1976) showed that poaching was the main factor that caused population decline in the late 1800s and early 1900s. In Luangwa valley, hippopotamus population increased greatly since 1939 after poaching was put under control and no disease incidences were mentioned as a major factor at that time (Attwell, 1963). A rinderpest epidemic however, occurred in the area at the beginning of the 1900s but there are no records to show that hippos were negatively affected (Pitman, 1931). Plowright, Laws and Rampton (1964), thought hippopotamus was susceptible to disease but Ford (1971) suggested it to be relatively immune. It was therefore, not clear whether mortality had a negative impact on the Luangwa hippopotamus population density or not. This study was therefore, designed to assess the influence of mortality on hippopotamus density, as it was hoped that such information would assist Zambia Wildlife Authority (ZAWA) (Now Department of National Parks and Wildlife – DNPW) in determining sustainable trophy hunting and culling quotas.

2. Materials and Methods

2.1Study area Location and Description

The location of the study area is the Luangwa Valley in eastern Zambia (Figure 1). The area currently holds the largest global hippopotamus population (Lewison, 2007; Chomba et al. 2013) and was found suitable for this

study. The study covered incidences of mortality on hippopotamus population along the 165 km stretch of the Luangwa River and the associated riverine habitat from the Chibembe pontoon (12° 48' S, 32° 03'E) to the Luangwa confluence (13° 24' S, 31° 33' E).

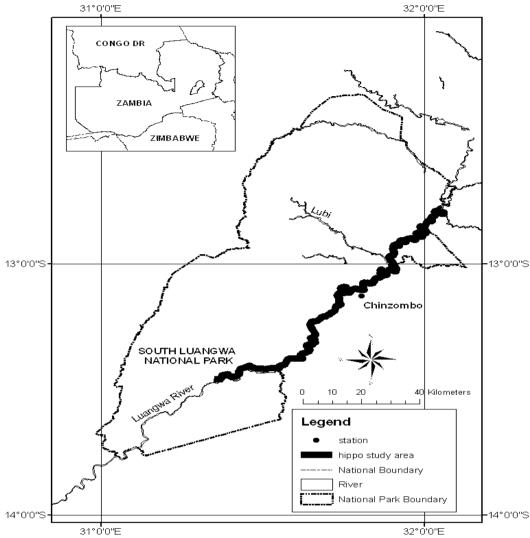


Figure 1: Location of the hippopotamus study in Luangwa Valley, Zambia.

2.2 Climate

The annual rainfall range from 400 - 800mm and minimum and maximum temperatures are 10° C (June - July) and 38° C (October) respectively. The hot rainy season is from late November to April, a cool dry season is from May to August, and a hot dry season from September to early November.

2.3 Data on Hippopotamus Mortality

Data on the number of hippopotamus killed through trophy hunting, control, poaching, disease and those dying from natural mortality were obtained from the records at ZAWA regional headquarters at Mfuwe. During the period 2005 - 2008 the research team during this study recorded numbers of hippopotamus dying from the six forms of mortality on data forms. Data on the number of hippopotamus dying from anthrax which was collected from ZAWA was verified by comparing with information from the Department of Veterinary and Livestock Development (DVLD) headquarters in Lusaka. At DVLD, information on disease out breaks and the number of animals dying from disease are recorded and stored in a data base. A summary table showing the number of hippos killed was developed. From this table it was easy to match and compare the number of animals dying from each mortality factor and hippopotamus density.

3. Results

3.1Mortality factors

The number of hippos killed by six mortality factors, poaching, control, trophy hunting, natural mortality, disease and culling varied significantly from year to year ($\chi^2 = 37, 205.87, DF = 21, \alpha = 0.05, P < 0.05$), being higher in some years and lower in others (Table 1).

Table 1: Numbers of hippopotami lost through culling, control, natural mortality, poaching, hunting and disease, Luangwa Valley, Zambia. Note: * represents hunting moratorium

No.	Hunt	Poach	Control	Disease	Culling	Natural mortality	Total
1	13	2	2	324	0	15	357
2	9	1	1	0	0	0	14
3	7	2	4	0	0	0	11
4	11	0	0	0	0	9	23
5	8	4	0	0	0	0	17
6	11	1	1	0	0	0	14
7	9	2	4	0	0	2	15
8	8	2	2	0	0	5	15
9	15	2	4	0	507	3	530
10	10	4	5	0	234	0	252
11	9	3	8	0	0	0	17
12	12	9	3	0	386	0	402
13	8	1	5	0	352	0	370
14	*	0	1	0	0	0	2
15	*	2	0	0	0	7	7
16	*	1	2	0	0	0	2
17	8	5	1	0	0	5	14
18	12	0	3	0	0	11	28
19	10	1	0	0	250	0	265
20	12	7		6	0	0	37
21	15	1	3	0	18	3	41
22	10	1	1	71	157	0	241
Mean	10.36	2.75	2.55	133.66	272	6.66	122
SE	2.3	2.2	1.9	5.3	160.4	4	

The total number of hippos killed during the period 1987- 2008 was 2,674 (mean 429). Single factor ANOVA (sensu Fowler et al. 1998) showed significant differences in the number of hippos killed by each mortality factor (Fo = 0.05 (1) 5, 73 = 3.76; P<<0.005). Further analysis of the data using Student NewMan's - Keuls Test (SNK) (sensu Fowler et al. 1998) showed that culling and disease took more individuals (95%) than the other four mortality factors combined (Table 2). Thus culling took (63 percent) and disease (32 percent) and the remaining four (4) mortality factors killed 5 percent (Figure 2).

Table 2: 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.

Parametre	Mortality category							
	Hunting	Poaching	Control	Natural mortality	Disease	Culling		
Mean	10.36	2.78	3.47	6.66	133.66	272		
Conclusion	Took the smallest number				Took the largest number			

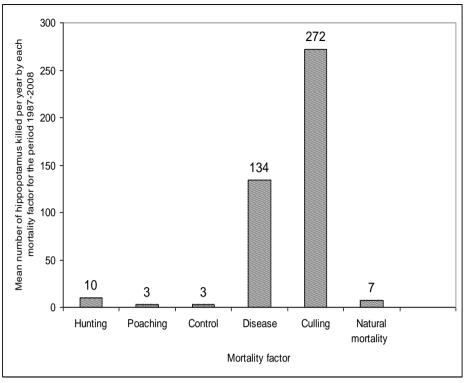


Figure 2: Mean number lost through each of the six mortality factors, Luangwa Valley, Zambia.

The number of hippos lost through mortality were too low and insignificant to negatively impact on population density. A variance Ratio F Test showed a significant difference between variances of population density and hippos killed (Fo = 0.05 (1) 5, 73 = 3.76; P<<0.005), implying that the mortality factors did not have a significant influence on the population size and density.

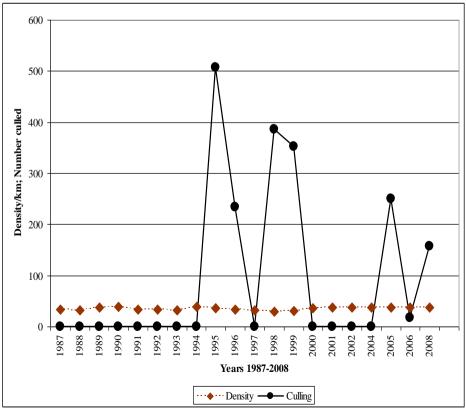


Figure 3: Impact of culling on hippopotamus population density, Luangwa Valley, Zambia.

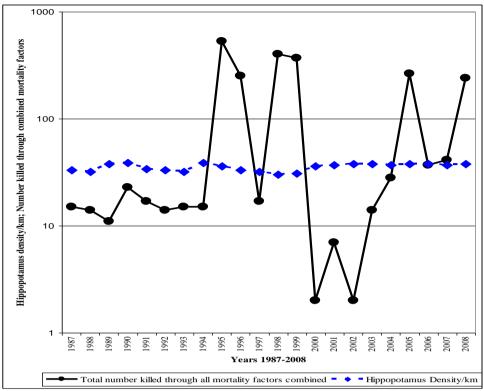


Figure 4: Impact of combined mortality on hippopotamus density 1987-2008, Luangwa Valley, Zambia

Hippopotamus population density appeared not to be affected by mortality as density did not fluctuate significantly in response to the number of hippos dying (Figure 3 and Figure 4). Hippopotamus population density remained relatively stable over the period 1987 - 2008 varying only between 30 - 38 individuals /km which was insignificant ($\chi^2 = 11.50$, DF= 31, $\alpha = 0.05$, P > 0.05), (Figure 3; Figure 4; Table 1), suggesting that mortality alone had no significant influence on hippopotamus population size and density.

4. Discussion

4.1Mortality Factors

Mortality did not have a significant impact on the population size of the hippopotamus. Culling and disease however, did take the largest number among all the six mortality factors investigated.

Loss of individuals due to disease was attributed to the poor nutritional status of the range resulting into poor body condition of the individuals particularly in the last quarter of the year (October - December) making them vulnerable to disease. Animals in poor condition have low resistance to disease (Caughley and Gunn, 1996). Anthrax outbreaks therefore, took advantage of the already weakened individuals. Human induced mortality such as poaching, control, and trophy hunting were insignificant. Predation was also insignificant mainly due to the size of the animal. Lion which is the largest predator in the Luangwa valley was reported by Jachmann (1996) to prefer buffalo, zebra and antelope species. Predation of hippopotamus by lion was rare and usually confined to years of drought when there were intra-specific fights as noted by Attwell (1963) who noted that during the 1958 drought for instance, adult males in particular were in poor body condition and ran away from dominant males after being wounded wandering great distances (exceeding 5 km) looking for food. Others died of wounds and were later eaten by either crocodile or lion (Attwell, 1963).

4.1.1 Culling

The culling quotas set by ZAWA in the previous culling programmes (Table 1) including the 2005 – 2011 were low. This was also earlier reported by Child (1999), that the problem of over population of the common hippopotamus population in the Luangwa valley since the 1960s had remained unabated as culling had no significant reduction of the population. The mean number culled per year in the last 32 years was not high enough to negatively affect the hippopotamus annual population change (Figure 3; Figure 4 and Figure 5). The very fact that there has been no recovery of the riverine vegetation implies that the number of hippopotamus removed since the mid 1960s has had no impact on the total hippopotamus population size and density (Child, 1999).

Caughley and Sinclair (1994) also noted that if the density of a population is lowered by control measures, the standing crop of renewable resources such as grass needed by any herbivore will increase because of the lowered use. Non-renewable resources such as wallowing or resting pools for instance will be easier for an individual to

find. Population reduction programmes such as control or culling, increases the resources available to the survivors of the operation. Their fecundity and their survival in the face of other mortality agents, is thereby enhanced (Caughley and Sinclair, 1994). The reduced density therefore, generates a potential increase, which become manifest if the control or harvesting is terminated as also recorded in Mweya peninsula in Uganda by Eltringham (1970) and response to culling in the Luangwa in the 1990s. The enhanced demographic vigour following reduction in density is a desirable outcome of a harvesting operation, and in fact the success of the harvesting is determined by such an effect. The further density is reduced the more the population seeks to increase. Thus control in the sense of enforcing a permanently lowered density, is simply a sustained yield operation that seldom utilizes the harvest. It is an attempt to drive a negative feedback loop in the opposite direction Caughley and Sinclair, (1994).

In culling the hippopotamus population of the Luangwa valley, this study reviewed the major objective as being mainly to prevent adverse habitat change. It was assumed that the major risk to the hippopotamus population in the Luangwa valley is habitat loss and food shortage, which contributes to drastic loss of body condition in the dry season. Poor body condition predisposes the species to environmental stress such as disease as experienced in the anthrax outbreak of 1987 and others (Table 1). High levels of hippopotamus population if not regulated may lead to environmental degradation and population crash as was observed in reindeer on St' Mathews Island by Klein (1968). Additionally, Lewison (2007) provided a useful model by measuring the impact of disturbances on the model hippopotamus population as the proportion of simulation runs in which the population dropped below one of the three-risk thresholds. Across the entire simulation time, habitat loss alone yielded the largest likelihood of crossing the population risk thresholds, although even the largest probabilities of decline for disturbance were low (P< 0.31).

To demonstrate that mortality had no impact on the population size in the period 1976 - 2011, it is important to look at the historical recovery of the population from excessive hunting and poaching in the late 1800s. The common hippopotamus population of the Luangwa valley experienced a sudden and dramatic increase from the low hundreds in the 1800s. At that time mortality through excessive hunting and poaching by the Portuguese explorers and local hunters respectively reduced the population to near extinction by the end of the 1800s (Attwell, 1963). However, the population managed to recover because the habitat was in good condition, implying that all habitat welfare factors such as food, wallowing and resting places were optimal to support the greatest growth rate possible. The population grew rapidly until the late 1970s, when the food base slowly became a limiting factor due to increased population size. Since the mid 1970s the habitat in the Luangwa Valley has been under stress and at great risk of degradation (Child, 1999). For instance, the thick *Phragmites, Ficus, Trichilia* and *Diospyros* riverine species reported by Darling (1960) no longer exist particularly in the northern sector of the study area. If this trend continued with no ameliorative measures taken, habitat degradation would lead to modification of the geomorphology of the Luangwa River through increased siltation and widening of the river channel as reported by Sichingabula (1998). This is because hippopotamus is known to significantly influence habitat structure including river geomorphology as reflected acknowledged by Naiman and Rogers (1997).

Culling therefore, should be considered as a management tool in the Luangwa Valley as was first determined during the culling of the 1970s and found to be stimulating hippopotamus population growth. In the culling of the 1970s, it was found that after the first culling scheme, 66 percent of the females were lactating.

During the 1970-1972 culling programme, calving rate for Luangwa hippopotamus was derived from the percentage of adult females lactating which was 66 %, almost double the pregnancy rate in the adult females examined previously during the first culling. It was noted that having a calving rate of 66 % was a consequence of freed food resources by removing some individuals through culling. Laws and Clough (1965) also found an increased annual calving rate of 50 percent after culling for Queen Elizabeth National Park. Culling was also reported to remove excess males which shifted the sex ratio from near parity to a ratio which was in favour of females (Laws and Clough, 1965; Bere, 1959; Pienaar et al. 1966). It was the biased sex ratio in favour of females that promoted increased recruitment after culling. Studies on the impact of culling on hippopotamus population in the Luangwa valley by Marshall and Sayer (1976) found a rate of increase of 4.3 percent per annum, which was derived from data for the Nsefu area (blocks A- C: Figure 1) where annual counts were carried out from 1953 to 1966, which later increased to 5.8 percent after culling. The mean age of puberty for females also declined leading to more prevalences of pregnancy and increased births after culling (Sayer and Rhaka, 1974).

This evidence therefore suggests that culling stimulates population growth rather than depress it. In this study, lower levels of increase were obtained in the 2005 - 2011 culling programme indicating that the culling quota was low and did not affect hippopotamus density.

The results obtained in this study which confirmed that mortality does not negatively affect hippopotamus population growth, implies that it would be possible to crop several hundred hippos a year in the Luangwa valley without reducing the density of the population (Figure 3; Figure 4; Figure 5). Such a takeoff could be accommodated within the subsisting hippopotamus density of 38/km. Heavier culling would result eventually in an increase in calf production through decrease in calving interval and age in puberty. There was an indication that the latter occurred during the earlier study in the 1970s by Marshall and Sayer (1976) when 5 percent of females in the seven to eleven year age group were pregnant in 1970 and 20 percent in 1971. These data may, however resulted from the marked difference in rainfall that occurred in the two years; the rainfall in 1970 –1971 was double that of 1969 – 1970. This

probably improved conditions for grazing animals during the 1971 conception season, although the effect of culling was also not ruled out.

Similar results were obtained in the 2005 – 2008/2011 culling seasons in which culling produced schools that had a higher ratio of females. It is therefore, advisable to cull hippopotamus to free food resources. Such reduction of population below K will stimulate population increase and reduce calving interval and lower calving age at puberty. The culling of hippopotamus also causes fewer conflicts with other wildlife utilization programmes because of their restricted distribution along the river. It is also possible to cull hippopotamus on an economic scale with minimum conflict with other recreation uses. However, massive population reduction as a vegetation conservation measure requires further investigation as stated earlier in order to know how much such a reduction of individuals through culling would affect the population of other grazing animals and thus the total grazing pressure. So far, culling, of hippopotamus in the Luangwa valley has been based on an economic justification, that since the common hippopotamus is a huge animal with a relatively short gestation period of about eight months, its potential for reproductive increase is high such that culling could be operated sustainably in those areas where densities are high and posing a threat to the integrity of the habitat and conservation of biodiversity in general. No monitoring systems have been set to monitor the impact of culling on the habitat and other species. It is important that before culling is conducted in future, parametres are set to assess the impact of culling on the habitat. Such parametres could be for instance recovery of species that are suspected to be negatively affected by the hippopotamus as the case was in Mweya Peninsula in Uganda of recovery of pastures (Eltringahm, 1996) and for the Lungwa valley as reported by Child (1999). The culling should not just be seen in terms of numbers and how much money can be realized from that operation but rather ecological benefits arising from such an operation. This has not been the case in the Luangwa valley, despite the over grazing incidences recorded in the area. Child (1999), also noted that no attempt had been made to match the numbers of hippopotami removed with the change in selected ecological parametres. These observations concur with that of Caughley and Sinclair (1994) who documented that more than the other two areas of wildlife management, conservation and sustained yield harvesting, culling is often flawed by lack of appropriate and clearly stated objectives. They noted that control in contrast to conservation and sustained yield harvesting is not itself an objective. It is simply a management action. It's use must be legitimised by a technical objective(s) such as increasing the density of a food plant of a particular species of bird, or mammal say, from 1/ha to 3/ha.

The control operations would therefore be aimed at a herbivore for which that plant was a preferred food. The success of the operation would be measured by the density of plants, not by the density of the herbivore or by the number of herbivores killed. Culling campaigns in many countries including the hippopotamus culling in the Luangwa valley, share a common characteristic. Very often the original reason for the management action is forgotten and the culling itself (lowering density) becomes the objective. The means become the end. Caughley and Sinclair (1994) gave an example from New Zealand which is probably one of the largest and longest running culling operations against vertebrates in the world. The programme started in 1920 and has continued to date (Caughley and Sinclair, 1994).

Caughley and Sinclair (1994) noted that where as the stated justification for the culling operations changed with time, those changes had virtually no effect on the management action. There were certainly changes in control techniques but, with the exception of the change in 1967, these were evolutionary adjustments in the management action itself. They were not driven by changes in policy. The means themselves were the end. Up until 1980, the reasons given for culling operations were that deer and other species caused erosion of the higher slopes and silting of lower rivers. However, in 1978, new meteorological, hydrologic, geomorphologic and stratigraphic research showed that deer, chamois (*Raupicara rupicara*) and thar (*Hemitragus jemlahicus*) had little or no effect on the rate at which river bends silted up or on the frequency and size of floods. Despite these data, deer culling continued after 1980 for no verifiable reasons. All that changed were the stated objectives which were variously for 'aesthetics' for 'proper land use' to ensure the 'continuing health of the forest', to 'protect intrinsic values' and to 'maintain the distinctive New Zealand character of the landscape'. But these reasons given by management were not open to scientific testing. Similarly in the Luangwa valley, the original objective for culling has often been forsaken at the expense of profits. This study therefore provided an opportunity for the management to set parametres that would be tested and monitored as culling progresses.

4.1.2 Disease

Where hippopotamus densities are high, such as in the Luangwa valley, their trampling and over utilization of grazing areas can cause soil erosion and control measures to reduce the numbers may be necessary (Child, 1999). Such conditions if left unchecked could lead to conditions of self-destruction through reduced food production (Child, 1999). Reduced food production leads to poor body condition, which makes the animals susceptible to disease. Disease therefore, comes in as a secondary factor in causing death. The high population density above *K* for a continuous period of time reduces the food base and causes loss of body condition which ultimately reduces the hippopotamus' resistance to environmental stress including disease.

Previous studies indicate that the main causes of hippopotamus mortalities were based on food supply (Attwell, 1963; Tembo, 1987; Child, 1999). Bere (1959) asserted that there was no known record of disease having

influenced hippopotamus populations in the Luangwa valley or else where in Zambia or sub Saharan Africa. Anthrax although recorded from hippopotamus in Luangwa valley and Uganda has not apparently proved to be a significant controller (Bere, 1959). Prins and Weyerhaeuser (1987) equally noted that anthrax epidemics in the Manyara and Serengeti ecosystems killed numbers of impala, while pneumonia killed elephants and rinderpest many buffalo in 1959 but not hippo. Such findings are consistent with the effect of anthrax on hippopotamus in the Luangwa valley, particularly after the anthrax out break of 1987 where recovery was almost immediate after a loss of more than 500 individuals. Other causes and not disease such as reduced food base and poaching if the area is not adequately protected like the one which occurred in the Luangwa valley in the 1800s, are more important than disease alone. Furthermore, the historical pattern of persecution described for Luangwa valley in the 1800 s and early 1900s also best describes the scenario for the Zambezi and Kafue Rivers. Pitman (1934) quotes informants as saying that both rivers contained 'very many' including schools of thirty and forty as recently as 1910, but by 1914 hippopotami there were only in twos and threes with the exception of certain places. The authors' count over part of the middle Zambezi and other counts from the Kafue river however, reflect considerably lower densities than in the Luangwa, despite the fact that the section of Kafue where the counts were done had had complete protection for many years being contained within the Kafue National Park (gazetted in 1950), and for many years before that being in the former Kafue Game Reserve. Isolated observations from other parts of the territory outside Game Reserves indicated that despite official protection, the species was diminishing. Pitman (1934) concluded that when analyzing the results and comparing them with the Luangwa valley counts, there were factors other than disease and hunting pressures to be considered, for instance the habitats themselves clearly must largely determine carrying capacity not the impact of disease.

This was also exemplified in the differences in population density between the upper and lower study blocks of the Luangwa valley. Studies conducted by Lock (1969) in Queen Elizabeth National Park and those by Attwell (1963) in the Luangwa valley, suggested that early burning appeared to induce more traveling for feeding purposes which increased stress on the animals which also exposed them to predation. In Kafue National Park for instance, hippos were concentrated in pools near available food, and ten animals were found dead in 1970 either killed by lion or intraspecific fights (Marshall and Sayer, 1976). Indeed the loss of food supplies due to man induced fire regimes at the critical time of the year might in it be a major factor in controlling density and not disease *per se*, (Mashall and Sayer, 1976). Vast areas of grassy plains in many areas of Zambia are fired and pasture denied to the species when it is most required. Loss of pasture to fire reduces the food base for the species and reduces its body resistance to environmental stress. Under such circumstances, disease comes in as a secondary factor, taking advantage of the nutritionally deprived individuals (Marshall and Sayer, 1976).

4.1.3 Predation

Regarding predation, it was assumed that on account of body size, the hippopotamus seemed not to have natural predators although lion is reported to take some individuals particularly calves and old or injured individuals (Jachmann, 1996). Studies by Jachmann (1996) showed that lions in the Luangwa valley appear to prefer buffalo, zebra and antelope species.

The use of sand bars usually surrounded by water as a nursery area for calves as was observed during the present study which also prevents lions from gaining access to the calves. Since the river has crocodile, it becomes dangerous for lion in many instances to wade through water in order to gain access to hippopotamus calves. When the calves are on a sand bar which is not surrounded by water, they are usually accompanied by adults for protection. It is on this account that it was assumed that predation and natural mortality were insignificant mortality factors on hippopotamus size and density.

It was concluded that mortality factors such as culling therefore, only serve as a useful management tool to secure the long-term survival of the common hippopotamus in the Luangwa valley and conservation of biodiversity and would not negatively affect the hippopotamus population growth rate as previously thought.

References

Astel, W.L. Phiri, P.S.M. and Prince, S.D. (1997). A dictionary of vernacular-scientific names of plants of the mid-Luangwa Valley. *Kirkia*, 6, pp 161 - 203.

Astel, W.L. Webster, R. and Lawrence, C.J. (1969). Land classification for management planning in the Luangwa Valley of Zambia. *Journal of Applied Ecology*, 6, pp 143 - 169.

Attwell, R.I.G. (1963). Surveying Luangwa hippo. Puku 1, pp 29 - 49.

Bell, R.H.V. (1986). Carrying capacity and off take quotas, in: BELL, R.H.V. and McShane-Caluzi, E. (eds) Conservation and Wildlife Management in Africa. U.S. Peace Corps, Washington, D.C.

Bourliere, F. and Verschuren, J. (1960). Introduction on the ecology of ungulates in Albert National Park. Congo Belgium, Brussels.

Chapman, J.L. and Reiss, M.J. (1999). Ecology, principles and applications. Cambridge University Press.

Chomba, C. Simpamba, T. and Nyirenda, V. (2013). Has the Luangwa (Zambia) hippopotamus (*Hippopotamus amphibius*) population stabilized after reaching its asymptote? What are the management implications? *Open Journal of Ecology* 3 (6), pp 395 – 406.

Darling, F.F. (1960). Wildlife in African territory. Oxford University Press, London.

Fanshawe, D.B. (1971). The vegetation of Zambia. Forest Bulletin. No. 7. Government Printer, Lusaka.

Finerty, J.P. (1980). The population ecology of cycles of small mammals. New Haven, Yale University Press.

FAO. (1973). Luangwa Valley Conservation and Development Project. Working Document No. I Game Management and Habitat. Manipulation. FO: DP/ZAM/68/510. F.A.O. Rome.

James, E. (2007). The influence of elephant ivory trade ban on population of common hippopotamus (*Hippopotamus amphibius*), a case study of Katavi-Rukwa-Lukwati ecosystem, Tanzania, MSc. thesis, University of Dar es Salaam, Dar es Salaam.

Klein, D.R. (1968). The introduction, increase, and crash of reindeer on St. Mathew island. *Journal of Wildlife Management*, 32, 350 - 367.

Lawton, R.M. (1964). The ecology of *Marquesia acuminata* (Gilg.) R.E. Fr. Evergreen forests and related chipya vegetation types of North-eastern Rhodesia. *Journal of Ecology*, 66, pp 467 - 479.

Lawton, R.M. (1978). A study of the dynamic ecology of Zambia vegetation. Journal of Ecology, 66, pp 175 - 198.

Lane -Poole, E.H. (1956). The Luangwa Valley. Northern Rhodesia Journal, 3, pp 154 - 163.

Lewison, R. (2007). Population responses to natural and human-mediated disturbances: assessing the vulnerability of the common hippopotamus (*Hippopotamus* amphibius), *African Journal of Ecology*, 45, pp 407-415.

Marshall, P.J. and Sayer, J.A. (1976). Population ecology and response of a hippopotamus population in eastern Zambia. *The Journal of Applied Ecology*, 13, pp 391-403.

Mduma, S.A.R. Sinclair, A.R.E. and Hilborn, R., (1999). Food regulates the Serengeti Wildebeest: a 40 year record, *Journal of Animal Ecology*, 68, pp 1101 - 1122.

Mentis, M.T.and Duke, R.R. (1976). Carrying Capacity of Natural veld in Natal for Large wild herbivores. *South Africa Journal of Wildlife Research*, 7, pp 89 - 98.

Mentis, M.T. (1977). Stocking rates and carrying capacity for ungulates on African Rangelands. South African Journal of Wildlife Research, 9, 90 - 98.

Michelmore, A.P.G. (1939). Observations on tropical African grasslands. Journal of Ecology, 27, 282 - 312.

Phiri, P.S.M. (1994). The relevance of plant taxonomic information for the conservation of the low altitude Luangwa Valley ecosystem in Zambia in: Seyani, J.H. and Chikuni A.C. (eds) Proc. XIII Plenary Meeting, Malawi, 2, 903 - 910.

Phiri, P.S.M. (1998). The vegetation types of the South Luangwa National Park and the surrounding Game Management Areas. National Parks and Wildlife Service, Chilanga.

Prince, S.D. (1971). A quantitative description of some mopane woodlands in the Luangwa Valley. Game Dept., Ministry of Lands and Natural Resources, Republic of Zambia, Lusaka.

Sayer, J.A. and Rhaka, A.M. (1974). The age of puberty in the hippopotamus (*Hippopotamus amphibius*) in the Luangwa River in eastern Zambia. *East African Wildlife Journal*, 12, 227 - 232.

Sichingabula, H. (1998). Hydrology, character of channel changes on Luangwa River, their impacts and implications on tourism, South Luangwa National Park and adjacent Game Management Areas. Report prepared for EDF/NPWS towards the development of a General Management Plan for South Luangwa National Park and adjacent Game Management Areas, Chilanga.

Sinclair, A.R.E. and Grimsdell, J.J.R. (1982). Population dynamics of large mammals. African Wildlife Foundation, Nairobi.

Vesey - Fitzgerald, D.F. (1963). Central African grasslands. Journal of Ecology, 51, 243 - 274.

Weger, M.J.A. and Coetzee, B.J. (1978). The Sudano - Zambesian Region in: WEGER, M.J.A Biogeography and Ecology of Southern Africa, The Hague.

White, F. (1962). Forest Flora of Northern Rhodesia. Oxford University Press. London.

White, F. (1983). The Vegetation of Africa. UNESCO.