The Ecology and Behaviour of the Common hippopotamus, *Hippopotamus amphibious* L. in Katavi National Park, Tanzania: Responses to Varying Water Resources

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Abstract

Katavi National Park (KNP) is a stronghold for hippopotami in Tanzania. To predict the probable effects of future changes in water availability, annual variations in rainfall, river level, river discharge, ground water levels and the lateral extent of swamps used by hippopotami, were related to annual variations in their behaviour, distribution and abundance in aquatic shelter sites.

Rainfall did not change consistently between 1950 and 2010. In contrast river levels and flow decreased over between 1990 and 2010. It is concluded that these reductions have been caused by an increase in irrigation of rice fields increasingly planted in upstream regions of the catchment area.

Rainfall fell in a pronounced annual cycle. The wet season started in December, increased in January, decreased in February reaching an annual peak in March. The dry season lasted from May to November. Variation in height, biomass and greenness of ground layer swards used by feeding hippopotami, closely mirror this annual pattern of rainfall.

As the dry season progresses hippopotami become increasingly aggregated in remaining aquatic shelter sites by day, to wallow and thermoregulate with concomitant depletion of the nocturnal feeding grounds close to remaining shelter sites.

Five observation sites were chosen, representing a gradient in the amount of water persisting through the dry season. Hippopotami showed spatial differences in their activity budgets and the frequency of behavioural events at these sites, which were consistent with the way they responded to variation in water availability between seasons.

Extrapolating these findings to predict responses to future changes in global climate and land use, I conclude consistent implementation of existing national laws governing diversion of water from rivers up-stream of the park will be crucial for maintaining vigorous populations of hippopotami in KNP. Similar problems of a catchment area scale occur in other National Parks in Africa.

Table of contents

Chapter 1: Introduction

2.0 Relevance of the study

Chapter 2: Study species and study sites

1. Target species

2. Study area

Chapter 3: Rainfall, river flow, discharge and soil saturation

2. Methods

3. Results

4. Discussion

Chapter 4: Hippopotami food resources

2. Methods

3. Results

4. Discussion

Chapter 5: Hippopotami abundance, immigration and emigration

Chapter 6: Spatial and temporal variations in behavioural activities

Chapter 7: Spatial and temporal variations in behavioural events

2. Methods

3. Results

4. Discussion

Chapter 8: Relationship between hippopotami, food and water resources

2. Methods

3. Results

4. Discussion

List of Tables

List of Figures

List of Plates

List of Appendix Chapter

List of Appendix Tables

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Chapter 1: Introduction

The Ecology and Behaviour of the common hippopotamus, *Hippopotamus amphibious* L. in Katavi National Park, Tanzania: Responses to varying water resources.

1.0 Introduction

1.1 Background to the study

A key reason for failure of mankind to find comparable life on another planetary system is that water in an aquatic phase appears to be extremely rare elsewhere in the universe. The existence of liquid water is essential for at least some stages of all forms of life as we know them here on earth. However the distribution of water on this planet is currently changing at an unprecedented rate as one of the consequences of anthropogenically induced climate change. Predicting how global changes in patterns and dynamics of the distribution of water will affect the ecology of living organisms is a major preoccupation in science today but cannot be considered in isolation because it is being accompanied by and in some cases, is driving major changes in land use. These are also impacting on the ecology of the biosphere. In this thesis I investigate impacts on the behaviour and ecology of one of the charismatic members of the mega-fauna: the hippopotamus, using a model population in Katavi National Park in Tanzania, East Africa.

Ecology is the scientific study of the distribution and abundance of organisms and the interactions that determine it (Begon *et al.*, 2006) modified from Krebs (1972) who defined ecology as the scientific study of the interactions that determine the distribution and abundance of organisms. This was a development of the definition given by Ernest Haeckel in 1869 quoted by Begon *et al.* (2006) that ecology is the scientific study of the interactions between organisms and their environment. The final goal of ecology is the understanding of the distribution, abundance and diversity of organisms.

Behavioural ecology or ethoecology is the study of the ecological and evolutionary basis for animal behaviour and the roles of behaviour in enabling an animal to adapt both internal (intrinsic) conditions and external (extrinsic) environment (McFarland, 2006; Martin and Bateson, 2007).

Behavioural ecology is concerned with functional questions about behaviour, especially how particular behavioural patterns contribute to the survival and reproductive success of an animal (Krebs and Davies, 1993). It is also concerned with the evolution of adaptive behaviour in relation to ecological circumstances (Krebs and Davies, 1993).

The challenges of ecology include developing an understanding of basic and applied problems (Begon *et al*., 2006), which may be unique and complex due to the variety of species of genetically distinct individuals, all living and interacting in changing ecosystems.

Among the current causes for changes to ecosystems are climate changes and land transformation due to human activities (Thuiller *et al*., 2006). Climate change is leading to temperature rise, sea level rise and unpredictable and extreme variations in precipitation leading to drought and flooding (IPCC, 2001a; 2001b). Such environmental problems have ecological impacts (Begon *et al*., 2006).

One animal species likely to be highly affected by changes in water flow is the hippopotamus because it is semi aquatic. Existing knowledge on hippopotamus behaviour and ecology is still inadequate despite their wide distribution in Africa and their interactions with humans (Dudley, 1998). A problem of water scarcity in their remaining habitats necessitates further understanding of their ecology and behaviour. Trends in water and environmental destruction are unlikely to be reversed (Lewison & Oliver, 2008) so their effects on wildlife are likely to be persistent.

Studying how hippopotami respond to the challenge of changing water flow will help to increase our understanding of ecological consequences of hydrological challenges. Little systematic study with regard to how the behaviour of a hippopotamus changes in response to the problem of water scarcity has been made. Population responses include variations in distribution and abundance, emigration and immigration, while behavioural responses may include changes in maintenance, social, sexual and aggressive behaviours.

All animals need to absorb water, either in liquid form or derived from their food. They require it for ionic regulation, to maintain osmotic homeostasis and some animals also use it to achieve evaporative cooling as part of their thermoregulatory strategies. One large mammal that relies on submerging in water for convective cooling is the common hippopotamus, *Hippopotamus amphibious* L. Changes in water availability are likely to significantly impact this species. In addition to the direct effects of water on the physiology of hippopotami, driving behaviours with strong implications for their ecology, there are also indirect effects of water availability due to rainfall determining the quality and quantity of food available. This leads to a behavioural trade-off resulting from selection pressures to optimise both sheltering and grazing. During the dry season there is a strong selective pressure to occupy a declining number of aquatic shelter sites which results in large numbers of hippopotami aggregating in fewer sites. As hippopotami are central place foragers, this leads to faster depletion of feeding sites close to the shelter which can, in extreme cases, lead to death by starvation (Mduma *et al.,* 1999; Sinclair *et al*., 2000); increased infanticide (Lewison, 1998) and increased disease transmission (Attwell, 1963; Marshall & Sayer, 1976; Turnbull *et al*., 1991, Lembo *et al*., 2011). Understanding the effects of changes in land and water use elsewhere in the catchment is essential to informed planning of Katavi National Park policy in the immediate future. To formulate long-term management strategies it is also essential to consider predictions of future changes in climate in East Africa region and how such changes might combine synergistically or detrimentally with the results of land use changes.

Existing knowledge on hippopotamus behaviour and ecology is inadequate despite their wide distribution in Africa and interactions with humans (Dudley, 1998). Problems of water scarcity in their remaining habitats are most appropriately addressed by studying their ecology and behaviour which will further help to increase our understanding of wider ecological consequences of hydrological challenges. Population responses include variations in distribution and abundance, emigration and immigration, while behavioural responses may include changes in maintenance, social, sexual and aggressive behaviours. Few systematic studies focusing on behavioural changes of hippopotami in response to the problems of water scarcity have been made.

Hippopotami live in close association with water in lakes, rivers, streams and swamps (Dunstone & Gorman, 2007). Alterations to their environment due to agriculture, deforestation and enhanced or decreased water flow may therefore threaten their survival (Dunstone and Gorman, 2007) if their aquatic habitats become less suitable.

This study is on the behavioral ecology of the common hippopotamus in response to varying water resources, one of the environmental problems in Katavi National Park (NP), in south western Tanzania. It has been prompted by an increase in human impact around the Park and the anticipated climate change on the environment. Findings are intended to help prepare the park management to address the environmental problems related to water scarcity.

1.2 Study objectives

There have been noticeable changes in the eco-hydrology of Katavi NP in recent years. This study is concerned with declining water resources and their consequences for the behaviour and ecology of hippopotami. The study compares the behaviours of hippopotamus populations in five habitats within the Park with differing conditions of water availability and during different seasons of the year. Rainfall in the region is strongly seasonal.

A crucial question in ecology concerns the factors that cause fluctuation in species abundance (Begon *et al.*, 2006). Among the factors responsible is the availability of resources. In this study, the distribution and density of hippopotami is examined along a wetness gradient in Katavi National Park to quantify spatial and temporal variations in hippopotami density between and within study sites and whether these might be related to food resources. An additional aim is to examine whether or not the total hippopotami populations in Katavi NP have changed significantly over recent decades. Given the sensitivity of hippopotami to natural disturbances and human-mediated threats, hippopotami were considered a good model species in which to examine the effects of both natural and anthropogenic factors on population size and behavioural responses to varying water resources. The extent to which animals experiencing important changes in their environment can compensate for such changes by altering their behaviour is also considered.

1.3 Justification for the study.

Katavi National Park is fed by the perennial Katuma River, which over approximately the last 13 years has been subject to declining water flows leading to earlier drying of the river and its tributaries. Human use of water in the upper catchment of the river and above the boundary jurisdiction of the Park has affected the water resources and in 2004 led to serious water scarcity when the river stopped flowing in August. The flow has since recovered but human impact may still be resulting in water scarcity in the park.

Behavioural responses of hippopotami to water scarcity have not been studied in Katavi. Due to their high dependence on water, variations of water resources are predicted to affect their behaviour. Studying such effects was central to this work. The study therefore had the following objectives:

I. To infer from patchy records of rainfall and river flow, changes from 1990 in the annual amount of water entering Katavi NP.
II. To study spatial and temporal variation in vegetation community attributes in Katavi in relation to seasonal drying. Such attributes include ground vegetation cover, sward greenness, height and grass plant mass.
III. To establish how varying water resources in Katavi National Park affect the distribution and behaviour of hippopotami.

IV. To study whether the population size of hippopotami has changed in Katavi since 1980s.

2. Relevance of the study

2.1 Scientific relevance

Ecological conditions in which animals live keep on changing. Animals interact with other animals and with their environment and may adapt to the changing conditions (Martin & Bateson, 2007). Resources such as water or food may become scarce and each species may respond differently. A lot remains to be learnt about the diversity and function of behaviour in response to a changing resource (Martin & Bateson, 2007). Information generated from this study will increase understanding of the ecology and behaviour of one of the most charismatic species of large mammal in Africa.

The study will add to our knowledge of such responses to changing resources and will increase understanding of the extent to which the species can respond plastically to environmental change and also what the tipping points of sustainability might be. The social life of hippopotami is relatively little known due to their aggressive behaviour (Eltringham, 1999; Blowers *et al*., 2008). This study will provide insights into this gap in our knowledge of social interactions between hippopotami.

2.2 Relevance to the management of Katavi National Park

Effective management of wildlife populations depends largely upon understanding and predicting their habitat requirements and accurately assessing habitat quality. The effects of the decline in standing water levels within Katavi need to be assessed (TANAPA, 2002; Meyer *et al*, 2005; Katavi, 2008). Similarly, assessment of past rainfall patterns and dynamics of the hippopotami populations need to be undertaken in order to ensure proactive management (TANAPA, 2002; Meyer *et al.*, 2005; Mlengeya *et al.*, 2008). Studying how hippopotami respond to the varying water resources is essential in understanding how they cope with their changing environment.

3. Organisation of the thesis

This thesis has been divided into nine Chapters. Chapter 1 gives the study objectives and explains the relevance of the study. Chapter 2 introduces the study species and describes the study area and sites including the biology and ecology of hippopotami and background information on the study area.

Chapter 3 deals with water resources including rainfall, river flow and discharge, variation in underground water levels and expansion and shrinking of the major water bodies. Chapter 4 is about food resources in the study sites including sward height, grass biomass, grass greenness and ground vegetation cover.

Chapter 5 investigates about hippopotami abundance, distribution, immigration and emigration in relation to the study sites and the park. Chapter 6 investigates hippopotami behavioural activities in the five animals study sites. Chapter 7 investigates behavioural events in the five animal study sites. Chapter 8 analyses the relationships between hippopotami abundance and behaviour and water and food resources. Chapter 9 is a general discussion of the whole study and general conclusions and recommendations from this study.

Some water quality measurements are presented in Appendix 1 as a complement to the Chapter 3.

Chapter 2: Study species, area and study site

1.0 Target species

1.1 The common hippopotamus

The common hippopotamus, *Hippopotamus amphibious* L. in the family Hippopotamidae is the third largest and heaviest land mammal after elephants, *Loxodonta Africana* (Annon.) and white rhinos, *Ceratotherium simum* (Burchell) (Grover, 1972; Laursen & Bekoff, 1978). The name hippopotamus comes from the Greek words 'hippos' and 'potamus' meaning horse and river respectively. Hippopotami are even-toed ungulates, hoofed mammals in the order Artiodactyla. Members of the family Hippopotamidae are non-ruminants artiodactyls whose mode of life makes them unique in Africa among the large mammals (Cerling *et al*., 2008). The other member of the family Hippopotamidae is the much smaller (about 200 - 300 kg) pygmy hippopotamus, *Choeropsis liberiensis.* The pygmy hippopotamus is limited to a very restricted range in West Africa. It is a shy, solitary forest dweller and currently classed as rare (Saragusty *et al*., 2010b).

Hippopotami were once widespread across wet habitats throughout Africa (TAWIRI, 2001; Lewison, 2007; Lewison & Oliver, 2008), particularly in lakes and rivers of sub-Saharan Africa (Grey & Harper, 2002; Cerling *et al*., 2008). The hippopotamus population in Africa was described as widespread and secure in 1996 (Lewison & Carter, 2008), however, there have been substantial population changes in the countries where they occur. Exploitation and habitat loss are reported to have reduced hippopotamus populations by 7-20% over the past two decades (Lewison and Oliver, 2008). Threats to hippopotami through exploitation for meat, retaliatory killing and habitat loss are likely to continue, and have already led the animal to be listed by IUCN as vulnerable (Lewison & Oliver, 2006) from lower risk or least concern in 1996. This is described in more detail in Section 1.5 of this Chapter.

The populations of many of the large mammals in Africa are decreasing (Owen-Smith & Mills, 2006). The bush meat trade is one of the explanations for these population declines across many parts of Africa (East, 1999; Brashares *et al*., 2004). From census of large mammals conducted in Tanzania from the 1980s to 2009, most species have declined with the exception of elephants and giraffes which maintained relatively stable populations across Tanzania (Stoner *et al*., 2006). Hippopotami population size was stable across most areas.

1.2 Ecology and importance of the hippopotamus as a keystone species

The hippopotamus is an instantly recognisable animal with a barrel-shaped body (Plate 2.1). Their height is 140-165 cm; males weigh 1600-3200 kg and females 655-2344 kg (Kingdon, 1982; Millar & Zammuto, 1983; Estes, 1992). Males are 119- 302 cm long with mean average of 270 cm while the female length ranges from 183- 302 cm with mean average of 272 cm (Eltringham, 1999). Hippopotami have two essential requirements; water in which to submerge and nearby grassland for foraging (Jablonski, 2004).

Plate 2.1: The common hippopotami (*Hippopotamus amphibious* L.) at Lake Katavi in Katavi NP, Tanzania

Hippopotamus life span is between 35-50 years with animals in captivity living longer (Laws and Clough, 1966; Sayer and Rakha, 1974; Eltringham, 1999). Age at maturity for females has been estimated at nine to ten years (Millar & Zammuto, 1983; Graham *et* *al*., 2002). Sayer and Rakha (1974) recorded puberty and maturity for female hippopotami at the age of seven and eight years respectively. However, the ages at which a half of the female population reached puberty and maturity were 11 and 13 years respectively, while in males puberty started at six years and maturity was reached at eight years (Sayer and Rakha, 1974).

Mating mainly takes place in water. Females first conceive at about nine years (ranging between 7 and 15 years) and calve at two-year intervals. Breeding in hippopotami is not strictly seasonal (Estes, 1992), but most conceptions occur in the dry season and birth peaks during the wet season. Female hippopotami have an average of 10-12 reproductive pregnancies during their lifetime (Lewison, 1998), with a gestation period of 6-8 months.

An expectant female separates from the rest of the herd and keeps away for a couple of weeks. Calving occurs in shallow water or on land and a newborn is helped by the mother to the land (Sayer & Rakha, 1974). Normally a single calf is born (Laws and Clough, 1966; Sayer & Rakha, 1974; Eltringham, 1999). Newborns are relatively small weighing about 25-55 kg (Sayer & Rakha, 1974; Eltringham, 1999). During this time they become fiercely defensive of the calf and can be dangerous to people. They are also aggressive towards other hippopotami whether territorial males or her own grown offspring.

Suckling of young takes place in water and on land. Lactation takes between 10-12 months, but some hippopotami have post-partum oestrus. A quarter of females examined during long term study in Uganda in the late 1950s to the early 1960s were pregnant and lactating (Laws & Clough, 1966).

A young hippopotamus begins to eat grass at about three weeks but continues to suckle for a year (Sayer & Rakha, 1974). Generally, weaning takes place from between six and eight months, with most calves being fully weaned by 12 months of age.

Hippopotami have an enlarged, chambered stomach similar to ruminants (Arman & Field, 1973) although, unlike ruminants, they do not chew the cud (Eltringham, 1999) and hence are referred to as pseudo ruminants (Estes, 1992; Eltringham, 1999; Cerling *et al*., 2008). The pseudo ruminant's stomach can effectively ferment grasses and other low quality foods (Arman & Field, 1973; Eltringham, 1999; Grey & Harper, 2002). In the hippopotamus stomach, two anterior diverticula and a large median chamber are responsible for fermentative digestion while the posterior chamber secretes gastric juice (Arman & Field, 1973). Despite their watery environment, hippopotami do not feed on aquatic vegetation to a great extent (Eltringham, 1999) and rather feed primarily on terrestrial vegetation (Kingdon, 1982; Eltringham, 1999; Grey and Harper, 2002; Cerling *et al*., 2008). Their diet consists mainly of grasses (Kingdon, 1982; Eltringham, 1999; TAWIRI, 2001); however, some current studies have reported that they may feed on dicotyledonous plants to a significant extent (Boisserie *et al*., 2005; Cerling *et al*., 2008). Studies using stable isotope ratios ($^{13}C/^{12}C$) have shown higher fractions of C_3 (trees, shrubs and forbs) biomass than estimated from previous observations (Bocherens *et al*., 1996; Boisserie *et al*., 2005, Cerling *et al*., 2008), emphasizing that they are not strictly grazers. Mugangu and Hunter (1992) reported instances of hippopotami in Virunga National Park in DRC Congo feeding more extensively on aquatic vegetation as a response to food shortage. Mugangu and Hunter (1992) and Grey and Harper (2002) reported hippopotami feeding on macrophytes aquatic vegetation to some extent in Lake Naivasha, Kenya, but aquatic plant remains formed a negligible proportion of their faeces. Field (1970) reported hippopotami eating the floating plants of the Nile cabbage (*Pistia stratiotes*) though it is unlikely that many were eaten. Holmes (undated) in the film titled "Hippos out of water" by the BBC showed that during the dry season, hippopotami fed on sausage-like fruits (*Kigelia Africana*), dried grass and leaves in Luangwa National Park, Zambia.

There have also been reports of carnivory in hippopotami (Dudley, 1998), however, these incidents are reported as rare and are thought of as fulfilling a nutritional need because vegetation often lacks essential nutrients or trace elements (Eltringham, 1999;

Grey and Harper, 2002). Hippopotami have a lifestyle which is energy-efficient and thus eat about 40 kg of grass a night which is only 1-1.5 % of their body weight (Eltringham, 1999; Grey and Harper, 2002; Clauss *et al*., 2007).

Hippopotami begin to commute to inland pastures shortly before dark, along branching paths up to 3-5 km long, up to a maximum of 10 km (Estes, 1992; Eltringham, 1999). After grazing for up to five hours, they return to the shelter before dawn (Estes, 1992). Though when feeding hippopotami are solitary, young calves and sub adults accompany their mothers, remaining with them until almost full grown at about 6-8 years. Females with new born young remain in water for several days for protection of a calf against possible attacks from predators.

Most feeding takes place on land at night followed by animals resting and digesting in water during most of the day. A large portion of ingested material is therefore defecated directly into water. Due to this tendency, hippopotami are considered as transporters of organic matter mediated through their gut (Eltringham, 1999; Grey and Harper, 2002; Spinage, 2012). The transported materials become available in a semi-processed form to aquatic consumers (Spinage, 2012). In Congo DRC, decline of hippo populations in Virunga National Park (Hart and Mwinyihali, 2001), resulted in decline of fish stocks because hippopotami dung provide nutrients for fish.

Ecologically, hippopotami play an important role in the ecosystem. Removal of hippopotami in Ruwenzori National Park in Uganda resulted in the increase of large mammals such as buffalo, elephants and waterbuck while that of bushbuck and warthog decreased (Eltringham, 1974).

Grazing by hippopotami may also influence plant community composition. Culling of hippopotami in Queen Elizabeth National Park in Uganda resulted in botanical changes such as decreases in grass basal cover, increases in bare ground and change in grass species composition, with tussock grasses such as *Sporobolous pyramidalis* increasing as a result of hippopotami removal (Thornton, 1971). Vegetation changes which may be associated with the combined effects of hippopotami grazing and fire across other parts of Africa have also been reported by Olivier and Laurie (1974).

Humans are the major predator of hippopotami while lions, hyena and crocodiles predate the young (Estes, 1992). Hippopotami mainly defend themselves and attack using large, long, sharp lower canines (Estes, 1992).

1.3 Water dependence and hippopotamus biology

Ecology requires attention to details of other aspects of the biology of a species apart from distribution and abundance (Begon *et al*., 2006). This section is intended to draw attention to some adaptations of hippopotami to their habitats. Hippopotami are unusual in being genuinely amphibious and this has a fundamental effect on their physiology and way of life (Eltringham, 1999). Water is required for their thermoregulation and animals are thus never found far from water (Cerling *et al*., 2008).

Hippopotami are well-adapted to aquatic life (Cerling *et al*., 2008; Herbison and Frame, 2008) which makes them unique in Africa among the large mammals (Eltringham, 1999; Cerling *et al*., 2008). Studies using oxygen isotope ratios ($^{18}O/^{16}O$) have shown that hippopotami are the most oxygen-depleted mammals, which directly reflects their semi-aquatic habitat (Bocherens *et al*., 1996; Cerling *et al*., 2008). Oxygen isotope analysis can help to provide information on mammal water balance and thermoregulatory strategies.

Hippopotami have unique skin consisting of a thin epidermis with no sweat glands. And as a result, they lose water much more quickly than other mammals (Jablonski, 2004). Out of water hippopotami risk rapid dehydration and overheating in hot weather (Estes, 1992). They must therefore retreat to water to keep their bodies cool because they do not sweat (Eltringham, 1999).

Hippopotami skin is almost hairless and they do not have sebaceous glands, but have mucus secreting glands which produce a thick oily pink fluid which helps to keep their skin moist (Saikawa *et al*., 2004). Although the fluid secreted is not strictly sweat, because it is produced by sub-dermal glands (Eltringham, 1999), it acts like sweat in helping to control body temperature. It is also thought to have antiseptic properties (Eltringham, 1999). The secretion is alkaline with pH 8.5-10.5 (Saikawa *et al*., 2004) and with two pigments; red and orange. The pigments act as sunscreen and have antibiotic function because, even at lower concentration to that of the hippopotamus skin, they can inhibit the growth of pathogenic bacteria *Pseudomonas aeruginosa* and *Klebsiella pneumonia* (Saikawa *et al*., 2004) and shield hippopotami from harmful ultraviolet rays.

The hippopotamus core body temperature is around 36°C (Luck and Wright, 1959; 1963; Cena, 1964; Noirard *et al*., 2008) and in order to reduce sun exposure, they have to move in water and bathe when environmental temperatures increases.

The large and wide head of the hippopotami has eyes, nostrils and ears set on the top, allowing them to partly submerge. Hippopotami can swim and dive well and their negative buoyancy allows them to walk along the bottom of water. When they are completely submerged their slit-like nostrils and ears are sealed off (Estes, 1992; Eltringham, 1999).

As an adaptation to its aquatic environment the feet are hoofed with membranes stretching between each of the four toes, helping the hippopotami to move through water. The fat beneath the skin is also an adaptation to its watery environment, making this large animal buoyant enough to float easily.

Young hippopotami can suckle under water by taking a deep breath, closing the nostrils and ears and wrapping their tongue tightly around the teat. They are reported to suckle in the same way while on land. While in water, newborn calves can climb on the back of their mother to rest.

1.4 Hippopotami behaviour

Hippopotami are highly gregarious, contact species and are territorial only when in the water (Olivier and Laurie, 1974; Estes, 1992). Males defend territories against other bulls but only if they challenge the incumbent male. Territories are established to defend mating rights rather than food which explains why they are non-territorial away from water. Females are non-territorial and are not necessarily confined to a single territory, although most return to the same area of water after grazing. A territorial system is not obvious and general mixing of individuals of all ages and both sexes can give the impression that territories are not held (Olivier and Laurie, 1974), however, more intensive studies have confirmed hippopotami territoriality (Klingel, 1991).

There are no social bonds between the adults within a group despite the fact that hippopotami lie in close contact with each other. The social bonds are between the mothers and daughters (Blowers *et al*., 2008). Males form separate bachelor groups.

1.5 Hippopotami distribution in Africa (historical data)

Hippopotami are among those species faced with vulnerability to extinction in Africa (Lewison and Oliver, 2006; Lewison and Oliver 2008). Their populations in most sub-Sahara African countries have declined in response to human disturbance (Lewison, 2007). They were once found throughout sub-Saharan Africa, although only estimated historic distributions are available. Currently, their distribution is primarily concentrated in a few parts of Eastern and South-eastern Africa where populations tend to occur in high densities (Lewison and Oliver, 2006; Lewison, 2007; Herbison and Frame, 2008). According to the World Conservation Union (IUCN), in many countries where hippopotami occur, their populations are declining (Fig. 2.1). In 1996, the species was categorised at lower risk or least concern by IUCN. By the late 1990s their numbers were estimated at only 170,000 individuals (Eltringham, 1999). Ten years later in 2006, hippopotami were listed as vulnerable (Lewison and Oliver, 2006). The declines have been attributed to two anthropogenic activities; habitat losses, as wetlands are converted to agricultural development and unregulated hunting for meat and ivory from the large canines and incisors (Lewison, 2007; Lewison and Oliver, 2008). Trampling and crop raiding by hippopotami led to early and determined efforts to exterminate them (Herbison and Frame, 2008; Kendall, 2011).

In countries such as Zambia, hippopotamus population surveys conducted between 2005 and 2008 are showing some improvement in their population size (Wilbroad and Milanzi, 2010). Zambia has the highest population size of any African country (Lewison, 2007; Lewison and Oliver, 2008) (Fig. 2.1).

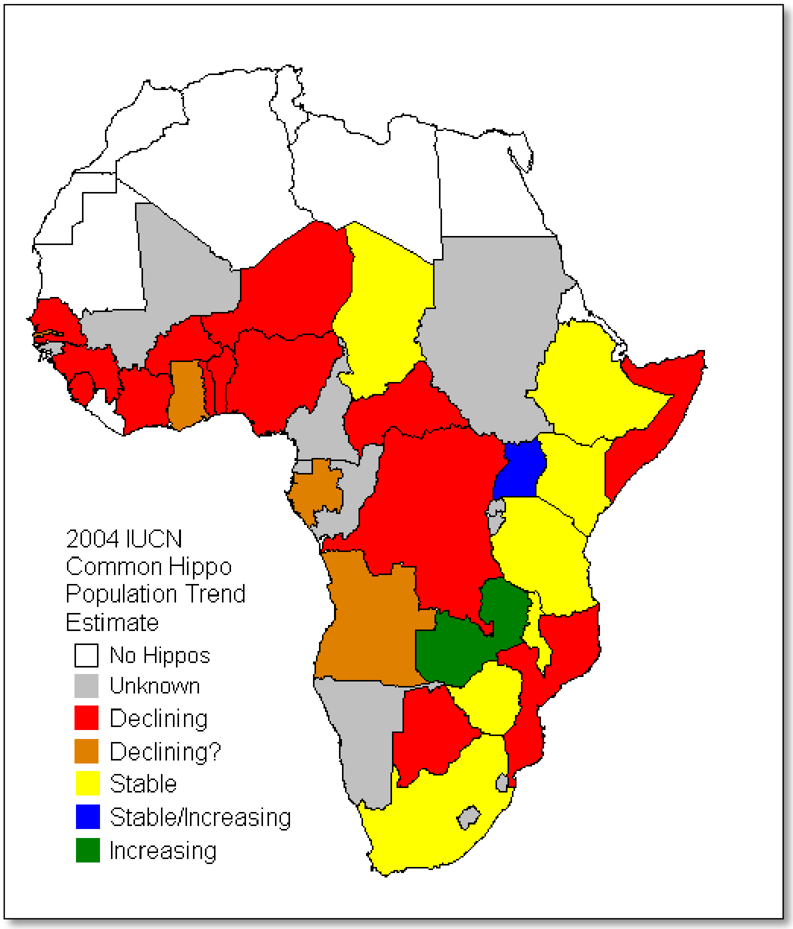


Fig. 2.1: Hippopotami population trends in Africa according to IUCN 2004. *Source*: Lewison and Oliver, 2008

2.0 Study area

2.1 Background to Katavi National Park

Katavi National Park (herein after referred to as the Park), with an area of about 4,471km^2, is located in Mpanda district, south western Tanzania, in the newly established Katavi Region (Fig. 2.2). The Park is located at 6°35'-7°05'S and 30°45'-31°25' E. Katavi National Park is Tanzania's third largest national park after Ruaha and Serengeti (TANAPA, 2002; Meyer *et al*., 2005; Katavi, 2008; TANAPA, 2008). Together with the neighboring game and forest reserves, it contains many different ecosystems covering an area of about 25,000 km^2 (Banda *et al*., 2007; Borgerhoff-Mulder, *et al*., 2007; TANAPA, 2008; Mlengeya *et al.*, 2008). The Park is one of the richest wildlife areas in Tanzania and was first recognised and protected in 1911 by the Germans as the Bismarck Hunting Reserve. It was upgraded to Rukwa Game Reserve by the British in 1957 (KRCD, 2004; TANAPA, 2005). The area was gazetted as a National Park in 1974 (Caro, 1999a; TANAPA, 2002) with an area of 2,253km^2. In 1996, several hunting areas were amalgamated with Katavi and it hence attained its present size (TANAPA, 2002; KRCD, 2004; TANAPA, 2008). The Park is named after Katabi, the legendary Chief spirit of the Wabende tribe who lived in Katavi.

Katavi encompasses a combination of ecological habitats ranging from woodlands, seasonally-inundated grasslands, riverine grassland and wetlands. Altitude ranges from 820 m a.s.l. in the valley floor to 1,560 m a.s.l on adjacent mountains of the escarpment surrounding the Park. The area is characterised mostly by alluvial soils (black cotton soils) on the plains and by red loams and red soils elsewhere (Banda *et al*., 2007).

The Park, being part of the extensive Katavi-Rukwa system, is renowned for its high biological richness. The ecological interest of the Park comes from a combination of factors including its size, diversity of habitats and the abundance and variety of its fauna and flora (TANAPA, 2008; Mlengeya *et al.*, 2008). The Katavi area consists largely of Miombo (*Brachystegia*) dry forest habitat characterised by *Acacia*, *Combretum,* *Commifora, Grewia, Kigelia, Pterocarpus, Brachystegia, Julbernadia, Isoberlinia and Terminalia* tree species (Rodgers, 1979; Caro *et al*., 2005). Miombo is deciduous woodland occurring in the largely unimodal rainfall areas of East and Central Africa on old acidic sand soils (Rodgers, 1978). Some plant inventory work in the ecosystem has been conducted (Mwangulango, 2003) and plant communities described (Meyer and Mwangulango, 2004). Under the shade of woodlands, the grass species are dominated by *Themeda triandra* (Forsk)*, Pennisetum polystachion* (L.), *Chloris gayana* (Kunth), *Dactyloctenium aegyptium* (L.), *Digitaria brazzae* (Franch.) Stapf and *Panicum repens* (L).

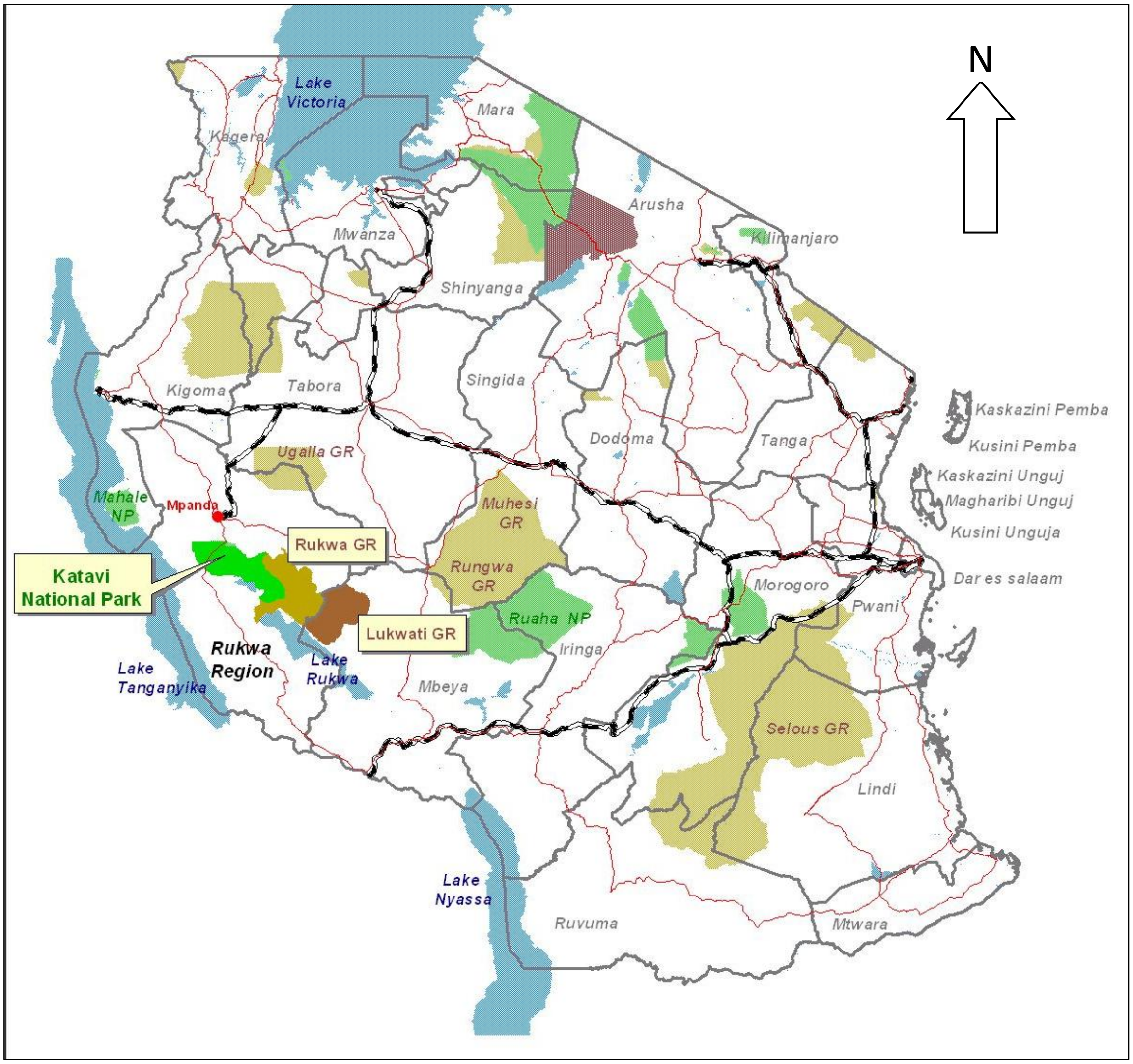


Fig. 2.2: Map of Tanzania showing location of Katavi NP and some Parks and Reserves. *Source*: Katavi NP/KRCD, 2009. Key: NP = National Park, GR = Game Reserve

The Katavi landscape is comprised of seasonally-flooded grassland plains interspersed with *Brachystegia* (Miombo) woodland on the well-drained hill sides. The major grass types on the elevated or hilly areas include species such as *Aristida kelleri* (Hack.), *Brachiaria brizantha* (A. Rich.) Stapf*, Digitaria brazzae* (Franch.) Stapf*, Eragrostis patens* (Oliv.), *Melinis repens* (Willd.) Zizka*, Sporobolus sanguineus* (Rendle)*, Cloris virgata* (Sw.), *Themeda triandra* (Forssk) and *Cyperus involucratus (*AGM)*.*

The major geophysical features of the Park include two seasonal lakes, Katavi in the north and Chada in the centre. The Katuma River flows across the plains connecting the lakes. Within the Park, there is an extensive network of floodplains, other rivers and wetlands. These hydrological features all drain southwards into Lake Rukwa. Seasons define much of the eco-hydrology of the Park (Meyer *et al.*, 2005; TANAPA, 2008; Mlengeya *et al.*, 2008). The seasonal lakes are reduced to grasslands during the dry season swelling into shallow lakes with the onset of rains. There are some seasonal creeks, swamps and swampy wetlands which retain and supply water to the flora and fauna of the Park in the dry season. These include Paradise and Katisunga swamps.

The major grass types in the seasonal lakes are *Hyparrhenia hirta* (L.) Stapf*, Echinochloa pyramidalis* (Lam.) Hitchc. and Chase*, Echinochloa crus-pavonis* (Kunth) Schult*, Sporobolus fimbriatus* (Trin.) Nees*, Sporobolus pyramidalis* (Lam.) Hitchc.*, Themeda triandra* (Forsk.), *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult**.** *, Digitaria ternata* (A. Rich.) Stapf. and *Pennisetum polystachion* (L.) Schult*.* In the transition zone of the lake-floodplain-woodland, the grass layer is short (up to 30 cm) and dominated by species including *Sporobolus fimbriatus, Echinochloa pyramidalis, Tribulus terrestris* (L.) *and Polygonum salicifolium* (Willd.).

Fresh water swamps at springs and adjacent to rivers are dominated by grasses, rushes, sedges and aquatic plants including *Cyperus papyrus* (L.), *Phragmites mauritianus* (Kunth), *Leersia hexandra* (Sw.), *Pennisetum purpureum* (Schumach.), *Echinocloa crus-pavonis, Echinocloa pyramidalis, Sporobolus fimbriatus, Typha domingensis* (Pers.) Steud.*, Pistia stratiotes* (L.), *Nymphaea caerulea* (Sav.), *Cyperus* *dives* (Delile), *C. articulates* (L.), *C. involucratus* (Rottb.) and *Mimosa pigra* (L.). Others are *Aeschynomene cristata* (Vatke Var.), *Neonotonia wightii* (Am.) Lackey and *Kotschya capitulifera (Baker) Dewit &P. A. Duvign.*

Various large and small animals depend on swamp and marsh grazing during the dry season for water and grazing on palatable grasses.

2. 2 Suitability of Katavi as a hippopotamus study site

It has been reported that Katavi is among those areas that support the greatest concentrations of hippopotami in Tanzania (Caro, 1999b; TANAPA, 2002). According to aerial census data collected during the late 1980s to early 2000s in seven wildlife areas in Tanzania, including Katavi, most populations of all large herbivores such as hippopotami declined in some parts of the country (Stoner *et al*., 2006). The survey further suggested that despite a network of protected areas in Tanzania and the conservation commitment, some large herbivores such as hippopotami populations need more conservation attention in order to remain stable. A preliminary foot survey was conducted in Katavi in 2004 (Stoner *et al*., 2006; Waltert *et al*., 2008).

Katavi National Park is among the sites that supports one of the healthiest hippopotami populations in Tanzania and harbours about 13% of the hippopotami population in Tanzania according to 2001 aerial census (TAWIRI, 2001). The Park provides suitable habitat with water for resting during the day and grazing grounds for feeding at night. Katavi is little disturbed by human activities. However, despite these attributes, land use practices in the areas adjacent to the Park and in the upper catchment of the main river are likely to have negative impacts on the water supply.

2.3 Challenges of water availability in Katavi

This research was not intended as a study of the hydrology or water resources of the Park. However, estimates of the amount of available water resource were made because behavioural response to water availability is the focus of the research. Water availability (quantity) has not been quantified systematically in the past.

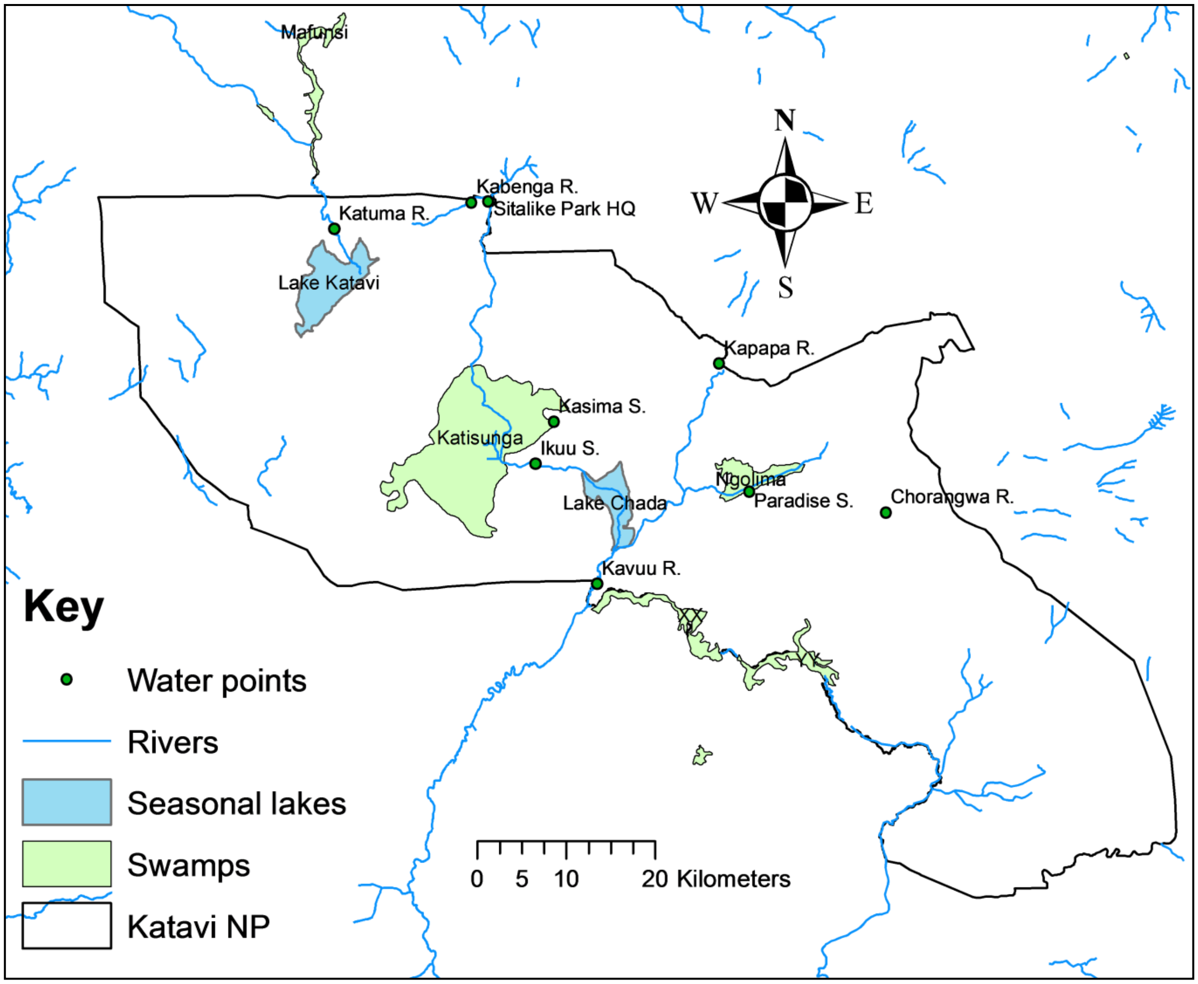


Figure 2.3: Map of Katavi NP and adjacent areas showing hydrography of study sites: *Source*: Katavi NP, 2009 and data collected during this study. NP= National Park, S=Springs, R= River.

Katavi depends heavily on rain and river water received from outside the Park area in the catchment of the Katuma River (Fig. 2.3). Although rainfall in the upper catchment at Katuma is about 1500 mm per year, it is exceeded by evapotranspiration (Meyer *et al*., 2005). According to Peterson (1973) and Wilhelm (1993) as quoted in 2005 (Meyer *et al*., 2005), rates of evaporation of standing water in lakes and pools in tropical regions such as Katavi can reach 2000 mm year^{-1}. As such, there is great pressure on the water resources of the Park.

The Park has six rivers of which the Katuma River is dominant (Fig. 2.3). The upper catchment areas of all the rivers are outside the Park, mainly to the North and East. Katuma River feeds the shallow Lake Katavi in the north of the Park, the Katisunga flood plains and Lake Chada, which also receives water from the Kapapa River (Fig. 2.3). Katuma and Kapapa Rivers join to form the Kavuu River. Kavuu River is the outlet for Lake Chada and flows towards Lake Rukwa. The most important areas which have high concentrations of animals, especially during the dry season (July-November), are Lakes Katavi, Chada and the Katisunga Plains (Caro, 1999b; 1999c). The others are Paradise Springs and along the Katuma, Kavuu and Kapapa rivers. Springs are another very important source of water in the Park and support a variety of species (Meyer *et al*., 2005; Mlengeya *et al*., 2008).

In recent years, the rivers feeding the Park, particularly the Katuma, have been drying in September or early October, approximately two months earlier than previous years when they dried in November. The situation has become much more severe since the early 2000 (Meyer *et al.*, 2005). The availability of standing water in Katavi appears to be decreasing at a substantial rate (Lewison, 1996; 1998; Meyer *et al.*, 2005; TANAPA, 2008). The most affected wildlife species include the hippopotamus. Declining surface water levels in Katavi have been reported anecdotally by park staff, but no data were collected before the 1990s (TANAPA, 2005).

Among possible reasons for the earlier drying of the Katuma River are deforestation and illegal damming of rivers upstream for irrigation of rice farms before the rivers enter the Park. In the Park, these competing demands on water resources have caused a noticeable drop in the water levels of the lake and wetland habitats in the Park for about 0.5 m between the 1990s and early 2000s (TANAPA, 2002; Meyer *et al.*, 2005; Mlengeya *et al.*, 2008; Caro *et al*., 2011). Intensive damming and irrigation systems in many villages in the drainage catchment area appear to be reducing the quantity and duration of water flow. As a result, this directly affects the availability of water for the flora and fauna downstream. Agricultural practices upstream also result in increased siltation of the Katuma River and other rivers and lakes.

Water supply is a key issue for the sustainability of Katavi National Park and the Rukwa Basin. This forms the context for the research presented in this thesis.

2.4 Climate and rainfall patterns

The National Park is defined as a climatically homogenous biome and the rainfall pattern is slightly bimodal (Banda *et al*., 2007) with wet periods in late November to January and March to April. The average annual rainfall for the period of nine years from 1997 to 2005 was 927 mm ± 126 mm (SD) (Meyer *et al*., 2005; TANAPA, 2008). Rainfall patterns are given in more detail in the introduction to Chapter 3. The inter-annual rainfall pattern and its effect on the hydrology are yet to be fully understood.

2.5 Human impacts on habitats

Currently, most wildlife is under human pressure (Haynes, 1998; Mwamfupe, 1998; Sherbinin & Freudenberger, 1998; Caro, 1999a; Songorwa, 1999; Madulu, 2001; Adams and Hutton, 2007). Human population increase around the Park is high, partly due to the influx of people from other areas for trade, settlement, agriculture and small-scale mining. Land is being cleared for agriculture while logging and deforestation are on the increase. From the mid-1970s, agro-pastoralists from northern Tanzania began moving to areas adjacent to Katavi. This has added further pressure to the Park and its resources, particularly to the North and South-west (TANAPA, 2008; Mlengeya *et al*., 2008).

Illegal and uncontrolled logging in the river catchments is increasing (TANAPA, 2005; Meyer *et al.,* 2005). Slopes are deforested for logging and agriculture leaving top soils bare and susceptible to soil erosion. Hardwoods are harvested for timber (Schwartz *et al*., 2002; Caro *et al*., 2005). The major impact of human activity is abstraction of water for irrigation in the upper catchment of the Katuma River, the impact of this on water resources of the Park is the subject of Chapter 3.

3.0 Study sites

Five observation sites were selected for recording behaviour, abundance, immigration and emigration of hippopotami. These were distributed in four main areas of the Park with varying availability of water resources over one annual cycle of wet and dry season. The selected areas spanned a wetness gradient due to different sources of water and retention properties of each site which represent different habitat types (a-e). The five sites are described (Table 2.1, Fig. 2.4, Fig.2.5 and Plates 2.1-2.5). Each selected study site was treated separately as they contained independent populations of hippopotami which did not mix.

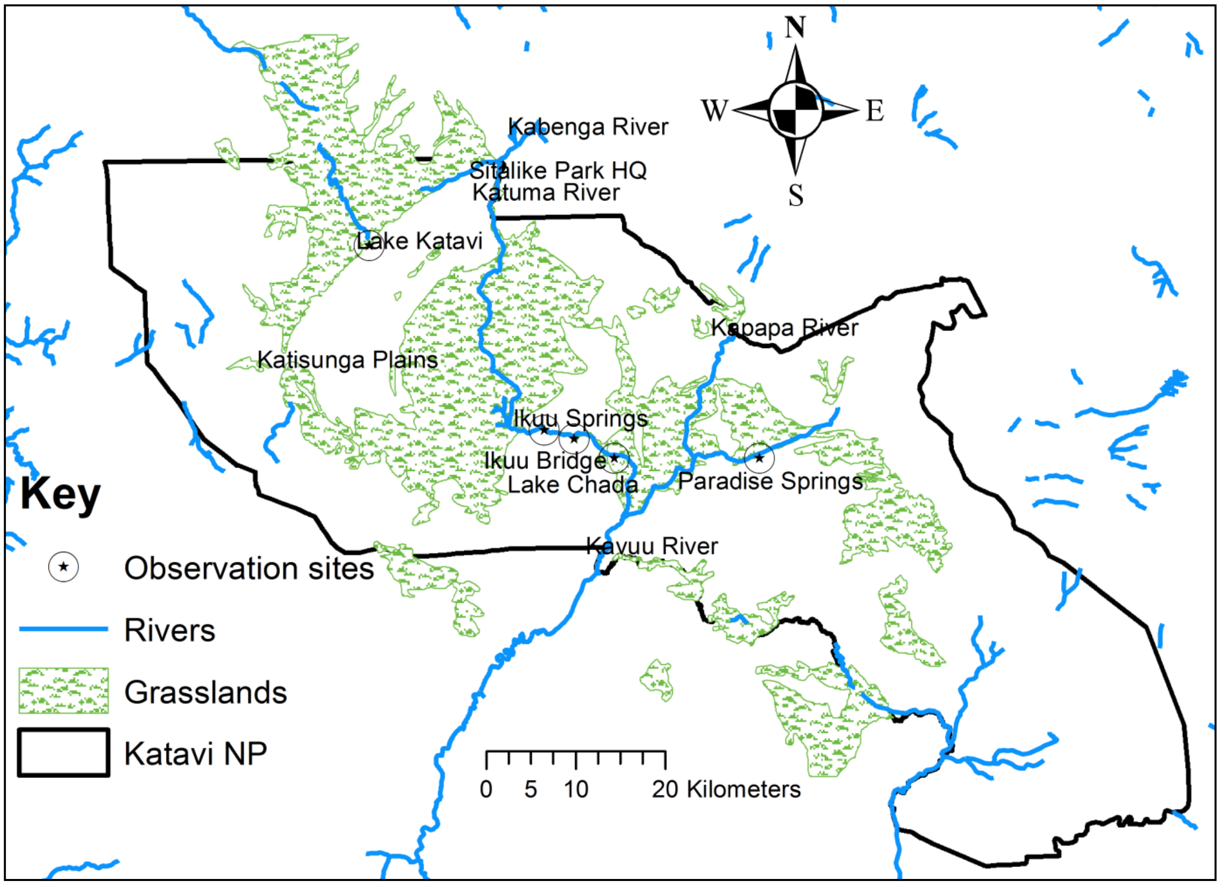


Fig. 2.4: Map of Katavi showing animal observation and recording sites. Grasslands are areas used by hippopotami for foraging. *Source*: Katavi NP and data collected during this study.

Table 2.1 Summary of main features of study site

Site name	GPS Position	Location	Main source of water
Paradise Springs	36M0323694	Adjacent Kapapa River	River + Springs
	UTM9233964		
Ikuu Springs	36M0299625	Adjacent Katuma River	Springs only
	UTM9237125		
Lake Katavi	36M0281050	Upperstream Katuma River	River + Springs
	UTM9258933		
Ikuu River	36M0303007	Along Katuma River	River only
	UTM9236110		
Lake Chada	36M0307464	Downstream Katuma River	River only
	UTM9233962		

a. **WETTEST Paradise Springs**. The perennially wet eastern tributary of the main Katuma River in riverine forest at the junction of the Kapapa River and Paradise Springs. This served as a control site due to the availability of water resources throughout the year.

The Paradise Springs study site is swampy grassland predominantly fed by perennial springs, receiving water from the springs within it and also from the Kapapa River which is perennial at this point as it emerges from the forest. It tends to retain some water throughout the year, although during the dry season water levels may fall dramatically. The study site is c. 5 ha surrounded by a total swamp and grassland area estimated at 50 km^2 (Plate 2.1).

The swampy area is separated from the main sandy grassland by a line of palm trees in the mouth of the spring. One side of the palms is perennially wet due to springs and the river, while the other side tends to dry out during the dry season because it depends on the rains. Further from the swamps to the grassland is black cotton soil grassland with scattered shrubs and trees starting within about one kilometre of the springs.

Plate 2.1: Paradise (Wettest)

Plate 2.2: Ikuu Springs (Wet)

Plate 2.3: Lake Katavi (Wet)

Plate 2.4: Ikuu Bridge (Dry)

Plate 2.5: Lake Chada (Driest)

Plates 2 (1-5) Photographs showing descriptions of each of the five hippopotami study sites in Katavi NP, Tanzania

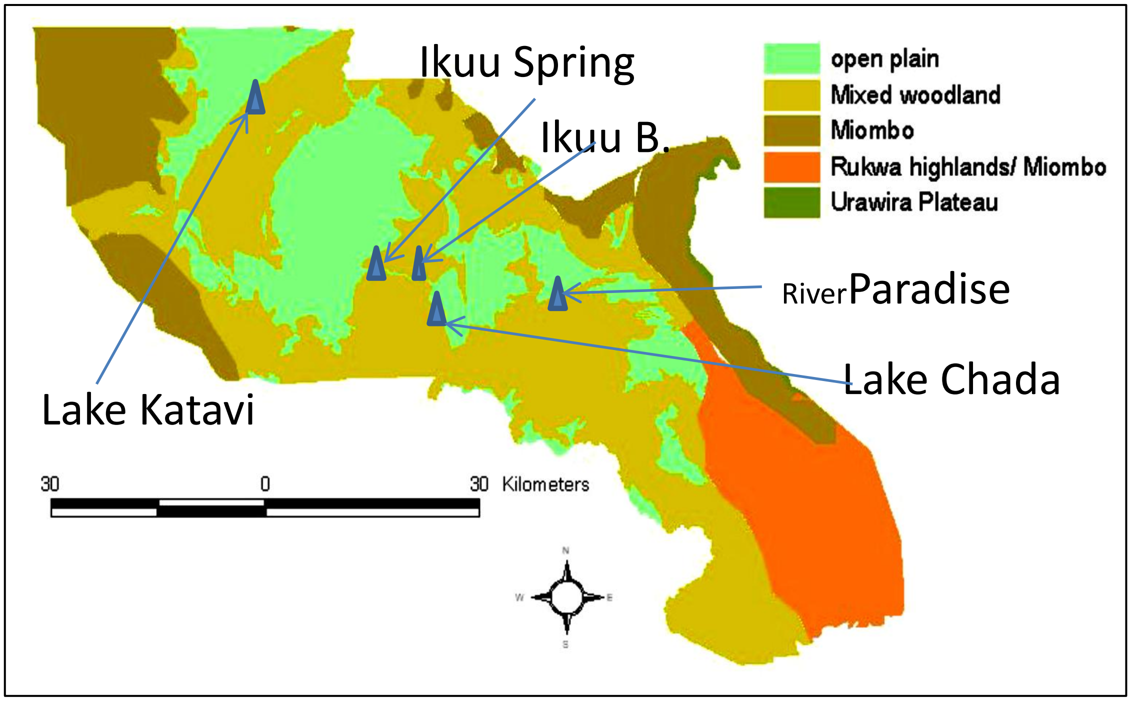


Fig. 2.5: Vegetation map of Katavi NP showing location of hippopotami observation sites in relation to the surrounding vegetation types. *Source*: Katavi NP. *Key*: Ikuu B = Ikuu Bridge, Paradise S = Paradise Springs

b. **WET Ikuu springs**: this site is predominantly spring-fed grassland. The area is also partly fed by the main Katuma River (only when in flood) which runs dry during the dry season. The springs supply water throughout the year to the hippopotamus shelter and the adjacent swamps. The spring area therefore remains relatively wet throughout the year. The total area of the spring is estimated at 0.5 km^2. The study site is surrounded mainly by the Katisunga grassland plains where most foraging took place and open woodland (Plate 2.2).

Many mammals use this site for dry season watering. The area surrounding the springs depends on rain as the major source of water and is also fed by the main Katuma River which bisects the grassland plain just above Ikuu Springs. There are also minor scattered springs which supply water as small pools, particularly during the dry season.

c. **WET Lake Katavi**. The wetter northern swamps at Lake Katavi. The area is mainly swampy and retains water for longer periods than Lake Chada. The area includes Lake Katavi which receives higher rainfall than other study sites (1000-3000 mm year^{-1}) and is the entry point into the Park for the Katuma River.

The Lake Katavi study site is predominantly swampy grassland fed by the Katuma River and from minor seasonal streams and springs. The grassland swells to swamp with the onset of rains while being reduced to dry grassland during the dry season. The area has some water holes which may retain some water during the dry season and which are used as shelters for hippopotami. During long drought, the holes may dry out completely. One water hole c. 5 ha was chosen for observing hippopotami. The total 'lake' area surrounding the site is estimated at 70 km^2 (Plate 2.3). The area is surrounded by Miombo woodland.

d. **DRY Ikuu Bridge**. Drier south-western riparian, seasonal grassland on the Southwest of Katisunga plains in the Ikuu area. Rainfall is between 800-900 mm year^{-1}. The site is fed mainly by the riparian seasonal Katuma River. It is surrounded by sparse woody vegetation cover.

This site dries out almost completely during the dry season although it may retain water in a few water pools in the river bed. One of these water pools was monitored at Ikuu Bridge. The total area of the study site and adjacent grassland is estimated at 0.25 km^2 (Plate 2.4). The area is surrounded by Miombo woodland and patches of grassland. Foraging takes place partly in this area but mostly in the nearby grasslands.

e. **DRIEST Lake Chada**. Driest western Miombo woodland on the south west of the Park. This area receives relatively low rainfall (800-900 mm year^{-1}), has less open water bodies except the 'lake' and hence retains little water after the rains.

The Lake Chada study site is open swampy grassland seasonally fed from rivers. The area is at the confluence of two rivers, Katuma and Kapapa. Both rivers are seasonal at this point, the area swelling into a swamp with the onset of rains, but reduced to dry grassland during the dry season. Some muddy pools remain during the dry seasons which become shelter sites for hippopotami. One such pool of *c*. 5 ha in area immediately after the rainy season but declining to less than 100 m^2 by the end of the dry season was monitored as a hippopotami sheltering site. The study site is surrounded by c. 40 km^{-1} of swampy grassland and woodland on the edge of grassland (Plate 2.5).

Several factors were considered for selecting the study sites. The areas are representative habitats of the Park which are wet and dry plains and forests. They were also selected according to accessibility all year round and for having been previously censused hippopotami. The main criterion for choosing these sites was varying availability of water resources.

At the five animal behaviour sites, sward height, greenness and ground vegetation cover were also measured within foraging range of the hippopotami to estimate the food resources. Water resources were quantified in a further seven sites. Water quality was measured in twenty six sites described in introductions of Appendix 1 and Chapter 3 and vegetation monitored as are described in Chapter 4.

Chapter 3: Rainfall, river flow and discharge and soil saturation

1. Introduction

Water resources raise some of the most important issues facing human beings (Coe & Birkett, 2004). Fresh water is critically scarce in many parts of Africa (UNEP, 2008). This is due to extremes in rainfall, high soil moisture deficits, increases in human population and dependence on irrigation. Water scarcity in some areas is becoming common due to climate change (IPCC, 2001; Coe and Birkett, 2004) and in some regions; scarcity is expected to become more acute. Problems of freshwater availability in Africa are complicated by highly variable precipitation (UNEP, 2008). This calls for a need to quantify water resources and their variability. Although field data are most commonly and accurately used for water resource analysis (Coe and Birkett, 2004) obtaining data consistently from remote regions can be very challenging.

Water crises in protected areas in Tanzania, with emphasis on the Katavi-Rukwa ecosystem, have been reviewed by Elisa *et al.* (2010). Little information on water resources exists for Katavi National Park yet water is one of the key issues in the management of the Park and the wider Rukwa Basin. The amount of water entering and remaining in the Park and flowing downstream to the Lake Rukwa basin appears to have been decreasing over recent years (TANAPA, 2005; Meyer *et al*., 2005; Mlengeya *et al*., 2008). Preliminary work on rainfall and water resources in Katavi, including partial measurements of water flow, has been conducted by Lewison (1996; 1998). Most of the data from that study are yet to be analysed by the Park authorities. The most important document to date is an unpublished report on water scarcity by Meyer *et al.* (2005) that brings together patchy data on rainfall and water levels over the period 1997/8-2004/5.

The research presented here is not intended as a detailed study of the hydrology or water resources of the Park. However, the size of the surface water resource has been measured because behavioural responses by hippopotami to water availability are the focus of this research. Water and distance to water affect the activity budget and strategies of hippopotami (Lewison and Carter, 2004), and hence their behaviour patterns.

Previous data have been compared with data gathered during this study to estimate the likely scale of any recent changes in the amount of water received by the Park. This has been achieved by using the scant water level records available at Regional Water Offices, rainfall and water level data collected as part of routine monitoring by Katavi Park staff and rainfall and flow data collected during 2009 and 2010 for this study.

Groundwater is an important source of water for the Park and springs support a variety of species (Meyer *et al.*, 2005; Mlengeya *et al.*, 2008) particularly in the dry season. Springs of groundwater are numerous in the Park and make an unmeasured contribution to the total water resource. Many ground water sources are in remote areas and access is limited during the wet season. This study did not attempt to estimate the size of the contribution of groundwater to the water resource of the Park.

1.1 Rainfall in Katavi

Katavi National Park and the adjoining ecosystem is defined as a climatically homogenous biome with a slightly bimodal rainfall pattern (Banda *et al*., 2007) with wet periods in late November or December to January and in March to April. The average annual rainfall for the nine years from 1997 to 2005 was 927 ± 126 mm (Meyer *et al*., 2005; 2006; Katavi 2008).

Lower altitude areas within the area of the Park receive 800-900 mm of rainfall per year and higher altitudes receive about 900-1000 mm (TANAPA/WD, 2004) (Fig. 3.1). The area to the north of the Park which includes the upper catchment of Katuma River receives between 1000 – 3000 mm of rainfall per year (IRA, 2004) as quoted in Meyer *et al*. (2006).

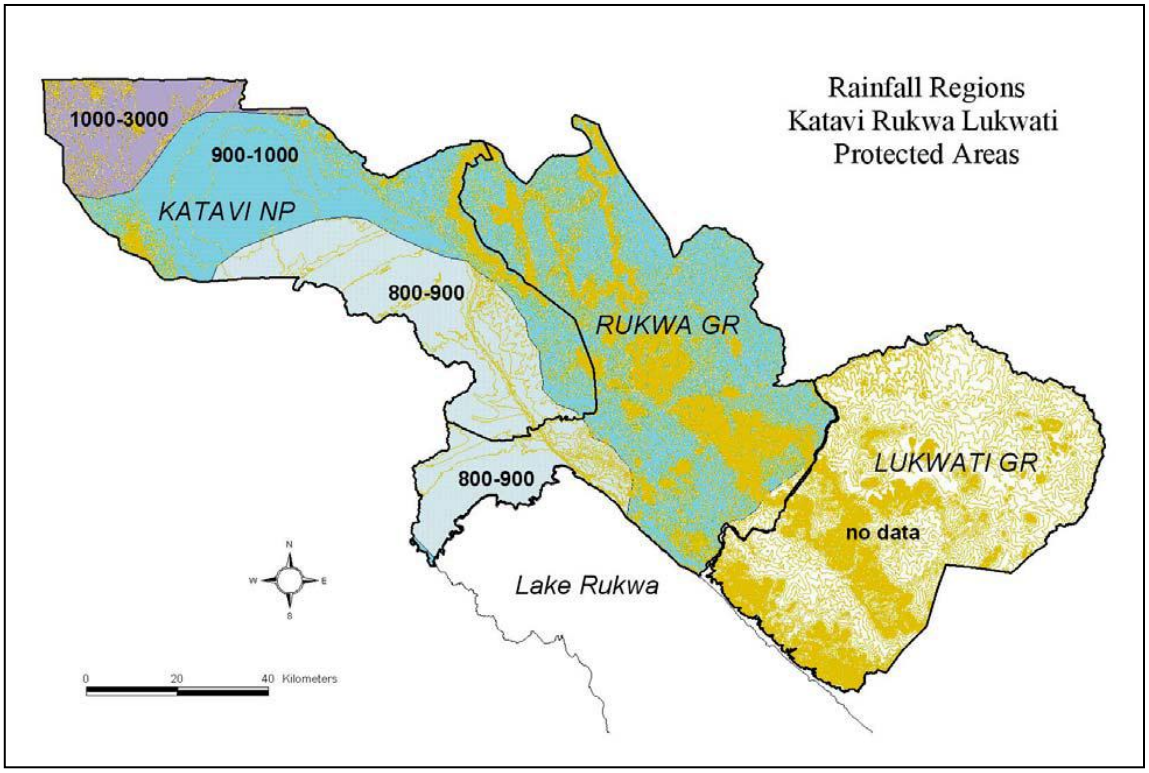


Fig. 3.1: Rainfall regions in Katavi National Park and adjacent areas. *Source*: Katavi NP, 2009.

1.2 Surface drainage pattern

The drainage catchments of all the six rivers that flow in the Park are mainly outside the Park boundary, mostly to the North and East. Katuma River dominates the surface drainage of the Park flowing into the shallow basin of Lake Katavi in the northern part of the Park, the Katisunga flood plains and then Lake Chada, which also receives water from the other rivers. The outflow from Lake Chada in the southern part of the study area is called Kavuu River which then flows further south towards Lake Rukwa (Fig. 3.2). Lake Katavi, the Katisunga Plains and Lake Chada are the most important areas for concentrations of animals in the Park, especially during the dry season (July-early November). Other key wildlife areas lie along the Katuma, Kavuu and Kapapa rivers. These areas also support high concentrations of animals in the dry season (TANAPA, 2002; Meyer *et al*., 2005). Areas where water is supplied by springs also support a variety of species (Meyer *et al.*, 2005; Mlengeya *et al.*, 2008) (Fig.3.2).

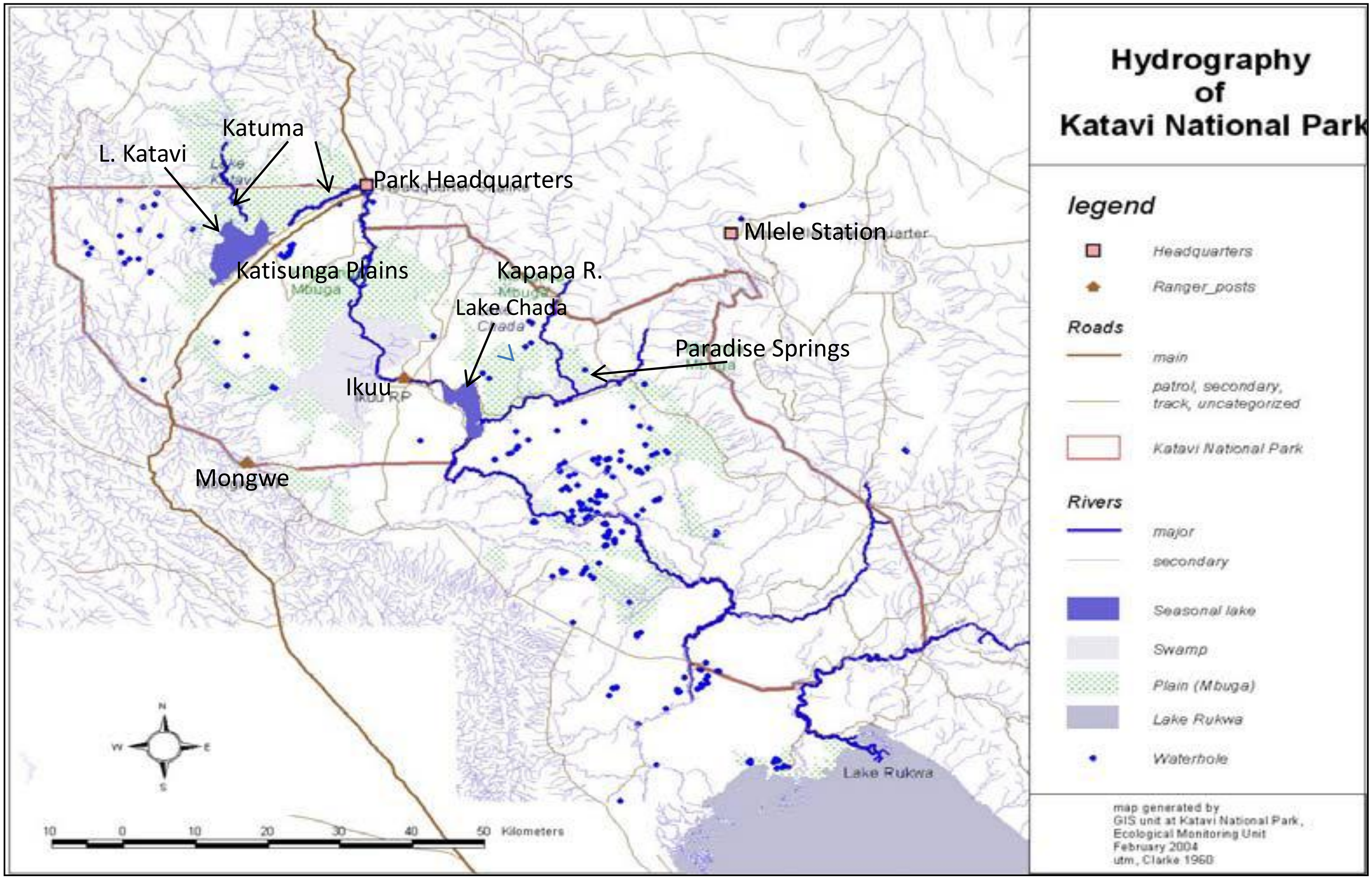


Fig. 3.2: Major sources of water in Katavi National Park, Tanzania. *Source*: Katavi NP, 2009.

1.3 Soil moisture deficit

With air temperatures varying between about 25 and 30°C, rates of evapo-transpiration exceed rainfall leading to high soil moisture deficits, particularly during the dry season in the hottest months of September and October (Meyer *et al*., 2005; Shorrocks, 2007). This leads to a negative water balance in the dry season (Shorrocks, 2007). According to Wilhelm (1993) as quoted in Meyer *et al*. (2005), rates of evaporation of standing water in lakes and pools in tropical regions can reach 2000 mm per year. Peterson (1973) reported evaporation about four times the annual rainfall received in the Tarangire ecosystem in Tanzania. With the driest areas of the Park receiving an average of 927 mm rainfall per year, the soil deficit is likely to be more than double the amount of rainfall received.

1.4 Aims and hypotheses

Anecdotal evidence suggests that the amount of water entering the Park *via* Katuma River has declined in recent years. This is tested using patchy historical data plus new data collected during this study. Rainfall data are used to detect changes in rainfall patterns that could explain any changes in river flow. Changes in flow that cannot be explained by rainfall might be linked to human impacts on flow in the upper catchments of the rivers that supply the Park.

The study also quantifies the water resource in key areas of the Park, including each of the five sites where hippopotami have been studied, to test for relationships between wetness both geographically and seasonally and the distribution, abundance and behaviour of the animals. Water also affects the size of the food resource for hippopotami so the availability of pasture is explored in Chapter 4.

Direct measurements of water depth in rivers and soils and of river discharge have been made over wet and dry seasons and in a range of sites to test the following hypotheses:

H_1: Rainfall in the study area has declined over the last six decades

H_2: River water levels in the study area have decreased over the last two decades

H_3: Water level varies between the five animal study sites

H_4: Water resources in the Park vary seasonally as discharge decreases and vary along the river

H_5: Tributaries with less human interference flow for more months and show less flow rate differences between seasons

2. METHODS

2.1 Study sites are described in Chapter 2

2.2 Rainfall measurements

Daily measurements of rainfall at the Park Headquarters at Sitalike, Ikuu Springs, Mongwe Ranger Post (R/P) and at Mlele (Fig. 3.3) are made as part of the routine ecological monitoring program of the Park. The longest and best continuous rainfall record started in the 1997/8 hydrological year (running from July to June of the following year) for the Park Headquarters. Data are sparse for the other stations (Meyer *et al*., 2005). Some historical records were obtained from the Katavi-Rukwa Conservation and Development Project (KRCD) and some from the 1950s (taken from Lewison, 1998) were obtained from the Regional Government Office. Records from the 1950s are by calendar years not hydrological years. Rainfall records for the upper part of the Katuma catchment area were obtained from Mpanda District Water Authority.

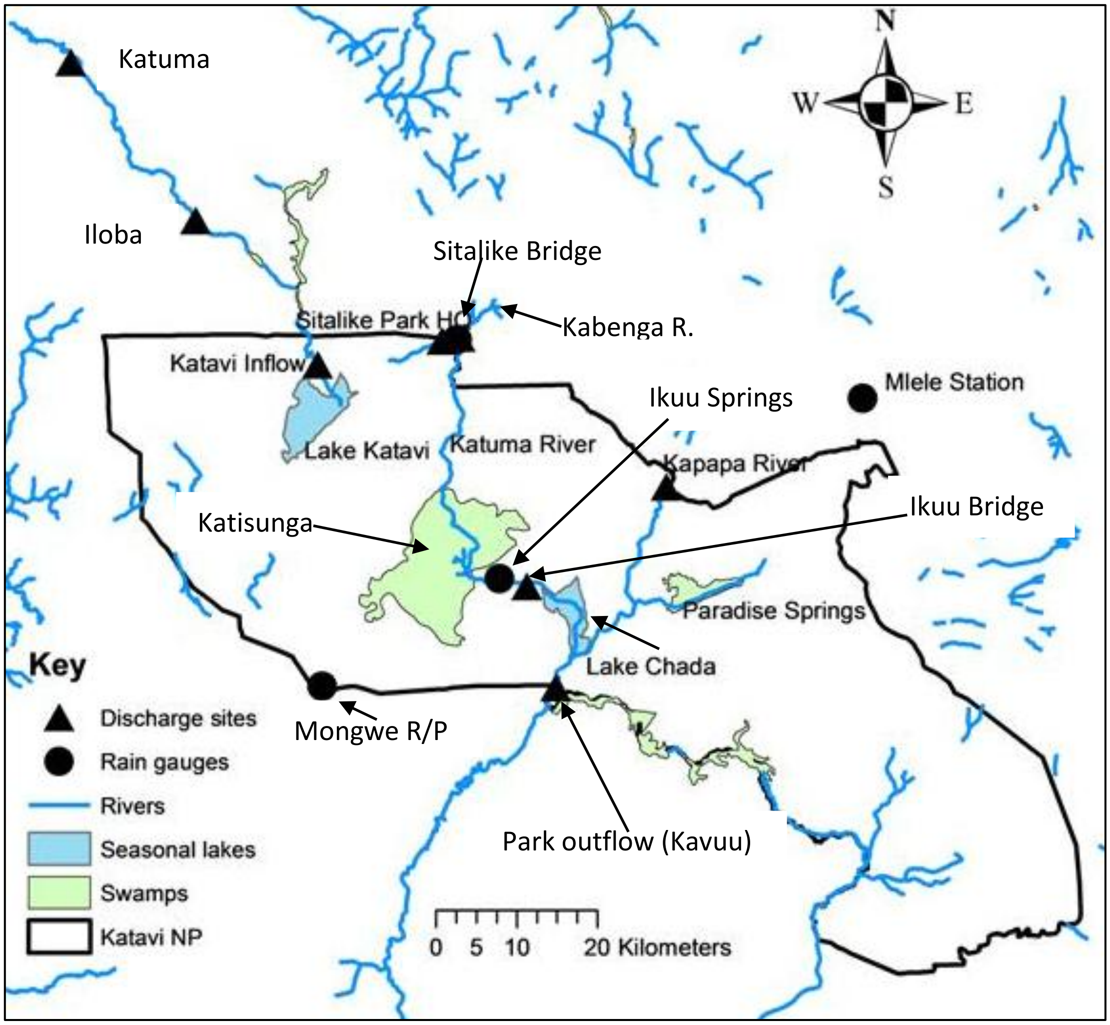


Fig. 3.3: Katavi National Park, Tanzania, showing rainfall and river measuring sites. *Source*: Katavi NP and data collected during this study. NP = Katavi National Park, R = River, R/P = Ranger Post.

At the Park Headquarters, a complete weather station, WS2350 with data logger, is used to record rainfall, wind speed, barometric pressure, temperature and humidity. Rainfall is collected in a standard Regenmesser 471003 stainless steel rain gauge with an internal 25 mm scaled plastic measure and a capacity of 165 mm. For the present study, additional gauges were installed in early 2000 in three stations. These were at Ikuu Springs, Mongwe and Mlele (Fig. 3.3). Daily rainfall data collected for this study were therefore from four stations distributed widely over the Park and rainfall at Katuma Village in the upper catchment was measured by the District Water Authority.

2.3 River levels

River level at Sitalike and Ikuu Bridge on Katuma River (Fig. 3.3. and Table 3.1) was measured as part of Park monitoring from 1990-1994 and again from 2005 at Sitalike and from 2009 for Ikuu Bridge to the present day. No other historical water level data were located.

For this study, river levels were measured at six additional sites. The locations of the eight sites in total and their main features are shown on Fig. 3.3 and in Table 3.1. Sites included the Katuma River at its inflow and outflow from the Park, sites near Lakes Katavi and Chada and two tributaries of Katuma River. The choice of station took into account the problems of access to remote areas and difficulty or impossibility of vehicle access in the wet season.

Permanent water depth measuring staffs made from angle iron were installed in sites where these did not already exist (in Kabenga, Iloba, Kapapa, Katavi Inflow and Park Outflow). Water depth was recorded on every visit that was made for measuring river discharge (Section 2.4).

Table 3.1: Locations of sites for river level measurements made in Katavi NP, Tanzania.

Site name	**GPS Coordinates (UTM system) and altitude (m a.s.l.)**	**Distance (km) downstream from source of main river**	**Description of the site**
		Main river	
Katuma Village	36M 0294723 9266730 *Alt.* 1094	15	The unfarmed upper catchment at a river bridge in Katuma village
Iloba Village	36M 0261919 9281260 *Alt.* 1010	18	The farmed upper catchment at a river bridge in Iloba village
Katavi Inflow	36M 0277023 9263437 *Alt.* 972	40	Inflow to Katavi NP near the Park's northern boundary
Sitalike Bridge	36M 0294723 9266730 *Alt.* 944	66	Downstream Lake Katavi at Sitalike Bridge
Ikuu Bridge	36M 0303007 9236110 *Alt.* 919	105	Downstream Katisunga Plains at Ikuu Bridge
Park Outflow (Kavuu)	36M 0306553 9223665 *Alt.* 916	125	The outflow from the study area at Kavuu corner, downstream Lake Chada
		Tributaries	
Kabenga tributary	36M 0292490 9266421 *Alt.* 963	67	A tributary that joins Katuma River below Sitalike. Measured at Kabenga Bridge near Sitalike Bridge
Kapapa tributary	36M 0320294 9248365 *Alt.* 961	110	A major tributary that joins Katuma River above the Park Outflow. Measured at Kapapa Bridge

Note: Distance of tributaries are from source of the main river to where they join the Katuma River

2.4 River discharge

River discharge was measured using the area-velocity method in the seven of the stations described for river level measurements. River discharge was not measured in Katuma Village in the high catchment but river levels were recorded. Most of the seven sites had road bridges from which flow measurements were made.

Channel cross sectional area

Channel (to bank full) cross sectional areas were surveyed in Katavi Inflow and Kavuu Outflow (the two un-bridged sites) during October/November 2009 in the peak of the dry season when river flows were at their lowest or river beds were dry. Surveying of the channel cross sectional area of bridged sites was possible at times when there was flow in the channel. Channel depth was measured at 2 m intervals across the channel and cross sectional areas were calculated as the sum of the areas (depth x 2 m width interval) of rectangular and triangular sub-sections.

River discharge

Measurements were made in all sites every two weeks. Velocity measurements started in December 2009 because until end of November 2009, water was yet to start flowing in Katuma River. However, there was some flow in the Kapapa tributary. In some places, water movements were noted, but were not strong enough to be recorded using the flow meter.

Flow velocity was measured at mid-depth using MFP126-S Geopack advanced flow meters.

River discharge, equal to the product of the cross sectional area of the river (A) occupied by water and its mean velocity (μ), was calculated as:

$$Q=A\mu$$

Where Q= Discharge ($m^3\ s^{-1}$), A= Cross-sectional area of the portion of the river occupied by the water (m^2) and μ= is the average flow velocity ($m\ s^{-1}$).

2.5 Seasonal change in soil water depth

Seasonal change in soil water depth in piezometer tubes was estimated in four of the animal behaviour sites and in Katisunga Plains. At each site, three piezometer tubes were installed in randomly chosen starting positions that were at equal distance from the river or other main water source. Water level either below or above the soil surface was recorded twice every month.

Piezometer tubes were made using perforated PVC pipes. These had a diameter of 10 cm and a total length of 210 cm. The length of the tube inserted into the ground was 190 cm and the length above the ground level was 20 cm. Water levels were recorded by inserting a measuring rod into the tube. Readings were taken as the distance from the point where the rod came into contact with water and the soil surface. Water depths above ground level were recorded by placing a measuring rod upward from ground level and recording water depth. Readings from each set of three piezometer tubes were averaged.

3. Results

3.1 Rainfall

From historical rainfall records from the 1950s to 2010 for the Sitalike area in Katavi, there have been fluctuations in rainfall (for example, the exceptionally high total rainfall of 2100 mm in 1979) but there has been no overall trend with time (r = 0.028 n = 58 NS) (Fig. 3.4).

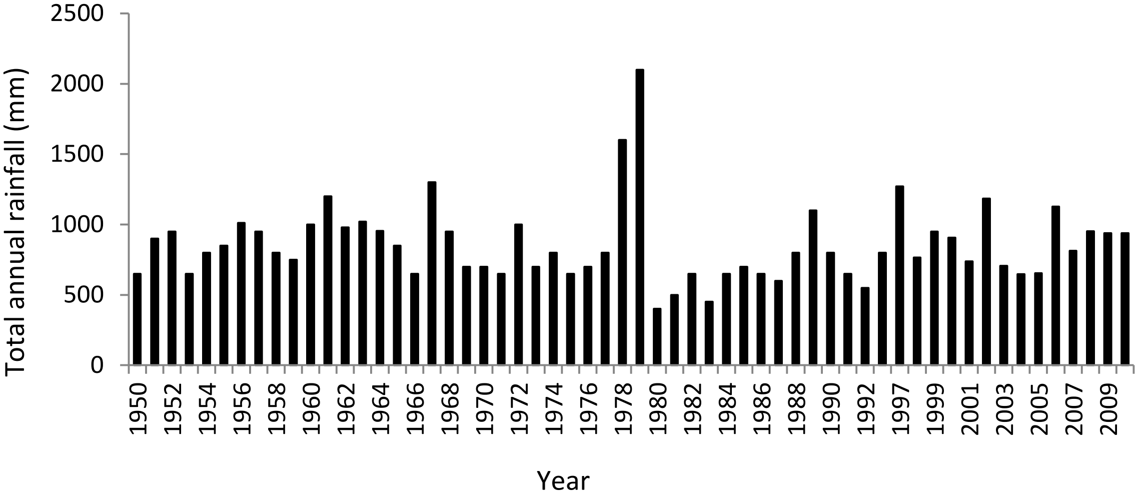


Fig. 3.4: Total annual rainfall (mm) recorded in Katavi NP from 1950-2010

The driest years in Katavi have been 1980, 1983, 1992, 2004 and 2005 (Fig. 3.4). Mean annual rainfall over the period 1950-2010 (58 years) was 854 ± 36.21 mm. The decade with lowest rainfall was 1980-1989 with a mean of 650 ± 199 mm (Fig. 3.5).

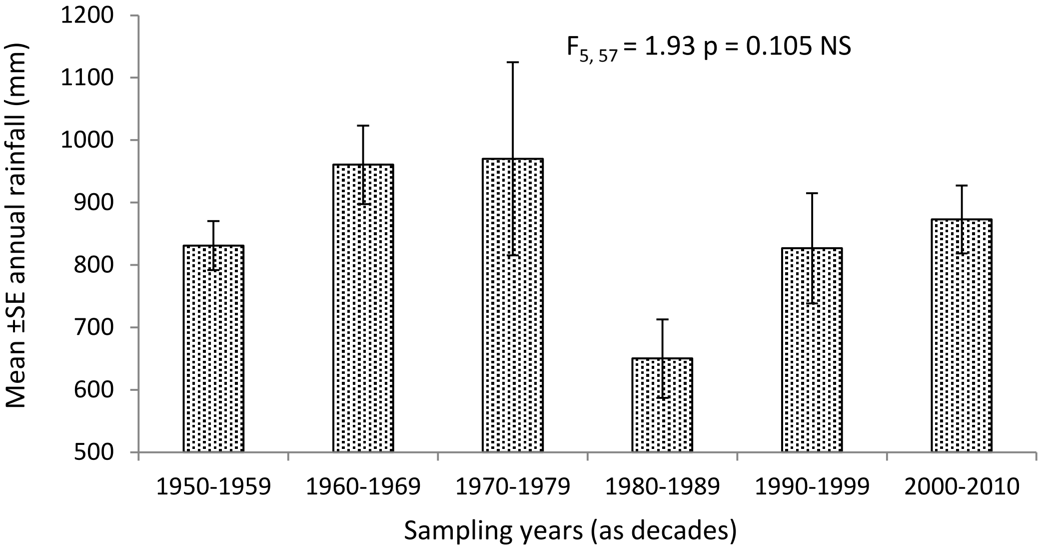


Fig. 3.5: Mean annual rainfall by decade since the 1950s. Error bars are standard errors around the decadal average.

A 13-year almost continuous rainfall record exists for the Park Headquarters at Sitalike. The highest total annual rainfall here was 1221 mm (in 1997/98) and the lowest was 804 mm (in 2006/2007) (Fig 3.6). Particularly high rainfall was recorded in 1997/8 and 2001/2 (Table 3.2).

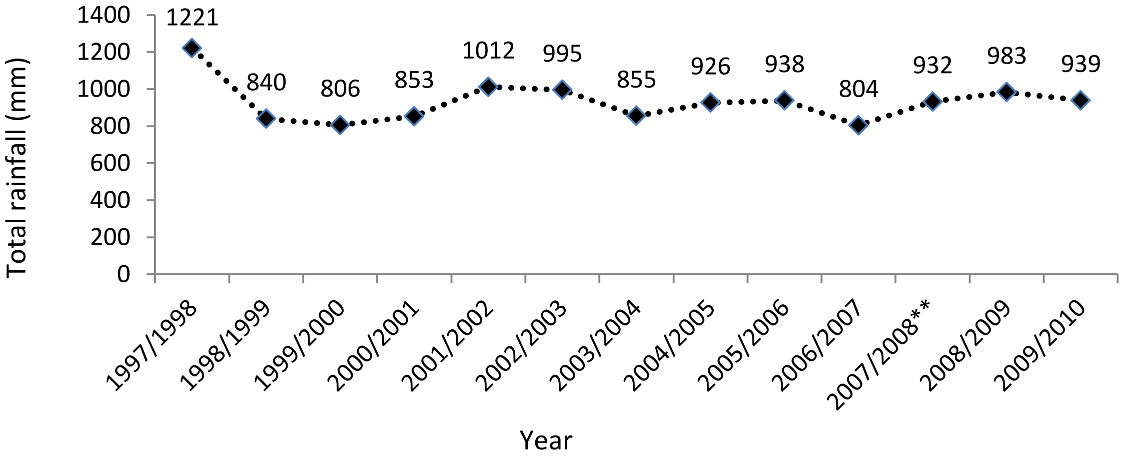


Fig. 3.6: Total annual rainfall (hydrological years from July to June) for Katavi NP recorded from 1997/98 to 2009/10 at Park Headquarters at Sitalike, Katavi NP, Tanzania. ** No records were taken in April-June 2007/8 so the total is an underestimate.

Table 3.2: Total monthly rainfall (mm) at Park HQ, Sitalike in Katavi National Park, Tanzania (1997/8-2009/2010 hydrological years)

Month	**1997/8**	**1998/9**	**1999/00**	**2000/01**	**2001/02**	**2002/03**	**2003/04**	**2004/05**	**2005/06**	**2006/07**	**2007/08**	**2008/09**	**2009/10**
July	0	0	0	0	0	0	0	0	0	0	3	0	0
August	0	0	0	0	0	0	0	0	0	0	13	0	0
September	5	4	4	0	0	0	0	18	0	0	0	0	16
October	25	14	36	104	55	0	44	10	14	8	35	17	9
November	233	21	195	157	78	177	15	142	85	178	155	167	95
December	349	118	32	108	120	249	177	248	47	150	139	180	198
January	250	168	117	109	319	145	155	142	193	169	175	157	112
February	32	26	180	84	66	16	164	71	135	78	87	212	171
March	173	363	153	210	209	244	152	264	128	128	326	120	283
April	123	124	90	53	132	65	147	28	158	77	-	106	37
May	32	2	0	26	33	0	0	3	179	13	-	26	18
June	0	0	0	2	0	0	0	0	0	4	-	0	0
Total	**1221**	**840**	**806**	**853**	**1012**	**895**	**855**	**926**	**938**	**804**	**932**	**983**	**939**
Mean	**102**	**70**	**67**	**71**	**84**	**75**	**71**	**77**	**78**	**67**	**104**	**82**	**78**
SE	**35**	**32**	**22**	**20**	**28**	**29**	**23**	**28**	**22**	**21**	**36**	**2**	**27**

The 13-year average seasonal rainfall pattern at Sitalike was slightly bimodal with one wet season from November to April, but with highest peaks in January and March and less in February (Fig. 3.7). March was the wettest month.

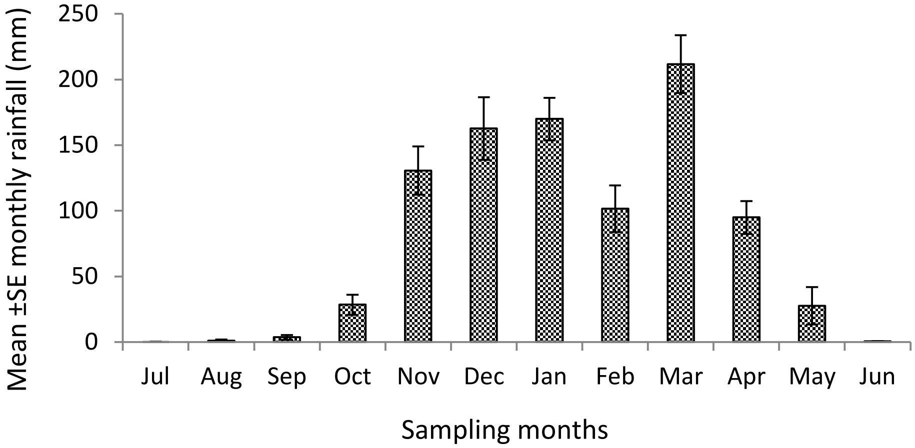


Fig. 3.7: Average monthly rainfall at Park HQ , Katavi NP, Tanzania over the hydrological years 1997/8 to 2009/10

This study began in August 2009, so in terms of relating water resources to animal behaviour, rainfall in 2009/10 is of greatest interest (Table 3.3). In 2009/10, rainfall stopped earlier in the season (in April) than in the previous year. May 2010 had a total rainfall of 18 mm compared with 26 mm for May 2009 (Tables 3.2 and 3.3). Generally, 2008/9 was slightly wetter at Park Headquarters than the following year although both years were around average in terms of the 13-year record. Animal behavior was therefore studied over a period with average rainfall. There was no rainfall from July to September 2010 at any of the four stations.

Table 3.3: Monthly total rainfall (mm) for four stations in Katavi NP, Tanzania during the study period, hydrological years 2008/9 and 2009/2010.

2008/2009	**Jul-08**	**Aug-08**	**Sep-08**	**Oct-08**	**Nov-08**	**Dec-08**	**Jan-09**	**Feb-09**	**Mar-09**	**Apr-09**	**May-09**	**Jun-09**
Park HQ	0	0	0	17	167	180	157	212	120	106	26	0
Ikuu Springs	0	0	0	15	97	42	28	35	47	152	20	0
Mongwe R/P	0	0	0	2	51	65	189	103	125	45	0	0
Mlele	0	0	0	83	149	122	156	142	206	282	1	9
2009/2010	**Jul-09**	**Aug-09**	**Sep-09**	**Oct-09**	**Nov-09**	**Dec-09**	**Jan-10**	**Feb-10**	**Mar-10**	**Apr-10**	**May-10**	**Jun-10**
Park HQ	0	0	16	9	95	198	112	171	283	37	18	0
Ikuu Springs	0	0	4	2	126	135	152	219	286	50	0	0
Mongwe R/P	0	0	0	0	144	165	103	227	112	19	0	0
Mlele	0	0	13	8	149	272	219	231	256	62	2	0

Over the study period, total annual rainfall (Fig. 3.8) and monthly rainfall as totals and averages (Table 3.3. and Fig. 3.9) varied greatly between the four gauging stations.

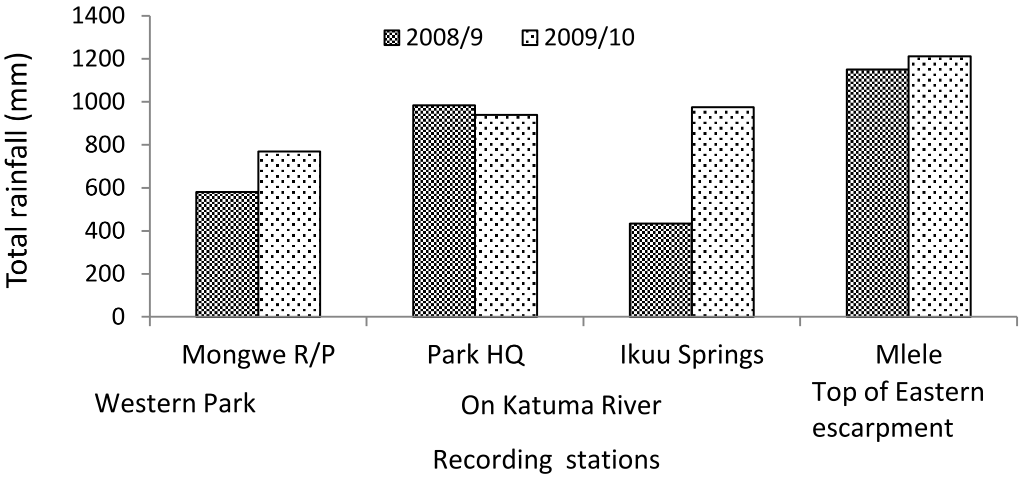


Fig. 3.8: Total annual rainfall in named sites in Katavi NP, Tanzania during 2008/9 and 2009/2010

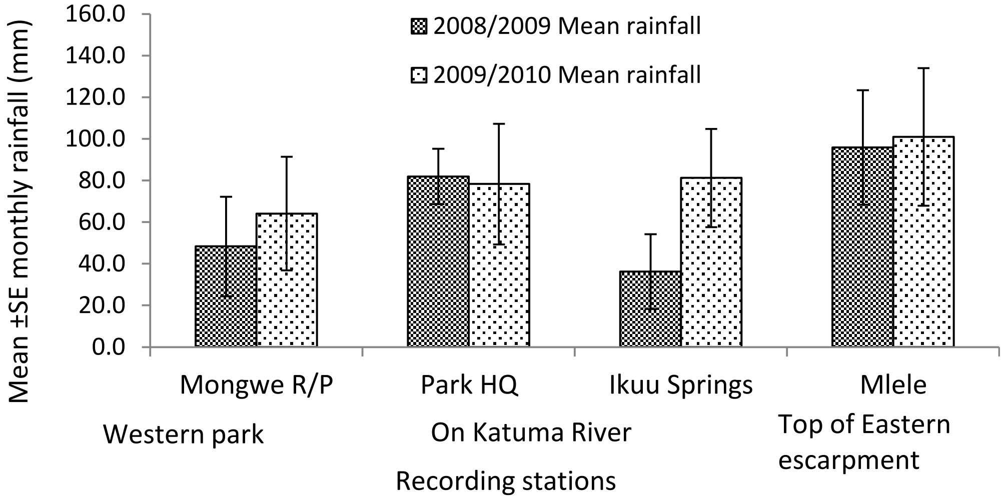
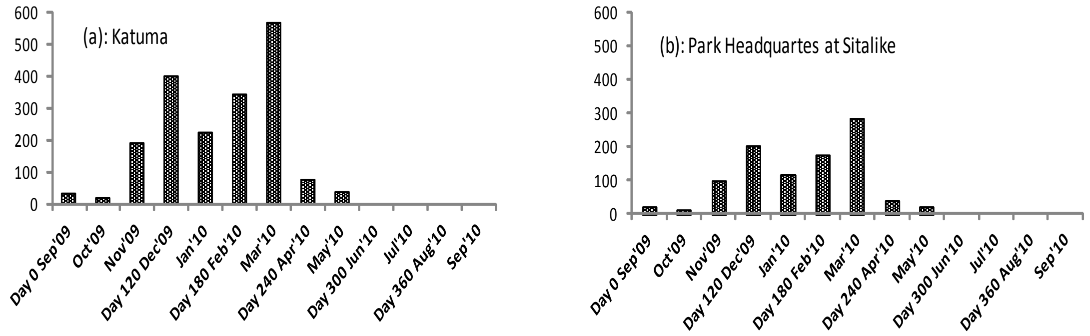


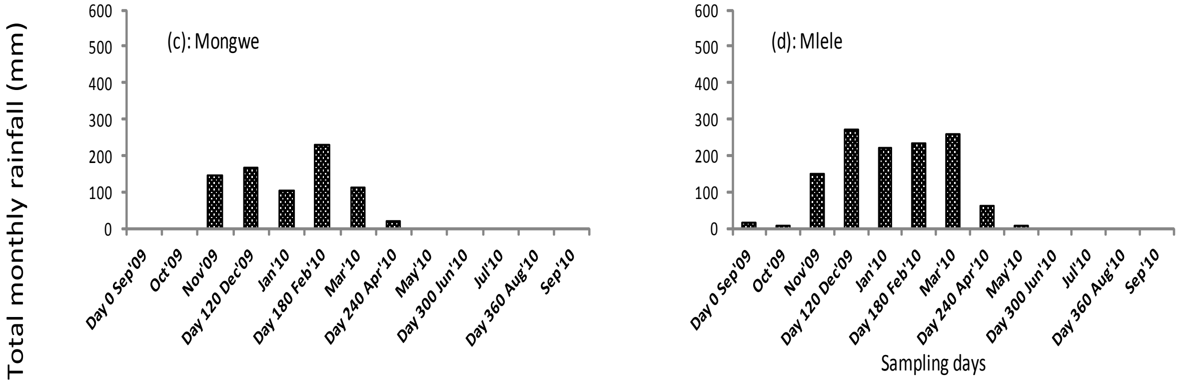
Fig. 3.9: Mean monthly rainfall for 2008/9 and 2009/2010 from named sites in Katavi NP, Tanzania.

Total monthly rainfall recorded over the study period in each of the sites is presented in Fig. 3.10. Values plotted in Fig. 3.10 are correlated with river discharge in Section 3.4 to test the closeness of rainfall-flow relationships.



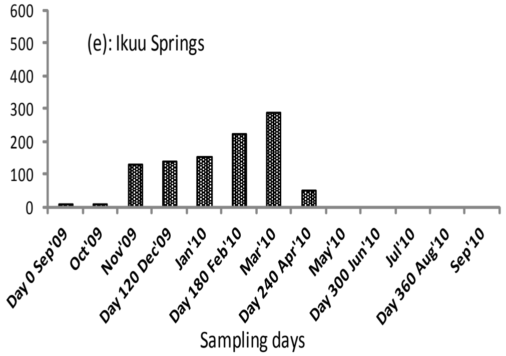
Flow at Iloba and Katavi inflow is matched to Katuma rainfall

Flow at Sitalike Bridge and Kabenga is matched to Park Headquarters rainfall



Flow at Ikuu Bridge is matched with Mongwe rainfall

Flow in the Kapapa is matched with Mlele rainfall



Flow at Ikuu Bridge and Park outflow are matched with Ikuu Springs rainfall

Fig. 3.10: Total monthly rainfall over the study period (September 2009 to September 2010) at the five rain gauging stations in Katavi NP with locations shown on Fig. 3.3. The footnote on each graph indicates how rainfall data from the site have been matched to river discharge data for testing rainfall-flow relationships in Section 3.4.

3.2 River Levels

A 10-year record of river levels exists for Sitalike Bridge (Fig. 3.11 and Fig. 3.12). At Sitalike Bridge, there were marked differences in annual mean river level over the ten sampling years ($F_{9, 112}$= 5.589, $p < 0.0001$) with much lower river levels in 2005-2009.

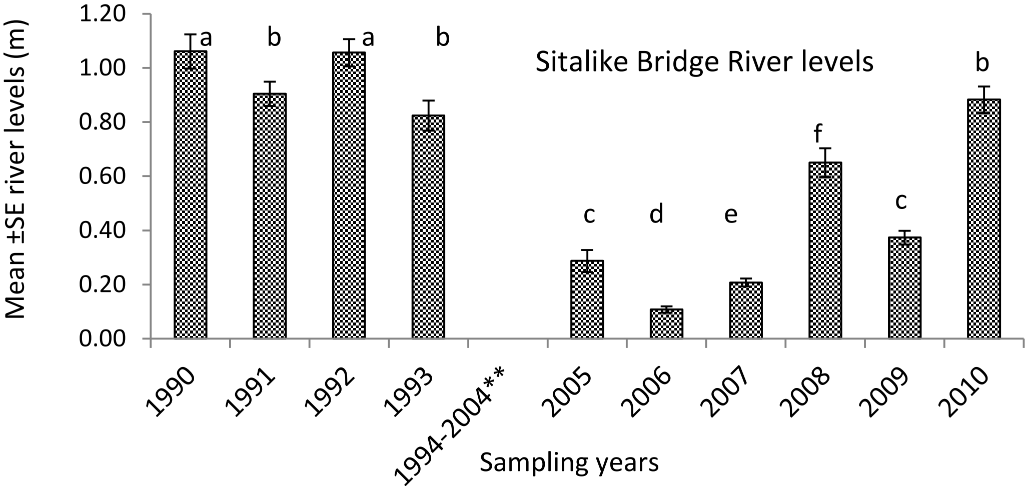


Fig. 3.11: Comparison of ten years annual mean river levels at Sitalike Bridge along Katuma River, Katavi NP, Tanzania. Error bars ±SE indicate variations between sampling months. ** No river level records exist for the period

Maximum river level occurred from March to May during the rainy season and minimum levels occurred in July to November during the dry season (Table 3.4).

Table 3.4: Annual maximum and minimum river levels recorded from 1990 to 2010 in Katuma River at Sitalike Bridge near the Park Headquarters in Katavi NP, Tanzania.

Year	**Annual max level (m)**	**Month with max level**	**Annual min level (m)**	**Month with min level**	**Seasonal range (m)**
1990	2.34	April	0.4	October, November	1.9
1991	1.73	April	0.2	August	1.5
1992	1.83	May	0.41	November	1.4
1993	1.66	March	0.01	October	1.7
Mean	**1.89**		**0.26**		**1.63**
2005	1.12	March	0.1	July	1
2006	0.41	May	0.03	August	0.4
2007	0.51	April	0.05	August	0.5
2008	2	April	0	September, October	2
2009	0.82	May	0	October	0.8
2010	1.65	April	0.2	September	1.5
Mean	**1.09**		**0.06**		**1.03**

There has been a decline in the mean annual maximum river level at Sitalike Bridge between the early 1990s and the late 2000s (Table 3.4). While mean level was 1.89 m in the early 1990s, the level for the late 2000s is 1.09 m being a decline of 0.8 m. Between 2005 and 2009 the River has experienced low annual maximum river levels and the river bed was dry in September and October in 2008 and in 2009. However, 2010 river levels were higher than those recorded in 2005-2007 and 2009. (Table 3.4). Monthly river levels in 2010 were higher than 9-year mean for most months although from October levels were lower than 9-year average for the months (Fig. 3.12). Over the study period, river levels at Sitalike were slightly higher than average over the wet season and lower than average in the dry season.

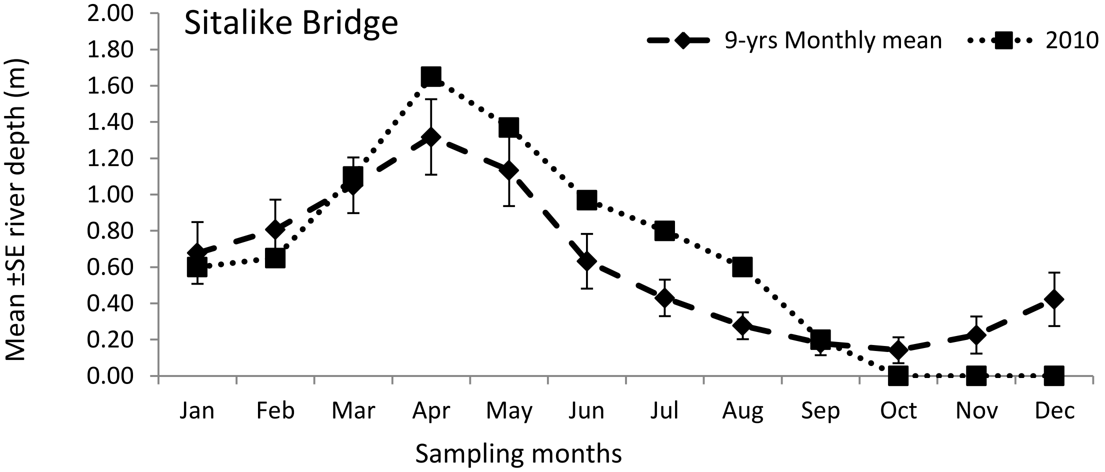


Fig. 3.12: Comparison of monthly mean river depth at Sitalike Bridge during 2010 with the 9-year average river depth in the same site. Error bars are ± SE

Annual mean river levels at Ikuu Bridge (about 40 km downstream of Sitalike) for six years are shown in Fig. 3.13. At 0.84 ± 0.19 m, the average river level in 2010 appeared lower than in previous years although there were no significant differences between the six years ($F_{5,\,58} = 2.049$, $p = 0.087$ NS).

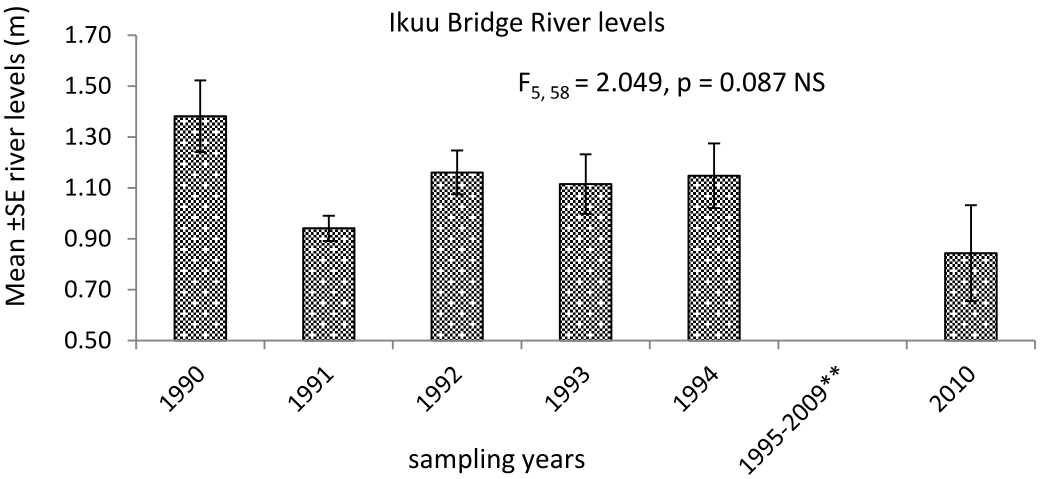


Fig. 3.13: Comparison of six years annual mean river level at Ikuu Bridge along Katuma River, Katavi NP, Tanzania. Error bars ±SE indicate variations between sampling months. ** No river level records exist for the period

Seasonal trends similar to Sitalike Bridge were observed at Ikuu Bridge, where the river stopped flowing in October 2010 (Fig. 3.14). Water levels at Ikuu Bridge from January to March 2010 were much lower than the mean over the previous six years (Fig. 3.14). Mean river levels in April and May 2010 were, however, slightly higher than the six-year average for these months.

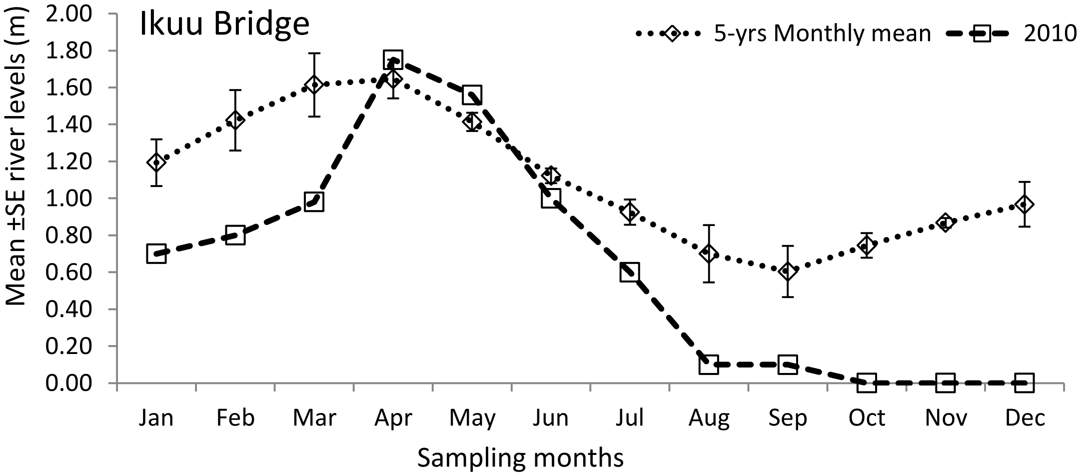


Fig. 3.14: Comparison monthly mean river depth at Ikuu during 2010 with the 5-year average river depth in the same site. Error bars are ± SE

For the years in which measurements were made at Ikuu Bridge, maximum annual level usually occurred in March with minimum levels in August and September (Table 3.5). In 2010, annual maximum level at Ikuu Bridge was slightly higher than the average level for 1990-1994 (Table 3.5). The River did not run dry at Ikuu Bridge between 1990 and 1994 but its minimum level in October 2010 was below 10 cm and not flowing. Dry season water level over the study period was therefore extremely low.

Table 3.5: Maximum and minimum river levels measured at Ikuu Bridge, Katavi NP.

Year	Annual max level (m)	Month with max level	Annual min level (m)	Month with min level	Seasonal range (m)
1990	2.02	March	0.87	October, November	1.2
1991	1.12	January	0.82	September, October	0.3
1992	1.65	March	0.72	October	0.9
1993	1.72	March	0.57	October	1.2
1994	1.69	March	0.52	September	1.2
Mean	**1.64**		**0.70**		**0.96**
2010	1.75	April	0.05	August, September	1.7

3.3 River discharge

The total volume of river water that entered the Park *via* Katuma River and its two tributaries from October 2009 to September 2012 was 9.77 x 10^8 m^3 yr^{-1}. River discharge increased steadily downstream until Sitalike Bridge (Fig. 3.15), then decreased.

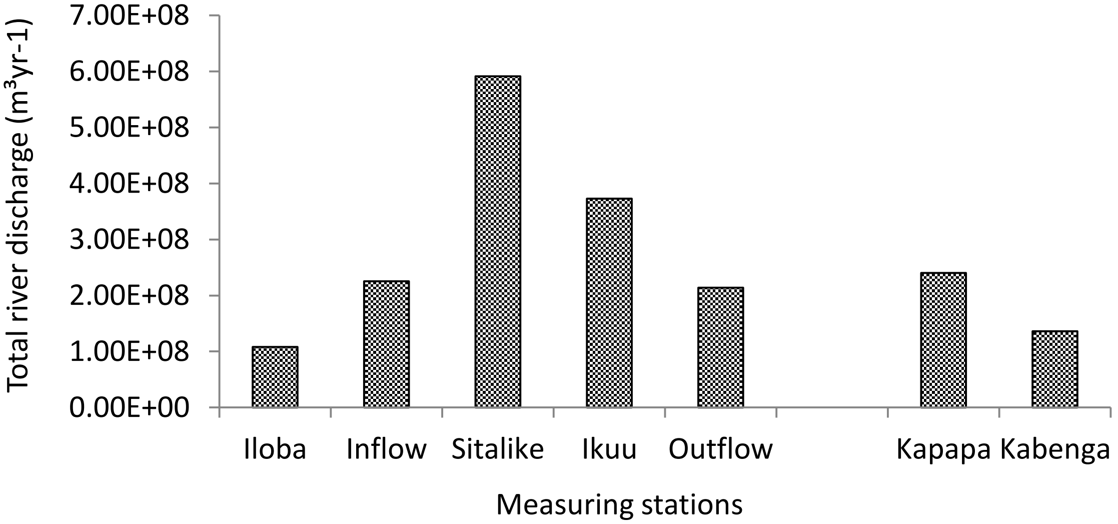


Fig.3.15: Annual total river discharge along Katuma River and the Kapapa and Kabenga tributaries October 2009-September 2010 in Katavi NP and catchment areas.

With the exception of the Kapapa tributary, there were marked seasonal changes in river discharge ($t_{94} = -6.114$ $p < 0.0001$) (Fig. 3.16), with highest discharges during the six rainy months. Discharge varied significantly between sites ($F_{7, 95} = 4.686$ $p < 0.0001$).

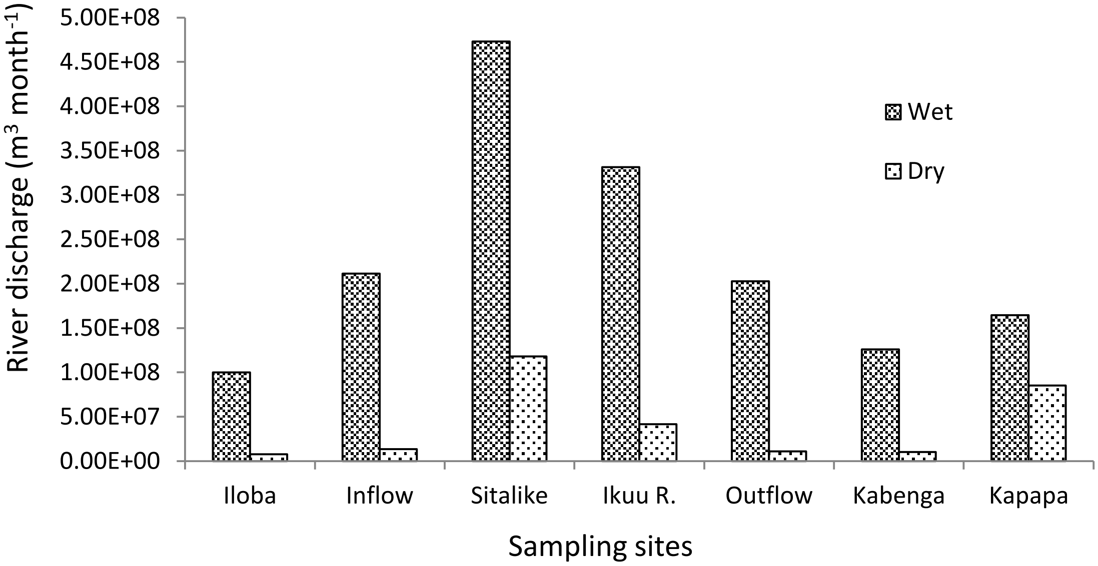


Fig. 3.16: Seasonal variations in river discharge at seven sampling sites during dry season (July-December 2009) and wet season (January-June 2010) in Katavi NP, Tanzania.

River discharge, as expected, varied significantly between sampling months ($F_{11, 95} = 4.427$ $p < 0.0001$), with significant increase in discharge during the rainy months of January- June compared to drier months (July-December), Fig. 3.17.

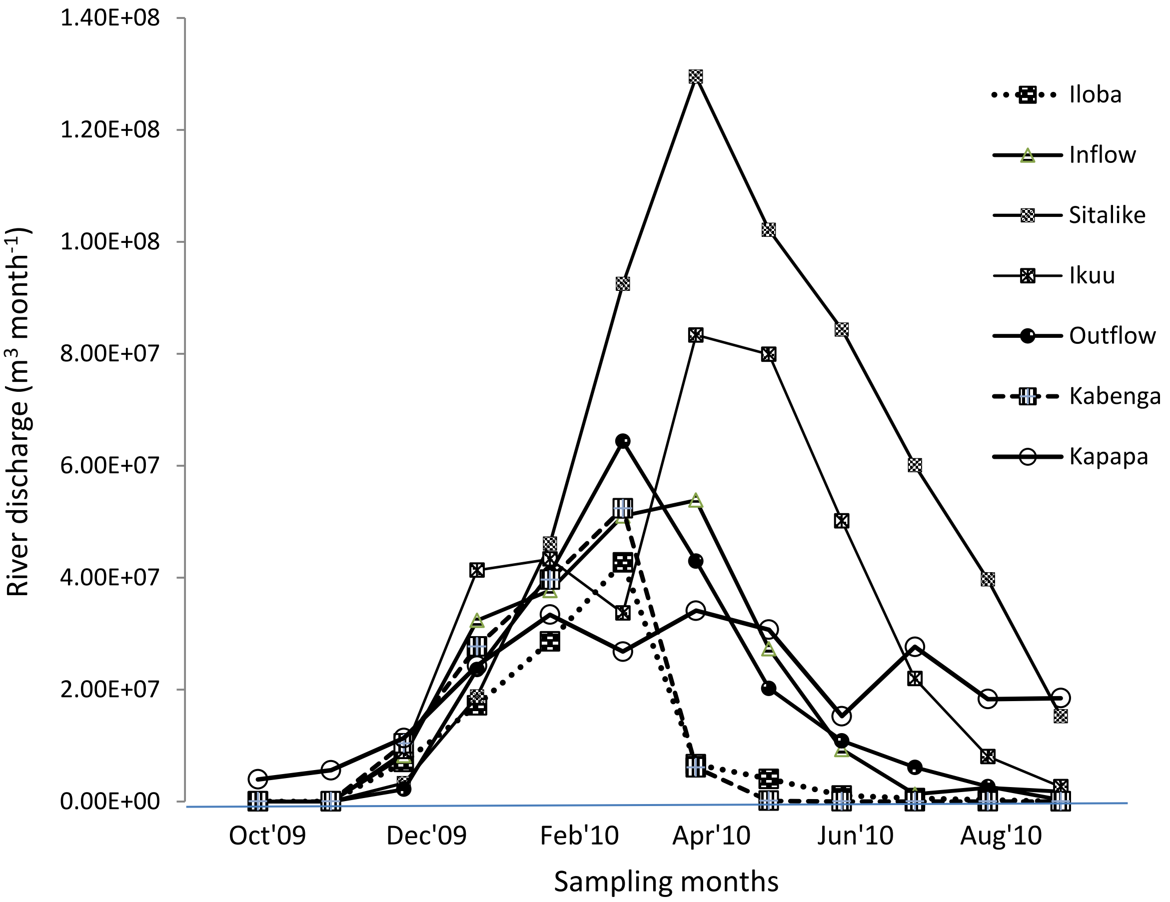


Fig. 3.17: Monthly river discharge (m^3 month^{-1}) at seven sites (five along Katuma River and two tributaries) October 2009-September 2010 in Katavi NP and catchment areas, Tanzania

Although discharge was not measured in Katuma Village near the source of the river in the upper catchment, water was flowing in the channel over the entire study period. However, there was no flow at Iloba Village below Katuma Village by the end of August and in September 2010 even though there was still flow upstream. River flow at Sitalike Bridge, Ikuu Bridge and the Park Outflow stopped during September and October 2009 and started flowing again during the second part of December 2009. The Kapapa tributary had flow throughout the year but the Kabenga ran dry during the second part of July 2010. The percentage of days when flow was estimated to have occurred in each site is shown in Fig. 3.18.

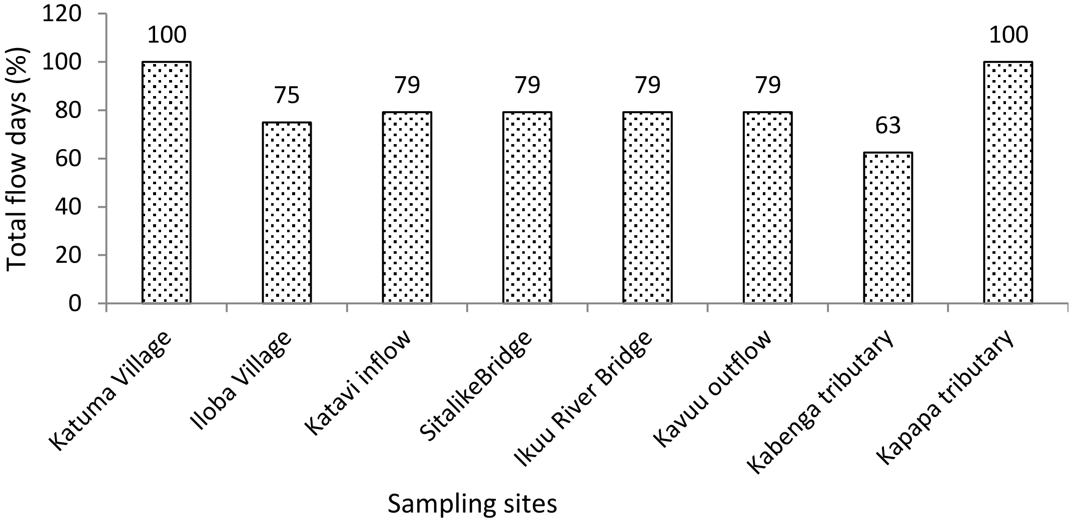


Fig. 3.18: Percentage number of days in a year (October 2009-September 2010) with water flow at the sampling stations in Katavi NP, Tanzania and in the upper catchment of Katuma River.

3.4 Rainfall-River discharge relationships

Relationships between river discharge and anticedant rainfall at the nearest upstream rain gauge (with the exception of Katuma) are presented in Fig. 3.19.

At Iloba in the upper catchment, there was a close and strong correlation between rainfall and river discharge ($r = 0.75$, $n = 20$ $p < 0.001$). River discharge increased as the rainfall peaked and dropped as the wet season ended (Fig. 3.19 (a)).

Rainfall and river discharge where the Katuma River enters the Park showed a similar pattern (Fig. 3.19 (b)), but discharge varied much less closely with rainfall ($r = 0.45$, $n = 20$ $p < 0.05$). As rainfall stopped, there was a corresponding decrease in river discharge.

At Sitalike Bridge, there was no correlation between rainfall and river discharge ($r = -0.14$, $n = 20$ NS) (Fig. 3.19 (c)). Discharge at Ikuu Bridge showed a strong correlation with upstream rainfall ($r = 0.84$ $n = 20$ $p < 0.001$) (Fig. 3.19 (d) and the same occurred at Kavuu where Katuma River leaves the Park ($r = 0.72$, $n = 20$ $p < 0.001$) (Fig. 3.19 (g)).

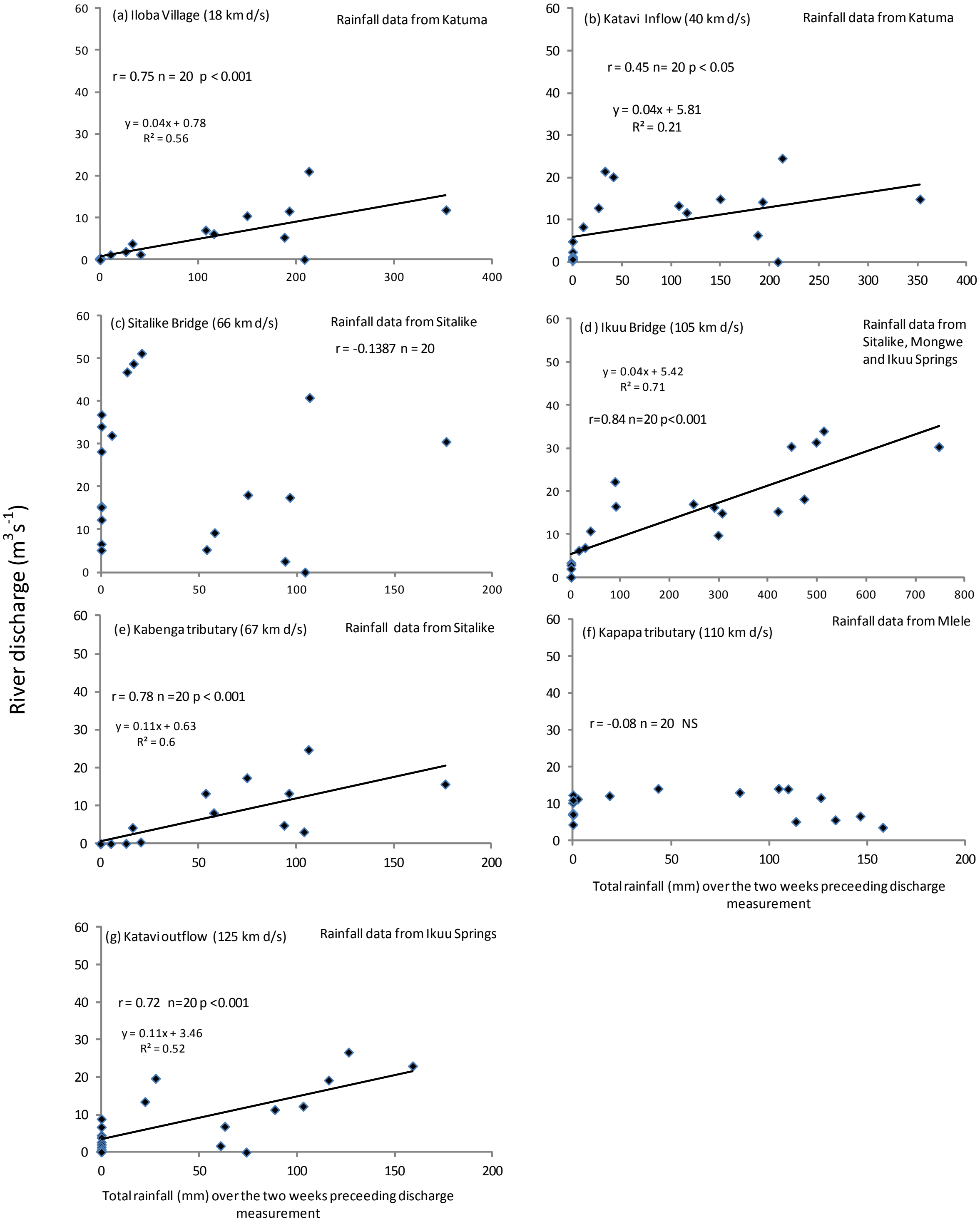


Fig. 3.19: (a-g): Correlation between rainfall and river discharge at five study sites along Katuma River and two tributaries in Katavi NP, Tanzania. Sites are ordered according to distance downstream from the source of the Katuma River. *Key*: d/s represents distance downstream from the source of Katuma River.

Flow in the Kabenga tributary corresponded positively with rainfall ($r = 0.78$, $n = 20$ $p < 0.001$) (Fig. 3.19 (e)) but in the Kapapa tributary, there was no correlation at all ($r = -0.08$, $n = 20$, NS) (Fig. 3.19 (f)). Correlations are summarised in Table 3.6.

Table 3.6: Summary of Pearson correlations between rainfall and river discharge at named study sites

Site name	Distance d/s (km)	r-value	n-value	p-value
Iloba Village	**18**	**0.75**	**20**	**0.001**
Park Inflow	**40**	**0.45**	**20**	**0.05**
Sitalike Bridge	66	-0.14	20	NS
Kabenga (tributary)	**67**	**0.78**	**20**	**0.001**
Ikuu Bridge	**105**	**0.84**	**20**	**0.001**
Kapapa (tributary)	110	-0.08	20	NS
Park Outflow	**125**	**0.72**	**20**	**0.001**

3.5 The Park inflow and outflow balance

Katuma River plus its two tributaries discharged a measured total of $1.72 \text{ X } 10^{9}$ $m^{3}yr^{-1}$ of water into Katavi National Park between October 2009 and September 2010 (Fig. 3.20). The contribution from Katuma River was 1.33×10^{9} m^{3} yr^{-1} with the Kapapa and Kabenga tributaries contributing a total of 3.86×10^{8} m^{3} yr^{-1}.

Water volume in Katuma River increased downstream until Sitalike Bridge when a large loss to flow was recorded (Fig. 3.15). This was despite addition of tributaries at Kabenga near Sitalike and the Kapapa River at Lake Chada. Over the year, the volume of water measured leaving the Park (at the Outflow site) was only about one third of the water volume of 5.91×10^{8} m^{3} yr^{-1} measured at Sitalike.

The amount of water flowing out of the Park *via* the Kavuu outflow was $2.14 \text{ X } 10^{8}$ m^{3} yr^{-1} over the same period. In terms of surface river flows only, the Park thus had a negative water balance from October 2009 to September 2010 of 1.50×10^{9} $m^{3}yr^{-1}$. This balance was therefore used in the Park with a proportion lost by evapo-transpiration and evaporation from open water and soils.

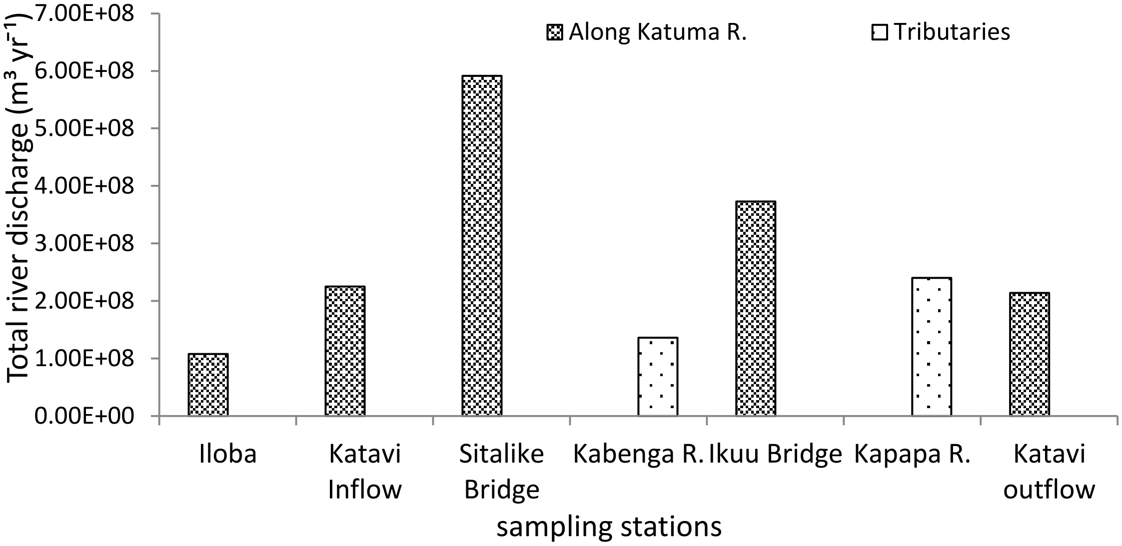


Fig. 3.20: Total river discharge recorded along Katuma River and two tributaries (shown in lighter shading) from October 2009 to September 2010 in Katavi NP, Tanzania.

3.6 Seasonal change in soil water depth

Generally, there was most variation in soil water level at Lake Katavi which was the only site that flooded (between February and April 2010) submerging the tubes. Soil water level remained below the surface in all other sites (Fig. 3.21). The driest month was November and in November 2009, the soil water level was between 150 cm and 180 cm below ground.

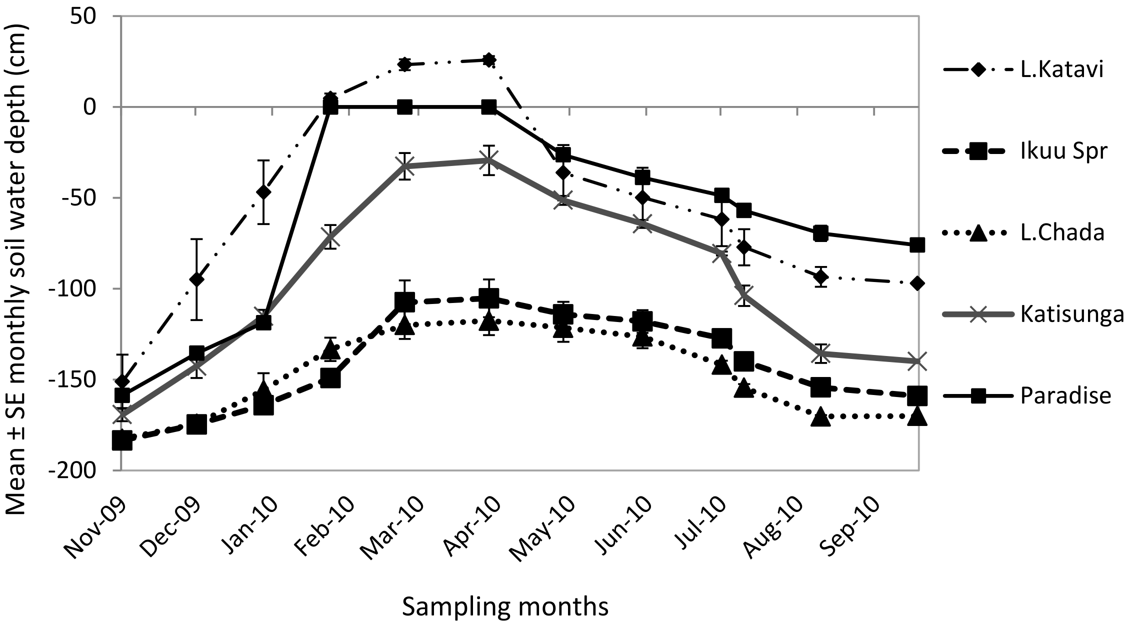


Fig. 3.21 : Depth of soil water in three replicate piezometer tubes at five study sites in Katavi NP, Tanzania from November 2009 to October 2010.

Ikuu Springs and Lake Chada were the driest sites with soil water 1 m or more below ground all year. Soil water depth in Katisunga Plains, one of the major feeding grounds for hippopotami, varied seasonally and although the site did not flood, soil was saturated below about 20 cm in the wet season (Fig. 3.21). Soil in Katisunga Plains and in Paradise Springs flooded quickly in response to rains but dried slowly. Although not recorded because access was impossible, there was evidence that Paradise Springs flooded between February and April.

The two wettest sites in terms of soil moisture were thus Paradise Springs and Lake Katavi and the two driest sites were Ikuu Springs and Lake Chada.

4. Discussion

4.1 Rainfall

With a 10-year average annual rainfall of around 920 mm, Katavi is probably wetter than other semi-arid savannah ecosystems such as Hwange National Park in Zimbabwe (about 700 mm yr^{-1}) and Ruwenzori National Park in Uganda with about 720 mm yr^{-1} (Valeix, 2011). Katavi is thought to benefit from convective rainfall (Meyer *et al*., 2006). The spatial pattern of rainfall in the Katavi region is, however, very patchy with much higher rainfall (1000 - 3000 mm yr^{-1}) in the mountainous upper catchment of the main river that feeds the Park. Southern parts of the Park receive the least rainfall due to their leeward position in relation to an escarpment (TANAPA, 2002, Meyer *et al*., 2006). Water scarcity does not necessarily occur in these areas though because of water supplied by Katuma River and its two main tributaries.

The longest record of rainfall inside the Park is for Sitalike, the Park Headquarters, and the 13-year record shows no trend in annual totals since 1997. Similarly, there is no trend since the 1950s in records from outside the Park. Caro (2008) who studied changes and declines in large mammal populations around Katavi concluded that there has been a small increase in rainfall in the Park since the 1970s and significant increases near the south east boundary of the Park. The IPCC (2001) subjectively predicts that anthropogenically induced climate change and land transformations will lead into an increase of up to 7 % in rainfall by 2050 in the East Africa Region (McDonald *et al*., 2012). However, rise in temperatures of about 0.7 ^{o}C in Africa between 1900 and 2005 (IPCC, 2007; Collier *et al*., 2008) are likely to have impacts on rainfall in the future (IAASTD, 2009).

There is no evidence that rainfall has changed over the recorded period so low rainfall cannot explain the unusually low river levels that occurred from the mid-2000s. Hypothesis one that rainfall in the study area has declined over the last six decades is therefore refuted as rainfall has not declined significantly over the last six decades.

4.2 River levels

Current river levels are lower than in the early 1990s but were particularly low around 2004/2005 when Katuma River stopped flowing for almost three months in the dry season. Water levels in the River at Ikuu in the middle of the Park and downstream on the Katisunga Plains, one of the major dry season feeding grounds for herbivores experienced especially severe declines. Low rainfall did not, however, explain years or periods of water scarcity. According to Meyer *et al*. (2005) and Caro *et al*. (2011), declines in water levels between the late 1990s and 2004 tend to coincide with the building of locally-constructed and illegal dams to store or divert water for irrigation in the upper catchment of Katuma River. Rice in particular is cultivated and this is a very water demanding crop. A similar situation has occurred in Ruaha National Park in Tanzania where rice cultivation and much larger-scale internationally-funded dams have led to the complete drying of the once perennial Great Ruaha River during the dry season (Kashaigili *et al*., 2006; Mtahiko *et al*., 2006; Epaphras *et al*., 2008; Kendall, 2011). Further evidence implicating human impact on water resources in Katavi is that in 2010, water levels in the Park appeared to recover during the wet but not the dry season. Recovery corresponded with regular visits in 2010 by water authorities to inspect upstream dams to ensure that they did not block downstream flow. Follow up visits probably persuaded farmers to release more water into the flow of Katuma River. Additionally, rainfall in 2010 was slightly lower than the previous year yet river levels were higher. However, dry season monthly flows were below average of the respective sites (Fig. 3.12 and Fig. 3.14).

Despite some recovery in 2010, mean river levels in the late 2000s at both Sitalike and Ikuu have declined against their 1990s means and at present, Katuma River runs dry during some months (Lewison, 1998; Meyer *et al*., 2005; Caro *et al*., 2011). Water scarcity during the dry season challenges animals that meet their water requirement mostly from surface waters (Douglas-Hamilton, 1973). The distribution of animals (Western, 1975) and their behaviour is likely to be affected, particularly during the dry season. This has started to be experienced elsewhere in Tanzania: in Ruaha NP (Barnes, 1983; Kashaigili *et al*., 2006; Epaphras *et al*., 2007; 2008), Lake Manyara NP (Fryxell and Sinclair, 1988) and Mikumi NP (Senzota and Mtahiko, 1990).

River levels between 2005 and 2009 support hypothesis that river water levels in the study area have decreased over the last two decades. However, river levels in 2010 at Sitalike do not support the hypothesis because 2010 was higher than previous years but still less than long term mean levels. Mean river levels also declined between early 1990s and late 2000s.

4.3 River discharge

There was flow in Katuma River near its source throughout the study period although in August and September, the River ran dry downstream at Iloba and was dry where the Katuma flows into the Park. Losses to flow between Katuma Village and Iloba which had the greatest effect on the Katuma during the dry season are interpreted as off-take from illegal dams for irrigation. Similar kind of water off-take has been affecting other parks such as Tarangire NP (Gereta *et al*., 2004a), the Mara River ecosystem in the Serengeti (Gereta *et al*., 2003) and Ruaha NP (Kashaigili *et al*., 2006; Mtahiko *et al*., 2006; Epaphras *et al*., 2007; 2008). In Rubondo NP in Lake Victoria in Tanzania, water levels are threatened by water up take for hydroelectricity dams (Elisa *et al*., 2010). Similarly, in Kenya, agricultural expansion in the Mara Region has affected the hydrologic aspects of the Mara River basin in Kenya and Serengeti in Tanzania (IUCN, 2000; Gereta *et al*., 2002; Kanga *et al*., 2011a; 2011b). In Asia, similar use of water resources resulted in some rivers running dry for some months during the dry season (Jablonski, 2004). Such kind of water uses has led to calls for more utilization of underground waters (MacDonald *et al*., 2012), as surface waters are unlikely to meet growing demands of the growing populations in Africa. This is coupled with the predicted declines in river flows due to projected increase in global temperatures (IPCC, 2001).

In terms of total annual discharge, Katuma River accumulated flow downstream until Sitalike when the total flow volume in the River decreased. This downstream pattern is affected by the Park's downstream sequence of very large seasonal swamps, Lake Katavi, Katisunga Plains and Lake Chada. These areas flood forming open water during the wet season and recede to dry savannah grassland during dry seasons. The swamps function as water stores accumulating water in the wet season and releasing water to downstream flow in the dry season. This pattern is likely to be essential for sustaining dry season flows in Katuma River.

Downstream water volume approximately doubled between where Katuma River flows into the Park and Sitalike. This increase may reflect additions of run-off from northern woodlands that receive high rainfall.

Between Sitalike and Ikuu Bridge, flow volume in the River decreased despite receiving water from the Kabenga tributary. The contribution from the Kabenga was relatively small and over the period of this study, the tributary stopped flowing during the dry season. The Kabenga drains cultivated land near the village of Sitalike and human impacts on flow are very likely. Reduced flow at Ikuu Bridge was more probably because the upstream flow recorded at Sitalike Bridge discharges into Katisunga Plains where losses *via* evapo-transpiration from the very large and flat plains will be enormous. The same process must have occurred in the shallow basin of Lake Chada in the southernmost part of the study area.

Rates of evaporation in the tropics are usually much higher than precipitation (Peterson, 1973; Wilhelm, 1993 as quoted in Meyer *et al*., 2005; Shorrocks, 2007) so water inputs to such areas will be greater than the downstream outflow and this is reflected in Katuma River's overall negative water balance in the Park. These natural processes leading to water loss probably explain the relatively low river discharge at the outflow to the Park compared to the inputs to the Park. Example of such water losses from tropical wetlands have been linked to fluctuations in water levels in Lake Naivasha in Kenya (Boar, 2006). Despite water losses, the seasonal swamps in the Park conserve and regulate water resources releasing water slowly to further downstream in the dry season.

The Kapapa tributary had a substantial discharge throughout the study period. This river arises from a forested sub-catchment that is much less influenced by human activities than the Kabenga. Although rainfall patterns were similar in the Kapapa and Kabenga sub catchments, the Kabenga had no flow during the peak of the dry season which may be linked to illegal cutting of forest. Forest clearance is on the increase outside the Park boundary and the water retaining capacity of the catchment is likely to be decreasing as a result. This adds a further human influence that is consistent with the recent changes and geographical variations in the flow and the duration of flow in Katuma River.

4.4 Relationships between rainfall and river discharge

There is a time lag between rainfall and river discharge response (Gordon *et al*, 1992). This is complex and the lag time is influenced by channel morphology, gradient, soils, infiltration rates and vegetation. In this study, a time lag of two weeks resulted in some fairly close correlations between rainfall and discharge. This suggests that inputs from ground water-fed springs are very much less important than direct rainfall in sustaining the flow of Katuma River. Correlations were not detected in two sites which were Sitalike Bridge and the Kapapa. Lack of correlations between rainfall and river discharge at Sitalike might be linked to water retention upstream in seasonal Lake Katavi although there was a rainfall-flow correlation at Ikuu Bridge, which is downstream Katisunga Plains where retention of flow would also have occurred.

The closest relationships were expected in sites with the least upstream human impact on flow, for example in the Kapapa tributary. There was, however, no detectable relationship between rainfall and discharge in the Kapapa. Rainfall (gauged in Mlele) stopped in May but the Kapapa continued to flow throughout the study period with maximum discharges recorded in January to March (maximum rainfall was in December, January and March). Lack of correlations might have been due to the long distance to the rain gauge which was on the top of the escarpment, the complication of the network of streams that drain the escarpment or a large contribution from water retained in its sub-catchment being released slowly. Dry season flow in the Kapapa was higher in relation to its wet season flow than in any other site. This suggests that water released from sub-catchment makes a large contribution to the dry season flow of this tributary. Springs have great local importance for wildlife in Katavi and two spring-fed sites are studied in the animal behaviour work. The contribution of groundwater to the flow of the main Katuma River is, however, unknown. According to MacDonald *et al*. (2012) and IAH (2012) ground water is a major source of fresh water in Africa with the greatest reserves in North African countries. In Tanzania and elsewhere in East Africa, however, aquifers are very deep and inaccessible (MacDonald *et al*., 2012) and open waters and rivers most usually result from runoff from surface drainage catchments. This is consistent with observations made in this Chapter in that significant contributions of groundwater within the boundary of the Park to the flow of the Katuma during the dry season are unlikely, given the observed drying of the River. In appendix 1 basic water quality monitoring data are presented which do not indicate any signals from base flow but this is also the case downstream from known springs such as Paradise Springs so does not preclude there being ground water input to the river.

4.5 Seasonal changes in soil water depth

Lake Katavi was the only site where flooding was measured. It is probable that flooding also occurred at Paradise Springs although this was not recorded because the site was not accessible at the time when peak levels occurred at other sites. Soil water depth responded to rainfall. This is probably because ground water is driven by recharge from the catchments (McCallum *et al*., 2011) which depend on rainfall. Rainfall, surface runoff and underground water inflow are the major determining factors for underground water levels (Cook *et al*., 2008). These sources of water in the ground have also been reported by Yuretich (1982) and Olago *et al*. (2009) in Kenya to determine water availability in East African rift valley lakes and hence underground water depth. In the Katisunga Plains, water level rose quickly in response to the beginning of the wet season. However, water levels did not go above ground at the measuring site. Soil wetness at Ikuu Springs and Lake Chada increased more steadily in response to rain than in the plains and did not decline as dramatically in the dry season as at the other three sites (Fig. 3.21).

On the three sites that responded most quickly to rains that fell in January and April 2010 (Lake Katavi, Paradise Springs and Katisunga), underground water levels dropped quickly after May 2010. The rate of soil drying was greatest in Katisunga, followed by Lake Katavi. Paradise Springs dried at a much slower rate. Differences in the rates at which the sites wetted or dried were obvious during visits to the sites and these differences are reflected well in the data collected from the piezometer tubes. Differences between the absolute wetness or dryness of the five sites are reflected less well by soil water depths because tubes were not positioned in the wettest parts of each site. The wettest parts of each site were the least accessible, usually the most vegetated with swamp grasses and often used by large animals (buffalo and elephant). The difference in elevation between the piezometer locations and the lowest and wettest point at each site also varied between sites. However, wetting and drying rates are reliable and the absolute soil water levels measured also serve to show that within areas used by hippopotami, in the dry season soils in some sites were not saturated until about 1.5 - 2 m below ground.

The results of this Chapter describe the seasonality of wetness along the Katuma River and the five sites in which hippopotamus behaviour was studied and will be linked to aspects of their distribution, abundance and behaviour in Chapter 8.

5. Conclusions

Amount of annual rainfall in the Katavi area have not changed consistently over the last 60 years. Although there have been relatively wet and relatively dry years, there is no overall trend. Years for the present study, 2009 and 2010 were about average in terms of total rainfall.

Low rainfall does not therefore explain observed declines in river level, flow volume or flow duration in some key wildlife areas of the Park. Particularly low river levels reported in the 1990s and 2000s (Meyer *et al*., 2005) were not due to low rainfall. Increased water scarcity is unlikely to be related to increases in evaporation or evapotranspiration because air temperatures recorded at the park have remained relatively the same since monitoring in the Park began in 1997/8. However, a general long term trend in Africa as a whole indicate rise in temperature between 1900 and 2005 (IPCC, 2007; IAASTD, 2009) and decreased precipitation.

Although essential to the wildlife ecology of the Park, particularly locally in areas such as Paradise Springs, groundwater is not thought to be significant in terms of sustaining the flow of Katuma River. Evidence for this is in the dry-season drying of the river and that river discharge is related to rainfall in almost all sites along the river. Ground water resources in the Park have not been quantified partly because of the remote locations of springs. This creates a gap in our knowledge about this important water source.

Declines since the 1990s in flow duration of the river and early drying of the river observed in this study implicate upstream loss of flow to small-scale illegal irrigation in the upper catchment of the river. Deforestation in the catchment remains a concern because of the resulting reduced capacity of soils and vegetation to retain wet season rainfall. Water scarcity may well continue in the Park. To safe guard the habitats of the Park and wildlife, there is a great need to continue monitoring river flows so that Park management can react and perhaps exploit deep ground water when surface flows are low.

Chapter 4: Hippopotami Food Resources

1. Introduction

This work is about hippopotami ecology and behaviour in relation to water resources. Study sites were chosen to span a wetness gradient assuming that food resources would be available and accessible to hippopotami in each of the sites. This chapter tests this assumption. Food availability is likely to vary from site to site and change over the course of seasons. Hippopotami are mainly herbivores (Arman and Field, 1973) and feed mainly on terrestrial vegetation (Laws, 1968; Field, 1970; Kingdon, 1982; Eltringham, 1999; Lewison and Carter, 2004) with a diet that consists mainly of grass. Measures of grass and other low-growing herbaceous species biomass have therefore been made seasonally in each of the five hippopotami study sites. Species cover, height, and greenness measurements were made seasonally in four of the hippopotami study sites and one feeding site.

The distribution of Katavi vegetation is mainly explained by geology, soils and relief (TANAPA/WD, 2004; Meyer *et al*., 2006). Katavi is almost exclusively situated in the Rukwa Rift Valley which is part of the East African Rift Valley (TANAPA/WD, 2004, 2004). Most of the surface area is 800-900 m a.s.l. and the Park is characterized by a flat and undulating terrain. In the northwest, southwest and northeast elevation increases to 1100 m a.s.l. (TANAPA/WD, 2004, 2004). Most soils in Katavi are alluvial originating from the plains and deposited in the valley bottom over the last 3 million years (Meyer *et al*., 2006). A major part of Katavi thus consists of young quaternary alluvial layers (Meyer *et al*., 2006). Generally, soils have high sand content and are rather infertile (TANAPA/WD, 2004, 2004). The soils are also acidic with very low organic content (Frost, 1996).

Katavi National Park is located almost entirely in the Miombo woodland which covers more than 70% of the Park. Miombo woodlands dominate the southern Africa region (Ryan & Williams, 2011). Apart from a diverse tree community (Coates Palgrave *et al*., 2002), Miombo harbours common grasses such as *Hyparrhenia, Andropogon, Loudetia* and *Digitaria* and the Miombo may support up to 20% of the grazer feeding or grass biomass (Frost, 1996). Grass biomass decreases with increasing tree biomass (Frost, 1996). Grassland on open plains in Katavi is dominated by grasses (Poaceae) and other herbaceous (non woody) plants or forbs (Meyer *et al*., 2005; 2006). Cyperaceae (sedges) and Juncaceae (rush) also occur. Savannas are characterized by a continuous cover of annual and perennial grasses and an open canopy of trees resistant to drought, fire and browsing. There may also be an open shrub layer. Grasses vary considerably in height within the grasslands.

Savanna grassland (herein referred to as grassland), is a major terrestrial biome with C_4 plants (in which carbon dioxide fixation occurs predominantly by the Hatch-Slack pathway (Cammack *et al*., 2008)) being the majority and with few and scattered C_3 plants (in which CO_2 fixation occurs predominantly by the reductive pentose phosphate cycle) (Beerling & Osborne, 2006; Cammack *et al*., 2008). C_4 plants are reported to dominate because they successfully inhabit hot, dry environments and have very high water-use efficiency compared to C_3 plants; C_4 pathways can double C_3 photosynthesis (Mayhew, 2009). Tropical savannas or grasslands are associated with uneven annual rainfall ranging from 760 – 1270 mm and a wet and dry climate. Rainfall in Katavi is strongly seasonal with the wet season followed by about five dry months.

About 25% of Katavi National Park area is savanna grassland on open plains (Fig. 5.1). The plains form the main feeding and resting habitats for hippopotami (and other herbivores). The grass available from the plains and woodlands in Katavi is therefore estimated to cover about 45% of the total Katavi area.

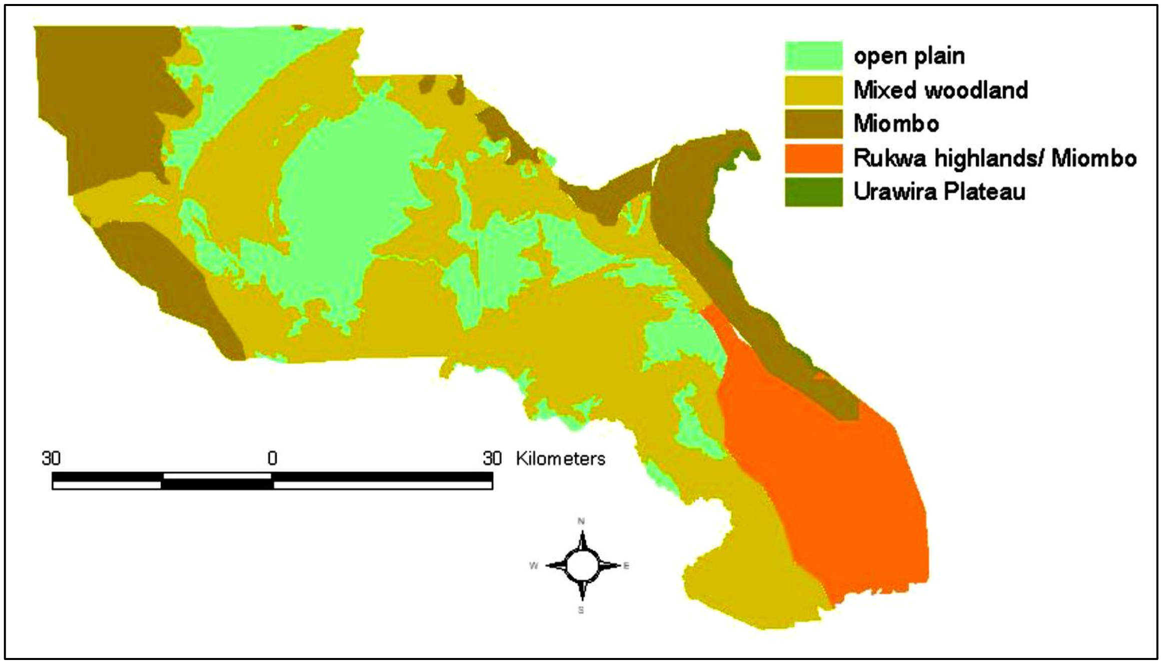


Fig. 5.1: Major vegetation types in Katavi National Park: *Source*: Katavi KRCD, 2006

Savanna ecology is influenced by periodic fires as well as rainfall and grazing (Ryan & Williams, 2011). Fire may influence grassland species composition and structure (Bond *et al*., 2005; Bowman *et al*., 2009). Edwards & Allan (2009) found correlations between areas of the country burnt and two year cumulative rainfall in Australia. It has been reported that under annual burning, Miombo woodland is converted to grassland (Furley *et al*., 2008), and that fire frequency determines tree cover. Katavi grasslands, as for other areas in savannas, are exposed to and strongly influenced by fires (Meyer *et al*., 2006).

Seasonality (wet and dry seasons) and grazing are likely to affect the food resource available to hippopotami. As with water availability, vegetation is an essential environmental resource for hippopotami and is likely to affect their behaviour on temporal and spatial scales. Apart from water resources, vegetation has been listed as the other limiting factor for hippopotami (Harris *et al*., 2008; Wilbroad and Milanzi, 2010; Chansa *et al*., 2011). This was the basis for including vegetation in this behaviour study. Hippopotami observation sites and vegetation study sites were located within savanna grassland of Katavi or the edges of Miombo woodland because these habitats are used for resting and feeding.

Hippopotami require aquatic habitat (Field, 1970) and forage primarily at night (Laws, 1968). This leads to spatial and temporal constraints on their foraging behaviour (Lewison and Carter, 2004). It has long been reported that their diet consists mainly of grasses (Kingdon, 1982; Eltringham, 1999; TAWIRI, 2001). Grass expansion in Africa during the Pliocene has been linked to success of early hippopotami (Boisserie & Merceron, 2011). However, some current studies have reported that they feed on dicotyledons vegetation to an extent too (Boisserie *et al*., 2005; Cerling *et al*., 2008; Harris *et al*., 2008). Mugangu and Hunter (1992) reported minor quantities of dicots in hippopotami diet in Zaire (DRC Congo). Grey and Harper (2002) reported hippopotami feeding on macrophytes or aquatic vegetation when plant stands were abundant in shallow water in Lake Naivasha, Kenya. More studies in East and Central Africa and Lake Turkana in Kenya using stable carbon ratios (analysis of hippopotami teeth enamel and hair tissues) showed a higher fraction of dietary non grass food materials in hippopotami diet than estimated by traditional observations (Cerling *et al.,* 2008; Harris *et al*., 2008).

Hippopotami select short grassland for feeding (Lock, 1972; McCarthy *et al*., 1998; Harrison *et al*., 2007), mainly with swards less than 15 cm tall (Lock, 1972; McCarthy *et al*., 1998; Spinage, 2012) but are non-selective in terms of grass species they eat particularly during scarcity. Nevertheless, some studies have reported them as selective grazers (Chansa *et al*., 2011). They ingest both standing dead as well as green material (Meyer *et al*., 2005). Lewison was quoted by Meyer *et al.* (2005) reporting that in times of scarcity in Katavi, hippopotami ate short grass unselectively ingesting sand, found later during postmortem analysis of stomach content. Harrison *et al*. (2007) reported highest hippopotami feeding intensity in areas with low growing grass in Malawi. Hippopotami cannot forage in tall grassland because they are unable to chop and grind their food but tears of by gripping using their lips (Spinage, 2012). In Malawi, highest grazing intensity was recorded by Harrison *et al*., (2007) in areas of flood plain and flood plain grassland with grass height at around 15 cm. Due to this feeding strategy, sward heights were measured in this study because this is also a measure of forage availability.

There have been reports of carnivory in hippopotami (Dudley, 1998). However, these are reported as rare and are thought to be fulfilling a nutritional need of hippopotami as vegetation often lacks essential nutrients or trace elements (Eltringham, 1999; Grey and Harper, 2002). Grasses in Miombo have low nutrient contents due to poor nutrient in the soils (Ryan, 2011).

Hippopotami mainly feed at night (Laws 1968; Field, 1970; Kingdon, 1982; Eltringham, 1999; Lewison and Carter, 2004; Chansa *et al*., 2011), but this study was not focused on feeding ecology and the study was restricted to day time behaviour only. Day time feeding is however, one of the behaviour traits recorded during this study. It has been reported that hippopotami employ foraging strategies that respond to vegetation characteristics such as vegetation quality, quantity and distance to water source (Lewison and Carter, 2004). This necessitated the study of vegetation in Katavi, particularly grasses in order to explain the possible relationship with hippopotami abundance and behaviour both on a temporal and spatial basis.

Ecological studies often involve measuring sward height (Stewart *et al*., 2001) and biomass. Sward height and biomass have been used as predictors of available pasture (Sharrow, 1984), and have been reported to closely correlate. It has been reported that biomass estimation by harvesting is costly and destructive (Reese *et al*., 1980). However, due to costs concerns, allometric relationships can be used to estimate understory biomass (Andariese & Covington, 1986). Despite costs or destruction concerns, biomass estimation has been found and remains essential (Reese *et al*., 1980). According to Guevara *et al*. (2002), plant destruction during biomass estimation is important and worthwhile.

Biomass has been reported by Collins & Weaver (1988) as the best indicator of the amount of material available for grazers. Biomass measures have also been reported to have many uses in the study and management of plant communities (Collins & Weaver, 1988), hence its adoption during this study, instead of measures of grass production that would involve much more frequent sampling effort than available in the present study.

In order to support the study on behavioural responses of hippopotami, some vegetation resources parameters were studied as forage forms a second important component in hippopotami habitat apart from water resources. Among the parameters measured in this study were plant mass (biomass + standing dead mass), sward height, percentage cover by vegetation and greenness in the five sites where hippopotami behaviour was observed. In vegetation sampling, some attention was paid to the selection of grazing sites for hippopotami or near resting sites. These were expected to help explain the patterns of behaviour observed. While results for food resources are presented in this Chapter, relationships between food resources and hippopotami distribution and abundance, immigration, emigration and behaviour are discussed in Chapter 8.

1.1 Aims and hypotheses

The aim of this work is to test the prediction that hippopotami resting sites have all year round feeding grounds and that their distribution and behaviour is not limited by feeding opportunity. It was anticipated that the effects of water and food availability on hippopotami distribution and behaviour cannot be separated. The major objective for plant sampling was to quantify total plant mass, biomass (g dry weight m^{-2}) and standing dead mass (g dry weight m^{-2}) in the five hippopotami key resting or shelter areas (behaviour recording sites). The study was also aimed at estimating variations in sward height, greenness and percentage ground cover between the feeding grounds in or near hippopotami's resting sites. The study therefore tested the following hypotheses:

Hypothesis$_1$: Green plant mass is available throughout the year within 5 km of all the sheltering or resting sites

Hypothesis$_2$: Sward height is not limiting hippopotami availability of ground biomass feeding.

Hypothesis$_3$: Plant biomass is the same in the five hippopotami study sites.

Hypothesis$_4$: There are seasonal variations in plant mass in the study sites

Hypothesis$_5$: Grass species dominate the ground vegetation community of the hippopotami feeding areas.

2 Methods

2.1 Site selection

This section gives descriptions that focus on the vegetation community present in each site, ordered in decreasing wetness. The main features of the sites are summarised in Table 5.1 and a map is shown as Fig.5.2. Each site has a different source or sources of water and taken as a whole, represent well the habitats of the National Park. All vegetation study sites were within 5 km of hippopotami resting or sheltering sites. Sward height, greenness, cover and plant mass (biomass and standing dead mass) were estimated for each of the sites. Sites are described in Chapter 2.

Table.5.1: Summarised descriptions of study sites in Katavi National Park.

Site Name	**Location**	**Main source of water**
a) Paradise Springs	Adjacent Kapapa River	Perennially River + Spring fed
b) Ikuu Springs	Adjacent Katuma River	Perennially spring fed
c) Lake Katavi	Katuma River (Northern site)	Seasonally River + Some minor spring fed
d) Ikuu River	Along Katuma River	Seasonally river fed
e) Lake Chada	Katuma River (Southern Site)	Seasonally river fed

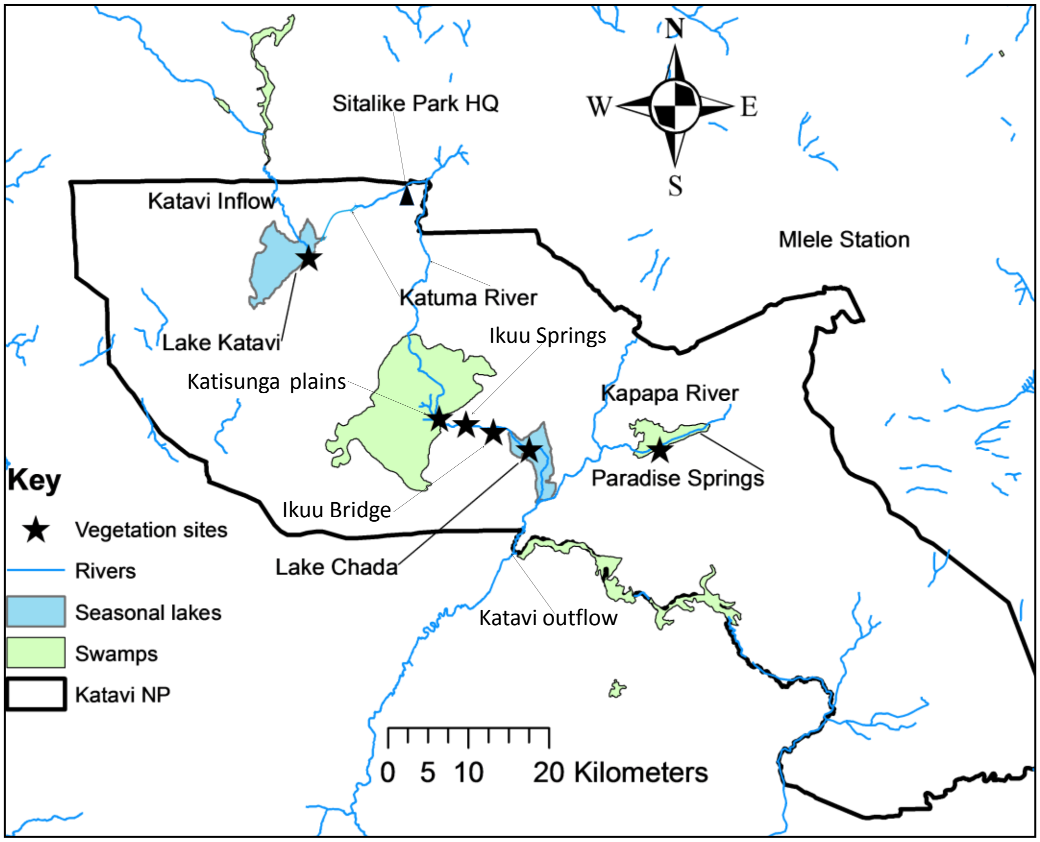


Fig. 5.2: Map of Katavi National Park showing five vegetation study sites.

Sward height, percentage greenness and percentage cover, were also monitored at an additional site, Katisunga Plains. This was added because of its size, and importance as a dry season feeding ground for a large numbers of herbivores in the Park, including hippopotami in the Ikuu sampling areas. Katisunga is predominantly flood plain grassland fed by the main Katuma River and some springs. The area covers about 250 km^2. The area has small dendritic channels that receive water from surrounding areas. The area was selected for sward height and greenness measurements because it is a major feeding ground for a large number of hippopotami from nearby hippopotami resting sites. The site was added to pair with Ikuu Bridge for measurements because the Ikuu Bridge resting site is a narrow (about 30 m) riparian strip. Many hippopotami tracks lead from Ikuu Bridge to Katisunga which is about 2.5 km from the Ikuu Bridge hippopotami resting site (Fig. 5.2).

2.2 Sampling frequency

Plant mass, biomass and dead mass were measured seasonally. Samples were taken in August/September 2009, (the driest months), January-March 2010 (the wet season) and May 2010, during the end of long rains, the wettest period. The last samples were taken in August 2010 to represent the beginning of the next dry season.

Sward height, percentage cover by ground vegetation and sward greenness were sampled monthly from October 2009 to September 2010. In February, March and April 2010, Paradise Springs was completely inaccessible and vegetation data are therefore missing.

2.3 Cover (%) by ground vegetation.

Vegetation cover was measured within the same quadrat used for sward height measurements in Section 2.4. While sampling sward height, percentage coverage of vegetation was estimated within the quadrat's 1 X 1 m area. This was done visually by estimating the proportion of the quadrat covered by vegetation and by bare ground.

2.4 Sward height

Sward height was measured using a sward stick. A sward stick is a calibrated 1.5 m metal rod in a 30 cm diameter disc made of aluminium sheet with a hole at the middle for sliding the disc along the metal rod. The disc area was 0.07 m^2 and weighed 0.41 kg and had a thickness of 2.5 mm. The rod was attached to the disc using soft wire string. The rod was calibrated to the nearest 5 cm, but more exact reading was done by reading to the nearest cm on the corresponding 5 m tape measure. When the sward height was relatively very low, only the tape measure was used to record the height as the disc was not effective in such cases. This was repeated using disc to calibrate the two methods.

At each site, a randomly selected plot measuring 100 m x 100 m was selected within which ten randomly selected sub-plots were located and measurements conducted for sward height. Sub-plot points were obtained by using a table of random numbers. At each of the ten sub-plots, a 1 x1 m quadrat was placed and sward height was measured at each corner. Measurement was carried out by lowering the sliding disc on the rod until the disc rested on the sward.

Average sward height was obtained by calculating the mean of the forty corners of the ten 1 X 1 m quadrats.

2.5 Sward greenness

Sward greenness was estimated within the same quadrat used for sward height measurements described in Section 2.4. Sward percentage greenness in the quadrat was estimated visually by observing and estimating the contribution of green vegetation to vegetation in the quadrat.

2.6 Plant mass, biomass and standing dead mass

Plant mass, biomass and standing dead mass were measured by cutting, drying and weighing vegetation in three replicates measuring 25 cm X 25 cm quadrats in each site. Quadrats were positioned at random within 100 m X 100 m sampling area.

All vegetation in each quadrat was clipped. Within each quadrat, only stems that emerged from within the quadrat area were included in the sample. Plant litter and any other material that was not rooted in the quadrat was removed. Thereafter, all attached stems were clipped at soil level and divided into green, living stems and standing dead stems. Stems were classed as living if 5% or more of their surface appeared green. Any herbaceous, non-grass species were sampled and kept separately.

Living stems, standing dead stems and other species were bagged separately and kept in labeled paper envelopes and air dried for 10 days. Envelopes were stored in a dry place before later oven drying at 60°C to constant weight and then weighing to the nearest 0.01 g on a Mettler top pan balance. Results are expressed as means of the three replicate quadrats scaled to per m^2. A total of 60 quadrat samples were collected over the study period. The total number of plant species was recorded for each quadrat giving a measure of species richness in each of the foraging sites.

2.7 Data analysis

Data were summarised and analysed using SPSS statistical software PASW 18 and the Microsoft Excel data analysis tool. Results were summarised as monthly, seasonal and annual means with their standard errors, correlations were performed using Pearson correlations and differences between sites or groups of sites were analysed using one way ANOVA.

3 Results

3.1 Cover (%) by ground vegetation.

Mean annual cover by ground vegetation varied between 50 ± 7.0 % at Lake Katavi and 58 ± 8.0 % at Ikuu Springs (Table 5.2). Cover by ground vegetation varied between months ($F_{11, 44} = 39.001$, $p < 0.0001$), and did not show significant variations between sites. Annual maximum cover by ground vegetation was recorded at Ikuu Springs while the minimum at 13 % was recorded at Lake Chada (Table 5.2).

Table 5.2: Summarised cover (%) by ground vegetation recorded at named study sites from October 2009-September 2010 in Katavi NP (% cover was not measured at Ikuu Bridge).

Study site	Annual maximum cover (%) by ground vegetation	Annual minimum cover (%) by ground vegetation	Mean annual cover (%) by ground vegetation
Paradise Springs	89	27	55 ± 8
Ikuu Springs	93	20	58 ± 8
Lake Katavi	84	19	50 ± 7
Lake Chada	88	13	55 ± 8

Some grass vegetation was present in all the study sites throughout the study period. Maximum vegetation cover was recorded in April 2010 at Ikuu Springs (93 ± 0.8 %) and the least was in October 2009 at Lake Chada (13 ± 1.9 %) (Fig.5.3)

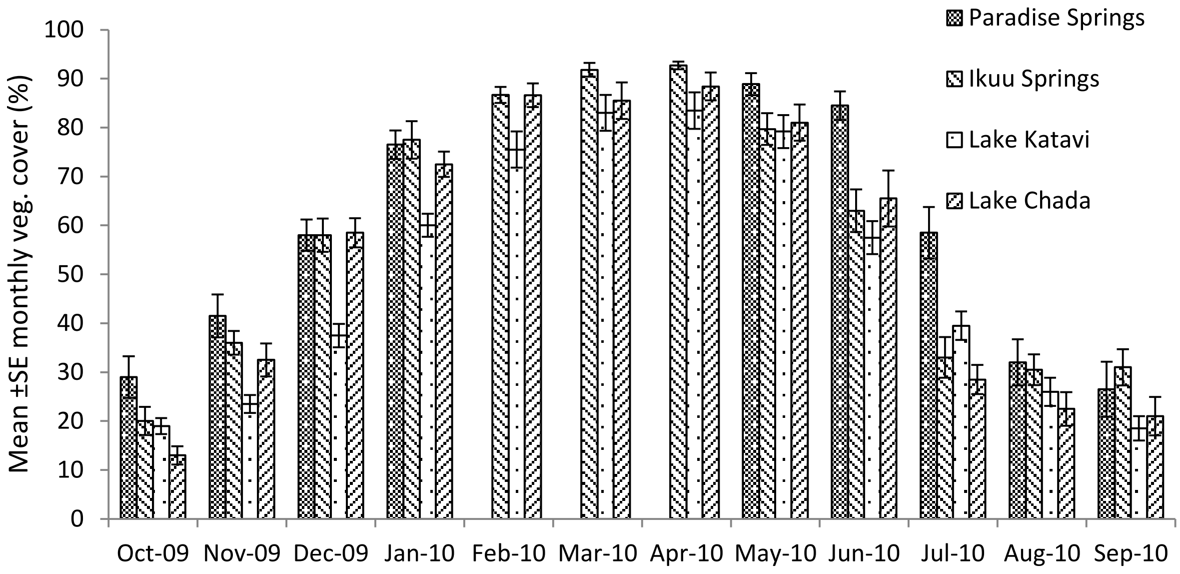


Fig. 5.3: Mean monthly cover (%)by ground vegetation in the four vegetation sampling sites in Katavi NP, Tanzania. Error bars are ± 1SE around monthly mean.

3.2 Sward height

Mean annual sward height ranged from 27 ± 6 cm at Lake Katavi to 32 ± 6 cm at Ikuu Springs (Table 5.3). Vegetation was generally tallest in April and May and varied between months ($F_{11,\ 44} = 22.079$, $p < 0.0001$), but not between the study sites. The maximum sward height of all sites was recorded at Ikuu Springs in April 2010 (68 ± 5.9 cm). The shortest sward height was 3.0 cm recorded at Lake Chada in October 2009 and September 2010 (Table 5.3 and Fig. 5.4).

Table 5.3: Summarised sward height (cm) recorded from October 2009 to September 2010 at the named study sites in Katavi NP.

Study site	Annual maximum Sward height (cm)	Annual minimum Sward height (cm)	Mean Annual sward height (cm)
Paradise Springs	66	5	31 ± 7
Ikuu Springs	68	6	32 ± 6
Lake Katavi	58	5	27 ± 6
Lake Chada	61	3	30 ± 6

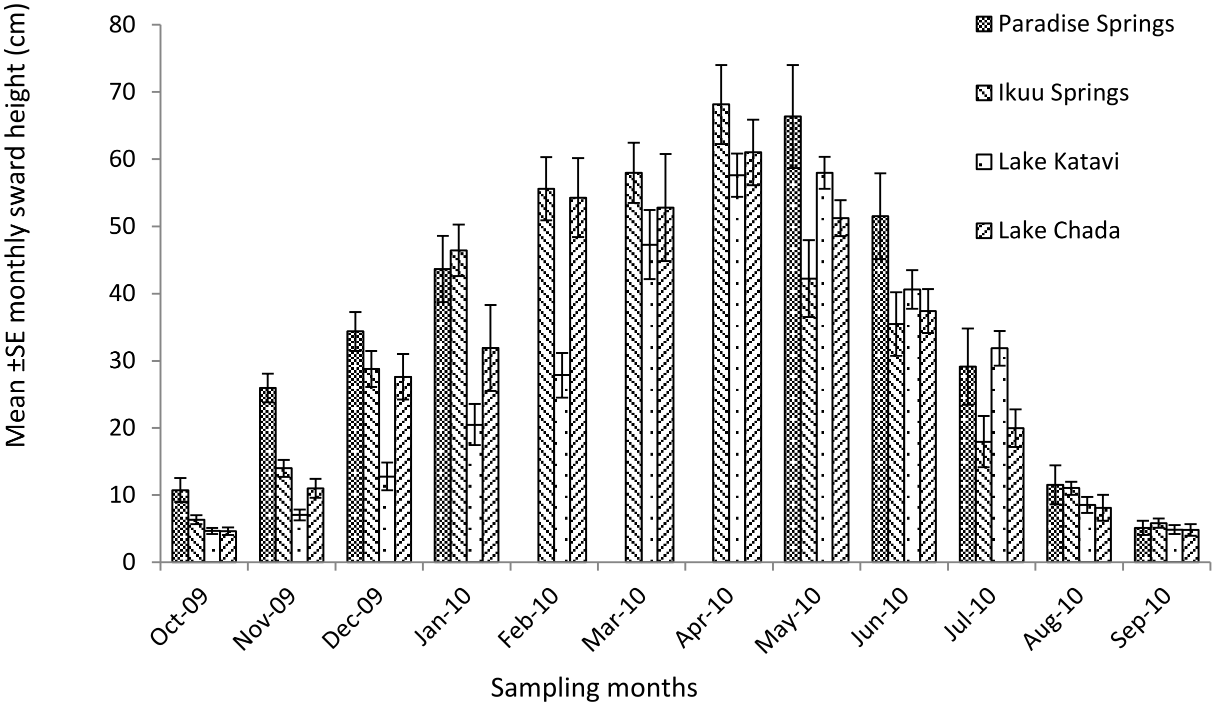


Fig. 5.4: Mean monthly sward height (cm) for ground vegetation in the four sampling sites in Katavi NP, Tanzania. Error bars are ± 1SE around monthly mean

The sward height in Katisunga Plains (Fig. 5.5) was within the range of other sites varying between 6.0 ± 1.3 cm in September 2010 and 82 ± 4.8 cm in April 2010. The annual mean sward height was 34 ± 8.0 cm.

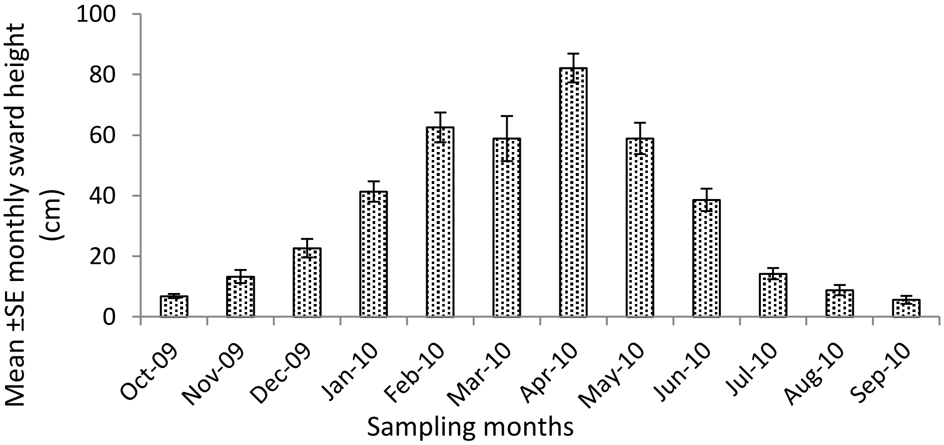


Fig. 5.5: Mean monthly sward height measured at Katisunga Plains site from October 2009-September 2010 in Katavi NP, Tanzania. Error bars are ± 1SE around monthly mean.

3.3 Greenness of vegetation

The maximum greenness was recorded at Ikuu Springs and Lake Chada while the minimum of 11 % was recorded at Lake Katavi and Lake Chada (Table 5.4). Mean annual greenness varied between 56 ± 9.0 % at Lake Katavi and Paradise Springs to 61 ± 9.0 % at Ikuu Springs (Table 5.4). Sward greenness varied significantly between months ($F_{11, 44} = 86.603$, $p < 0.0001$) (Fig. 5.6). However, greenness did not vary between sites.

Table 5.4: Summarised greenness (%) of vegetation from October 2009-September 2010 at the four named study sites in Katavi NP

Study site	Annual maximum greenness (%) of vegetation	Annual minimum greenness (%) of vegetation	Mean annual greenness (%) of vegetation
Paradise Springs	88	27	56 ± 9
Ikuu Springs	96	16	61 ± 9
Lake Katavi	94	11	56 ± 9
Lake Chada	96	11	58 ± 10

Vegetation was therefore at least 5% green, which corresponds to the definition of living for the purpose of this study, in all the study sites all the year round. Maximum greenness was recorded at Ikuu Springs and Lake Chada in March and April 2010 with 96 %. Minimum greenness was recorded at Lake Katavi in September 2010 (11 ± 2.0 %) and at Lake Chada in August 2010 (11 ± 2.7 %). Mean monthly greenness values are presented in Fig. 5.6.

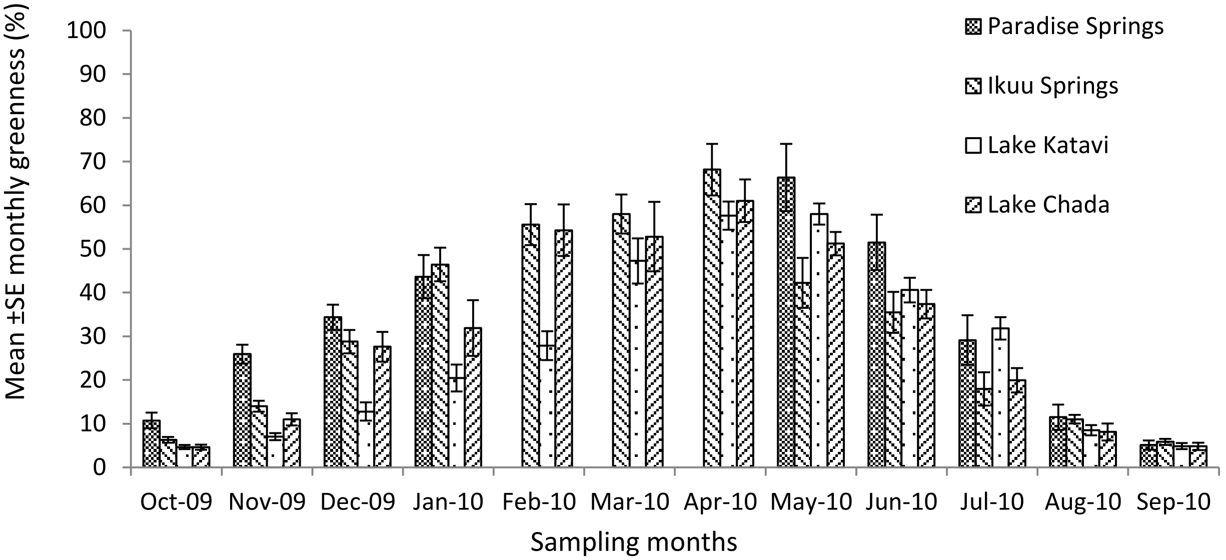


Fig. 5.6: Mean monthly greenness (%) of vegetation in the four listed vegetation sampling sites in Katavi NP, Tanzania. Error bars are ± 1SE around monthly mean.

Greenness of vegetation at Katisunga Plains varied between 11 ± 3.5 % in September 2010 to 97 ± 0.4 % in March 2010 with an annual mean of 60 ± 10 % (Fig. 5.7).

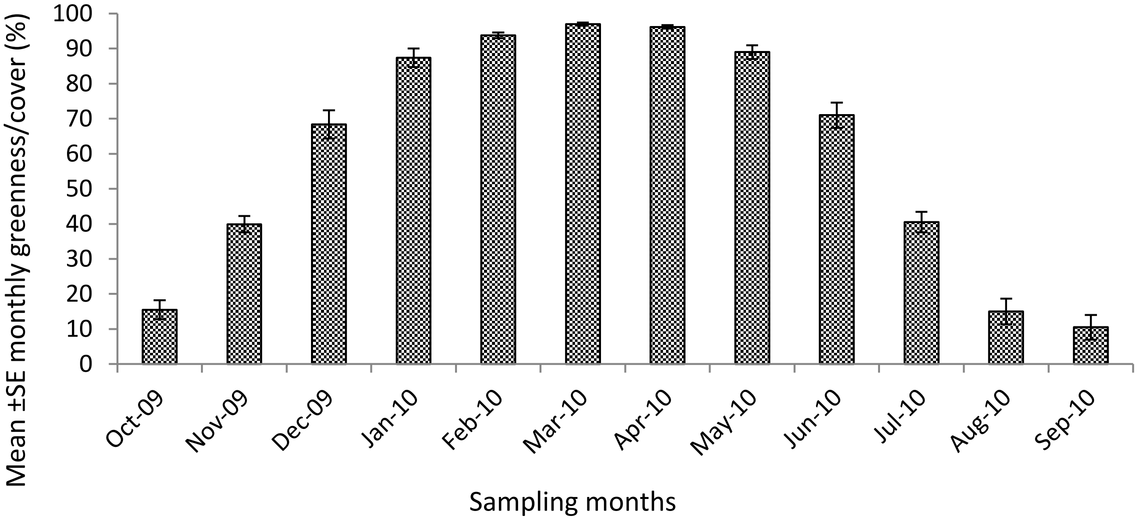


Fig. 5.7: Mean monthly greenness (%) of vegetation at Katisunga Plains site in Katavi NP, Tanzania. Error bars are ± 1SE around monthly mean.

3.4 Plant mass, biomass and standing dead mass

The highest mean seasonal plant mass recorded was 960 g dry weight m^{-2} in May 2010 at Lake Chada. The lowest was 66 g dry weight m^{-2} at Ikuu Springs in August 2009 (Fig.5.8). Paradise Springs was inaccessible in January 2010, so no data are available. Mean plant mass varied significantly between the four sampling seasons ($F_{3, 19} = 4.388$, $p < 0.02$). However, there were no significant differences in mean plant mass between study sites.

Maximum annual plant mass was 2880 g dry weight m^{-2} recorded in May 2010 at Lake Chada while the minimum annual plant mass was 198 g dry weight m^{-2} recorded in August 2009 at Ikuu Spring (Table 5.5). Ground vegetation was present in all seasons and in all sites sampled.

Table 5.5: Summarised annual maximum and minimum plant mass (g dry weight m^{-2}) from August 2009-August 2010 at the four named study sites in Katavi NP.

Sampling site	Annual maximum plant mass (g dry weight m^{-2})	Annual minimum plant mass (g dry weight m^{-2})
Paradise Springs	1233	301
Lake Katavi	1967	492
Ikuu Springs	2165	198
Ikuu Bridge	1684	793
Lake Chada	2880	594

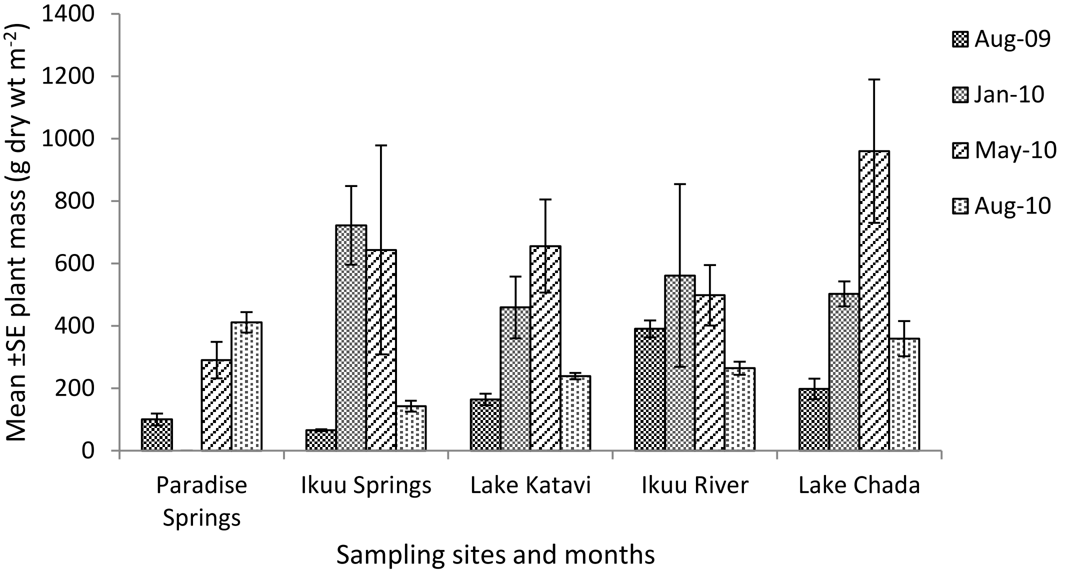


Fig. 5.8: Mean seasonal plant mass (biomass + standing dead mass) (g dry wt m^{-2}) for five study sites in Katavi NP during the 2009/2010 study period.

Mean seasonal biomass varied between the four sampling seasons ($F_{3, 19} = 3.923$, $p < 0.028$). However, there were no significant differences in seasonal biomass between study sites. Variations in mean seasonal biomass and standing dead mass for individual study sites are presented in Fig. 5.9.

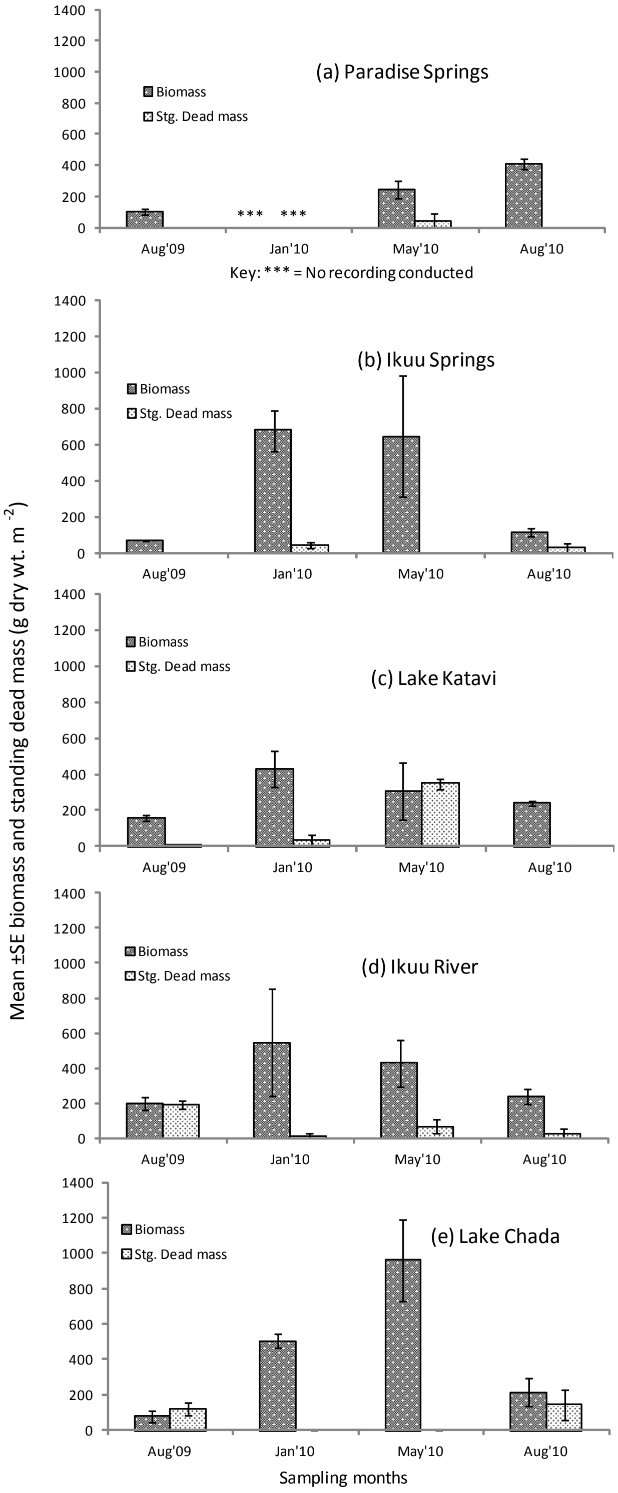


Fig. 5.9: Comparison of mean seasonal biomass and standing (Stg) dead mass (g dry wt. m^{-2}) for the named study sites August 2009-August 2010 in Katavi NP, Tanzania. Error bars are ±SE around the seasonal sampling mean.

The mass of standing dead stems did not vary seasonally between study sites. The highest seasonal mean standing dead mass was at Lake Katavi in May 2010 (378 g dry weight m^{-2}), while the least was also at Lake Katavi in August 2009 (6 g dry weight m^{-2}) (Fig. 5.9). The ratio of living to dead stems is shown in Table 5.6.

Table 5.6: Summary of annual mean biomass, standing dead mass and the ratio of biomass to standing dead mass in the five named study sites August 2009 to September 2010 in Katavi NP. Error bars are ±SE around annual mean.

Site	Annual mean biomass (g)	Annual mean standing dead mass (g)	Ratio of biomass to standing dead mass
Paradise Springs	757 ± 269	132 ± 44	6 : 1
Ikuu Springs	1126 ± 495	54 ± 33	21 : 1
Lake Katavi	849 ± 171	290 ± 252	3 : 1
Ikuu Bridge	1056 ± 247	229 ± 121	5 : 1
Lake Chada	1316 ± 585	199 ± 116	7 : 1

Ikuu Springs was the site with the highest ratio of biomass to standing dead mass (Table 5.6). Lake Katavi had the lowest ratio.

3.5 Species richness of the sward.

A total of ten low-growing plant species were found across all five sites. Grasses represented about 62% of the species found (Table 5.7). Number of grass and herbaceous species did not differ significantly between study sites. However, number of grass and herbaceous species varied significantly between the four sampling sessions ($F_{3, 56} = 3.108$ p = 0.034 and $F_{3, 56} = 5.648$ p = 0.002 respectively) (Fig. 5.10).

Table 5.7: Maximum number of grass and herbaceous species recorded in Katavi NP

Sampling site	Number of grass species	Number of herbaceous species
Paradise Springs	5	3
Lake Katavi	4	5
Ikuu Springs	4	4
Ikuu Bridge	5	4
Lake Chada	4	4

4. Discussion

4.1 Ground cover

For an organism to reproduce and maintain a viable population, the basic needs (food, cover, space and water) must be available in the appropriate quantity and quality (Fulbright and Ortega, 2006). One of the prerequisites for habitat management is therefore to identify limiting factors and optimum levels for food, cover, space and water (Johnson, 1980). The type and availability of these requirements are likely to have some impacts on hippopotami behaviour, abundance and movements on temporal and spatial scales.

The results of this chapter make a link between hippopotami behaviour, distribution and abundance with feeding resources. The correlations presented in Chapter 8 show that sward height, cover by ground vegetation and greenness of vegetation correlated inversely with some hippopotami characteristics such as abundance, immigration, emigration and behaviour. There were no correlations with some other characteristics such as hippopotami aggregations with vegetation variables. Details of such correlations are presented in Chapter 8.

All sampling sites had cover by grass and several herbaceous plants during the whole period of this study. Despite variations in the amount of ground cover, during the driest period, at least 10 % of the ground in each site was covered with green forage. In terms of vegetation cover, forage was thus geographically available all year in all of the sites. However, such availability depends on other sward characteristics such as minimum sward heights required for optimal foraging and bite size. Vegetation cover did not vary between sites, despite variations in wetness between sites. Rainfall in East Africa controls much of forage (McNaughton, 1985; Sinclair, 2000). Although rains stopped after the rain season, its impact in sustaining forage was assisted with local factors during the rest of the year. This might account for the availability of cover all year.

4.2 Sward height

Some studies have found that the quantity and quality of food for herbivores and other key processes in ecology (such as plant succession) in grass ecosystems are affected or may be affected by sward height (Stewart *et al*., 2001). For some animal species, such as cattle and their calves, feeding rate (intake per bite and rate of intake) is sensitive to sward height (Hodgson, 1981; Laca *et al*., 1992). It has also been reported that hippopotami feeding rate seems to be affected by sward height (Lock, 1972; Olivier and Laurie, 1974; Harrison *et al.*, 2007), preferring and foraging successfully in short grass with sward height at about 15 cm. Sward height correlated inversely with hippopotami density for both juvenile and adults. More hippopotami were recorded when swards were shorter. However, this is not necessarily a causative relationship because hippopotami select short swards. However, very short swards may be limiting. In Katavi, very short sward led to hippopotami eating grass mixed with sand (Meyer *et al*., 2005) probably due to inability to select using their lips. Foraging height of hippopotami tends to close with that of wildebeest in the Serengeti where mechanistic model and field observations showed that they maximize energy intake on swards between 3 and 10 cm (Wilmshurst *et al*., 1999). Wildebeest were observed preferring short and intermediate swards of moderate greenness. However, selectivity of forage was higher towards greenness and not on grass height (Wilmshurst *et al*., 1999). There are various sward characteristics which may explain the reasons for the hippopotami preferring short swards. These are discussed in Chapter 9. They include morphology of hippopotamus, dentition (Lock, 1972; Spinage, 2012) and sward quality or digestibility, assimilation and handling or bite rates (Fryxell, 1991; Hassall *et al*., 2001; Drescher *et al*., 2006).

Grazing intensity among hippopotami in Liwonde NP, Malawi was highest in the sites with sward height around 15 cm high. The lowest grazing was in sward heights of up to 50 cm high. It was proposed by the authors that habitat type had a greater effect on hippopotami grazing than distance from water (Harrison *et al.*, 2007). In the coastal grassland of Transkei, South Africa, greatest concentrations of forage biomass were recorded in the shortest swards (Shackleton, 1990), as grazing marginally reduce the biomass (Shackleton, 1991). This might explain why hippopotami tend to feed on short swards, apart from its morphology. They are likely to get more net energy by feeding in the short swards with more digestible biomass rather than longer swards. This is in line with forage maturation hypothesis (Fryxell, 1991).

Sward heights in Katavi averaged between 30 and 40 cm. This can be considered as above optimum height for hippopotami and therefore was inaccessible for grazing during half of the year. The months of January to June supported taller swards which might have been well above the optimal for hippopotami. Forage may not have been available near their shelter sites. However, grazing pressure by other ungulates such as buffalo and zebra may transform tall grasslands into patches of varying sward heights (Kanga, 2011) and hence make it accessible for foraging. In Masai Mara Game Reserve in Kenya, hippopotami have been effective in maintaining short swards and are said to be important in vegetation dynamics (Kanga, 2011). Also alternate feeding between areas by hippopotami may have been essential in resource utilization as inaccessible sward at an area at one time becomes accessible at a later season. This may enable forage to be available to other ungulates at most of the time during the year by resource partition (Schoener, 1974; McNaughton, 1985). Similarly, many herbivores are known to migrate in response to a varying resource such as forage (Wilmshurst *et al.*, 1999).

Hippopotami select certain areas for grazing. Due to the sward height recorded during most of the wet season, they might have been foraging in other areas. In Lundi River, Gonarezhou NP, in Zimbabwe, hippopotami used areas close to the river during the wet season and foraging further away during the dry season (O’Connor & Campbell, 1986) possibly due to sward height. Shackleton (1992) in Mkambati Game Reserve in South Africa found that grazing in areas which had long swards was very low. Similar observation has been reported in Malawi (Harrison *et al.*, 2007). In Ruaha NP, Tanzania, more hippopotami raided crops during the rainy season (Kendall, 2011), probably because of sward height being higher than their optimum heights. Sward heights are also associated with maturity of the grasses. As the grasses mature their tensile strength increases hence reducing digestibility (Hassall *et al*., 2001), this might be the reason for hippopotami preferring short, previously grazed swards.

In general, all the study sites were affected by burning and rapid drying of grasses. Some of the areas such as the Katisunga plains were burnt to avoid hot fires during the peak of the dry season. This affected the sward height and quality as estimated arbitrarily by levels of greenness. This also forced some animal species particularly hippopotami to concentrate their feeding in fewer areas hence reducing sward height at a much faster rate.

At Ikuu Springs, maximum sward heights were recorded in March and April. Sward heights dropped abruptly in May-July probably due to increased concentration of animals at the beginning of the dry season (May–July 2010). Animals of various species congregated at the site for feeding and watering at the springs and Katuma River. After burning of adjacent areas, the number of animals grazing at Ikuu Springs increased and this led to more utilization hence reducing the sward height at a much faster rate. This is consistent with the inverse correlations between vegetation variables and immigration and emigration reported in Chapter 8.

Ikuu Springs was used heavily as a dry season refuge. Before the start of the dry season, animals were few and scattered. With the beginning of dry the season, animals started to congregate at Ikuu Springs possibly in anticipation of the coming dry season. During this time (May to July), the main Katuma River nearby had some flowing water, and hippopotami that moved here contributed to the rapid decrease in sward height.

In the Katisunga plain, maximum sward height was recorded in April but dropped rapidly in May-July, most probably due to heavy grazing and fires. Throughout the year, the Katisunga Plain was used by various animal species, more so when rains stopped and water levels receded. After the end of the rains, water levels dropped rapidly. Also, the impact of early burning which took place in late May and June and accidental fires were observed to affect sward height.

At Paradise Springs and Lake Katavi, there were slow decreases in sward height mainly due to low densities of animals. During May-July, animals were still scattered and the number was still low hence underutilization of the area. During managed burning, these areas were not affected because they were still greenish and wet. This caused fires not to affect the sward heights in these two study sites. At Lake Chada, there was an increase in the number of animals and rapid rates of drying, which affected sward heights during the months of May-July.

In all the areas, sward height responded quickly to the onset of rains in November. Before November, green vegetation was still supported by remaining river waters in muddy pools; springs and some areas had some green vegetation after the previous burning. Because of this, all the sites responded in the same way.

It can therefore be concluded that at some point in the year, sward height was limiting in the feeding of hippopotami near their shelter sites. However, this does not indicate that there was less or no food as the vegetation study concentrated in the areas near their shelter sites. Animals had more foraging ground to feed from further from the shelters but would have to expend more energy in travelling and time.

4.3 Greenness of Vegetation

Vegetation greenness was taken as an indication of sward quality, with more greenness reflecting increased quality. Some green forage was available in all study sites in Katavi during the study period despite seasonal reduction in percentage greenness. In the Serengeti, green forage was recorded during the dry months only in high rainfall areas

(McNaughton, 1985) within the Park. There were correlations between hippopotami density and greenness of the vegetation. These are discussed in Chapter 8.

The year round greenness of forage in Katavi was partly contributed to by springs, minor water pools and some areas that were burnt towards the beginning of the dry season producing green shoots during the dry season. However, rainfall was a major dictating factor for plant greenness. In the study of utilization of natural pastures by wild animals in the Rukwa valley, Tanzania (Foster & FitzGerald, 1964), it was found that grazing pressure results in pasture rejuvenation. They observed that sequence of animals, heavier ones followed by lighter ones, use the different pastures in rotation during the year and as a result, alternate periods of optimum use and rest occur, and the harmful effects of overgrazing do not appear. This can explain why the hippopotami use the short swards which rejuvenate in the course of their feeding (Shackleton, 1992). Dry periods favor the fauna whereas extremely wet ones are unfavorable (Foster & FitzGerald, 1964; O'Connor & Campbell, 1986). This can further explain that during the wet season, green forage may be plenty but inaccessible to animals. The grass rejuvenation principle might help to explain why green vegetation was recorded throughout the study period, in addition to water and effects of burning. Hippopotami do not eat selectively (Lewison, 2004) as quoted in Meyer *et al*. (2005), therefore it is also probable that food was available at all times despite a decline in green plant mass.

In the Serengeti, foraging by wildebeest was found to be influenced by sward greenness rather than sward height (Wilmshurst *et al*., 1999), preferring moderate greenness regardless of season. However, because greenness increases with age of the sward, this led to the wildebeest preferring short to intermediate swards which have moderate greenness. During wildebeest migrations, the animals foraged on green flush of grasses stimulated by localized rainfall (Wilmshurst *et al*., 1999). This is thought to be a strategy of maximizing energy intake.

Hypothesis one is therefore accepted in that green plant mass was available throughout the year within 5 km of all the hippopotami sheltering or resting sites.

4.4 Plant mass, biomass and standing dead mass

The highest total plant mass was recorded in May at Lake Chada which was the driest site, however, this coincided with the end of the rains. In January, Ikuu Spring (the second wettest site) recorded the second highest plant mass over the whole study period. The least plant mass was recorded in August at Ikuu Springs and Paradise Springs, both wet sites. Plant mass did not therefore correspond closely to the wetness of the site, but rather to rainfall. As it was with sward height, all the sites responded in the same way in terms of plant mass. Wetness was however concentrated at the resting site while foraging took place at a much larger area around the shelter site. The impact of wetness might have been less of forage, hence plant mass. It has also been reported that forage in east Africa mainly depends on rainfall (McNaughton, 1985, Sinclair *et al*., 2000).

Low plant mass in the two wettest areas might have been contributed to by controlled burning of the areas during June. After burning, biomass concentrations become temporarily low for some few months (McNaughton, 1985; Shackleton, 1990). Some possible explanation for low plant mass at Ikuu Springs might be due to the effect of grazing. During August, the area is grazed by animals going to and from the springs and water pools along the Katuma River for watering. Similarly, Paradise Springs is highly used by hippopotami and other grazers for feeding and watering. Their feeding impact is thought to have contributed to low plant mass during the dry season. The highest biomass was at Lake Chada and was probably due to a low intensity of grazing.

Generally, plant mass in Katavi grasslands is comparable to other grass lands. Singh & Yadava (1974) found that above ground biomass, standing dead and litter showed a maximum of 1, 974 g dry weight m^{-2} in a tropical grassland in India. They found that maximum biomass was during the wet season. Ni (2004) found that above ground biomass in temperate Northern China had peaks ranging from 20-2021 g dry weight m^{-}

^{2} with a mean of 325 g dry weight m^{-2}. As in Katavi, Ni (2004) found that grassland productivity and biomass had significant positive relationship with rainfall. In East and Southern Africa, similar relationship between rainfall and grasslands has also been reported (McNaughton, 1985; Shackleton, 1990; Sinclair, 2000). In Mali, Diarra & Breman (1975) found that rainfall is a decisive factor for grass production. In Free Orange state, South Africa, plant mass, biomass and dead mass production in grazing areas were found to be affected by seasonal rainfall among other factors (Snyman & Fouche, 1993). O'Connor (1994) in Gazankulu, South Africa found that abundance of dominant grass in African savannas grassland was more responsive to rainfall variability than grazing.

4.5 Species richness of the sward

Ten species of ground flora were recorded in the study sites. Also there was no seasonal change in species composition between and within the study sites. Lack of seasonal change in species richness suggests that plants were mostly perennial rather than annual. Results showed that grass species dominated the ground flora in foraging areas. Species available are important because despite hippopotami being unselective during the time of forage scarcity, they have preferences in the grass species. In Mkambati Game reserve, Transkei, South Africa ungulates grazed intensively on *Cymbopogon* and *Digitaria* species (Shackleton, 1992). O'Connor (1994) reported *Aristida bipartite* as unpalatable grass species while in the genera *Heteropogon, Themeda, Digitaria* and *Setaria* were palatable. Chansa *et al*. (2011b) observed that hippopotami in Luangwa River in Zambia utilized grass species depending on availability, although grass species in the genera including *Panicum, Urochloa, Cynodon, Echinocloa* and *Hermathria* dominated their diet. Also in Zambia, areas with *Cynodon dactylon* and *Echinocloa* species along Luangwa River were found to harbour many hippopotami suggesting that these were most palatable grass species (Wilbroad and Milanzi, 2010).

Although few species were recorded during the present study in the study sites, more species have been recorded in Katavi (Mwangulango, 2004). Similarly, species recorded are among those listed as palatable to hippopotami. Despite being unselective, presence of more grass than herbaceous species may indicate more choice for the hippopotami.

In Masai Mara, in Kenya (Kanga, 2011), hippopotami were thought to influence vegetation dynamics including seasonal variations in grass species due to the effects of feeding. This was less so in Katavi as there were no seasonal variations in species richness and there was low species variation between study sites. However, this may also indicate that effects of hippopotami grazing were not heavier in their feeding sites near the hippopotami shelter sites in Katavi, probably due to availability of forage.

5. Conclusions

Forage accessibility by hippopotami in terms of sward height is not thought to have been a major constraint during the dry season. However, during most of the year, sward height, were higher than the optimum height preferred by hippopotami. Other nearby foraging areas are thought to have been used by hippopotami at times when sward heights near shelter sites were much higher. This is because hippopotami tracks were see leading to various foraging sites from the shelter sites. This is also due to the fact that many large herbivores migrate in response to variations in availability of resources.

Although herbaceous vegetation resource availability and accessibility varied seasonally, forage was not thought to be a limiting factor for hippopotami in Katavi during the period of this study. Apart from above optimum sward heights in the study sites during some months

Despite seasonal variations in vegetation greenness, hippopotami resting and feeding grounds nearby had green swards during the whole year and thus their distribution and behaviour were not limited, but may have been affected by grazing opportunities. Some green forage plants were available within 5 km throughout the year. Greenness which was considered as a measure of forage quality was recorded throughout the year.

This study was conducted during the average year as rainfall was slightly below the previous year but slightly above 13-year average for the park. Water therefore did not limit as anticipated during the dry year. This supported plant mass during the whole study period.

Some sward greenness was recorded throughout the year in the hippopotami feeding ground or near sheltering sites. As greenness was recorded to represent sward quality, it can be argued that despite a decline in percentage greenness during the dry season, there was quality forage throughout the year.

Due to rainfall trends over the last six decades, there is no concern over the availability of forage for the hippopotami in Katavi at present, except for the few dry years. There is no evidence to suggest that forage will be limiting in the near future if the projected climate change will lead into increased precipitation (IPCC, 2001a; 2001b; 2006; IAH, 2012). This is because forage in East Africa depends largely on rainfall, and remains to be the major determinant of forage availability.

Despite projected increase in rainfall (IPCC, 2001; 2001b; 2006; IAH, 2012); the park may be faced with drought if there is no addition of water from the catchments. This is because of the higher rates of evapotranspiration as temperatures are set to increase (IPCC, 2007a; 2007b; IAASTD, 2009). Projected increase in temperature and rates of evapotranspiration coupled with uncontrolled water use may cause the forage to dry out much earlier hence leaving the hippopotami with low quality or no forage during the years with prolonged drought.

Short sward particularly if predominantly brown may result in higher travel costs and hence lower net energy gain.

Higher hippopotami density coincided with lowest sward heights. This might be the evidence of trade-offs between serving the benefits of aggregating and its foraging costs.

Chapter 5: Hippopotami abundance, immigration and emigration

1. Introduction

Ecology is concerned with two main subjects, distribution and abundance of organisms (Krebs, 1972; Begon *et al*., 2006). Distribution and abundance are linked by interactions that determine them. There are spatial and temporal variations in abundance. Temporal variations can be between decades, within decades, annual and seasonal. Animal abundance is influenced by natality, mortality, immigration and emigration (Begon *et al*., 2006). Long term (generation time) changes in abundance are most likely to be influenced by changes in natality and mortality. Short term changes in abundance (within generation time) are mainly due to changes in distribution brought by seasonal dispersion and migration (immigration and emigration) as animals move in and out of their present habitat. Habitat is the place where an organism lives and it includes all the resources and conditions present in that area that produce occupancy including survival and reproduction (Hall *et al*., 1997; Krausman, 1999). The relationship between animal population density and their habitats has been addressed by ecological theories including resource concentration (Root, 1973; Connor *et al*., 2000).

Within generation changes in abundance due to immigration, emigration and dispersion are often responses to changes in habitat quality. Habitat quality is the ability of the environment to provide conditions appropriate for survival and reproduction (Fulbright & Alfonso Ortega-S, 2006). The major environmental conditions and factors affecting habitat quality include environmental resources (food, shelter or space, water) and seasonal changes in weather conditions (temperature, wind and rainfall) (Begon *et al*., 2006; Fulbright & Alfonso Ortega-S, 2006). When habitat provides less than that needed it may cause the animal to move from the present habitat in search of better habitat.

Changes in distribution result from variations in abundance between sites. This may be due to physiochemical conditions, the type and amount of resources available, the life cycle of the species and the influence of external factors such as competitors and predators (Begon *et al*., 2006)

Native fauna in Africa is declining (Bouche´ *et al*., 2011). Natural and human mediated disturbances influence abundance and populations (Thuiller *et al*., 2006; Lewison, 2007). Climatic factors such as rainfall have many effects on wildlife population dynamics (Hone & Clutton-Brock, 2007). For a number of years, hippopotami populations in Africa have been decreasing (Lewison and Oliver, 2008), predominantly as a result of hunting and habitat loss (Lewison and Oliver, 2008; Kanga *et al*., 2011a; 2011b) (Fig. 6.1). Understanding dynamics of small population is essential in conservation particularly of endangered species (Begon *et al*., 2006). This is particularly important for species such as hippopotami which in 2006 was categorized as vulnerable by IUCN compared with former category of wide spread and secure in 1996 (Lewison and Oliver, 2008).

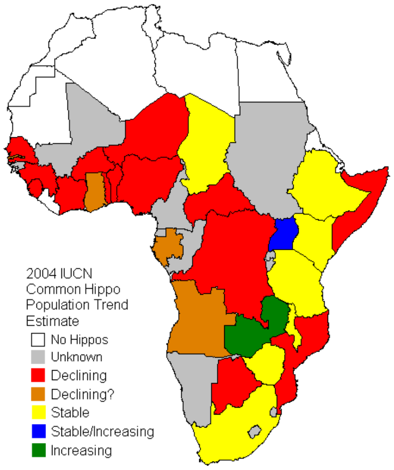


Fig. 6.1: Hippopotami population trend in African countries. *Source*: Lewison and Oliver (2008)

Hippopotami contribute to an ecosystem in a number of ways. They are mega herbivores that have large spatial and temporal influences on natural ecosystems (Lewison and carter, 2004) by altering physiognomic habitat structure and creating a mosaic of habitats for smaller organisms (Field, 1970; Field and Laws, 1970; Kanga *et* *al*., 2011a; 2011b). Moderate hippopotami densities can prevent the spread of small fires by maintaining habitat mosaics. Hippopotami are therefore often considered as keystone species (Eltringham, 1999; Boisserie *et al*., 2011). High hippopotami density has been reported to cause over grazing, erosion and decreased plant and animal diversity (Field, 1970; Thornton, 1971; Eltringham, 1974; Chansa *et al*., 2011a). In Queen Elizabeth National Park in Uganda, high density led to the culling of about a half of the population size in 1958 (Thornton, 1971; Eltringham, 1999). Hippopotami culls were also conducted in Ruwenzori National Park, Uganda (Eltringham, 1974). In Zambia, high population density in Luangwa River also led to culling of hippopotami (Sayer & Rakha, 1974). In Kruger National Park, South Africa, culling was also carried out from 1962 to the late 1980s in order to maintain an optimum density of the hippopotami population (Viljoen, 1980; Viljoen & Biggs, 1998). Reduced water depth in the shallow lakes in Katavi in the 1990s was thought to have been partly caused by the large populations of hippopotami that the Katavi water systems support (Lewison, 1996).

Hippopotami have also been involved in conflicts with humans (Dunham *et al*., 2010; Kanga *et al*., 2011a; 2011b). Hippopotami live in lakes and rivers, some of which border human settlements. Human-hippopotami conflicts have led to increased killing and culling of hippopotami (Kendall, 2011). In Mozambique, hippopotami have been identified as causing the third most deaths due to wildlife in Africa (Dunham *et al*., 2010). Hippopotami cause damage to crops (Dunham *et al*., 2010; Kendall, 2011).

Effective management and conservation of wildlife populations such as of hippopotami requires knowledge of occurrence, abundance and factors that influence spatial and temporal patterns of these variables (Thorn *et al*., 2010). Conservation, particularly of threatened species relies on information on their population estimates and trends (Collen *et al*., 2011). Due to spatial and temporal resource distributions, hippopotami, as for other animals, make seasonal movements in search of better resources or to escape from major changes in food or climate at the current habitat. This may influence abundance both temporally and spatially.

Protected areas have been regarded as pillars for global conservation efforts (Craigie *et al*., 2010). National Parks are among the key conservation areas for protecting species (Thuiller *et al*., 2006), hence the need to estimate density of hippopotami in Katavi. Despite the importance of protected areas, their performance in maintaining populations particularly in Africa are still poorly documented (Craigie *et al*., 2010). Protected areas are essential because many wild animals in Africa survive poorly outside protected areas due to anthropogenic effects (Caro, 1999; Rannestad *et al*., 2006; Stoner *et al*., 2007). While counting hippopotami in Tanzania in 2001, 80 % of the recorded hippopotami were found inside protected areas (TAWIRI, 2001), suggesting the species can hardly tolerate human habitation. Recording and estimating density helps to identify the most important sites (Olivier and Laurie, 1974). Estimation of population size is also the raw material for study of abundance (Begon *et al*., 2006).

Hippopotami are widespread in Tanzania but detailed population estimates are lacking for most areas (TAWIRI, 2001). The first country-wide systematic reconnaissance flights (SRF) aerial census in Tanzania was conducted in 2001. From minimum total counts, 20,079 hippopotami were counted along 20 major rivers and six other water bodies (Fig .6.2) (TAWIRI, 2001). The survey concentrated on potential hippopotamus habitats, however, some rivers and other potential water bodies were not surveyed due to logistical limitations (TAWIRI, 2001). The habitat and activity patterns of hippopotami deemed them particularly difficult to accurately count from the air (TAWIRI, 2001; Stoner *et al*., 2006; 2007). Difficulties in counting hippopotami from the air and time limitation mean that their numbers were most probably underestimated.

According to aerial census of 2001, most of the hippopotami were recorded in southern and western Tanzania, and about 80 % of these were found in protected areas (National Parks and Game Reserves) (TAWIRI, 2001). Important sites were Selous

Game Reserve, the Katavi-Rukwa ecosystem, Ugalla and Malagarasi Rivers and the Mara River in the Serengeti National Park (Fig. 6.2) (TAWIRI, 2001).

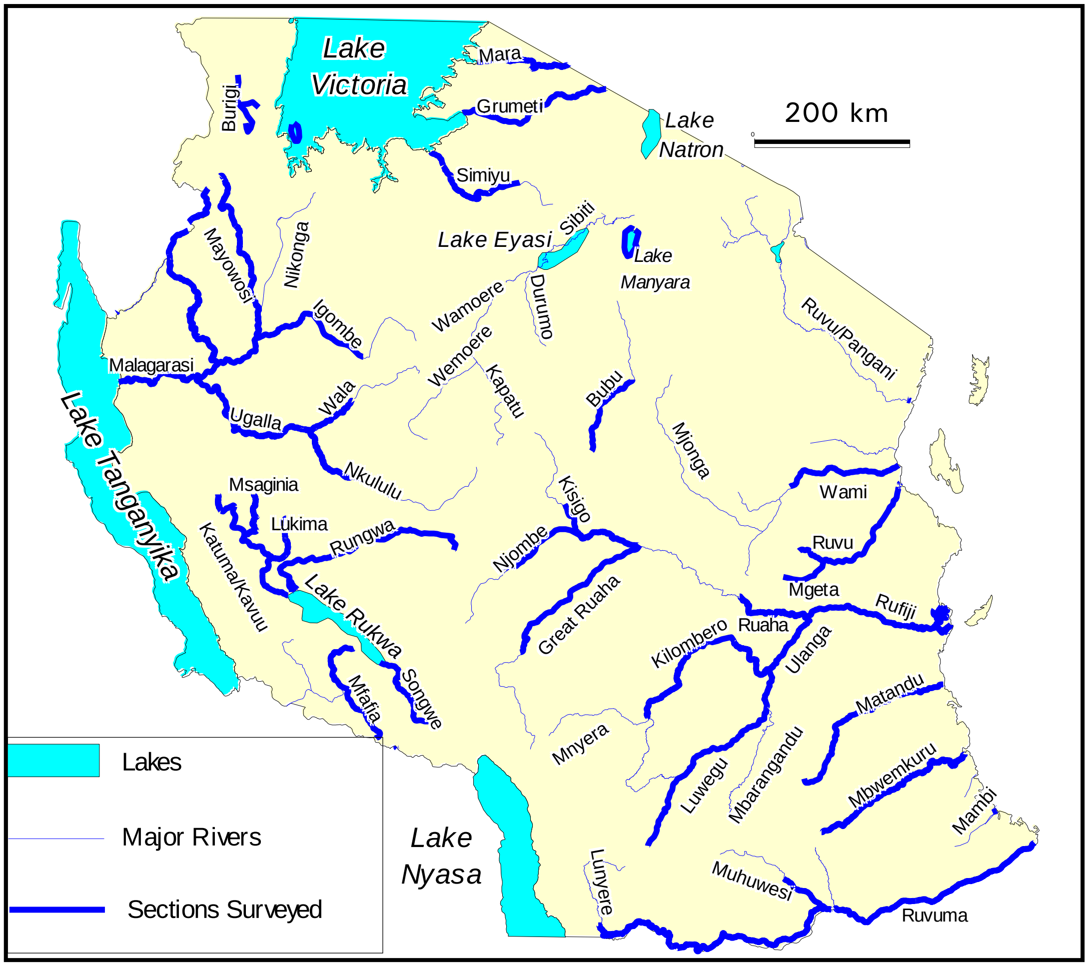


Fig. 6.2: Areas surveyed in 2001 for hippopotamus in Tanzania. Source: TAWIRI/CIMU 2001.

During the large mammal census undertaken in 1986 in Selous Game Reserve in Tanzania, the population for the area was 15,483 while in 1989, an estimated 24,169 hippopotami were recorded (TAWIRI, 2001). Game (1990) counted hippopotami on the major rivers in the same area and estimated a population of 20,598 hippopotami and 1,189 hippopotami in the Mara River in the Serengeti National Park.

Apart from their abundance, hippopotami move overland in search of grazing (Eltringham, 1974; 1999; Lewison and Carter, 2004; Harrison *et al.,* 2007). In the course of their movement they impact their environment in various ways (McCarthy *et al*., 1998). Studying movement of hippopotami to and from their resting or sheltering ground was intended to record baseline information on their movements through seasonal immigration and emigration in Katavi. Understanding spatial and temporal movements will help in acquiring information for proper management and management strategies. The study therefore had the following aims:

1.1 Aims and hypotheses

The aim of estimating hippopotami abundance in Katavi was to determine if there were significant changes in their distribution over the years.

It was also aimed at assessing changes in hippopotami populations in Katavi National Park over recent years and to provide preliminary assessment of seasonal dynamics in hippopotamus abundance, immigration and emigration in selected sites in the Park. The study involved the following:

1. Comparing hippopotamus abundance over censuses years
2. Comparing hippopotamus abundance of adult and juveniles at five study sites.
3. Comparing rate of emigration and immigration of hippopotami in the five sites

The study therefore tested the following hypotheses

H_1 The index of the total hippopotamus population in Katavi National Park shows a decline over time scales larger than their generation time

H_2 Hippopotamus abundance in Katavi NP varies between seasons

H_3 Patterns of seasonal immigration and emigration of hippopotami in Katavi vary between sites

2. Methods

2.1 Aerial and ground counts

Long term hippopotamus aerial censuses for Katavi exist although they were not the primary target species. Few records exist on spatial and temporal variations in hippopotamus populations in the Park.

To estimate the number of hippopotami in Katavi National Park, three methods were used; two involved estimating hippopotamus numbers in the whole of Katavi while the third was confined to the five study sites. The first two were conducted by Park staff and research personnel while the third formed part of this study. Results for each hippopotamus counting method are presented and analysed separately. The methods were

a) Aerial counts or census
b) Minimum total counts
c) Direct counts

Aerial counts using Systematic Reconnaissance Flight (SRF) have been conducted in Katavi since 1977 using Cessna 206 light aircraft. However, more regular counts began effectively in 1987 (Table 6.1). Most of the counts were not specifically for hippopotami (with exception of September 2001), but they did provide estimates of hippopotami abundance. Wherever possible, two or more aircraft were used simultaneously to reduce double counts by finishing the counts in a shortest time possible. During these counts, flight height from the ground varied between 60-150 m depending on the terrain. Most flights were conducted at 100 m on the plains and 120-150 m on the hilly or mountainous areas. Inter distance between two transects were 1-5 km apart depending on required sampling intensity whether reconnaissance or detailed. In order to systematically calibrate transect width on the ground, it was necessary to indicate respective strips to the observers. This varied between observers depending on the height of the eyes of observer above the seat or position that each observer adopts while observing (Swanepoel, 2007). In order to confine the observations zone to a strip approximately 150 m wide on the ground, markers were attached to the wings of the plane at approximately 50-70 cm apart depending on the height of the observer. The markers were individually calibrated for each observer. Two observers and a recorder were involved in each plane.

Table 6.1: Years and months when aerial census were conducted in Katavi

Aerial census Sampling years and months in Katavi									
1987	1988	1991	1995	1998	2000	2001	2002	2006	2009
October	May and November	November	December	October	October	May	November	July	September

Minimum total count involved ground counts of all hippopotami in the areas in which they were seen or known to occur in the park following aerial reconnaissance surveys conducted using light aircraft over the whole Park. Shortly after the aerial survey, foot counts were made, using different teams for each area to reduce census duration and minimize possibilities of double counting. A total of twelve transects for hippopotamus counting were established. Counting was conducted in October 2004, 2005 and 2010. October was chosen as the hottest month in Katavi with high evapo-transpiration and low water levels making hippopotami more obvious. However, due to logistical and time constraints during the counts, some areas were not covered and in some larger areas only proportions were intensively covered. This is among the sources of possible underestimation.

Direct observation at ground level

The third method was the one used during this study which involved counting hippopotami using 10 X 50 binoculars in behavioural observation sites. Animal counts were conducted in estimated quadrats measuring 0.2 km X 0.25 km (200m X 250m) making an area of 5 ha (0.05 km^2). Estimated total area size of each site is given under each site descriptions in Chapter 2 and summarised in Table 6.2. Sites are arranged according to predicted wetness gradient. Distance estimation was made using Leica LRF 900 Scan laser range finder by Leitz, Wetzlar, Germany.

Table 6.2 Summary of description of study site and their characteristics

Site	Est. total Size (km^2)	**Location**	**Main source of water**
Paradise Springs	50.0	Adjacent Kapapa River	River + Springs
Ikuu Springs	0.5	Adjacent Katuma River	Springs only
Lake Katavi	70.0	Upper stream Katuma R.	River + Springs
Ikuu Bridge	0.25	Along Katuma River	River only
Lake Chada	40.0	Downstream Katuma R.	River only

2.2 Site selection

Five sites were chosen for recording hippopotamus numbers. These are the same sites as those at which behaviour observations of hippopotami were made. Their main features are described in Chapter 2, summarised in Table 6.1 and shown in Fig. 6.3.

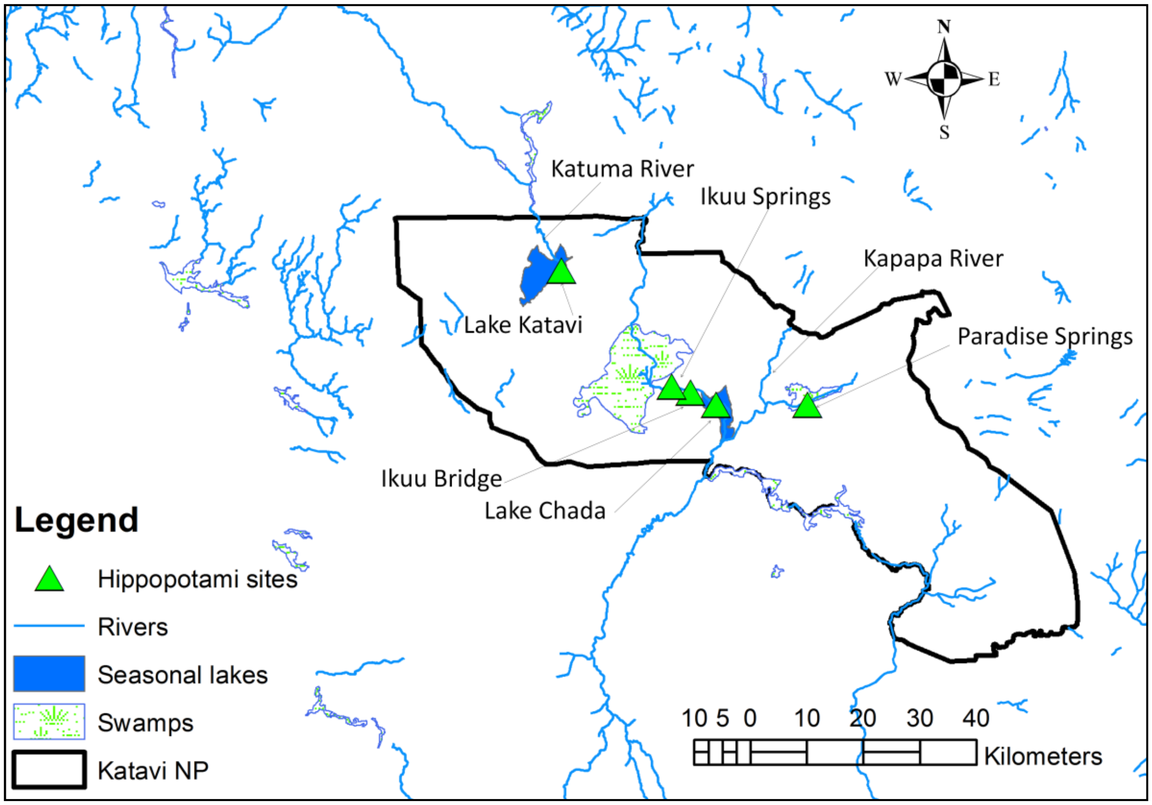


Fig. 6.3: Map of Katavi National Park showing hippopotamus observation sites. *Key*: NP = National Park.

2.3 Data recording

Observation and counting were conducted at two week intervals within a month from September 2009 - September 2010. On each of the two days, counts were conducted three times a day (morning, noon and late afternoon) with 30 minutes for each count making a total of six counts a month. Average numbers of hippopotami per site per day were calculated and monthly means derived. Adults and juvenile were recorded separately. Emphasis was on the following aspects:

- Temporal changes in abundance (in relation to seasons and months)
- Spatial differences in abundance between five sites

The months of June to November were considered as dry season while December - May were the wet season months.

2.4 Data analysis

Abundance was calculated as the number of hippopotami in each quadrat of 5 ha or 0.05 km^2 at each of the five study sites and hippopotamus density calculated as number of individuals km^{-2} at each of the five sites.

Correlation and analyses of variance (ANOVA) were performed using the SPSS statistics package software (PASW Statistics 18) by IBM.

Rates of immigration and emigration (expressed as percentage change) were calculated as percentage change in abundance derived as number of hippopotami during the present month minus number of hippopotami during the previous month divided by number of hippopotami during the previous month.

$$Rate = \frac{Abundance\ current\ month - Abundance\ previous\ month}{Abundance\ previous\ month} X\ 100\%$$

3. Results

3.1 Change in abundance between decades.

Aerial census data covering the period from 1980s to 2009 were obtained from Tanzania Wildlife Research Institute (TAWIRI), Tanzania Conservation Information Monitoring Unit (CIMU) and Tanzania Wildlife Conservation Monitoring (TWCM) and analysed. Aerial census results indicate fluctuating, declining hippopotami abundance (Fig. 6.4). However, the trend is not clear and not significant at 95% ($R^2 = 0.08$ df = 9 p = 0.43 NS). Changes over the years between 1980s and 2009 were not consistent, the population increasing to a peak in November 1991 followed by a decline and second peak in 2002. The lowest abundance was recorded in October 2006 (Fig. 6.4).

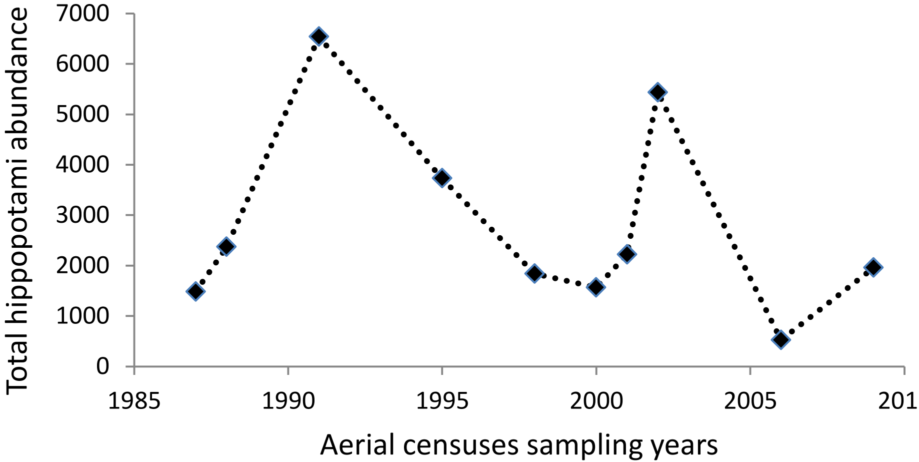


Fig. 6.4: Aerial censuses annual variations in hippopotami abundance between sampling years in Katavi NP, Tanzania

Data Source: Tanzania Wildlife Conservation Monitoring (TWCM), 1995; 1998; Tanzania Wildlife Research Institute/Conservation Information Monitoring Unit (TAWIRI/CIMU, 2010).

Summarizing the data for decades (Fig. 6.5), shows that there is not a consistent trend in annual censuses of hippopotami abundance ($R^2 = 0.08$, df = 9 P = 0.427 NS). However, if fluctuations in abundance are summarised between decades (Fig. 6.5), it is apparent that abundance of hippopotami was low in the 1980s, increased significantly during the 1990s, but that the decline to 2000-2009 levels was not significant (Fig. 6.5).

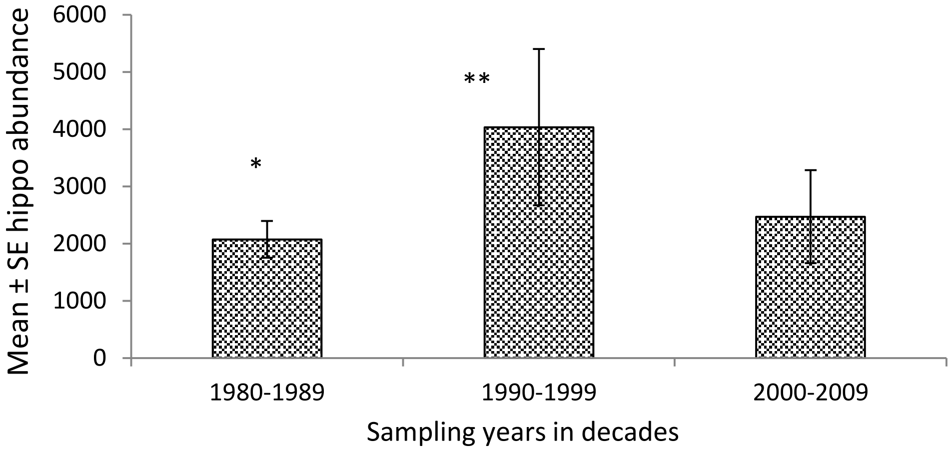


Fig. 6.5: Mean decadal hippopotami abundance in Katavi NP using data from aerial census. Error bars indicate ± 1SE around the decade's mean.

Data Source: Tanzania Wildlife Conservation Monitoring (TWCM), 1995; 1998; Tanzania Wildlife Research Institutes/Conservation Information Monitoring Unit (TAWIRI/CIMU, 2010).

3.2 Change in abundance within a decade: minimum total counts

A total of 4434 hippopotami were counted in October 2004 and 3726 were counted in 2005 and 4579 hippopotami in 2010 on the same locations (Table 6.3). Using percentage of means for each site for the three years did not indicate major changes. There was no significant difference in hippopotami abundance between three sampling years ($F_{2, 20} = 1.101$ $p = 0.354$ NS).

Table 6.3: Minimum total counts results for hippopotami in Katavi National Park, Tanzania

Counting Location	**2004**		**2005**		**2010**		**Mean**	**SE**
	Count	**% of mean**	**Count**	**% of mean**	**Count**	**% of mean**		
Ikuu Springs	1011	91	1052	95	1254	113	1106	75
Upper Ikuu Springs	670	86	654	84	1026	131	783	121
Upper Lake Katavi	850	119	238	33	1050	147	713	244
Paradise Springs	645	102	879	139	369	59	631	147
Sitalike airstrip	561	127	462	105	301	68	441	76
Sitalike Camp	478	124	441	114	239	62	386	74
Sitalike Bridge	219	118	0	0	340	183	186	99
Total	**4434**	**104**	**3726**	**88**	**4579**	**107.8**	**4246**	
Ikuu Bridge	**		**		834		**	**
Lake Katavi	**		**		190		**	**
Kapapa Hills	**26**		**23**		**		**25**	**2**

Data Source: Meyer *et al.*, 2005; Katavi National Park Ecological Monitoring Unit., 2010
Key: **=No data. Sites are arranged according to magnitude of mean abundance

Locations of all sites are shown on Fig. 2.3 and Fig. 2.4 (Chapter 2) and some GPS coordinates for the centre of sites are presented in Appendix 2.

3.3 Spatial variation in abundance

Of the areas surveyed, hippopotamus abundance was highest at Ikuu Springs, Upper Ikuu Springs, upper Lake Katavi, Paradise Springs and Sitalike (Fig. 6.6). Ikuu Bridge was only counted in 2010 when abundance was fourth highest.

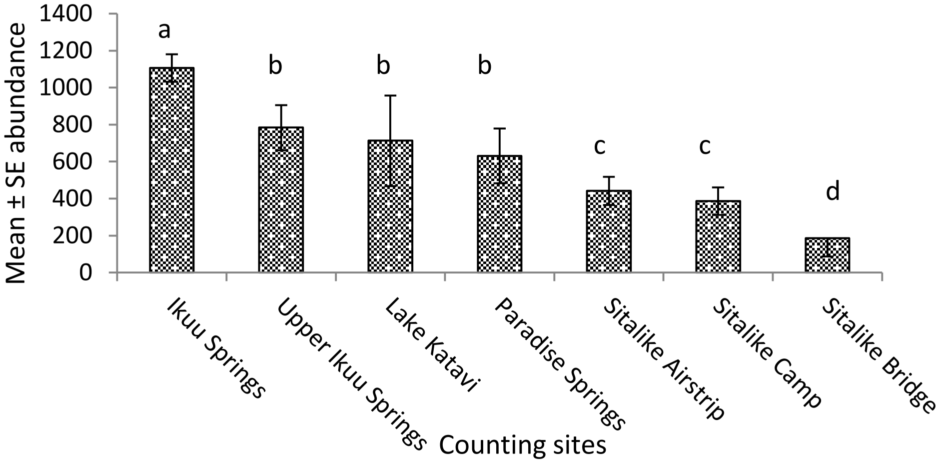


Fig. 6.6: Mean 3-year hippopotami abundance in selected sites using minimum total count data in Katavi NP. Error bars are ± 1SE around 3-year mean.

Mean annual adult hippopotamus abundance varied significantly between study sites ($F_{4, 81} = 2.935$, $p < 0.026$) (Fig. 6.7). Adult hippopotamus abundance was highest at Ikuu Springs followed by Lake Katavi while Lake Chada had the least. Mean annual abundance of juvenile hippopotami varied between sites ($F_{4, 81} = 3.081$, $p < 0.021$) (Fig. 6.7). Juvenile hippopotamus abundance at Paradise Springs, Lake Katavi and Ikuu Bridge was the highest while Ikuu Springs and least at Lake Chada (Fig. 6.7).

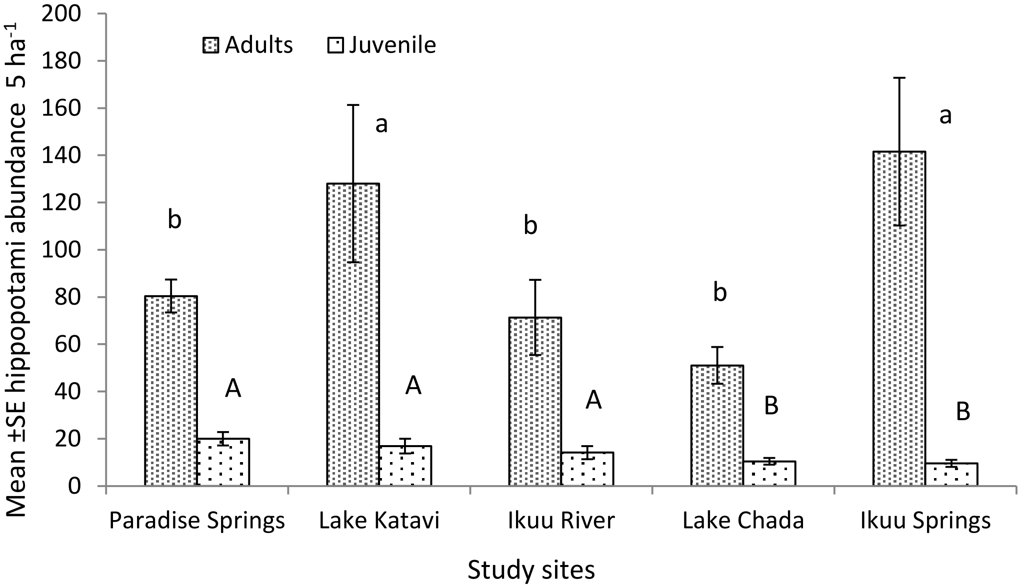


Fig. 6.7: Mean hippopotami annual abundance in 5 ha plots for adult and juvenile hippo in five study sites in Katavi NP, Tanzania. *Key*: Means with the same letter do not differ significantly at $p < 0.05$. Capital letters are for juveniles while lower cases

3.4 Temporal variations in abundance

(a) Seasonal variations in abundance

Abundance among adult hippopotami varied significantly between the dry and wet seasons at Lake Katavi, Ikuu Springs and Ikuu Bridge ($F_{4, 82} = 2.905$ $p = 0.027$). Abundance was significantly higher in the dry season at Lake Katavi, Ikuu Springs and Ikuu Bridge ($t_{80} = -2.183$, $p < 0.032$). However, mean hippopotami abundance on other sites did not show any significant seasonal variations (Fig. 6.8). August, September, October and November were the driest months of the dry season while January, February, March and April were the wettest in the wet season.

Abundance among juvenile hippopotami varied significantly between the dry and wet seasons at four out of five study sites ($F_{4, 82}$= 3.444 p = 0.012). Only at Paradise Springs was the difference between seasons not significant (Fig. 6.9). Abundance at other sites varied significantly between the wet and dry season (t_{80} = -2.926 p = 0.019).

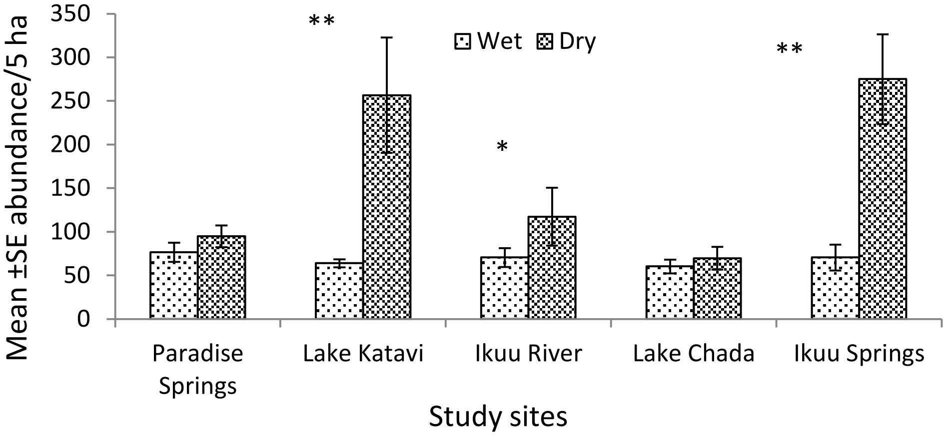


Fig. 6.8: Differences in adult hippopotamus abundance between dry months (August-November) and wet months (January-April) in Katavi NP, Tanzania

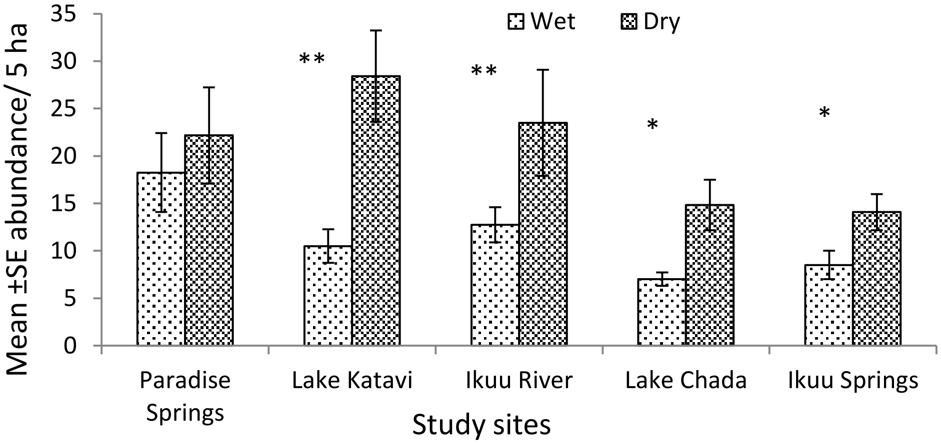


Fig. 6.9: Differences in juvenile hippopotamus abundance between dry months (August-November) and wet months (January-April) in Katavi NP, Tanzania

(b) Monthly variations in abundance and density

Abundance varied between months for both adults and juveniles. There were significant variations in abundance between months for adult hippopotami ($F_{16,\ 81}$= 3.981 p = 0.0001) and between sites ($F_{4,\ 81}$ = 2.938 p = 0.026) (Fig. 6.10).

Juvenile hippopotami abundance varied significantly between months ($F_{16,\ 81}$ = 5.442 p = 0.0001). There were also significant differences in monthly abundance between sites for juveniles ($F_{4,\ 81}$ = 3.142 p = 0.019) (Fig. 6.10).

Hippopotami abundance at Paradise Springs had steady annual variations in all the months, with only small fluctuations. However, there was a common trend at three other study sites, Lake Katavi, Ikuu Springs and Ikuu Bridge where density increased from September to a peak in November. At Paradise Springs and Lake Chada, some similar general trends were observed; however, density did not change significantly as at the other three sites (Fig. 6.10).

From December, with exception of Paradise Springs; density declined in all of the four sites and by May, June and July, density was minimal. Decline in density at Ikuu Springs and Lake Katavi was much more rapid than other sites. Nevertheless, all sites reached their minimum density between April and July (Fig. 6.10). Density started increasing again from August, with similar patterns for all sites.

Abundance in juvenile hippopotami increased during the dry months beginning from September as for adults. Density reached its peak in November and December. Density trends were as in adults in that it decreased during the wet months of February to July before starting to increase in August. Density increase at Ikuu Springs during August-September 2010 was lower compared to the same period in 2009. Fewer juveniles were recorded in 2010. Although density at Paradise Springs did not decrease significantly during the wet month of January, during the dry season from August to September 2010 higher densities were recorded compared with the same period in 2009 (Fig. 6.10).

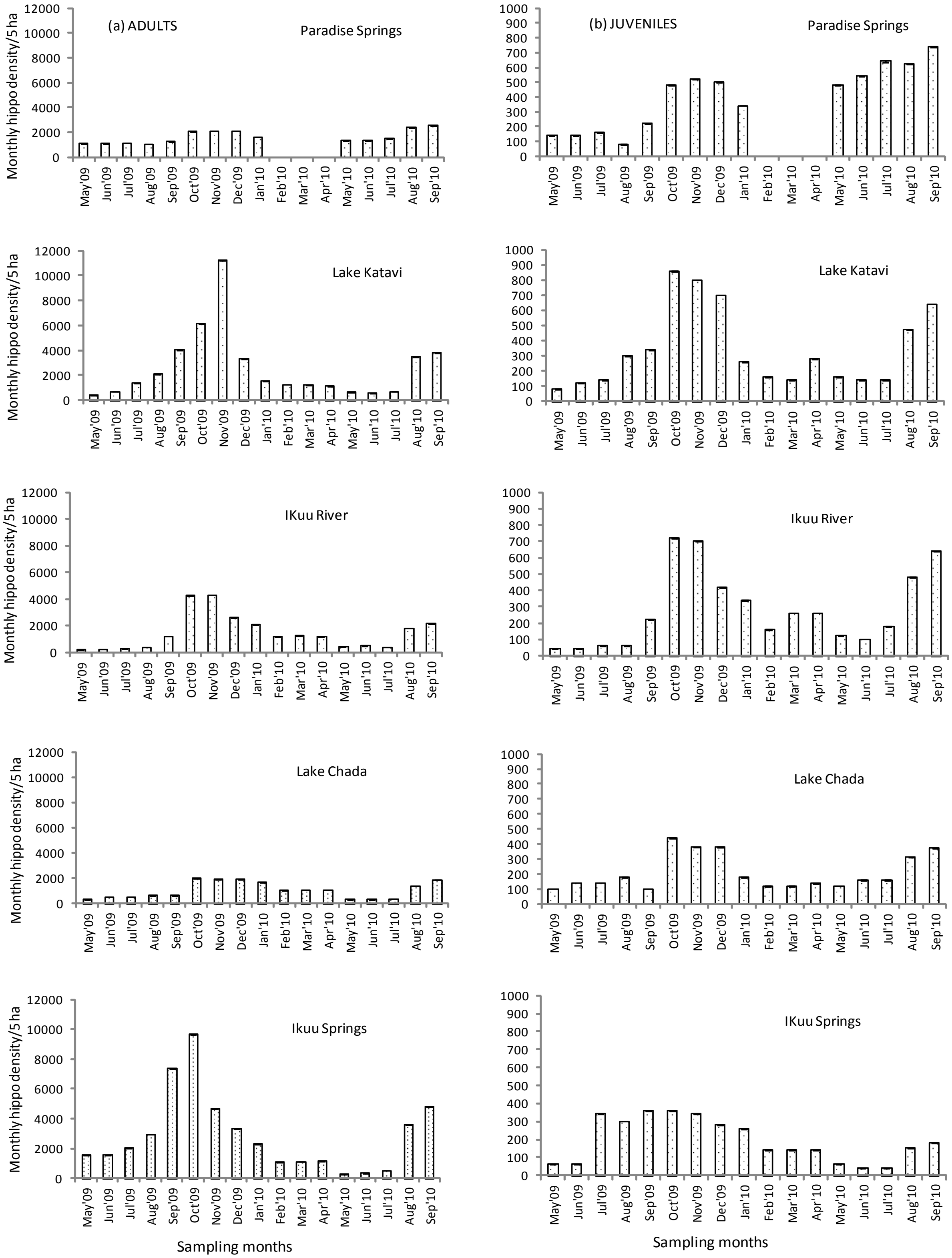


Fig. 6.10: Monthly variations in hippopotamus density (May 2009-September 2010) among (a) adults and (b) juveniles in the five named study sites in Katavi NP, Tanzania

3.5 Immigration and emigration

Monthly rates of immigration and emigration for both adult and juvenile hippopotami at the five study sites are presented in Fig. 6.11. There were significant monthly variations in immigration and emigration ($F_{16, 81} = 5.323$, $p < 0.0001$). There were also significant seasonal differences in immigration and emigration among adult hippopotami ($t = 3.566$ $df = 80$, $p < 0.001$) (Fig. 6.10). Rates of immigration and emigration for adult hippopotami did not vary between sites (Fig. 6.11).

There were significant monthly variations in immigration and emigration among juvenile hippopotami ($F_{16, 81} = 3.188$, $p < 0.0001$) (Fig. 6.11). Rates of immigration and emigration among juvenile hippopotami did not vary between sites (Fig. 6.11).

As with variations in abundance, most emigrations were recorded between December and July. Immigration was more prominent between August and October. Among all sites, Paradise Springs had the lowest rates of immigration and emigration while at Ikuu Springs and Lake Katavi the rates were highest (Fig. 6.11).

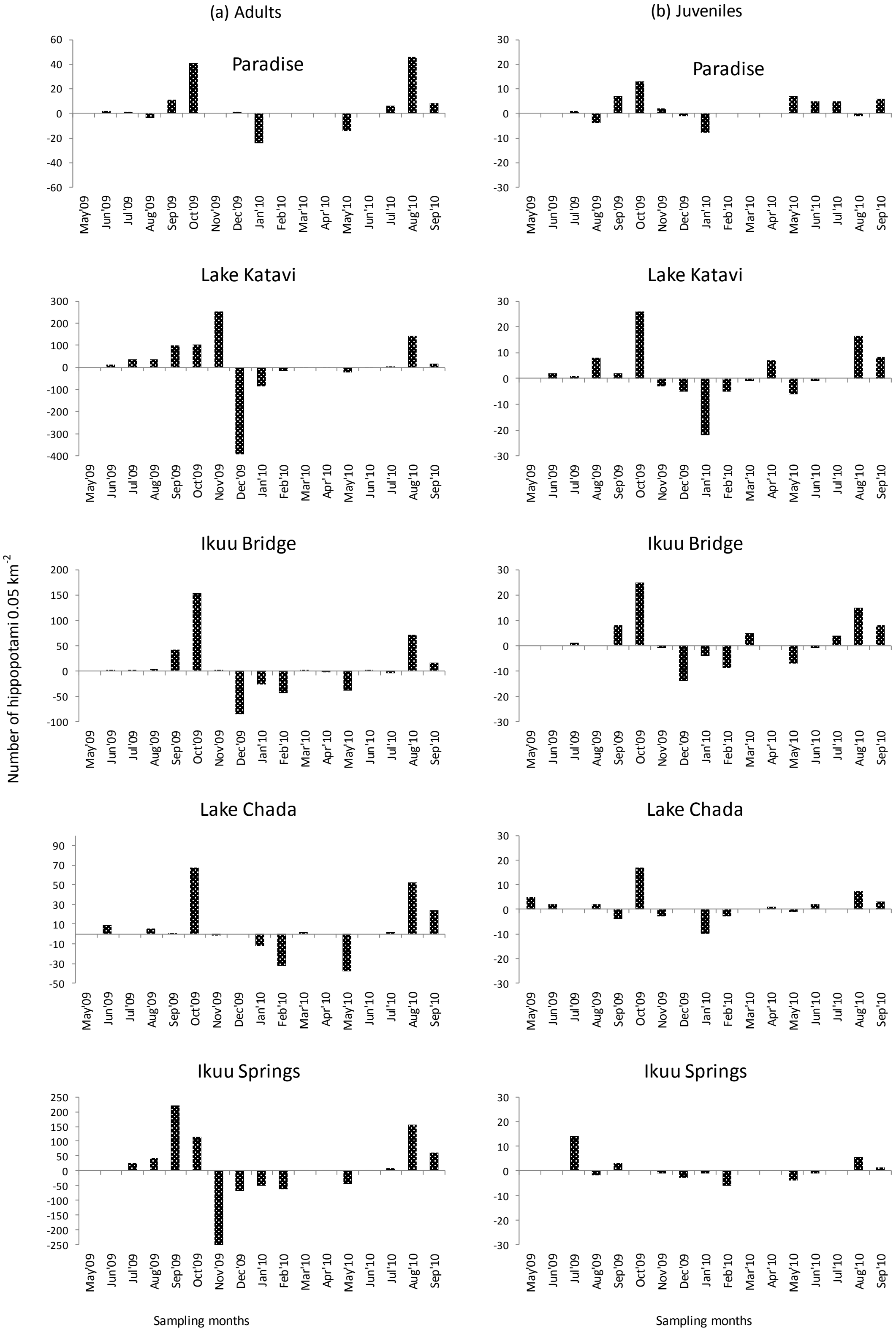


Fig. 6.11: Monthly variations in Immigration and emigration of hippopotami in Katavi NP for adults and juveniles expressed as number of individuals. *Note*: different Y-axis scale within and between (a) and (b).

4 Discussions

Abundance can vary between decades, within decades, seasonally and spatially.

4.1 Change in abundance between decades.

Among the factors which may cause fluctuations in hippopotami abundance over greater than a generation time span are habitat loss and incompatible land uses, drought (affecting availability of both water and food), poaching (due to increased trade in hippopotami meat and ivory) and diseases. The other threat has been retaliatory killing due to conflicts with humans (Kanga *et al*., 2011a; 2011b; Kendall, 2011). In countries with civil unrest such as Congo DRC, hippopotami populations have suffered the most (Lewison and Oliver, 2008; Kendall, 2011). Among these, habitat loss and poaching have been listed as being most important (Oliver, 1993; Graham, *et al*., 2002; Lewison and Oliver, 2008), leaving their future in jeopardy.

Diseases such as anthrax has also been reported to affect hippopotami population in the Serengeti (Lembo *et al*., 2011), although its effect on the population has not been quantified. In Zambia, anthrax in 1987/8 killed over 4,000 hippopotami in Luangwa River affecting its populations (Turnbull *et al*., 1991). In Kruger NP, South Africa, incidences of anthrax in the dry seasons of the early 1990s affected local hippopotami populations with relative vulnerability at 2.1% (Viljoen and Biggs, 1998). Rinderpest in the early 1900s in Luangwa River in Zambia was thought to have contributed to hippopotami scarcity in the 1930s (Attwell, 1963; Marshall and Sayer, 1976), however this was disputed by Ford (1971) who suggested the species to be relatively immune to the disease. In Katavi, there are no recorded reports of significant effects of either disease (Caro, 2008). However, drought in 1988 was the major cause for the decline of hippopotamus abundance in Kruger NP in South Africa (Viljoen and Biggs, 1998).

In Asia, historical extinction of hippopotami was associated with increased seasonality in patterns of rainfall and river flows which resulted in rivers remaining dry for several months of the year (Jablonski, 2004). In Ruaha NP, Tanzania, hippopotamus populations declined by 7.7 % between 2004 and 2007 thought to be due to reduced river flow (Epaphras *et al*., 2008). Population decline due to reduced water and possibly retaliatory killing of hippopotami in Ruaha NP was also reported by Kashaigili *et al*. (2006) and Kendall (2011).

However, in some areas, there have been increases in hippopotami population despite these factors. In Kenya, hippopotamus populations increased between 1997 and 2008 in the Mara while deteriorating habitats and drought were increasing (Kanga *et al*., 2011a; 2011b) due to the presence of microhabitats with water and forage leading to the increase. Also, drought and deteriorating habitats reported in Kanga *et al*. (2011a; 2011b) are thought to have been temporary and short lived. Prolonged drought and habitat loss are likely to be detrimental to hippopotamus population growth. In Kruger NP, in South Africa it was observed that the availability of dams in or near the rivers and suitable pools in rivers played a key role in maintaining hippopotami density during drought or periods of reduced river flows (Viljoen and Biggs, 1998). Similar observations were made in Queen Elizabeth NP in Uganda where seasonal use of temporary wallows led to maintaining hippopotami abundance (Field and Laws, 1970). Some of their water wallows temporarily dried out after the wet season (Field and Laws, 1970). During the dry season hippopotami were confined to river channels, lakes and some few permanent water pools. During the wet season, most of the animals exploited much of the areas by moving into temporary water pools (Lock, 1972).

Among the factors that determine abundance include natality, mortality, immigration and emigration. There has been a decline in populations of most herbivores in Tanzania from the 1980s to the early 2000s (Stoner *et al*., 2006; 2007). Highest hippopotami abundances were recorded in 1991 and 2002. Lowest abundances were in 1987 and 2006 (Fig. 6.3 and Fig. 6.4). Aerial census data indicate an increase and decline in hippopotami abundance in Katavi (TAWIRI, 2001; Caro, 2008). The decline is however, not significant. Although hippopotami populations are declining (Lewison and Oliver, 2008), the Katavi population has remained relatively stable. In 2006, the lowest record in hippopotami abundance in Katavi was observed. Abundance peaked up in 2009.

Various reasons might explain the increase in abundance. The first is new born hippopotami, as represented by the number of young observed. The second is immigration from other localities. Lewison (1998) noted that increase in hippopotami in early 1990s in Katavi was thought to be due to animals coming in from outside Katavi as the result of habitat destruction in the areas bordering the Park. The same might help in explaining the current observations, that there is an increasing trend in habitat destruction. However, very few hippopotami sites were observed outside the Park and hence natality is thought to be the major abundance contributing factor.

Results have shown that in the 1980s, hippopotami abundance was low before it peaked in the 1990s (Fig. 6.4). Since then, in the 2000-2010 decade, abundance has declined to a certain extent. However, from aerial census data presented, hippopotami population trends are not very clear, partly because hippopotami are irregularly recorded through aerial count due to their aggregation habit and most of the time during counts they are in or under water (TAWIRI, 2001). Grouping patterns of hippopotami make it difficult to count from the air (TWCM, 1995; 1998), hence the high standard errors. Large groups may be missed completely and hence affect the results. This can help to explain the observed fluctuations in abundance results.

However, despite the possible influences in estimating abundance, the observed trend might be reflecting actual trends on the ground. The 2006 lowest abundance recorded might be explained by the severe drought reported during the 2004/5 in Katavi (Meyer *et al*., 2005). Natality in hippopotami is severely affected by drought (Lewison, 2007); the effects of this drought might have had an impact during the 2006 counts. Fewer females calving, mortality due to drought and under nutrition among both adults and juveniles is likely to have affected abundance. Similar factors are thought to have affected other years with lower abundance. Human influence by poaching or hunting was also cited as another possible reason for the hippopotami mortality (Meyer *et al*., 2005), however, this has been shown to have a less significant effect in Katavi (Caro, 2008).

Calving in hippopotami is not strictly seasonal but peaks in calving have been associated with increased rainfall (Graham *et al*., 2002). During drought, proportion of hippopotami females likely to conceive declines significantly from about 30 % to 5% (Lewison, 2007) due to poor conditions brought by poor nutrition. This may have significant influence on the fluctuation of the population. Local drought in Kruger NP rivers in 1991/2 led to a decline in hippopotamus population during the following census (Viljoen & Biggs, 1998) and can help to substantiate effects of drought on population growth.

Similar fluctuating trends in hippopotamus populations due to different reasons have been reported from other protected areas in Africa. In Masai Mara National Reserve in Kenya an increase by about 170 % in hippopotami abundance was recorded between 1971 and 1980. However, between 1980 and 2006, there was no increase within the reserve although hippopotamus abundance increased by about 360 % outside the reserve (Kanga *et al*., 2011a; Kanga *et al*., 2011b). The increase was recorded despite deteriorating habitat conditions. This led to the assumptions either that the population was increasing or its spatial distribution was being compressed due to range contraction (Kanga *et al*., 2011a; Kanga *et al*., 2011b). When hippopotami increased, other large mammals declined. Similar trends in hippopotami population over the decades were recorded in Gonarezhou National Park in Zimbabwe where from 1965-1982 significant increase was recorded (Zisadza *et al*., 2010). However, between 1983 and 1997, a significant decline occurred before increasing again between 1997 and 2008 (Zisadza *et al*., 2010). Drought, siltation of rivers and persecution were thought to be the major causes for a decline of hippopotami between 1983 and 1997. Contrasting trends were recorded in Luangwa River in Zambia where from 1970 to 1987, when a 7 % increase in hippopotami population was recorded annually (Tembo, 1987). The increase led to more than a doubling of population density when compared with the density in Queen Elizabeth National Park in Uganda in the late 1950s (Tembo, 1987; Eltringham, 1999). However, populations did not increase significantly from 1988. It was thought that the population had reached its carrying capacity 100 years after the population was severely affected in the 1890s (Attwell, 1963). In Sabie River, Kruger NP in South Africa, drought experienced during the 1991/2 reduced the once growing hippopotami population by about 13 % (Viljoen, 1995). Viljoen & Biggs (1998) reported several hippopotamus deaths in Kruger National Park South Africa following severe drought during 1991/2. Meyer *et al*., (2005) reported an increase in hippopotami carcasses during the 2004 drought in Katavi.

In Lundi River, Zimbabwe, hippopotami increased by 330 % between 1958 and 1980 before the population stagnated because of drought and killings (O'Connor & Campbell, 1986). In Luangwa River, Zambia, high mortality due to anthrax which killed over 4,000 hippopotami between 1987 and 1988 (Turnbull *et al*., 1991) affected the growing population trends reported by Tembo (1987). These may indicate similar patterns in the hippopotami population growth between Katavi and elsewhere. Some cases of stagnated population due to possibility of reaching carrying capacities include wildebeest in the Serengeti (Mduma *et al*., 1999) and reindeers in Saint Matthew Island (Kirkpatrick *et al*., 1968). In these cases it was thought that environmental resources such as food, spaces for basking and wallowing were the causes for reduced birth rates. The environmental factors are known to determine the points at which population stabilizes (Bothma & Toit, 2010). However, the Katavi population is not thought to have reached its carrying capacity, although dry season resting sites are shrinking and may be limiting during the dry season.

Similar trends in increasing and decreasing populations have been observed for wildebeest (*Connochaetes taurinus* Burchell, 1823) in the Serengeti, Tanzania and for buffalo (*Syncerus caffer* Sparrman 1779) in Arusha NP, Tanzania. In the Serengeti, wildebeest population increased between 1963 and 1993 and stabilized before declining during the 1993-1994 due to drought (Mduma *et al*., 1999; Sinclair *et al*., 2001). Drought was the major reason because 75 % of carcasses observed were found to be under nutrition and food supply continued to limit population increase particularly during the dry season. Mortality was greatest in wildebeest under one year of age (Sinclair *et al*., 2001). This could also be the cause for the 2006 lowest abundance of hippopotami in Katavi. Mortality of juveniles might have contributed significantly to the decline as drought during the previous two years might have affected many juveniles. Meyer *et al*., (2005) observed more hippopotami carcasses during the dry season in 2004, which was drier than normal in Katavi. The use of water upstream for irrigation contributed to the drought more than rainfall, which was average for that year. The year 2006 had the lowest river levels for similar reasons. Sinclair (2008a; 2008b) found buffalo populations in the Serengeti to be regulated by adult mortality caused by under nutrition as a result of food shortage. However, food shortage among ungulates has been described as a general situation in eastern Africa (Sinclair, 2008a; 2008b).

Aerial censuses reported in this study were conducted during different times of the year which might contribute to the observed trends. Different conditions prevailing at the time of surveys are likely to result in different values of abundance. During the wet season, groups in water are likely to submerge and thus be invisible to the observers from the aircraft. In Mara River, Tanzania, Olivier and Laurie (1974) found hippopotami populations became more dispersed and mean group size decreased after a rise in water levels and vice versa. Such variations may lead to differences in abundance estimation results. Similar trends were recorded in Liwonde NP in Malawi (Harrison *et al*., 2007). In Katavi NP, similar observations occur. This causes variations in hippopotamus density during censusing at different times of the year. Stoner *et al*., (2006) reported that wildlife estimates are likely to fluctuate between counts conducted during different seasons. This was based on observations that many ungulates congregate more at water sources during the dry seasons. During the wet seasons, hippopotami are partly submerged in water hence becoming less detectable. Vegetation during the wet season is also responsible for reduced visibility (Stoner *et al*., 2006). In order to increase success, aerial counts in Kruger National Park, South Africa have been conducted between June and August at the mid dry season when water depth were shallower because of reduced water flow and clearer waters which allowed counting of submerged individuals (Viljoen & Biggs, 1998). In Zimbabwe, aerial censuses were conducted in November during the dry season, mainly to increase ability of detecting the hippopotami (Zisadza *et al*., 2010).

Variations in aerial hippopotami census in Katavi might also be influenced by variations in sampling effort or intensity, observers and areas covered during the census. Sampling efforts between sampling years varied between years. In 1995, one aircraft was used to conduct census in the area of 13,341 km^2 including Katavi while in 1998 three aircrafts were used to census a total area of 12,321 km^2 including Katavi, and counts were lower despite the apparently greater sampling efforts. This is likely to give varying results. In studying abundance of hippopotami in Kruger NP, South Africa between 1984 - 1994 it was found that during aerial counts, hippopotamus density was significantly lower than estimated during total counts (Viljoen & Biggs, 1998). In order to minimize the effects of observers on the counts, Field and Laws (1970) proposed the use of the same personnel wherever possible. This can further help to explain the observed variations between years.

However, despite these possible factors for fluctuations, the counts have shown a general trend of increase and decline of hippopotami populations in Katavi. There is a need to conduct continued census during similar times and seasons from where long term results can be comparable. Dry season counts provide more reliable population estimates.

4.2 Change in abundance within a decade

From minimum total counts between 2004 and 2010, the number of hippopotami has remained largely stable with exception of 2005. Water scarcity, reduced natality and poaching were thought to have attributed to the 2005 decline (Meyer *et al*., 2005). However, these estimations were minimal, because some areas where hippopotami are present were not covered. This is among the sources of underestimation.

In 2010, there was an increase in hippopotami abundance when compared to 2004 and much larger when compared to 2005. This pattern of abundance supports the report that less water in Katavi started to be experienced in 2004 after illegal damming upstream the Katuma River (Meyer *et al*., 2005) refer Chapter 3. This can help to explain the lowest abundance recorded during the 2005 counts reflecting the possible effects of 2004/5 drought on hippopotami abundance as drought significantly affects natality and survival of hippopotami (Lewison, 2007). In Kruger NP in South Africa, localized drought in 1988 in some sections of the rivers, resulted in hippopotami die offs, the decrease being reflected in censuses during the following year (Viljoen & Biggs, 1998). However, despite damming and subsequent water reduction in Katavi, hippopotami abundance increased during the 2010 counts.

Increase in the hippopotami abundance in Katavi can be seen as small, but, it is a 23 % increase in abundance over five years and thus the increase is fairly substantial. Larger increases have been reported in Zambia (Tembo, 1987; Wilbroad and Milanzi, 2010), Zimbabwe (O'Connor and Campbell, 1986) and Kenya (Kanga *et al*., 2011a; 2011b). In Liwonde NP in Malawi, hippopotami population increased by 54 % during a period of 16 years from 1987 to 2003 after which there was no noticeable increase (Harrison *et al*., 2007).

In the Katavi hippopotamus population, there is a near balance in the forces determining abundance. Natality and immigration were slightly higher than mortality and emigration hence a small increase in population abundance over years compared to a 7 % annual increase recorded in Zambia (Tembo, 1987). This is supported by the fact that there were many calving incidences and calves observed during the study period, while observed dead hippopotami were very limited in number when compared with the population of hippopotami in each of the study sites. Increase in abundance from 2005 to 2010 may help to support this suggestion. The increase in abundance occurred despite natural mortality or human induced mortality reported in Katavi (Caro, 1999a; Meyer *et al*., 2005). Increase of hippopotami in Zambia was after severe declines in the early 1900s due to diseases, hunting and drought (Marshall and Sayer, 1976).

There may be underestimation of abundance using minimum total counts due to its limitations. However, despite any shortcomings, obtained results shows that the hippopotamus populations in Katavi are stable and has not varied significantly over the years. Repeated aerial census between 1977 and 2009 and transect counts from 1995 in Katavi have indicated declines in other large mammals; however, hippopotami is not among the declining species (Caro 2011, Caro *et al*., 2011).

Results also indicate some important patterns in distribution and abundance of hippopotamus in Katavi NP. The most important sites where higher abundances were recorded were the sites which had water during the dry season such as Ikuu and Paradise Springs. Also, microhabitat provided by artificial water pools at some drier sites such as Ikuu Bridge and at Lake Katavi enabled hippopotami to reside during the dry season.

Counting hippopotami using ground transects is efficient although costly, slow and time consuming (Tembo, 1987; TWCM, 1995; 1998; TAWIRI, 2001; Kanga *et al*., 2011a), hence minimum total counts presented in this Chapter were necessary. Some consistency has been noted in hippopotami counting using ground surveys during the three years records and more detailed estimates in change of abundance were derived from minimum total counts (Table 6.2). In Queen Elizabeth NP in Uganda, counts using boats proved to be effective as repeated counts of submerging or hiding hippopotami were possible (Field and Laws, 1970). This helps to emphasize the usefulness of ground transects.

Several factors may have contributed to the observed stability and small increase in hippopotami abundance. Forage is one of the most important requirements for hippopotami apart from water (Sinclair *et al*., 2000; Harrison *et al.*, 2007). There has been no significant decline in rainfall in Katavi, and therefore it can be assumed that food has been available throughout the sampling years. This has possibly led to increasing population despite decline in water levels. Timing of food supply and availability (phenology) is listed as one of the factors which determine birth seasons in tropical ungulates (Sinclair *et al*., 2000). Due to this, it is probable that hippopotamus timing of birth has largely been determined by food supply which has been stable over the years, hence the increase in population. Prolonged drought would have led to shortened period of food supply and hence affect the birth success of hippopotami. However, this has not been reported over the census time with the exception of the year 2004.

Mortality, both natural and through hunting and diseases were ruled out as affecting hippopotami population apart from 2004 where ‘many’ carcasses were reported (Meyer *et al*., 2005). Hippopotami were not on the list of most hunted species in Katavi (Caro, 2009; Caro *et al*., 2011), and hence an increase in abundance despite damming and decline in water level or reduced flow.

According to Waltert *et al*. (2008), Katavi National Park has an estimated 5694 hippopotami or a density of 1.33 hippopotami km^{-2}. This abundance equals the one in Kruger NP in South Africa where 2,600 counted in the 1998 in an area of 19,485 km^2 was considered as stable population (Viljoen & Biggs, 1998), while the entire country had an estimated 5,000 hippopotami (Eltringham, 1999). Katavi with an area of 4,700 km^2 can thus be considered to have a more viable population. Factors such as reduced natality during some years are thought to be a natural phenomenon, not entirely due to temporarily limiting resources. This is because reduced natality has also been reported among hippopotami in zoos (Pluhacek, 2008). Reduced natality among hippopotami in captivity occurred despite controlled environment and habitat which provide optimal physiological conditions for hippopotami (Wheaton *et al*., 2006). This may help to explain further the stability and smaller increases in Katavi hippopotami.

Drought remains to be a major threat to hippopotami populations as indicated by other studies reported in Section 4.1 and 4.2 and the possible effects experienced in 2005 counts. Prolonged low or no river flows might exacerbate this even further apart from inadequate forage, as rainfall which determines forage availability has remained largely unchanged over the past six decades.

4.3 Spatial variations in abundance

Density and abundance of hippopotami varied between sites. Adult hippopotami density and abundance was highest at Ikuu Springs and Lake Katavi. Lake Chada had the least adult density among the five sites. Paradise Springs and Ikuu Bridge were the intermediates. This observation might be explained by nature of the study sites as discussed in Chapter 2. Caro (1999a) observed higher hippopotami densities at Lake Chada and Lake Katavi.

The distribution of large mammals is influenced by a number of factors including vegetation, permanent or temporary surface water, fire, predators and human activities (Field & Laws, 1970). There are several factors which make a site suitable for hippopotami. Availability of water, particularly during the dry season is one of the major pre-requisite for occupation of a site by hippopotami (Graham *et al*., 2002; Dunstone & Gorman, 2007; Jablonski, 2004). Nearby foraging grounds is another major requirement (Viljoen & Biggs, 1998; Eltringham, 1999; Harrison *et al*., 2007). Apart from stationary waters, sites with slow moving waters such as river bends, river confluence and lagoons increase the suitability of the sites for hippopotami (Chansa & Milanzi, 2011). Areas of slow and relatively shallow, gently sloping banks are favoured as it enables hippopotamus to lie half immersed while resting (Laws & Clough, 1966; Field, 1970, Olivier & Laurie, 1976; Viljoen & Biggs, 1998). Spatial variations among hippopotami in other areas in Africa have been high e.g., in Kruger National Park (Viljoen & Biggs, 1998) and in Zambia, (Wilbroad & Milanzi, 2010).

Selection of suitable sites by hippopotami is emphasized by observations in Zambia and South Africa where in Kruger NP, 94 % of its population was recorded in six rivers. Out of the six rivers, 81 % was recorded in three rivers (Viljoen & Biggs, 1998). In Zambia, about 62 % of its entire hippopotami population of 40,000 were located in Luangwa River out of nine lakes and dams and 18 rivers surveyed (Wilbroad & Milanzi, 2010).

Within Luangwa River about 76 % of its hippopotami population was found in river bends (Chansa & Milanzi, 2011). Similar patterns were observed in Tanzania while surveying abundance of hippopotami where 80 % of its population were concentrated in some few rivers in southern and western parts of the country within protected areas (TAWIRI, 2001). These emphasize the importance of habitat selection by hippopotami.

Slow flowing waters at the river bend are the possible reasons for the Ikuu Bridge site to accommodate many hippopotami almost throughout the year despite being in a drier part without a substantial nearby foraging ground. Hippopotami prefer structurally suitable pools to pools which are closer to foraging areas (Smithers, 1984). This emphasizes the importance of water and shelter sites to hippopotamus.

The wettest site, Paradise Springs was the most suitable for hippopotami among the five sites. This is because it provided water and forage throughout the year and thus hippopotamus abundance was maintained. However, as resources are likely to vary over seasons (Western, 1975; Western & Lindsay, 1984; Fryxell & Sinclair, 1988), sites which provide resources during the dry seasons are highly important. This was represented by sites such as Ikuu Springs where hippopotami took refuge during the dry season. Although Lake Katavi, Lake Chada and Ikuu Bridge provided refuge to hippopotami during the dry season, they were not as 'suitable' as Ikuu and Paradise Springs. This is because their waters were more seasonal and hence in case of prolonged drought they are likely to dry out and force the animals to disperse to other locations which are not easily available, especially during the dry season.

Between the two, water and forage, the former has been listed as the factor which determine distribution of mammals (Western, 1975; Smithers, 1984; Western & Lindsay, 1984; Fryxell & Sinclair, 1988; Gereta & Wolanski, 1998; Wolanski & Gereta, 2001). In Katavi, Ikuu Springs and Lake Katavi were the sites with the highest abundance. However, these had temporary high abundance. The wettest site at Paradise maintained higher abundance due to provision of forage and water throughout the year. The two driest sites supported hippopotami during the dry season due to the presence of microhabitats which provided shelter for the hippopotami, without which the sites would have been inhospitable over the dry season. Similar observations were recorded in Kruger NP (Viljoen & Biggs, 1998) where dams and water pools along the river helped to maintain abundance during the dry season. Similar observations of hippopotamus using temporary shelter were recorded in Uganda (Field & Laws, 1970; Lock, 1972; Eltringham, 1999).

Availability of water particularly during the dry season is thought to have contributed to the observed variation in hippopotami abundance between sites. High hippopotamus variance in abundance at the two sites Ikuu Springs and Lake Katavi may be explained by bigger monthly fluctuations in water availability, the factor which might have contributed to the observed results. Paradise Springs being the wettest site had the highest water supply throughout the year hence maintained relatively constant hippopotami abundance throughout the year (Fig. 6.6). This is because resources, mainly water and forage availability, dictates seasonal movements of mammals (Western, 1975; Western & Lindsay, 1984; Fryxell & Sinclair, 1988). This can help to explain the observations at Lake Katavi and Ikuu Springs where abundance was seasonal.

Among juvenile hippopotami, Paradise Springs was the site with the highest density while Ikuu Spring was the least. This observation is linked to the availability of water resources and nature of use of the areas by hippopotami. Paradise Springs was the site with highest supply of water throughout the year, whereas Ikuu Springs was mainly a dry season refuge for adult hippopotami hence, it had fewer juveniles than any other site. Availability of water throughout the year at Paradise Springs was a possible reason for calving throughout the year and hence more juveniles unlike Ikuu Springs (Fig.6.6, Fig. 6.7 and Fig. 6.8). At Ikuu Springs, being a dry season refuge, few mating events were observed and this would have led to fewer juveniles.

Spatial variations in hippopotami may reflect environmental variables such as water and vegetation. In Luangwa River in Zambia, hippopotami density distribution was reported to be influenced by diversity of grass species, biomass and grazing capacity (Chansa *et al*., 2011b). Wilbroad & Milanzi (2011) reported influence of grass species and abundance on hippopotami distribution and abundance in Zambia. Harrison *et al*. (2007) reported hippo abundance to relate to vegetation type in Malawi.

In Katavi, abundance was highest in the sites that provided water during the dry season, while it was lower in the driest site. During the wet season abundance was more evenly spread over many areas of the Park. This suggests that water supply to the sites was a major factor for the observed trends. Wildlife distribution in general responds to and depends mainly on surface waters (Douglas-Hamilton, 1973), and distribution reflects variations in water availability (Western, 1975). Hippopotami distribution is likely to be particularly affected because the rivers tend to dry out between September and November. The hippopotami then select sites with dry season water availability. Nevertheless, the site which had more water supplies throughout the year, Paradise Springs was not the site with highest abundance, but it did have the most constant abundance throughout the year.

Apart from water and forage availability, humans may also affect hippopotami distribution and abundance (Caro *et al*., 1998). In Okavango Delta, Botswana, it was observed that hippopotami avoided some suitable habitats due to poaching and hunting. Indigenous and crocodile hunters used hippopotami meat as baits for crocodiles (McCarthy *et al*., 1998). However, this is not thought to be the case for Katavi, where availability of water largely determined differences in abundance between sites.

4.4 Temporal variations in abundance

(a) Seasonal variations in abundance

Hippopotami abundance varied between seasons at Lake Katavi and Ikuu Springs. At these sites, high abundances were recorded during the dry season. Availability of spring water at Ikuu Springs and water pools at some locations at Lake Katavi were the major reason for the observed seasonal variation in abundance. During the wet season, hippopotami dispersed to other resting sites. Similar observations were made by Olivier and Laurie (1974) in the Mara River, Serengeti where hippopotami groups were found to disperse as water levels in the river increased. Seasonal pattern has been reported for different large mammals (Coe *et al*., 1976; Western, 1975; Western & Lindsay, 1984; O'Connor & Campbell, 1986; Fryxell & Sinclair, 1988), with movements being in search of quality forage or water (Senzota & Mtahiko, 1990).

Despite having the highest abundance, Ikuu Springs was mainly used as a dry season refuge. With the onset of rainfall in November, the group at the site dispersed leaving very few individuals until after the end of the wet season. Similar observations were made at Lake Katavi. The group size and abundance increased with the decrease in water levels. This led to significant seasonal variations in hippopotami abundance at the two sites (Fig. 6.7).

At Paradise Springs, the wettest site, hippopotami did not enter or leave the site in large numbers during the dry or wet seasons. This was the main cause for lack of significance in seasonal changes in abundance at the site. At Ikuu Bridge and Lake Chada sites, effects of microhabitat played a crucial role in maintaining hippopotami abundance over the cause of seasons (Fig. 6.7). This was due to the availability of water pools in the two sites which were used by hippopotami as resting sites well into the dry season. Many hippopotami at the pools remained throughout the year hence the seasonal variations in abundance was minimal.

Among the factors that are responsible for seasonal variations in abundance are food, shelter and water availability (Coe *et al*., 1976; Western, 1975; Western & Lindsay, 1984; Fryxell and Sinclair, 1988). These affect habitat quality on a seasonal basis. Habitat quality is the ability of the environment to provide appropriate conditions for persistence of organism (Hall *et al*., 1997; Krausman 1999). Food for hippopotami is the major limiting factor where water is not limiting (Harrison *et al*., 2007). In habitats where hippopotamus are found, poor availability of daytime sheltering space during the dry season can regulate their abundance (Olivier and Laurie, 1974; Tembo, 1987; Harrison *et al*., 2007). Chansa *et al*. (2011b) reported hippopotami density to be influenced by grass species diversity and grass biomass which determined grazing capacity. However, in Katavi, seasonal variations were mainly observed to be due to water at the shelter sites and much less due to forage.

Apart from food resources, during the dry season, water scarcity and higher temperatures (Manteca & Smith, 1994) are the other major environmental parameters which are likely to influence hippopotami distribution, abundance and behaviour. In Katavi, sites with least wetness and a single source of water were more affected by seasonal variations in hippopotami abundance than the sites with more wetness or multiple sources of water.

Seasonal variations in hippopotamus distribution and abundance have been reported in different studies mainly in response to environmental variables (water and food). Shift in hippopotami abundance and distribution was reported by Harrison *et al*. (2007) in Shire River in Malawi. Hippopotami moved into temporary water sources which occurred as the wet season advanced. Although the river was perennial, this led to seasonal variations in abundance. Similarly, such seasonal patterns were reported in Queen Elizabeth NP in Uganda (Field and Laws, 1970, Lock, 1972).

Water availability was therefore the main cause for seasonal variations in abundance. Lack of seasonal variations in abundance at Paradise Springs was due to availability of water throughout the year within the site. Little variations at Ikuu Bridge and Lake Chada were contributed by microhabitat conditions which existed during the study period. At these two sites, water pools which went well into the dry season made the sites habitable for hippopotami throughout the year, although less so at Lake Chada.

(b) Monthly variations in abundance

Paradise Springs was the only site where few monthly variations in abundance among the five study sites were recorded (Fig. 6.9). At this site, hippopotami abundance remained relatively constant throughout the year. However, in the rest of the sites, maximum abundances were recorded in August, September, October and November during the dry season months before declining again in December after the onset of rainfall. Months between February and July recorded minimum abundance in the four sites. Similar observations are reported from Mara River, Serengeti (Olivier & Laurie, 1974) and similar areas. Harrison *et al*. (2007) reported shift in hippopotami abundance in Liwonde National Park, Malawi, due to increasing water in the main river.

The beginning of dry season saw more hippopotami congregating at the study sites hence increasing abundance. At Paradise Springs, few animals dispersed and increased distance between them but the majority did not move out of the study site, hence little variation in monthly abundance.

Many large herbivores move out of their habitats during the transition of seasons in response to resource availability or quality (Western, 1975; Western & Lindsay, 1984; Fryxell & Sinclair, 1988). Wetter sites particularly Paradise Springs provided optimum resources throughout the year. This was also observed in drier sites but which had some microhabitats within them providing water during the dry season where hippopotami were recorded throughout the year. Monthly variations in abundance were mainly due to the changing water availability.

During aerial censuses reported in this study, highest abundance was recorded in November. This was during the period when hippopotami congregated just before they dispersed following the rains. This shows that the trend has been relatively the same over the last three decades, because water availability mainly depends on rainfall which has not changed significantly.

Abundance of juvenile hippopotami increased during the dry season months. Peaking of juvenile abundance during the dry months was observed to be a result of both returning immigrants and natality during the wet season. Natality was seen to contribute to this due to the number of young hippopotami observed as the dry season started. However, Ikuu Springs was different from other sites. This was due to the low number of juveniles. The site was dominated by adults, probably male hippopotami with few juveniles. The site was thought to be difficult for young hippopotami possibly due to crowding. This is the only site during the study period, where juvenile hippopotami carcasses with wounds were observed. Five in total were seen.

At Paradise Springs, natality increased the number of juvenile. Although calving was more regular during the wet season, hippopotami were seen calving throughout the year, except at Ikuu Springs.

A quick decline in abundance at Ikuu Springs and Lake Katavi in November and December was due to the re-occurring of water pools after the beginning of rains. At Lake Katavi, after the swamps swelled in December, most hippopotami spread out to other shelter sites. Density decline at other sites occurred more slowly (Fig. 6.9). Seasonal movements of large herbivores during the transition months in the season are a response to changing resources (Western, 1975; Barnes, 1988; Senzota & Mtahiko, 1990). This is also thought to be the reason for the observed monthly variations in Katavi.

4.5 Immigration and Emigration

Among the five study sites, Paradise Springs was the site which showed the lowest rates of immigration and emigration for both adults and juvenile hippopotami. This was followed by Lake Chada and Ikuu Bridge. Ikuu Springs and Lake Katavi recorded the highest rates of immigration and emigration. Many large herbivores migrate seasonally in search of resources mainly water and forage (Fryxell & Sinclair, 1988), with migration happening during transition between the dry and wet season. Migration is the response to seasonal change in resources availability or quality (Western, 1975; Western & Lindsay, 1984; Fryxell & Sinclair, 1988). This can be a major reason for little variation in rates of immigration and emigration at Paradise, the wettest site, where resources changed only slightly over the wet and dry season. In response to changing habitat conditions, animals may also seek a new shelter. In Liwonde NP in Malawi, hippopotami moved to temporary shelter as water in the main river increased

(Harrison *et al*., 2007). This was also observed at one site in Katavi, Ikuu Bridge where hippopotami abundance declined during the wet season as the river waters flowed much faster. This is because hippopotami mainly avoid fast moving waters. In Luangwa River in Zambia, about 76 % of hippopotami population concentrated in river bends or meanders (Chansa *et al*., 2011a) to avoid fast flowing waters. Seasonal variations in hippopotami distribution and abundance due to immigration and emigration in response to variation of environmental resources has been reported in different studies including in the Mara River, in the Serengeti (Olivier & Laurie, 1974), Malawi (Harrison *et al*., 2007), in Kenya (Kanga *et al*., 2011a; 2011b), Okavango in Botswana (McCarthy *et al*., 1998), in Lundi River in Zimbabwe (O'Connor and Campbell, 1986) and Zambia (Chansa *et al*., 2011b). East (1984) indicated a positive correlation between large herbivore abundance or biomass and rainfall. Tall swards may limit hippopotami foraging ability and thus are likely to compel hippopotami to immigrate and emigrate because of their morphology (Spinage, 2012). In Malawi, hippopotami avoided areas with taller swards while feeding (Harrison *et al*., 2007).

At Paradise Springs, more and reliable water from the springs and the river was available throughout the year compared to other sites. Wet swamps at Ikuu Springs were only crowded over the dry season. At other study sites, water levels went well below the surface during the dry season and in others only muddy pools remained. This determined the rates of immigration and emigration of each site. The observed low rates of immigration and emigration at Paradise were because of hippopotami avoiding fast moving or deep waters. In Liwonde NP in Malawi, increase in water in the Shire River caused hippopotami to move into temporary water sources as the wet season advanced (Harrison *et al*., 2007). Similar patterns were observed at Paradise Springs where despite availability of water, they moved and spread further as water levels increased, avoiding the deeper sites. Similar avoidance of fast moving waters during the wet season was observed at Ikuu Bridge.

Hippopotami at Ikuu Springs, being a dry season refuge started aggregating in Late July, probably in preparation for the next dry season. By November 2009, the site area was crowded. After the first rains in Late November more than 90% of the population had moved out of Ikuu Springs. The site remained with few hippopotami until the following July when the dry season started. At this site, water springs seemed to play a crucial role in immigration and emigration.

Ikuu Springs was the site with the highest abundance, with abundance peaking during the dry season. Lake Katavi had the second highest abundance. Similar conditions to Ikuu Springs were observed. Congregation of hippopotami resulted from the expansion and contraction of Lake Katavi waters. Onset of rains saw the majority of hippopotami disperse to the rest of the lake while contraction led to congregation of hippopotami into the remaining water pools. Water in these pools is thought to have come from springs within the ‘lake’ area and waters remaining from the Katuma River.

Ikuu Bridge had less immigration and emigration of hippopotami due to the micro habitat at this site, because a water pool remained throughout the year which later into the peak of dry season remained as a muddy pool. The pool sustained a good number of both adult and juvenile hippopotami throughout the year. The pool is thought to have affected the normal immigration and emigration of hippopotami from this site.

Similar conditions to that at Ikuu Bridge were observed at Lake Chada, although the pools were much smaller than the former. In all, in river sections without muddy pools during the dry season, hippopotami migrated to other places.

5. Conclusions and recommendations

Although hippopotami abundance in Katavi has increased and declined over a period of generations, the decline is not significant. It can therefore be concluded that the Katavi hippopotami population has remained relatively stable over the period of 1980-2010.

Although aerial census indicated noticeable fluctuations, minimum total counts conducted on the ground indicate a slight increase in Katavi hippopotami abundance.

Despite some fluctuations in the hippopotami abundance in Katavi, and despite reduced water flows in the Park, the picture is not gloomy for Katavi hippopotami abundance because there has been some population increase. This is an indication that the population is likely to increase if conservation efforts are increased.

There were seasonal variations in hippopotami abundance at the study sites. This was particularly so in study sites with a single source of water for the hippopotami.

Hippopotamus distribution varied over seasons. Water was the main factor in the distribution of hippopotami. Wettest site with water supply throughout the year had relatively constant number of hippopotami while drier sites which had water during the dry season attracted large number of hippopotami during the dry season from other nearby sites. Availability of water was thought to be determinant of how the animals were distributed.

Differences in hippopotami distribution are related to differences in shelter site conditions. Study sites with dual sources of water particularly during the dry season favoured higher abundance. The distribution of hippopotamus populations was therefore determined by the availability of suitable day living space, with animals moving into the preferred temporary water sources in the wet season and retreating back into their previous sites when temporary sites started to dry up. This was not the case for the wettest site.

Seasonal patterns in immigration and emigration of hippopotami did not vary between sites. There were similar patterns in movements although the number was highly dependent on the water conditions of the individual sites. The wettest sites had minimum immigration and emigration due to availability of water and forage resources throughout the year.

Chapter 6: Spatial and temporal variations in hippopotami behavioral activities

1. Introduction

Behaviour is the way an animal responds to stimuli in its environment (Raven *et al*., 2008). Environment may be either internal or external. Stimuli may include detection of food, water, or other resources such as mate, predators or enemies. Behavioural ecology is defined as the study of the ecological and evolutionary basis for animal behaviour and its roles in enabling an animal to adapt to its environment (Dunstone and Gorman, 2007). The final goal of ecology is to understanding the distribution and abundance of organisms (Begon *et al*., 2006). It thus deals with interactions that determine distribution and abundance, many of these interactions involve behaviours. Animals occupy different environments with diverse challenges which affect their survival and reproduction (Raven *et al*., 2008); with both internal and external environment shaping the way an animal behaves.

Any change to the habitat of animals is likely to have some impacts on individuals and populations. Different species respond differently to impacts of habitat destruction (Maclean *et al*., 2006), but any change is likely to be manifested through behaviour. Environmental change is reported to cause simultaneous responses in population dynamics, gene frequency and morphology of some species (Coulson *et al*., 2011). Large animals for instance, have been found to behave differently in hunted and un-hunted areas, with those in hunted areas being more easily disturbed (Caro, 1999a). Hippopotami are reported to avoid suitable habitats due to poaching (McCarthy *et al*., 1998) and also respond by increasing their aggressiveness (Patterson, 1976). Marshall & Sayer (1976) observed hippopotami becoming more timid during the cropping program in Luangwa, Zambia. However, their external environment is not the only influence causing changes in behaviour. Coulson *et al*. (2011) have reported that same species populations living in different environments differ genetically or phenotypically. Studies of genetics in human twins reveal similarities in some behaviours independent of environment (Raven *et al*., 2008), emphasizing the role of the internal environment in influencing behaviour.

Hippopotami are regarded as keystone species in river and lake habitats (Eltringham, 1999; Boisserie *et al*., 2011). Hippopotami are among animals which have the tendency of aggregated dispersion (contagious or clumped distribution) (Begon *et al*., 2006). This is a patchy distribution brought about by patchy distribution of resources which enable them to enhance their reproduction and survival. Patchy resource distribution is both spatial and temporal (Begon *et al*., 2006). Resources therefore vary with location and time. A major factor which brings hippopotami together to aggregate, particularly during the dry season, is water resources. This is because the animals are rather solitary when on the feeding ground. Variations to their resting habitats due to variations in water regimes are likely to alter the way they respond. As introduced and discussed in Chapter 3 of this study, it is thought that water challenges in Katavi are exaggerated by habitat destruction particularly in the catchment and areas adjacent to the Park.

Hippopotami live in close association with rivers, streams and lakes (Graham *et al*., 2002; Dunstone & Gorman, 2007; Dunham *et al*., 2010). These places are used as suitable and safe resting places mainly during the day time. Alterations to their environment affect them differently in different sites. Reactions to the changing conditions in sheltering or resting and feeding grounds are likely to be manifested through their behaviour. Due to various reasons, water supplies to the hippopotami resting and feeding sites in Katavi NP have been fluctuating over the last twelve years from the early 2000 (Lewison, 1996; 1998; Meyer *et al*., 2005) as reported in Chapter 3 of this study. This decrease in water is likely to affect the behaviour of hippopotami. Observation of their behaviour might indicate some of the resulting effects of water dynamics on hippopotami at the study area. Behaviors observed are not likely to be the direct result of water dynamics only, but may serve as indicators. This is because it is not always the case that behaviour shown by individuals reflects adaptive response to the environment (Raven *et al*., 2008). Both nature (instinct) and nurture (experience) play significant roles. Animals have therefore been reported to alter their behaviour as a result of previous experience or learning (Raven *et al*., 2008).

Hippopotami are animals with some spatial and temporal environmental limitations. Foraging behaviour is influenced by availability of aquatic habitats for resting (Field, 1970), and mainly occurs at night (Laws, 1968; Lewison & carter, 2004). Temperature, forage and water are therefore among key requirements in determining their activity patterns.

There have been different reports on the decline of hippopotami populations from various areas in Africa (Caro, 1999a; Stoner *et al*., 2006; Lewison and Oliver, 2008). Understanding their behavioural changes at local levels would help inform conservation measures under the changing environments. Katavi is one of the areas in Tanzania which supports large concentrations of hippopotami. If there is a negative impact of any change on the Katavi population, this could be indicative of changes across the country. Changes in the Katavi water regime are leading to early drying of the water sources in the Park. Drought is regarded as one of the factors that can limit populations of species (Raven *et al*., 2008). This is often mediated by behavioural responses such as increased competition for limited remaining wet sites.

There have also been hippopotami-human conflicts due to crop raiding or human killings resulting from changing habitat conditions in the protected areas. Although this conflict is not yet serious in Katavi, it occurs in other areas (Kendall, 2011; Nyirenda *et al*., 2011). Dunham *et al*. (2010) reported such conflicts in Mozambique and across Africa. Hippopotami live in rivers which sometimes border human settlement hence causing conflicts outside the protected areas (Dunham *et al*., 2010; Kendall, 2011). Timely and pro-active management is needed, bearing in mind the current shrinking of suitable habitats due to water related challenges and encroachment of protected areas by human settlement and agriculture. Information from studies like the present one could help our understanding of hippopotami behaviour and could help to plan so as to avoid or alleviate such conflicts. Studying hippopotami behavioural activity pattern can be important in informing their conservation and management.

Behaviour patterns can be divided into activities or states and events (Martin and Bateson, 2007). Both are dealt with in this study. However, for convenience, the two have been separated into two different Chapters; events are dealt with in Chapter 7. Activities or states and events were recorded separately in order to record as many behaviour categories as possible. Behaviour activities are behaviour patterns of relatively prolonged duration such as body posture, sleeping, feeding, moving or resting (Martin and Bateson, 2007) as opposed to events which are of relatively short duration such as body movement, scratching, barking or other vocalization. The major feature of behaviour activities is their duration, how long they last in a certain time frame. For events, the major feature recorded is the frequency of occurrence.

1.1 Aims and hypotheses

There have been reports of decreasing amount of water entering and remaining in the Park leading to earlier drying of water bodies (Chapter 3). This is likely to affect species that depend on water. The aim of this study was to observe how the behaviour of hippopotami changes in relation to the decreased water supply, particularly during the dry season.

The main aim was to study the impact of reduced water flow on the behaviour of hippopotami (*Hippopotamus amphibious*), between different study sites and different seasons. The study therefore tested the following hypotheses:

H_1 There are variations in behaviour patterns between hippopotami at different study sites in Katavi.

H_2 Hippopotami rest more in the dry than wet season

H_3 More time is spent feeding in the dry than wet season

H_4 Social behaviour of hippopotami is displayed more in the wet season

H_5 There are spatial and seasonal variations in hippopotami aggregation

2 Methods

2.1 Site selection

Five observation sites were selected in Katavi NP for hippopotami data recording. These were distributed in areas with varying habitat conditions as representative of the different habitats in the Park. The areas selected were expected to span the wetness gradient due to different sources of water and retention properties for each site. Locations of the sites are shown in Fig. 7.1 and characteristics are as described in Chapter 2.

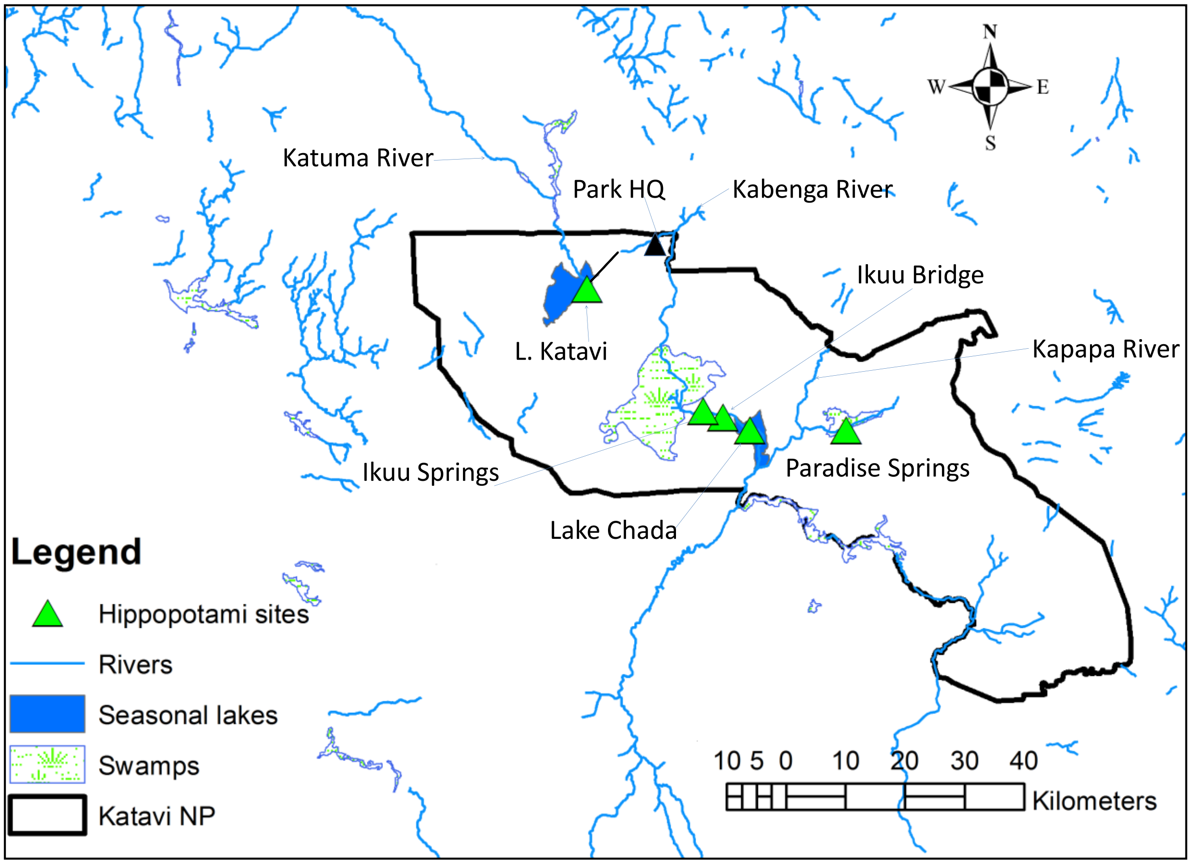


Fig. 7.1: Map of Katavi NP showing location of five behaviour study sites.

2.2 Data recording

From September 2009-September 2010, at each of the five sites selected for hippopotami behaviour observation, two days each month were spent in recording behaviour and aggregation of hippopotami. Animal behaviour was recorded in a quadrat measuring 0.2 km X 0.25 km (200 m X 250 m) making an area of 0.05 km^2.

This study is based on directly observed behaviour. At each of the sites, observations were carried out from a vehicle or on foot from a hidden position in order to minimize interference. Animals were watched either directly or using a pair of binoculars, distances were minimized consistent with health and safety constraints. If hippopotami were disturbed for any reason, behaviour recording stopped until they appeared to calm or settle and ignore the cause of disturbance.

The study was conducted between 0600 and 1930 hours for safety reasons. Observations in the wet season were made between December 2009 to May 2010 and in June to November 2010 for the dry season. Activity scans were conducted in 30 minute blocks, six times a day from 0700 to 1930 hours at approximately 0700-0730, 0900-0930, 1100-1130, 1500-1530, 1700-1730, 1900-1930 hours. Total time for activity scans was three hours per day for two consecutive days each month each site. In total, activity patterns were observed for 390 hours. Adult and juveniles behaviours were recorded separately.

Observations were only recorded at the specific sheltering or resting grounds shown in Fig. 7.1 and described in Chapter 2. Behavioural activities recorded were resting, standing, walking, feeding and passive touching. Aggregation was also recorded during wet and dry seasons. These behavioural categories were defined as: 1) **resting:** lying on water bank or on land without leg movements. In this state, they were immobile and may be passively touching each other. 2) **Standing:** also involved staying stationary with no or very limited leg movements. For some analyses resting and standing were combined as one category of no leg movement behaviour.

3) **Walking**: all activities on land involving leg movements, except when feeding, including searching for feeding sites. 4) **Feeding**: involving head movements associated with cutting and ingesting food. 5) **Passive touching** was a social activity involving non aggressive lips or body contact between hippopotami. It was significantly longer than active touching dealt with in behavioural events.

Aggregation of hippopotami was estimated from distances measured as the inter-individual distance between two randomly selected individual hippopotami in a study site. At most, a total of 25 pairs of hippopotami were randomly selected for sampling from which inter-individual distances were recorded.

Two recording methods were used to record behaviour and complemented each other due to their importance. These were as follows:

1. Direct recording or logging into a palm top Psion Logix 10 computer using the software 'Observer Mobile' professional system for field observations. The Psion uses the Observer XT mobile kit for the Psion Work about Pro. Before recording in the field, a coding scheme (ethogram) was designed on the laptop. In the scheme, every subject and behaviour to be recorded was specified. The coding scheme was transferred to the palm top computer. At the end of each session, data from the palm top computer were transferred onto the laptop PC which has been installed with the Observer XT base package for Windows. Data were summarised using the Observer software installed into the PC.
2. Recording onto data sheets. Data sheets were used as a backup or alternative to the handheld equipment. While using these, data were recorded and entered onto a PC after every session in the field.

   Before actual recording, video recording was conducted. Videos were used to record behaviour before recording started (during the preliminary observations) to measure intra observer reliability. Video was also occasionally used when recording was not done using the palmtop. Videos gave an exact visual record of behaviour before actual recording. Video records were useful for recording and noting behavioural activities that were very rapid. Similarly, videos helped to capture behaviour that might have been missed by the palmtop or data sheet method. Despite its advantages, video recording was not used as the primary recording medium or to supplement the palm top and data sheet. Videos were only used for familiarization and consistency in training before actual behaviour recording started.

Recording methods

Sampling rules

Behavior observations were made predominantly by scan sampling according to Martin & Bateson (2007) and Lehner (1996). A group of hippopotami was rapidly scanned for five minutes and the behaviour of each animal recorded at that instant. This was followed by a recession of five minutes before recording continued for another five minutes until the 30 minutes period ended.

Recording rules

Behaviour sampling was conducted according to Martin and Bateson (2007) and Lehner (1996) using continuous (all occurrences) recording for the behaviour categories identified or coded. This measured true frequencies and durations and times at which behaviour patterns started and stopped, making it possible to record several different categories of behaviour simultaneously. It employed continuous sampling, divided into successive time intervals.

2.3 Data analysis

Data were summarised into frequency tables and analyses including 1-way ANOVA, 2-way ANOVA, t-tests and correlations were performed.

Seasonal variations were tested using t-tests. Spatial and temporal variations were analysed using analysis of variance (ANOVA) while multiple factors were analysed using 2-way Analysis of Variance. Relationships were tested using correlations.

3. Results

3.1 Comparison of activity budget between adults and juveniles

Adult hippopotami spent about 46.7 ± 1.3% of their day time resting and 9.0 ± 0.4% standing making a total time of about 56% with no active leg movements (Fig. 7.2). 19.1 ± 1.2% was spent walking and 20.7 ± 1.2% feeding making a total time of about 40% moving. 4.3± 0.6% was spent on social activities mainly touching each other.

Juvenile hippopotami spent about 39.7 ±1.6% resting, significantly less than adults (Fig. 7.2), and 11.2 ±0.7% standing significantly more than adults, making a total of about 51% with no leg movements (in resting state). 17 ±1.2% of juvenile hippopotami time during the day was spent walking while 17.9 ± 0.9% was spent in feeding making a total time of 35.6% moving, slightly less than that of adults. 13.4 ± 1.1% was spent in touching activities, which was significantly higher than for adults (Fig. 7.2).

Some activity budgets varied significantly between adults and juvenile hippopotami. Adults spent more time resting and feeding than juveniles ($t_{24} = 3.999$, $p < 0.002$ and $t_{24} = 4.659$, $p < 0.004$), while juvenile spent more time standing ($t_{24} = -2.796$, $p < 0.010$) and touching ($t_{24} = -7.403$, $p < 0.0001$) than adults. However, there were no significant differences between age groups in time spent walking (Fig. 7.2).

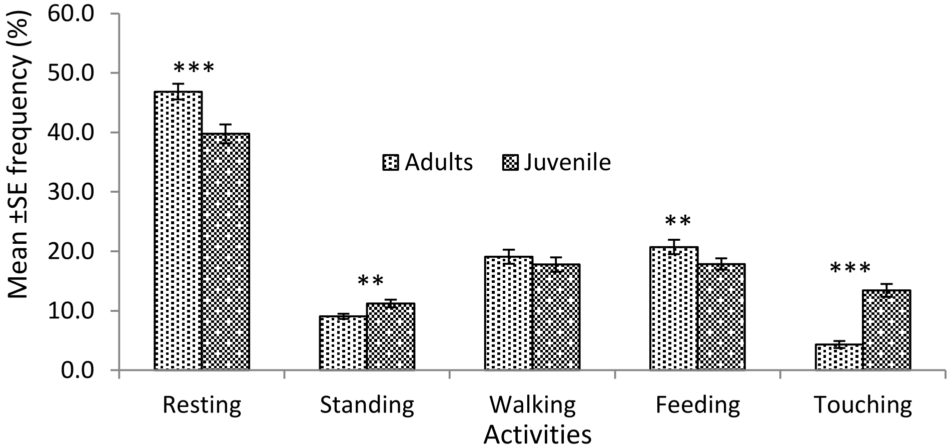


Fig. 7.2: Summarised annual activity budget for adult and juvenile hippopotamipotami in five study sites in Katavi NP, Tanzania (September 2009-September 2010)
Key to Fig. 7.2: ***=p<0.001, **=p<0.01, *=p<0.05

3.2 Seasonal variations in activity budget.

There was significantly more time spent walking (t_{33} = 3. 923, $p < 0.001$) and touching (t_{33} = 3.386, $p < 0.002$) during the dry than wet season among adult hippopotami in Katavi, and more feeding (t_{33} = -2.421, $p < 0.02$) in the wet season (Fig. 7.3 (a)). There were no significant variations over the wet and dry seasons for resting and standing.

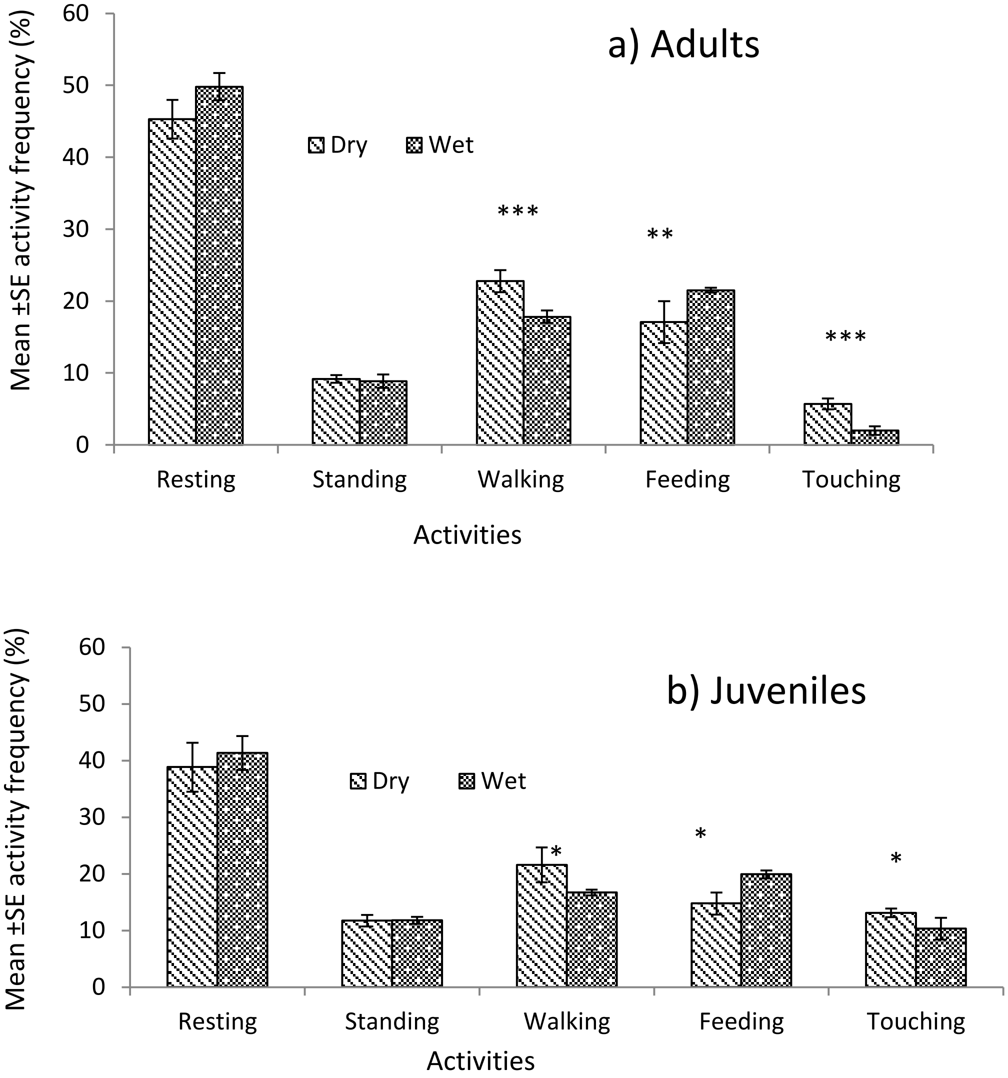


Fig. 7.3: Differences in activity budget among (a) adults and (b) juvenile hippopotami between the dry months (August-November) and wet months (January-April) in Katavi NP, Tanzania
Key to Fig. 7.3:, * = $p < 1.05$

Juvenile hippopotami spent more time walking ($t_{33} = 2.335$, $p < 0.026$) and touching ($t_{33} = 2.214$, $p < 0.034$) during the dry than wet season. Feeding activity ($t_{33} = -2.436$, $p < 0.02$) as for adults, increased significantly during the wet season, whereas there were no significant variations between the seasons for resting and standing among juveniles (Fig. 7.3 (b)).

3.3 Monthly variations in activity budget

The activity budget of adult hippopotami showed significant monthly differences for resting ($F_{12, 389} = 3.193$, $p < 0.0001$), walking ($F_{12, 389} = 3.891$, $p < 0.0001$), feeding ($F_{12, 389} = 2.013$, $p < 0.022$) and touching ($F_{12, 389} = 6.554$, $p < 0.001$). Standing activities showed some variations but such monthly variations were not significant. Activity frequency for both adults and juveniles is summarised in Appendix 2 and shown in Fig. 7.4.

Juveniles showed significant monthly differences in activity budget for resting ($F_{12, 389} = 2.168$, $p < 0.013$), walking ($F_{12, 389} = 2.431$, $p < 0.005$) and touching ($F_{12, 389} = 5.484$, $p < 0.0001$). Standing and feeding did not vary significantly between months for juvenile hippopotami.

Maximum frequency of resting among adult hippopotami was recorded in March, while the minimum was recorded in September 2009 (Appendix 3, Fig. 7.4). However, the range between the highest and lowest for all the months was small (13.2%). In October, February, April and May there was also higher frequency of resting although it did not vary significantly between months. Standing among adult hippopotami was highest in November and lowest in March. Nevertheless, the months of September, December, January and February are the months in which higher frequencies for standing were recorded (Appendix 3, Fig. 7.4).

Juvenile hippopotami rested more in October although less than adults, while they rested least in January, significantly less than for adults. Maximum standing was in December while minimum standing was in October and July (Appendix 3, Fig. 7.4).

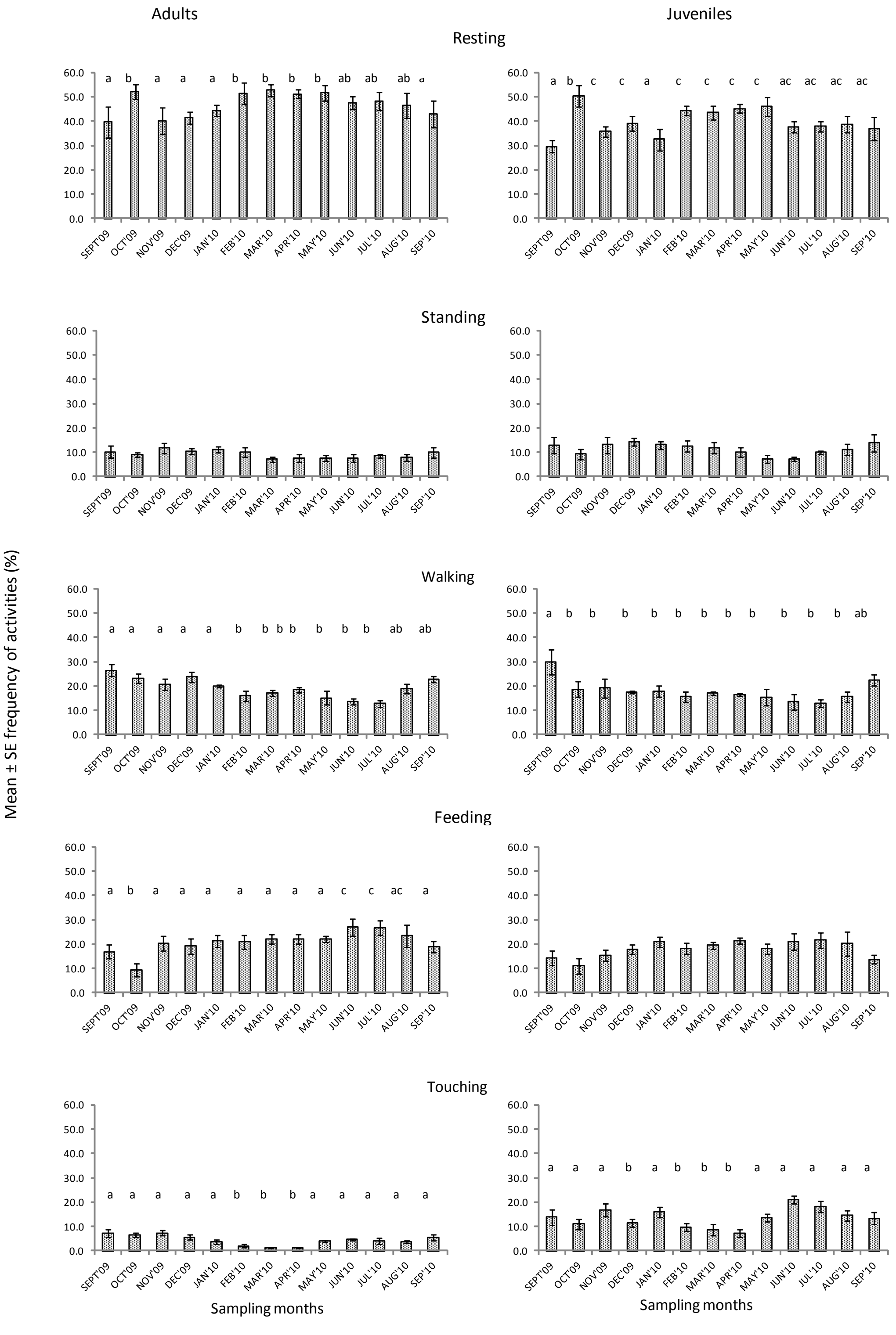


Fig. 7.4: Mean monthly variations in frequency of activities (September 2009-September 2010) among adult and juvenile hippopotami in Katavi NP, Tanzania. *Note*: Means not showing the same letter differ by $p < 0.05$.

Walking among adult hippopotami was more frequent in September 2009. June and July were the months with the least walking. Feeding in June and July were the highest among all months. October recorded the lowest feeding frequency among adult hippopotami (Appendix 3, Fig. 7.4).

Walking among juveniles was higher in September 2009 than in all other months, while it was at its lowest in July and June. Feeding among juvenile was higher in July and April. Minimum feeding was recorded in October followed by September 2010 (Appendix 3, Fig. 7.4).

Touching among adult hippopotami was most frequent in November, closely followed by September 2009. Least touching was recorded in April and March (Appendix 3, Fig. 7.4)

Maximum touching among juvenile hippopotami was in June, while minimum touching was in April followed by March (Appendix 2, Fig. 7.4).

3.4 Time specific activity budgets

Some components of the activity budget varied significantly with time of the day in all study sites during both the wet and dry season (Fig. 7.5). Resting, standing, walking, feeding and touching varied significantly at different times of the day over the study period (Fig. 7.5).

Both adult and juvenile hippopotami at Ikuu Bridge showed significant variations in all components of their activity budgets at different times of the day (Table 7.1).

All activities at Lake Chada varied significantly over different times of the day for both adult and juvenile hippopotami (Table 7.1).

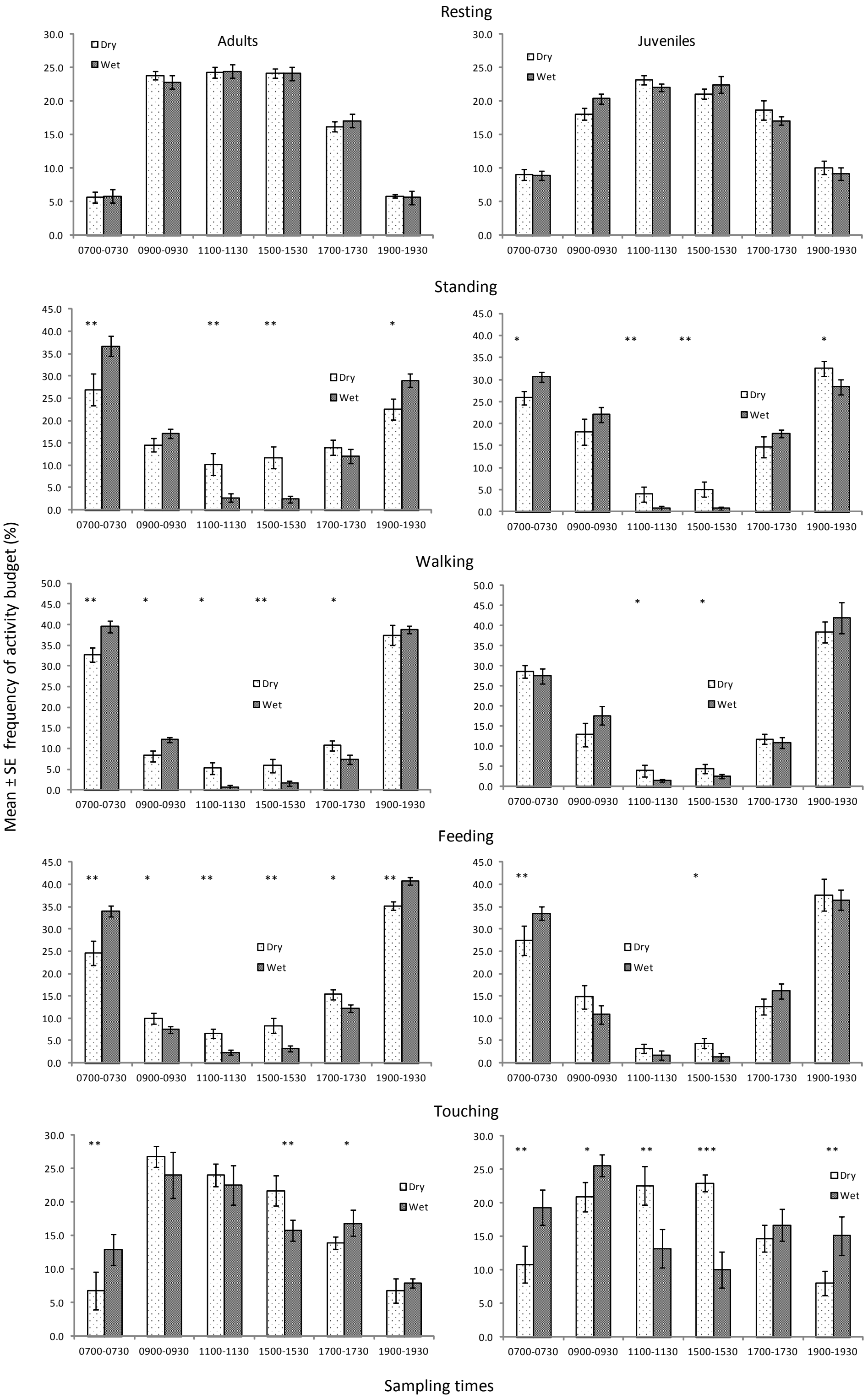


Fig. 7.5: Variations in mean behavioural activities for (a) adult and (b) juvenile hippopotami between different times of the day during the dry and wet seasons in Katavi NP, Tanzania. Key: ***= $p < 0.001$, **=$p < 0.01$, *= $p < 0.05$.

With exception of touching, adult hippopotami at Lake Katavi showed significant differences with time of the day (Table 7.1). All activities at Lake Katavi site varied significantly over different day times for juvenile hippopotami (Table 7.1).

Table 7.1: Summary of statistical tests for variations of activity patterns among adult and juvenile hippopotami at different times of the day at Katavi NP, Tanzania

		Adults		**Juveniles**	
		df= 5, 77		**df= 5, 77**	
Study site	***Traits***	***F-value***	***p***	***F-value***	***p***
Ikuu Bridge	Resting	82.217	0.0001	41.78	0.0001
	Standing	14.078	0.0001	14.68	0.0001
	Walking	43.764	0.0001	37.96	0.0001
	Feeding	39.648	0.0001	30.98	0.0001
	Touching	4.483	0.001	2.732	0.026
Lake Chada	Resting	39.18	0.0001	25.181	0.0001
	Standing	10.593	0.0001	3.937	0.003
	Walking	38.302	0.0001	14.58	0.0001
	Feeding	49.42	0.0001	35.593	0.0001
	Touching	11.353	0.0001	7.01	0.0001
Lake Katavi	Resting	25.799	0.0001	17.923	0.0001
	Standing	6.858	0.0001	7.305	0.0001
	Walking	20.653	0.0001	11.823	0.0001
	Feeding	13.792	0.0001	9.619	0.0001
	Touching	**	NS	2.492	0.039
Paradise Springs	Resting	8.414	0.0001	5.184	0.0001
	Standing	**	NS	2.426	0.043
	Walking	9.828	0.0001	5.251	0.0001
	Feeding	10.232	0.0001	8.847	0.0001
	Touching	4.643	0.001	3.908	0.003
Ikuu Springs	Resting	86.602	0.0001	25.072	0.0001
	Standing	7.049	0.0001	7.896	0.0001
	Walking	38.441	0.0001	19.149	0.0001
	Feeding	31.882	0.0001	25.505	0.0001
	Touching	**	NS	**	NS

Key: ** denotes test not significant at $p < 0.05$.

With exception of standing, all other activities showed significant differences over times of the day at Paradise Springs (Table 7.1). Juvenile hippopotami at Paradise Springs showed significant differences in all activities between times of the day (Table 7.1).

All adult and juvenile activities varied significantly with time of day at Ikuu Springs with the exception of touching (Table 7.1).

3.5 Variations of activity budgets between study sites

Differences in activities between sites are shown in Fig. 7.6. Resting ($F_{4,\ 389} = 7.459$ $p < 0.0001$), feeding ($F_{4,\ 389} = 4.114$ $p < 0.003$) and touching ($F_{4,\ 389} = 5.852$ $p < 0.0001$) among adults were significantly different between study sites. However, there were no significant differences in standing and walking between study sites.

A similar range of activities were different for juvenile hippopotami between the five study sites; resting ($F_{4,\ 389} = 4.254$ $p < 0.002$), feeding ($F_{4,\ 389} = 3.670$ $p < 0.006$), and touching ($F_{4,\ 389} = 3.112$ $p < 0.015$) had significant differences between sites (Fig. 7.6), but so did standing ($F_{4,\ 389} = 3.188$ $p < 0.014$), leaving walking as the only activity that did not show any differences between study sites.

The most resting among adult hippopotami was recorded at Ikuu Springs and the least at Lake Katavi (Fig. 7.6). Juvenile hippopotami at Ikuu Bridge rested more than in other sites with a resting frequency less than that of adults. Least resting for juveniles occurred at Lake Chada with a frequency slightly lower than that for adults (Fig. 7.6).

Adult hippopotami spent most time feeding at Lake Katavi, and least at Ikuu Springs (Fig. 7.6). Feeding by juveniles was most frequent at Lake Katavi and least at Ikuu Bridge closely followed by Ikuu Springs (Fig. 7.6). Touching in adults was highest at Paradise Springs and least at Ikuu Springs (Fig. 7.6). Touching in juveniles was more frequent at Lake Chada and Ikuu Bridge. Minimum touching between sites occurred at Lake Katavi and Ikuu Springs (Fig. 7.6).

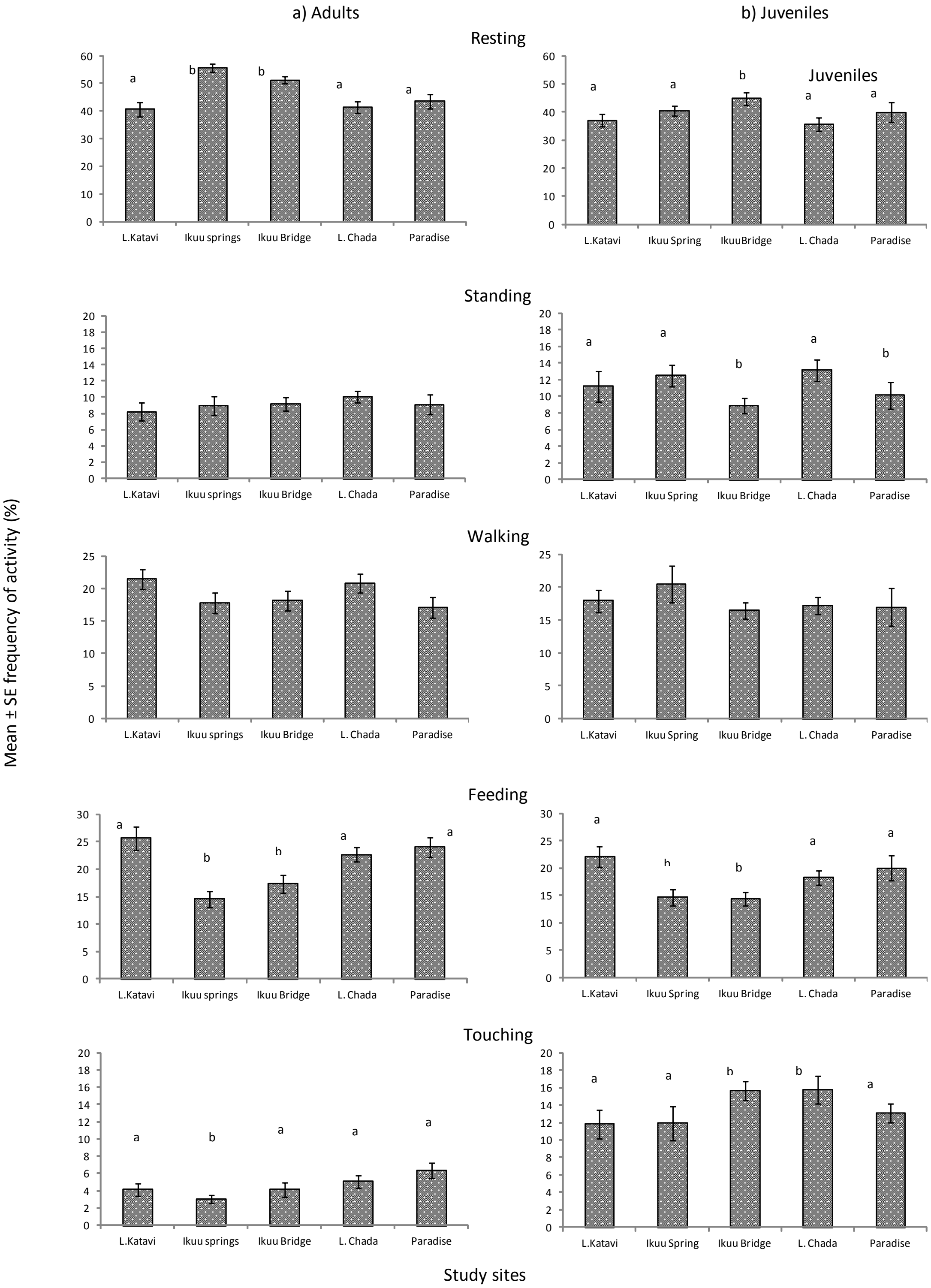


Fig. 7.6: Summary of mean activity budget for adult and juvenile hippopotami at five study sites (September 2009-September 2010) in Katavi NP, Tanzania. Bars not sharing the same letter differ by $p < 0.05$.

3.6 Comparison of seasonal variations in activity budget between sites

Adult hippopotami at Ikuu Bridge exhibited significant seasonal differences in the proportion of time spent standing (t_5= -3.256, $p < 0.023$), walking (t_5= 8.487, $p < 0.001$) and touching (t_5= 3.704, $p < 0.014$). Resting and feeding did not differ (Fig. 7.7).

Juvenile hippopotami at Ikuu Bridge showed significant seasonal differences in proportion of time spent standing (t_5= -3.054, $p < 0.028$) and touching (t_5= 4.273, $p < 0.008$). Resting, walking and feeding did not show any seasonal variations (Fig. 7.7).

Standing and touching (t_5= 3.135, $p < 0.026$ and t_5= 2.792, $p < 0.038$ respectively) were the only activities which showed significant seasonal differences among adult hippopotami at Lake Chada. Resting, walking and feeding did not vary significantly between the wet and dry season (Fig. 7.7).

Among juveniles, touching activities were the only ones that varied seasonally at Lake Chada site (t_5 = 2.811, $p < 0.037$). Resting, standing, walking and feeding did not show any significant seasonal differences (Fig. 7.7).

At Lake Katavi site, resting and walking activities showed significant seasonal differences among adult hippopotami (t_5= -3.094, $p < 0.027$ and t_5= 3.166, $p < 0.025$ respectively). Standing, feeding, and touching did not show any significant seasonal differences (Fig. 7.7).

Juvenile hippopotami at Lake Katavi showed significant seasonal differences in the time spent resting (t_5= -6.336, $p < 0.001$). Nevertheless, other activities did not show any seasonal variations. Standing, walking, feeding and touching did not vary between the wet and dry season (Fig. 7.7).

There were no significant seasonal differences in activity budget among adult or juvenile hippopotami at Paradise Springs over the study period (Fig. 7.7).

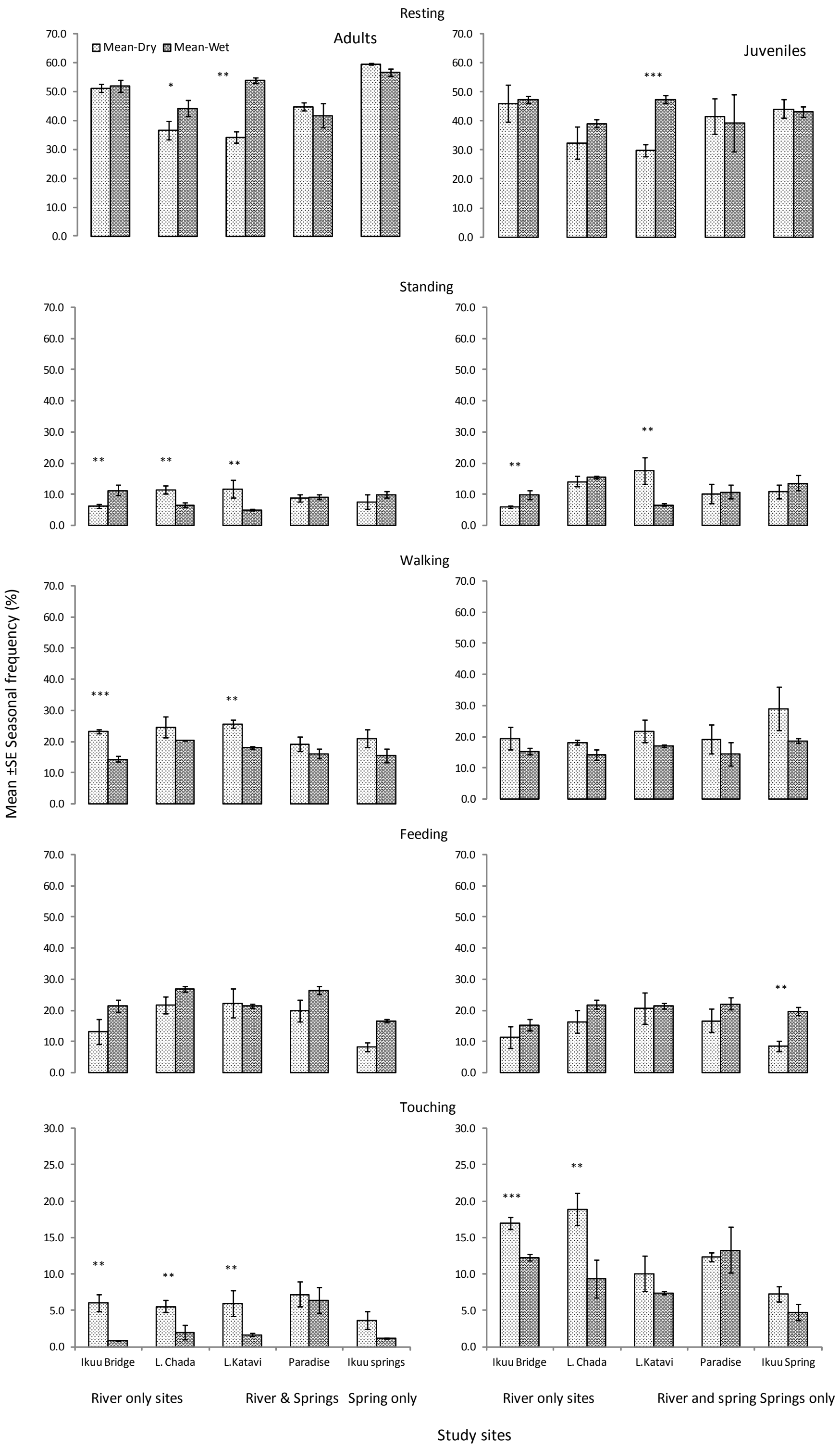


Fig. 7.7: Spatial variations in activity budget (September 2009- September 2010) between five study sites for adult and juvenile hippopotami in Katavi NP, Tanzania. ***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$

3.7 Aggregation

Comparison of aggregation between sites

The highest inter-individual distances in the five study sites were at Ikuu Springs, while the least were at Paradise Springs and Ikuu Bridge (Fig. 7.8). There were no significant differences in inter-individual distances between the five study sites.

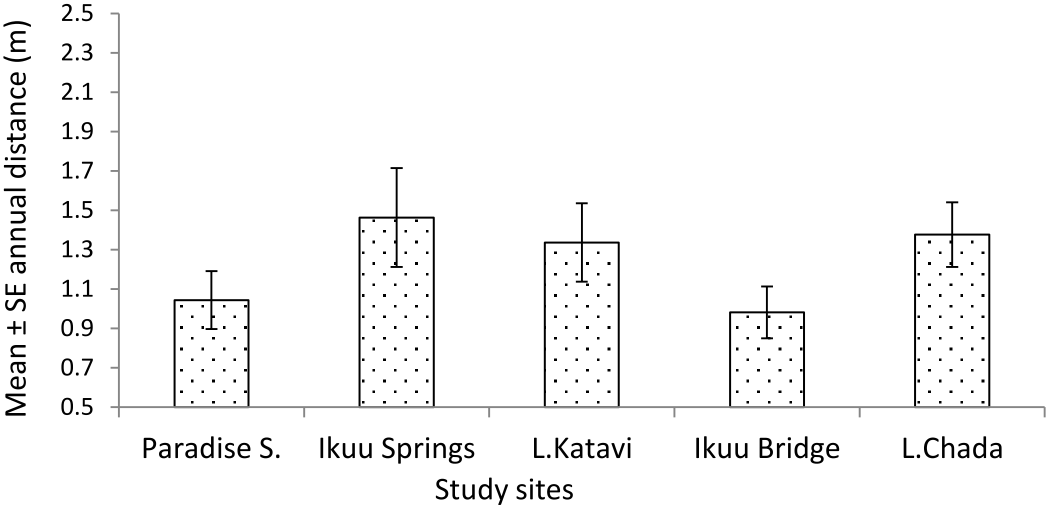


Fig. 7.8: Comparison of mean annual hippopotami inter-individual distance (aggregation) between the five study sites in Katavi NP, Tanzania.

Seasonal variations in aggregation (inter-individual distances)

Mean aggregation of hippopotami at Paradise Springs (t_{84} = 14.992, $p < 0.0001$) was least in the wet season and significantly lower than in the dry season (Fig. 7.9).

Wet season inter-individual distances were significantly lower at Paradise Springs than at the other sites (t_{84}= -9.182 $p < 0.0001$) (Fig. 7.9). Inter-individual distances during the dry season did not vary between the five sites.

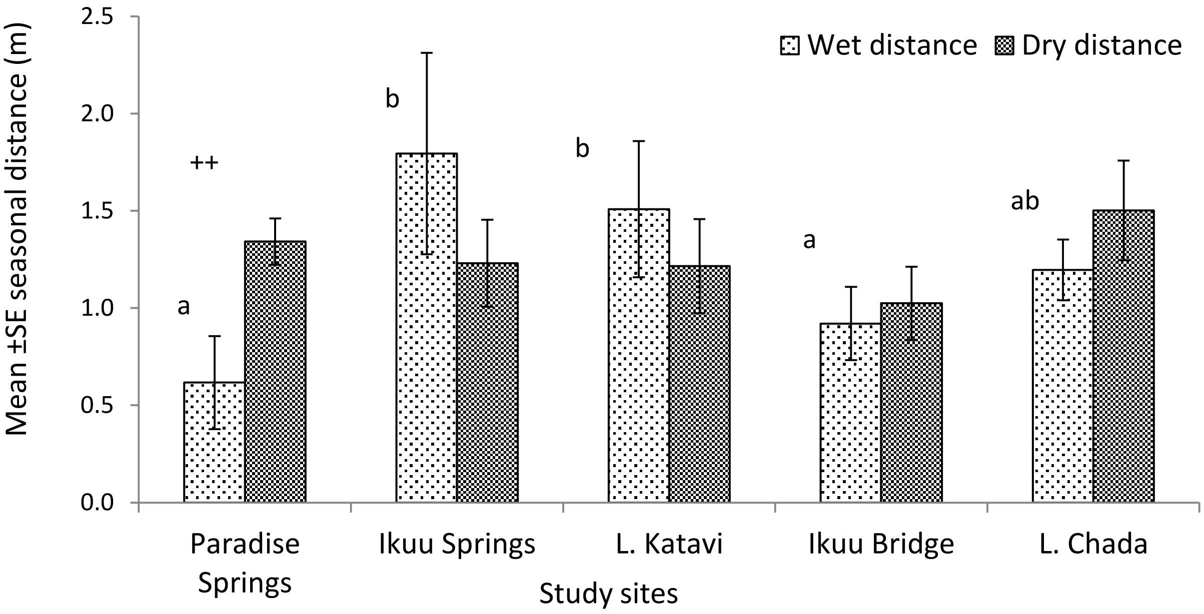


Fig.7.9 : Differences in inter-individual distances between dry months (August-November) and wet months (January-April) for hippopotami in the five study sites in Katavi NP, Tanzania. Note: ++ = No recording was done between February-April in Paradise Spr

Monthly variations in hippopotami aggregations

Aggregation (mean inter-individual distance) varied significantly ($F_{16,\ 84} = 2.629$, $p < 0.003$) (Fig. 7.10), with the lowest inter-individual distances during driest months.

The lowest inter-individual distances between hippopotami were during the dry months of October, November and December (Fig. 7.10) with least aggregation recorded in May 2009.

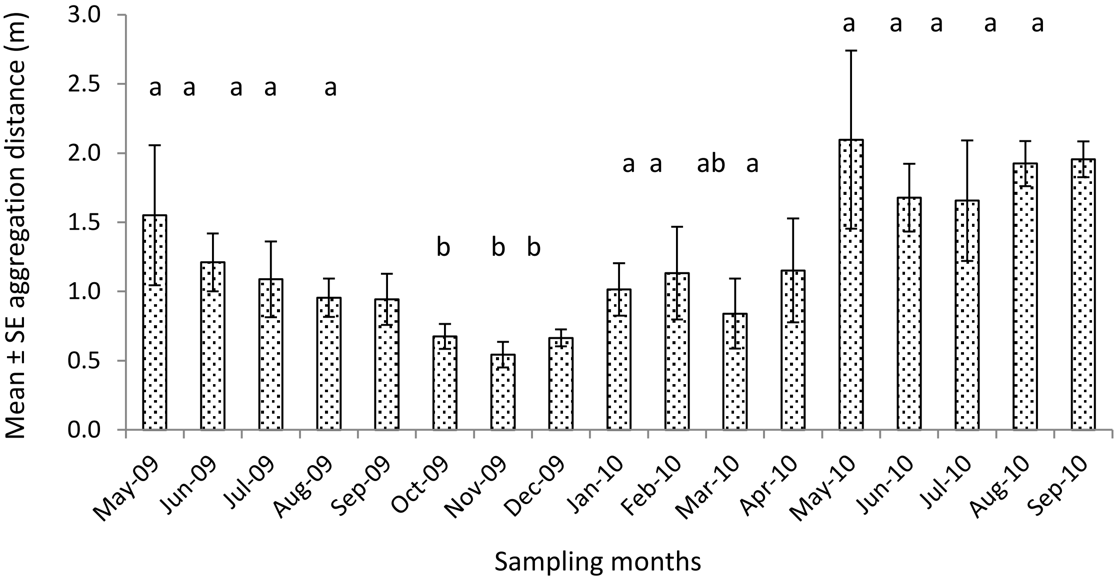


Fig. 7.10: Overall mean monthly variations in inter-individual distance between hippopotamis in Katavi NP, Tanzania. Bars with the same letter are not significantly different at $p < 0.05$.

Monthly variations in aggregation between study sites

The highest inter individual distances were at Ikuu Springs in May 2010 (4.6 ± 1.3 m) followed by Lake Katavi with 3.4 ± 0.5 m in May 2009. The lowest inter-individual distances occurred in November 2009 at Lake Katavi (0.3 ± 0.1 m), July 2009 at Ikuu Springs (0.4 ± 0.1 m) and in October and November at Ikuu Bridge with 0.4 m in both months (Fig. 7.11).

At Lake Katavi, the highest mean inter-individual distance (about 3.5 m) was in May 2009 with the lowest (less than 0.5 m) in November 2009. The next lowest was in September with 0.5 m. In August and December 2009 the mean inter-individual distance was just above 0.5 m. In August and September 2010 it was just less than 2.5 m. This was greater than the mean inter-individual distance during the same period in 2009 (Fig. 7.11).

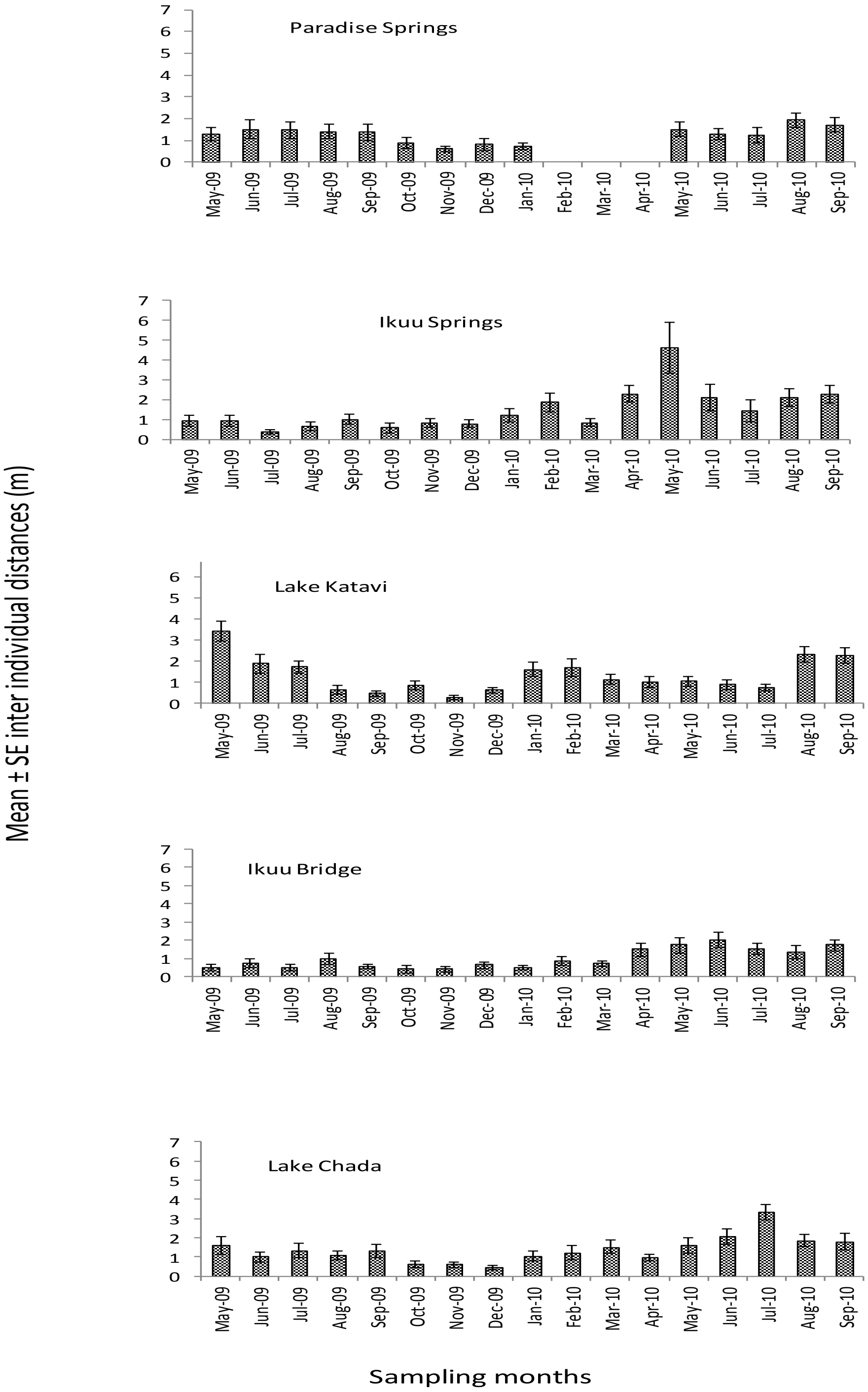


Fig. 7.11: Mean monthly aggregations (inter-individual distances) between hippopotami in five study sites in Katavi NP, Tanzania.

Mean monthly distance between individuals at Paradise Springs did not vary greatly during the study period compared with the other sites. Nevertheless, the lowest mean inter individual distance was in November 2009, this was about 0.5 m. Generally, in October 2009-January 2010 mean distances were below 1.0 m. During the other months, hippopotami were more than 1.0 m apart but less than 2.0 m apart. In August 2010 the mean distance was just below 2.0 m (Fig. 7.11).

At Lake Chada, the highest mean inter-individual distance of about 3.5 m was in July 2010. In June 2010, distance was about 2.0 m while in August and September 2010 mean distance was just less than 2.0 m. In December 2009 the least inter-individual distance with a mean of less than 0.5 m apart was recorded. In October and November 2009 mean distances were just above 2.0 m (Fig. 7.11).

Low mean inter individual distances between May 2009 and March 2010 was at Ikuu Bridge. Within these months, the lowest mean distance of about 1.0 m was in August closely followed by February 2010 with mean distance just below 1.0 m apart. In June 2010, mean distance was 2.0 m. This was closely followed by mean distances just below 2.0 m in September and May 2010 while the lowest mean distance of about 0.5 m was in October and November 2009 and January 2010 (Fig. 7.11).

At Ikuu Springs the highest mean inter-individual distances (about 4.5 m) were in May 2010, while the lowest mean distance (less than 0.5 m apart) was in July 2009. Low mean distances of less than 1.0 m occurred in October-December 2009. Mean inter-individual distance of between 1.5 to about 2.5 m were in February, April, June, July, August and September 2010 (Fig. 7.11).

Directions of effects and impacts of reduced water resource to the behavioural activity patterns of hippopotamus are summarised in table7.2.

Table 7.2: Summary of activity budget of the adult and juvenile hippopotami showing the direction of effects of declined water resources

		Adults		**Juveniles**	
Traits	**Source of variations**	**Direction of effects of less water**	**Description of variation**	**Direction of effects of less water**	**Description of variation**
Resting	Seasonal	No direction	No significant difference between seasons	No direction	No significant difference between seasons
	Monthly	Negative	Slightly more resting during the wet season months	Negative	Less during the dry season
	Spatial	Positive	More resting at drier sites (Ikuu Springs and Bridge)	Positive	More at drier site Ikuu Bridge
Standing	Seasonal	No direction	No significant difference between seasons	No direction	No significant difference between seasons
	Monthly	No direction	No significant difference between months	No direction	No significant difference between months
	Spatial	No direction	No significant variations between sites	Positive	More at drier sites (Ikuu Springs and Lake Chada)
Walking	Seasonal	Positive	More walking during the dry season	Positive	More walking during the dry season
	Monthly	Positive	More walking during the dry season months	Positive	Slightly more walking during the dry season months
	Spatial	Positive	More walking at drier sites (Lakes Chada + Katavi)	Positive	More at drier sites (Lake Katavi and Ikuu Springs)
Feeding	Seasonal	Negative	Less feeding during the dry season	Positive	Less feeding during the dry season
	Monthly	Positive	Slightly less feeding during the dry season months	No direction	No significant variations between months
	Spatial	Negative	Less feeding at drier sites (Ikuu Springs and Ikuu Bridge	Positive	Less at drier sites (Ikuu Springs and Ikuu Bridge)
Touching	Seasonal	Positive	More touching during the dry season	Positive	More touching during the dry season
	Monthly	Positive	More touching during the dry season months	Positive	More touching during the dry season months
	Spatial	Positive	Lowest at drier sites (Ikuu Springs), higher at wettest site	Positive	More at drier sites (Ikuu River and Lake Chada)
Aggregation	Seasonal	Positive	Only the wettest site maintained abundance hence varied aggregation	Positive	Only the wettest site maintained abundance hence varied aggregation
	Monthly	Positive	More aggregation during the dry season months	Positive	More aggregation during the dry season months
	Spatial	Negative	Drier sites differed from the wettest site at Paradise Springs	Negative	Drier sites differed from the wettest site at Paradise Springs

4. Discussion

Although adult hippopotami spent more than half of the day time resting, nearly half of the day time was spent performing other activities particularly those related to feeding. This was slightly less for juveniles, for which feeding represented about 36% of their time. Walking and feeding occupied about the same time in adults and juveniles. However, juveniles fed slightly less because juveniles did not always feed when adults were feeding. This was the probable reason that more standing and touching were recorded in juveniles than adults. Adults spent more time resting than juveniles (Fig. 7.2). Adults once in their resting sites were more settled than juveniles. Juveniles, apart from resting were involved in other activities mainly social. This led to less resting than adults. In the study of behavioural responses of captive hippopotami, active behaviours for adults and juveniles had a frequency of about 32 % for both groups (Chen *et al*., 2010). This is slightly less than that observed in Katavi.

With the exception of resting and touching, all activities recorded were affected either positively or negatively by the availability of water and forage (Table 7.2). Seasonal feeding activities were negatively affected as water decreased at the shelter sites leading to less foraging near their shelters. Walking and social touching were positively affected, increasing as water decreased during the dry season.

Although there were no significant differences in aggregation between sites, at Paradise Springs, there was a difference in aggregation between seasons. This was because abundance of animals was relatively constant throughout the year at this site. During the wet season, hippopotami spread out, possibly to avoid deeper and fast moving waters and increased distances between them. However, most of them were within the same study site. In drier sites such as Ikuu Springs and Lake Katavi, abundance varied significantly between seasons but their grouping patterns did not vary significantly.

Minimum inter-individual distances or maximum aggregations were recorded during the dry season, increasing steadily as the wet season advanced and maintained during the wet season. There was less aggregation as water receded.

Less water made the animals aggregate more and increase touching and body contacts between each other. There was less water and significantly more close contacts during the dry than wet season. On some occasions, contacts turned confrontational. Touching more during the dry season was due to hippopotami being in closer contact than during the wet season when animals spread and dispersed further.

Aggregations of animals on a site have effects on forage through their consumption, trampling and excretion (Drescher *et al*., 2006). This is more effective in areas where animals such as hippopotami live and forage as their aggregations may be higher, hence affecting quality, quantity and structure of forage much more quickly. In turn, forage structure may affect foraging behaviour (Ginnet *et al*., 1999; Drescher *et al*., 2006); hence, understanding how resources are exploited is crucial (Illius *et al*., 2002). Change in behaviour may be due to increased distances or increased intake rates and time spent feeding as may lead to increased resource depletion at foraging sites. This can help in explaining variation of distribution of hippopotami in relation to study sites and seasons. At the wettest site, hippopotami had more resources hence their abundance and degree of aggregation were maintained while at drier sites, they aggregated more in wet shelters only during the dry season. This was consistent with the results of consequences of aggregation on dynamics of forage (Fryxell, 1991). According to the forage maturation hypothesis, among the advantages of hippopotami aggregating can be maintaining swards at optimum heights through their feeding and hence increased production of young and softer sward tissues (McNaughton, 1979). Short swards and emerging shoots have a direct impact on forage intake by determining rates of intake and digestion (Fryxell, 1991), as growth and age of forage have an inverse relationship with forage quality (Hassall *et al*., 2001; Drescher *et al*., 2006).

With the exception of Paradise Springs during the wet season, inter-individual distances were not significantly different between sites. Mean inter-individual distances at Ikuu Springs were contributed by the fact that from late November 2009, most hippopotami moved out of this site leaving behind few individuals until the next dry season in July 2010. During the time when fewer individuals remained, grouping patterns did not vary in terms of inter-individual distances. This might be the result of changing tradeoffs linked to aggregation. As hippopotami are basically solitary when foraging, it may be unnecessary to aggregate during the wet season when temporary wallows or shelter and forage are available. During the wet season, aggregation is less essential as there are more resources so intra-specific competition for optimal length sward may be reduced. Hippopotami aggregate more during the dry season to utilize the diminishing water resources in the shelter sites but this may have a cost of foraging areas near to the shelters becoming depleted.

Seasonality in behaviour in relation to group size and bonding may differ within species, sexes, age groups and individuals (Lehner, 1996). In the Mara River in the Serengeti, studies have shown that groups tend to split more often during the wet than dry season (Olivier and Laurie, 1974). This may be due to food availability but mainly due to water resource availability because group size decreased after a rise in water levels. During dry months from October to December the lowest inter-individual distances between hippopotami was recorded. This was during the period when most of the shelter sites were dry or relatively dry.

At Paradise Springs, the wettest site, non of the behavioural activity categories differed significantly between seasons while some components of behavioural activities varied between seasons at the four other sites. Water, forage close to the shelter sites and environmental temperatures were the main factors which determined most of the activity patterns of the hippopotami. Hippopotami are highly dependent on permanent water because of the anatomy and physiology of their skin (Eltringham, 1999; Luck & Wright, 1963; Saikawa *et al*., 2004; Jablonski, 2004), and hence have to forage close to water sources. The limitation requiring them to be close to water sources is that they lose water quickly when out of water in hot weather. Luck and Wright (1963) measured hippopotami in Uganda losing water through evaporation at about 7.2 - 9.9 mg^{-1} 5 cm^{-2} /10 min from their skin at air temperature between 32 – 39°C. They however have to maintain their core body temperature at about 36°C (Cena, 1964; Noirard *et al*, 2008). This is likely to be one of the major drivers of diurnal and time specific activity budgets. Manteca and Smith (1994) listed environmental temperatures as among the major factors affecting activity patterns of mammals. According to Schneider and Kolter (2009), temperature between 21-28°C may be optimal for the hippopotami. However, in Katavi maximum temperatures of 35°C were recorded during the months of September, October and November when water was limiting. With mean annual temperatures being between 27 ± 0.8 and 31 ± 0.8°C, it is likely to affect them in their activity patterns, particularly in the absence of water.

Water is central to the diurnal, time specific activity budgets of hippopotami as they have to spend their time resting in order to thermo-regulate their bodies. This is because they reduce sun exposure by getting into water when environmental temperatures become higher (Eltringham, 1999; Noirard *et al*., 2008). Water temperatures, which are relatively stable compared to air temperatures (Noirard *et al*., 2008) help to cool the hippopotami. This is despite the fact that water temperatures vary with seasons, but less so than air temperatures. Rise in air temperatures and absence of water for cooling in some drier sites in Katavi during the dry season of 2009 led the hippopotami to seek refuge in the shade of trees. Presence or absence of water for cooling determined how long hippopotami spent performing particular behavioural activities during the day at different times of the year. This is supported by the observed differences between the wettest and the drier sites and between seasons.

Availability of forage near shelter sites was another factor which determined the diurnal activity budget of the hippopotami. During the wet season when environmental temperatures were cooler and forage was available near the resting sites, hippopotami spent more of the day time feeding than during the dry season when forage was less available and temperatures much higher. Conducive temperature and availability of forage influences the desire to feed near their shelter sites in order to reduce travel distances while maximizing energy intake (Luck and Wright, 1963; O'Connor and Campbell, 1986; Spinage, 2012).

Availability of forage near the shelter sites enabled animals to feed more during the day within their sheltering sites in order to fulfill their energy demands. In addition, this resulted in more walking while also feeding and so to spending less time resting. Hippopotami are primarily night time feeders (Laws, 1968; Lewison and Carter, 2004), more day-time feeding may suggest that forage is limiting near shelters during the dry season. There is a possibility that a smaller quantity of more fibrous foods are eaten during the dry season leading to more time spent digesting while resting. In a study of buffalo in Meru, Tanzania, total grazing time per day did not differ between seasons. However, ruminating time increased during the dry season as the result of more fibrous food (Sinclair, 2008b). Manteca and Smith (1994) observed varied patterns as animals had to alter their activity budget as resources become scarce. This might be the cause for less feeding during the day time in dry season.

Similarly for juveniles, there were less resting and more walking and touching during the dry than wet season. This is thought to have been due to less forage and water. During the dry season, more time is spent looking for resources than during the wet season. Animals had to adjust their behaviour pattern to fit with less resource as observed by Manteca and Smith (1994). It is therefore thought there was less time foraging due to there being less water.

This activity of feeding near shelter sites may indicate that the animal had less forage during the previous night, possibly due to the distances between shelters and foraging grounds or simply taking advantage of forage availability close to where they rested. It is probable that hippopotami would utilize a nearby foraging ground if available in order to meet their nutritional requirements. Subject to climatic conditions mainly air temperatures, hippopotami feed during the day or lie out of water while basking (Luck and Wright, 1963; Spinage, 2012). In Zimbabwe, hippopotami foraged within 1 km of the river bank during the wet season, although they had to travel much further inland during the dry season (O'Connor and Campbell, 1986), as forage became depleted within the 1 km stretch. This can help to explain why hippopotami at drier shelter sites in Katavi left just after the first rains in order to be close to their feeding grounds. This is because there was less forage near the drier shelter sites particularly during the dry season. This led to hippopotami travelling further for foraging. In Uganda, Eltringham (1999) and Field & Laws (1970) observed hippopotami creating temporary shelters for minimizing travel distances between shelter sites and foraging grounds. Time used for travel may influence diurnal activity budgets such as animals having to rest instead of feeding.

Most hippopotami continued to feed near their resting sites after returning from foraging and before they started their dusk feeding trips. This was especially frequent during the wet season when forage was available near their shelter sites. It was also most frequent at the wettest site. In the drier sites, there was less feeding near shelter sites due to less forage during the dry season. This led to less feeding being recorded at drier sites. Feeding near shelter sites allowed hippopotami to feed, wallow and bask with less energy expenditure. This was restricted in the drier sites; hence variations in activity budget between sites.

Impacts of less water on hippopotami led to increased movements among hippopotami and increased touching. Hippopotami had to adjust their patterns and adopt new patterns in order to cope with the available resources. However, during this study, availability of forage and water was well above the expected or previously reported levels of drought. Moe drought is likely to have led to a more drastic change or variations in behavioural patterns. In Ruaha NP, Tanzania, extended periods of low or no river flow disrupted normal behaviour patterns of animals and led to changes in their behaviour (Kashaigili *et al.*, 2006).

Less resting among adults and juveniles were observed in the dry months of September, November and December before increasing in January. Feeding near resting sites contributed to variation of activity patterns between different times of the day. Availability of food, water resources near resting grounds and environmental temperature dictated the activity budget over times of the day. During the morning after the animals returned from feeding, they spent some hours basking and moving back to water and hence were unsettled. During the hot time of the day most of them were resting. Luck and Wright (1963) and Blowers *et al.* (2008) observed that animals keep on basking and getting into water frequently during hot days. In Katavi this was mainly observed during the time when water for immersing was available. During the late morning to late afternoon most hippopotami were resting. However, during the wet season animals spent more day time actively feeding, hence a more spread activity budget over the times of the day.

Variation of activity budget within time of the day is also related to changes in weather conditions particularly for the purpose of thermoregulation. As environmental temperatures increases, hippopotami move into water while they bask when temperatures declines (Eltringham, 1999). Noirard *et al*. (2008) in Niger found that hippopotami basked more when waters were cold.

Ikuu Springs was the site where the highest resting activity was recorded among adults. This is because of the use of the site as there was less feeding ground at this site. Hippopotami at Ikuu Springs therefore had to spend more day time resting. However, few fed within the site.

Forage is among the factors that influences activity patterns of hippopotami in various ways. In Zambia, Wilbroad and Milanzi (2010) observed that poor pasture at a site induced more travelling among hippopotami. This tends to be supported by Manteca and Smith (1994) who suggested that less food during the dry season leads to animals spending more time traveling and feeding. Hippopotami at the wettest site had forage during most of the time and hence were more active. Feeding by both adults and juveniles was highest at Lake Katavi.

Ikuu Springs, despite being a wet resting site for hippopotami throughout the year, had much less foraging opportunities within the shelter site which almost disappeared when hippopotami abundance increased.

5. Conclusions and recommendations

Some components of activity patterns varied significantly between seasons. Variations observed during the dry season are indicators that water dynamics have an impact on behaviour patterns of hippopotami in Katavi.

Differences in wetness between sites show that water had a major influence on differences in hippopotami activity patterns between sites. Hippopotami in the wettest site showed little seasonal variations in activity patterns and aggregation compared to the drier sites.

Availability of forage and air temperatures are thought to have contributed to the observed variations in activity patterns between sites and seasons.

Availability of water, varying air temperature and availability of forage near resting sites determined variations of activity patterns during different times of the day.

Due to hippopotami depending on water for thermoregulation, it can be concluded that most diurnal behavioural patterns responded to thermoregulation constraints (Wright, 1964; Noirard *et al*., 2008). Apart from the need hippopotami have to feed, the skin anatomy and physiology can be considered as major determinants of the activity budget.

Chapter 7: Spatial and temporal variations in behavioural events

1. Introduction

Animals interact with their environment in different ways (Lehner, 1996; Raven *et al.*, 2008) and environment plays a crucial role in shaping behaviour. External and internal factors and forces affect the behaviour of individual animals (Raven *et al.*, 2008). Behaviours are not random (Lehner, 1996) but are instinct or learned. Sampling relative frequency and duration of different behaviours enables quantification of behavioural acts (Lehner, 1996). Behavioural acts can be arbitrarily sub divided into two categories: activities or states and events. This subdivision depends on the duration of the act (Martin and Bateson, 2007). Behavioural activities are presented in Chapter 6 and behavioural events in this Chapter.

Events are behavioural patterns of relatively short duration such as vocalization or discrete body movements (Martin and Bateson, 2007), as opposed to behavioural activities which are behavioural patterns of relatively longer duration such as standing, resting or feeding. The major feature of events is their frequency of occurrence while duration of activity is the major feature in behavioural activities (Martin and Bateson, 2007). Behavioural activities are measured as the amount of time taken performing a particular activity or activities within a certain period, such as time spent feeding in an hour. However, behaviour events are measured in terms of frequency of occurrence within a certain period of time such as number of grunts or barking made by an animal per minute.

This Chapter is about spatial and temporal variations in events. The wider context of this Chapter is given in Chapter Six on behaviour activities. Events were separated from behavioural activities to simplify recording. Separating recording of events from behavioural activities simplified the recording protocol and improved reliability of the data because events being behavioural patterns of short durations were likely to have been missed if recorded at the same time as recording behavioural activities.

Separating scan sampling for the two fundamental types of behaviour, activities and events thus enabled more information to be acquired, as noted by Ruiter (1986), Lehner (1996) and Martin and Bateson (2007).

1.1 Aims and hypotheses

The overall aim of the study is to investigate the impact of a varying water resource on the ecology and behaviour of hippopotami. The environment provides for the proper development and expression of behaviour (Lehner, 1996). It is therefore through the study of such behaviours we can express the impact of environment on hippopotami.

A total of eight events in four categories which are described in section 2.2 were measured during this study. These include aggression (threats and biting), sexual (courtship and mating), social (active touching and grooming), and maintenance events (yawning, rolling, ear flicking and splashing water over the backs). The study therefore tested the following hypotheses concerning hippopotami in Katavi.

H_1: There are differences in frequency of behavioural events between adults and juveniles.

H_2: There are broad seasonal variations in event patterns

H_3: There are differences in event patterns between study sites

2. Methods

2.1 Site selection

The five observation quadrats selected for recording events were the same study sites used for recording behavioural activities. Locations of the sites are shown in Fig. 8.1 and characteristics and criteria for selection are described in Chapter 2.

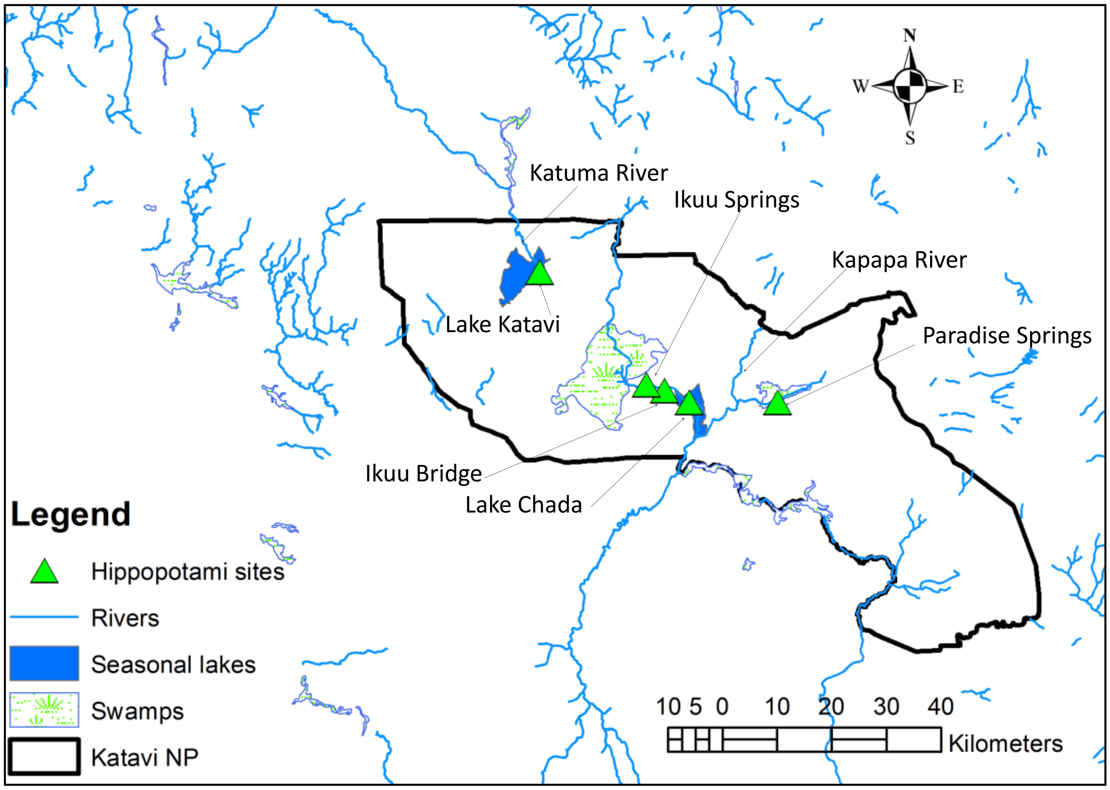


Fig. 8.1: Sketch map showing hippopotami behavioural events study sites in Katavi NP.

2.2 Data recording

Animal observations were made from September 2009-September 2010, at each of the five sites selected for hippopotami behaviour observation. Two days each month were spent in recording hippopotami behavioural events at each site.

This study is based on directly observed behaviour according to Lehner (1996) and Martin and Bateson (2007). At each of the sites, observations were carried out from a vehicle or from a hidden position in order to minimize interference. Animals were watched either directly or using a pair of binoculars. Observations distances were minimized but in accordance with health and safety constraints. If hippopotami were disturbed for any reason, recording stopped until animals appeared to calm or settle and ignore the cause of disturbance.

The study was conducted between 0600 and 1930 hours for safety reasons. Observations in the wet season were made between December 2009 to May 2010 and in the dry season from September-November 2009 and June to September 2010. Event scans were conducted for 4 h day^{-1} in 60 minutes blocks, four times a day from 0700 to 1900 at approximately 0800-0900, 1000-1100, 1600-1700 and 1800-1900 hours for two consecutive days each month on each site. In total, events patterns were observed for 520 hours. Adult and juvenile behavioural events were recorded separately.

Observations were only recorded at the specific sheltering or resting grounds shown in Fig. 8.1 and described in Chapter 2. Four behavioural events categories (aggressive, sexual, social and maintenance) were recorded and were sub divided as a) aggressive events comprising events defined as: 1) **Threats**: this comprised confrontation without actual fight or attack. Threats involved opening their mouth wide, displaying their jaws and moving head, charging and chasing others and excluding others from a resting site and 2) **biting:** which involved use of teeth to attack parts of the body of other hippopotami and slashing with a tusk.

b) **Sexual events**: this included 1) **Courtship**: involved a male hippopotamus moving towards a female and following it for some time until the female was ready for mating. Courtship also included friendly chase in water and 2) **Mating**: which was the actual event of copulation after courtship. C) **Social events**: these included all non-confrontational interactions, active touching or contact and grooming when lying down as well as when active. d) **Maintenance** events which were divided into 1) **Yawning**: yawning in vertebrates is the involuntary opening of mouth while taking a deep breath of air. It is non-confrontational opening of the mouth upward towards the sky and not directed to another individual, seen as a friendly gesture. Possible functions of yawning are discussed in Section 4.1 2) **Rolling**: turning the body round in water or mud. This happens when water is not deep enough to immerse the whole body. Rolling was taken as either full roll with movement from one side to another with all four legs in the air or half roll where the animal turned half way with at least two legs in the air and back again to the same side. It was thought rolling was aimed at cooling the back. 3) **Ear flicking**: twitching ears vigorously and 4) **Water splashing**: flicking tail from side to side in water in order to splash water over the back. This was thought to be for cooling their back when water was not deep enough. At times of drought, mud was also used for splashing. Possible functions of ear flicking and water splashing are discussed in Section 4.1.

In the same ways described in Chapter 6, two complementary methods were used to record behaviour: direct logging into a palm top Psion Logix 10 computer using the Observer Mobile Professional system for field observations software. The Psion uses the Observer XT Mobile kit for the Psion Work about Pro and use of data sheets as described in Chapter 6. Prior video recording for familiarization were also made as described in Chapter 6.

Recording methods

Sampling protocol

Hippopotami behavioural events were monitored mainly by scan sampling according to Martin and Bateson (2007) and Lehner (1996). A group of hippopotami was scanned rapidly for five minutes and the behaviour of each animal recorded at the instant it occurred. This was followed by a pause of five minutes before recording continued for another five minutes, until the 60 minutes period ended.

Recording protocol

Events were recorded using all occurrence recording divided into successive time intervals. This measured frequencies of behavioural event patterns, hence making it possible to record several different categories of behaviour simultaneously.

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2.3 Data analysis

August, September, October and November were grouped as dry season while January, February, March and April were wet season months. Statistical analyses were performed using the SPSS statistics package software (PASW Statistics 18) by IBM. Data were summarised into frequency tables.

Seasonal variations were tested using t-tests. Spatial and temporal variations were analysed using 1-way analysis of variance (ANOVA) while multiple factors were analysed using 2-way analysis of variance. Relationships were tested using correlations.

3 RESULTS

3.1 Comparison of frequency of events for adults and juveniles

Maintenance events were the most frequent in both adults and juveniles making up a total of 89 ± 2.1 % and 81 ± 1.6 % for adults and juvenile respectively (Fig. 8.2). There were more social events among juveniles while more aggressiveness was observed in adults. There were some sexual events in adults amounting to about 1% of the total events observed (Fig. 8.2)

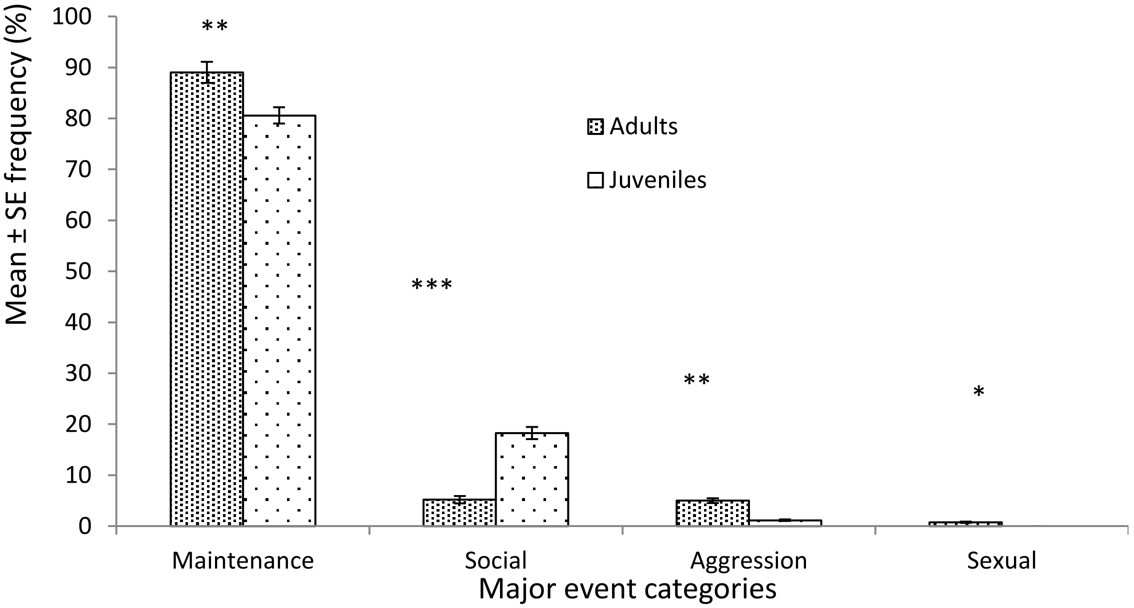


Fig. 8.2: Annual means of behavioural events observed for adult and juvenile hippopotami combined for the five study sites in Katavi NP, Tanzania. Key: ***= p <0.001, ** = p <0.01, * = p <0.05

Amongst adults, yawning was the most frequent (33.7 ± 3.2 %) behavioural event (Fig. 8.3), closely followed by ear flicking. Water splashing was the third most frequent event followed by social interactions. Threats and rolling had similar frequency. Events involving biting and sexual encounter had the lowest frequency of total events recorded for adult hippopotami (Fig. 8.3).

Ear flicking was the most frequent event in juvenile hippopotami recording a 40.9 ± 2.5 % of total events. Yawning and social were the next most frequent (Fig. 8.3). There were significant differences in frequency of water splashing, threats and rolling. There were only a few isolated observations of biting by juveniles (0.1 ± 0.1 % of total events), and no sexual events among juveniles (Fig. 8.3).

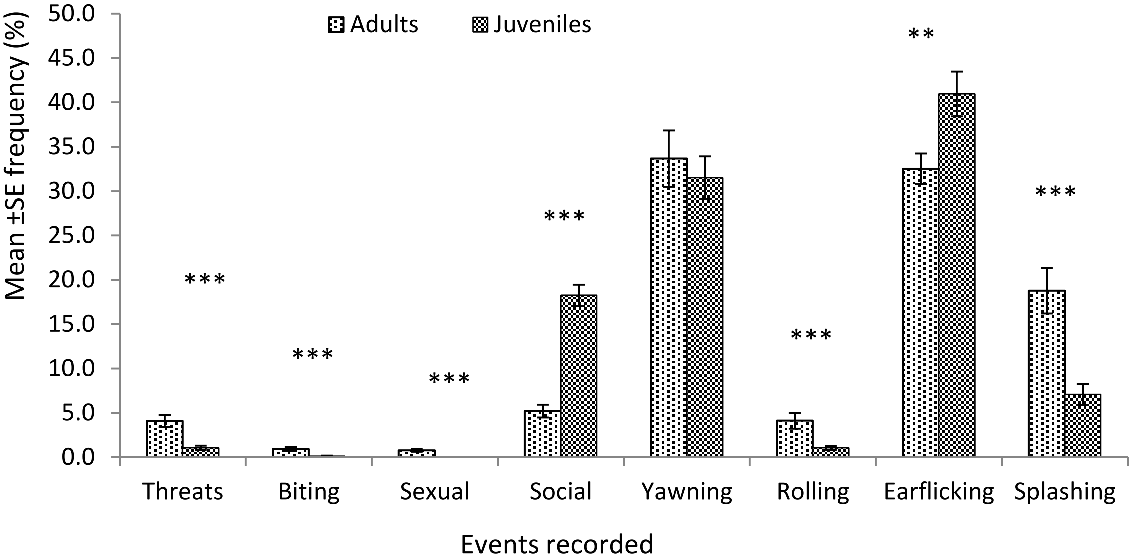


Fig. 8.3: Annual means of behavioural events observed for hippopotami combined for the five study sites in Katavi NP, Tanzania (September 2009-September 2010). Key: ***= $p < 0.001$, **= $p < 0.01$, *=$p < 0.05$

There were significant differences in the frequency of behavioural events between adults and juvenile hippopotami (Table 8.1). Of the eight events recorded, yawning was the only one for which there was no significant differences between the two age groups (t_{24} = 0.566, p = 0.577). Differences between adults and juveniles were significant for all other categories of behavioural events (Table 8.1 and Fig. 8.3).

Table 8.1: Independent sample t-test for differences in events between adults and juvenile hippopotami in Katavi NP, Tanzania

S/No	Factor	t-value	Df	p-value
1	Threats	4.184	24	0.0001
2	Biting	3.287	24	0.003
3	Sexual	5.043	24	0.0001
4	Social	-9.262	24	0.0001
5	Rolling	3.319	24	0.003
6	Ear flick	-2.744	24	0.011
7	Splashing	4.123	24	0.0001

Adults showed more aggressive (threatening and biting), sexual and maintenance (rolling and splashing) behaviours while juveniles showed more social behaviour and ear flicking (maintenance) (Fig. 8.3).

3.2 Seasonal variations in events

Amongst adults, maintenance events were more frequent during the wet season and aggression was more frequent during the dry season (Fig.8.4). Sexual events were higher during the wet than dry season. Social interaction had relatively similar frequency in the two seasons (Fig. 8.4).

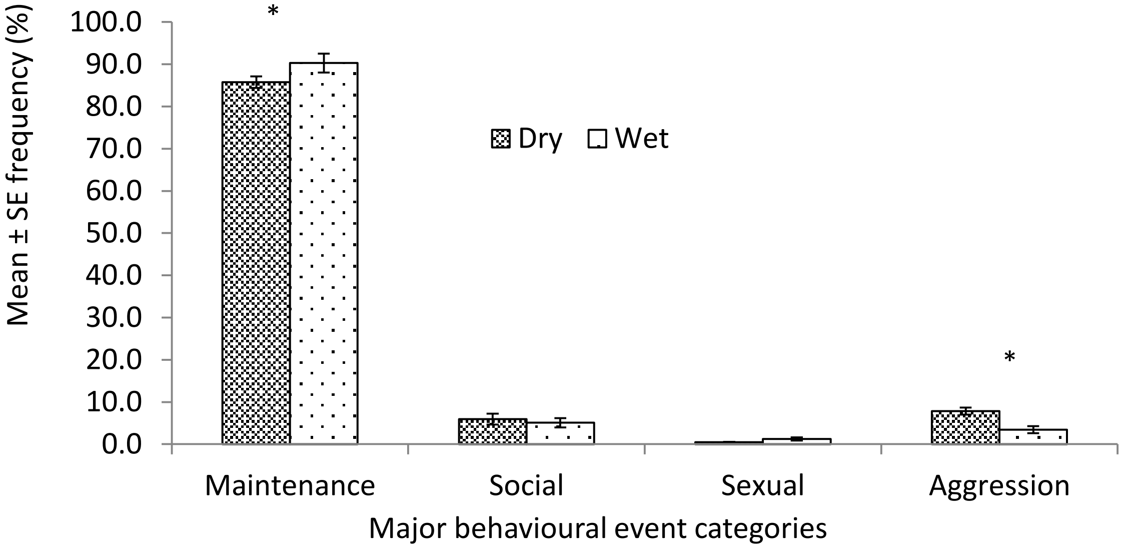


Fig. 8.4: Variations in frequency of behavioural events observed during the dry and wet seasons for adult hippopotami combined for the five study sites in Katavi NP, Tanzania. Key: *=p<0.05.

Social events amongst juvenile were the only events with significant seasonal variations with more social events during the wet season (Fig. 8.5). Although maintenance was the most frequent behavioural event, this did not vary seasonally for juveniles. There were only a few isolated observations of aggression and these were mainly during the dry season and there was no difference between seasons (Fig. 8.5).

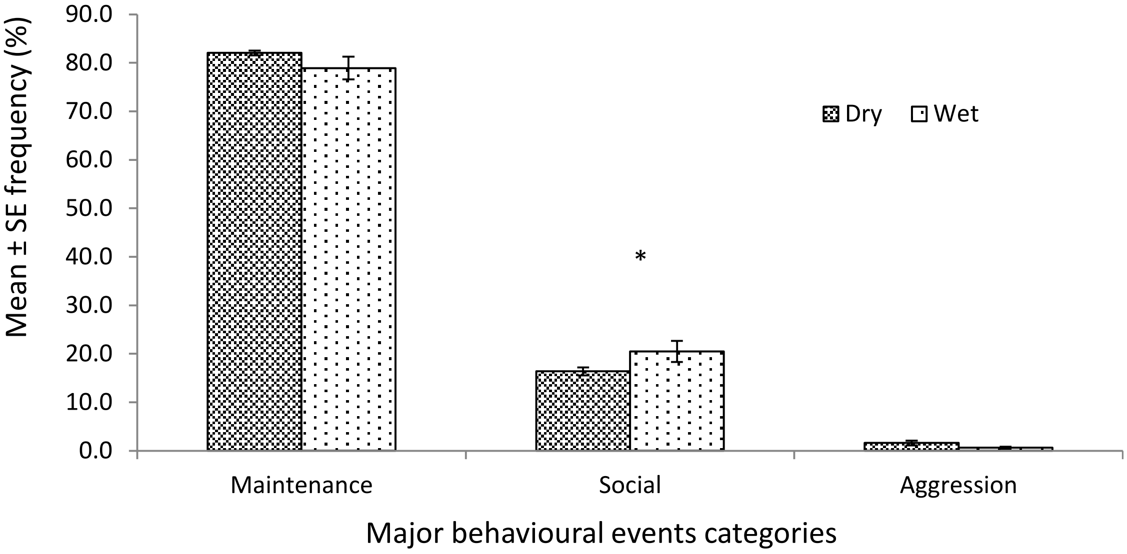


Fig. 8.5: Variations in frequency of behavioural events observed during the dry and wet season for juvenile hippopotami combined for the five study sites in Katavi NP, Tanzania. Key: *=p<0.05

For adults, there were differences between wet and dry seasons in biting ($t_{11} = 2.744$, $p < 0.019$), sexual events ($t_{11} = -2.216$, $p < 0.049$), yawning ($t_{11} = -4.102$, $p < 0.002$), rolling ($t_{11} = 3.972$, $p < 0.002$) and water splashing ($t_{11} = 4.883$, $p < 0.0001$) (Fig. 8.6). Aggressive behavioural events (threats and biting) were most frequent in the dry season as were the maintenance behaviours of splashing and rolling. Yawning, ear flicks, sexual and social behaviour were more common in the wet season (Fig. 8.6).

There were no significant differences in threats, social events and ear flicking between the wet and dry seasons among adult hippopotami (Fig. 8.6).

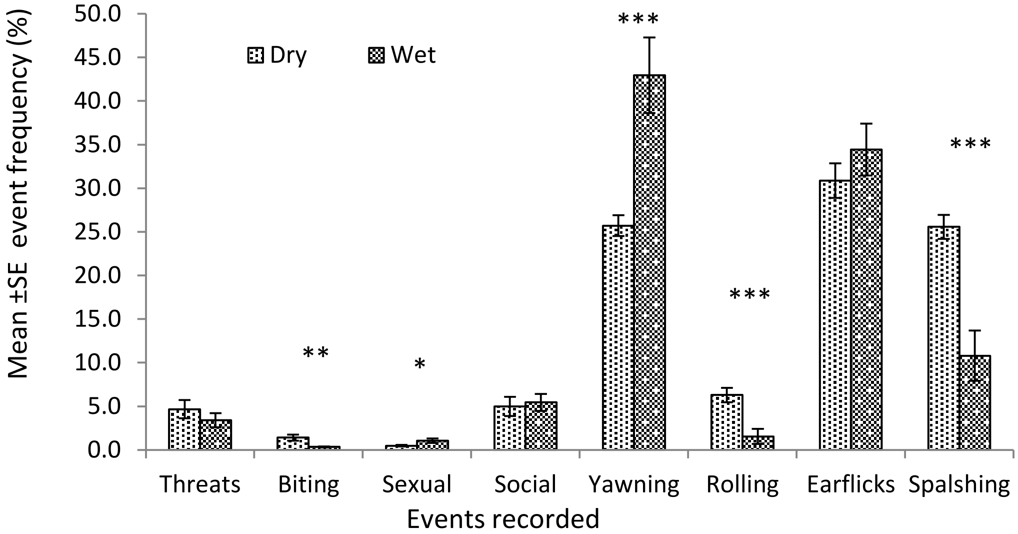


Fig. 8.6: Seasonal variations in events among adult hippopotami in Katavi NP, Tanzania (September 2009-September 2010). Key: ***=p<0.001, **=p<0.01, *=p<0.05

For juveniles, the only significant differences between seasons were in social and water splashing events (t_{11} = - 1.873, p < 0.03) (Fig. 8.7). There were more social events in the wet than dry season. As for the adults, there was more splashing during the dry than wet season. There were no differences in the other six event categories between the dry and wet season (Fig. 8.7).

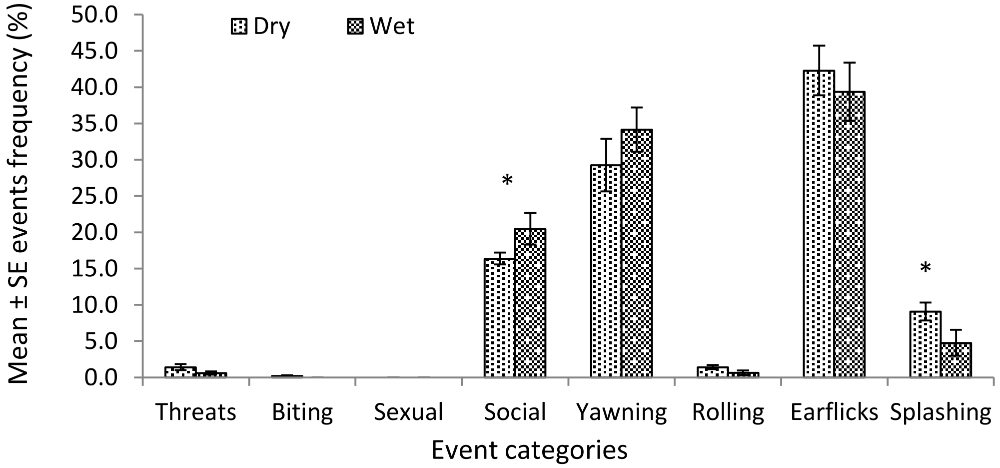


Fig. 8.7: Seasonal variations in events among juvenile hippopotami in Katavi NP, Tanzania (September 2009-2010). Key: *=p<0.05

3.3 Monthly variations in events

To identify more precisely when within season frequency of events changed, variations between individual months were analysed (Fig. 8.8, Fig. 8.9 and Fig. 8.10). There were significant monthly variations in all events observed among adult and juvenile hippopotami (Table 8.2).

Table 8.2: ANOVA results for monthly variations in events among adult and juvenile hippopotami in Katavi NP, Tanzania

		Adults			**Juveniles**		
S/No	**Factor**	**F-value**	**df**	**p-value**	**F-value**	**df**	**p-value**
1	Threats	5.366	12, 258	0.0001	3.322	12, 259	0.0001
2	Biting	4.752	12, 251	0.0001	1.775	12, 252	0.053
3	Sexual	4.162	12, 259	0.0001			
4	Social	8.342	12, 259	0.0001	2.43	12, 259	0.005
5	Yawning	2.624	12, 259	0.003	3.4	12, 259	0.0001
6	Rolling	17.1	12, 259	0.0001	2.361	12, 259	0.007
7	Ear flicks	4.29	12, 259	0.0001	4.548	12, 259	0.0001
8	Splashing	7.844	12, 259	0.0001	6.36	12, 259	0.0001

Aggressive behaviour peaked in September and October, with most threats among adult hippopotami during the months of October and November (Fig. 8.8 and Fig. 8.10), while April, June and July were the months with least threats among adults (Fig. 8.10). There were a few isolated threat events among juvenile hippopotami during August and October (Fig. 8.10). However, these were not as serious as for adults. No threats were recorded in March and April, with few in June, making these months the least in threat events among juveniles (Fig. 8.10).

Biting by adult hippopotami was most frequent in September 2009, August and September 2010. Least biting was observed in February and April (Fig. 8.10). Few and isolated non serious biting by juveniles occurred in August, September and October (Fig. 8.10). However, they were very isolated incidences amounting to less than one percent of the total events recorded (Fig. 8.10).

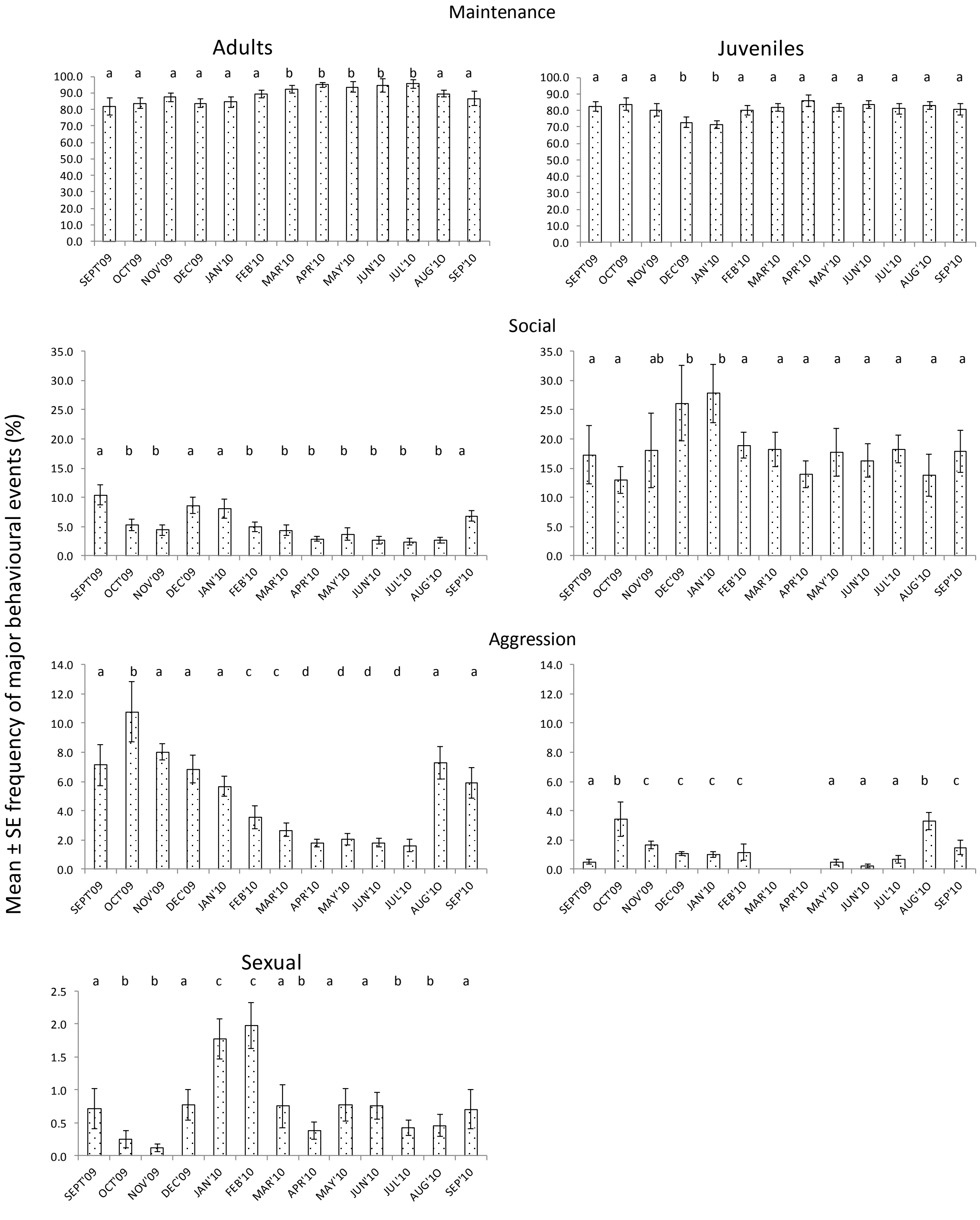


Fig.8.8: Variations between months in mean frequencies in maintenance, social, aggression and sexual behavioural events for adult and juvenile hippopotami in Katavi NP. Bars sharing the same letter are not significantly different at $p < 0.05$.

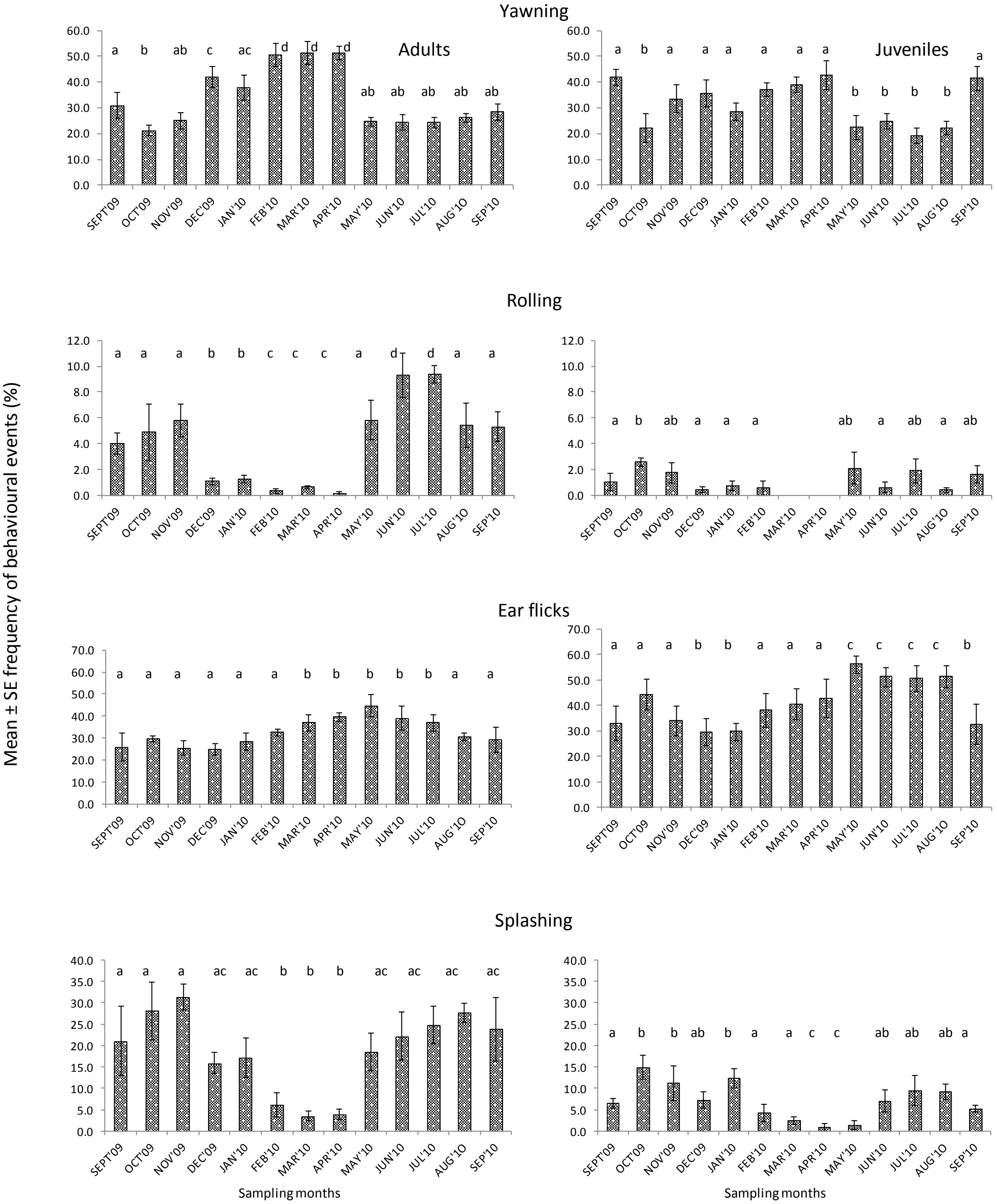
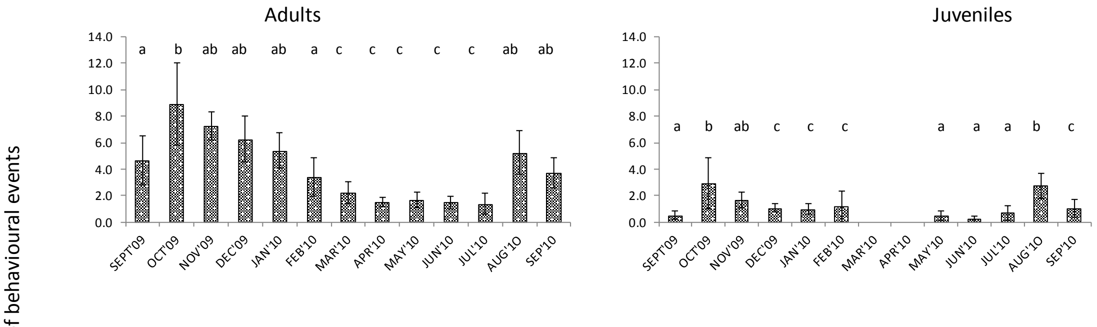


Fig. 8.9: Variations between months in mean frequencies of separate components of maintenance behavioural events for adult and juvenile hippopotami in Katavi NP. Bars sharing the same letter are not significantly different at $p < 0.05$.

a) Threats



b) Biting

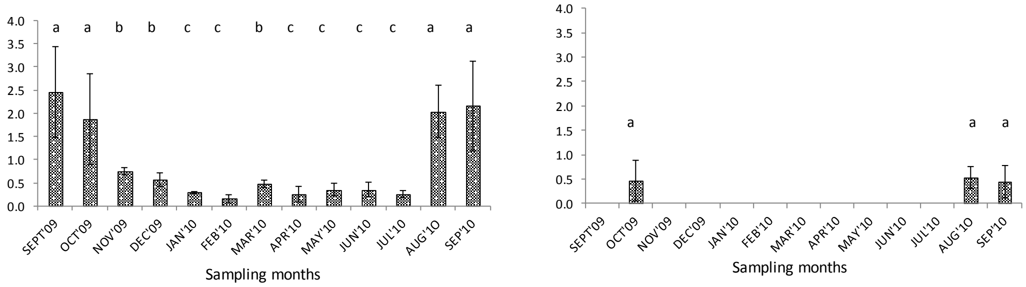


Fig. 8.10: Variation between months in mean frequencies of separate components of aggressive behaviour for adult and juvenile hippopotami in Katavi NP, Tanzania. Error bars are ± SE around monthly mean. Bars sharing the same letter are not significantly different at $p < 0.05$.

Most sexual events among adult hippopotami in Katavi were observed during the middle of the wet season in January and February (Fig. 8.8). Fewest were observed in October and November (Fig. 8.8).

Social events among adults were significantly higher in September and December 2009, while the least was recorded in June, July and August (Fig. 8.8). Social events among juvenile hippopotami were more frequent during the months of December and January. Least social events were recorded in August and October (Fig. 8.8).

Maintenance behavioural events (yawning, rolling, ear flicks and splashing combined) showed a clear annual pattern among both adults and juveniles (Fig. 8.8). They slightly peaked up in February until July. However, monthly variations were very gentle with no sharp increase in frequencies (Fig. 8.8).

More yawning in adult hippopotami was recorded in February, March and April while the least yawning was recorded in October (Fig. 8.9). Yawning events among juveniles also peaked in April but were also high in September 2009 and 2010. Least yawning events were recorded in July (Fig. 8.9).

Most rolling by adult hippopotami was in June and July with generally more in May-September than December to April (Fig. 8.9). Rolling by juvenile hippopotami was most frequent in October, with no rolling recorded in March and April (Fig. 8.9).

Ear flicking showed a clear annual pattern among adult hippopotami with more flicking in April and May and least in November and December (Fig. 8.9). Ear flicking by juvenile hippopotami had the highest frequencies in May, closely followed by June, July and August (Fig. 8.9). The fewest ear flicks were recorded in December and January.

Adult hippopotami splashing water on their backs was most frequent during the driest months of October and November with least water splashing in March and April (Fig. 8.9). For juveniles, splashing water was most frequently observed in October and January and least in April (Fig. 8.9).

3.4 Spatial variations in events

There were significant spatial variations between study sites. With exception of social, ear flicking and splashing behaviours for adults, all other event categories differed significantly between sites (Table 8.3).

For juveniles, there were significant variations in social events, yawning, rolling and ear flicks between sites (Table 8.3). Threats, biting and water splashing did not vary significantly between sites.

Table 8.3: ANOVA results for spatial variations in events among adult and juvenile hippopotami in Katavi NP, Tanzania

		Adults			Juveniles		
S/No	**Factor**	**F-value**	**Df**	**p-value**	**F-value**	**df**	**p-value**
1	Threats	8.061	4, 258	0.0001			
2	Biting	8.99	4, 258	0.0001			
3	Sexual	3.519	4, 258	0.008			
4	Social				8.793	4, 259	0.0001
5	Yawning	2.634	4, 258	0.035	7.786	4, 259	0.0001
6	Rolling	2.859	4, 258	0.024	2.689	4, 259	0.032
7	Ear flicks				3.682	4, 259	0.006

Most aggression (threats and biting) between adults was recorded at Ikuu Springs and least at Paradise Springs (Fig. 8.11 and Fig.8.13). Similarly, the few, isolated threats by juvenile hippopotami were more prominent at Ikuu Springs and least at Paradise Spring (Fig. 8.11 and Fig.8.13). The even fewer incidences of biting by juveniles followed the same pattern (Fig. 8.13).

Sexual events were most frequent at Ikuu Bridge and Paradise Springs and least at Ikuu Springs (Fig. 8.11).

Lake Katavi and Paradise Springs had the most social events among adult hippopotami (Fig. 8.11). Social interaction also was less at Ikuu Springs than at the other four sites (Fig. 8.11). Social events among juvenile hippopotami were most frequent at Lake Chada. Ikuu Spring had the least social events by juveniles (Fig. 8.11), significantly less than other sites.

Among adults, yawning events was most frequent at Lake Katavi and least at Paradise Springs (Fig. 8.12). Juveniles yawned more at Ikuu Springs while there was least yawning at Paradise Springs (Fig. 8.12).

Adults rolled the most at Paradise Springs and least at Ikuu Bridge and Lake Katavi (Fig. 8.12). Few rolling incidences were recorded among juvenile hippopotami (Fig. 8.12).

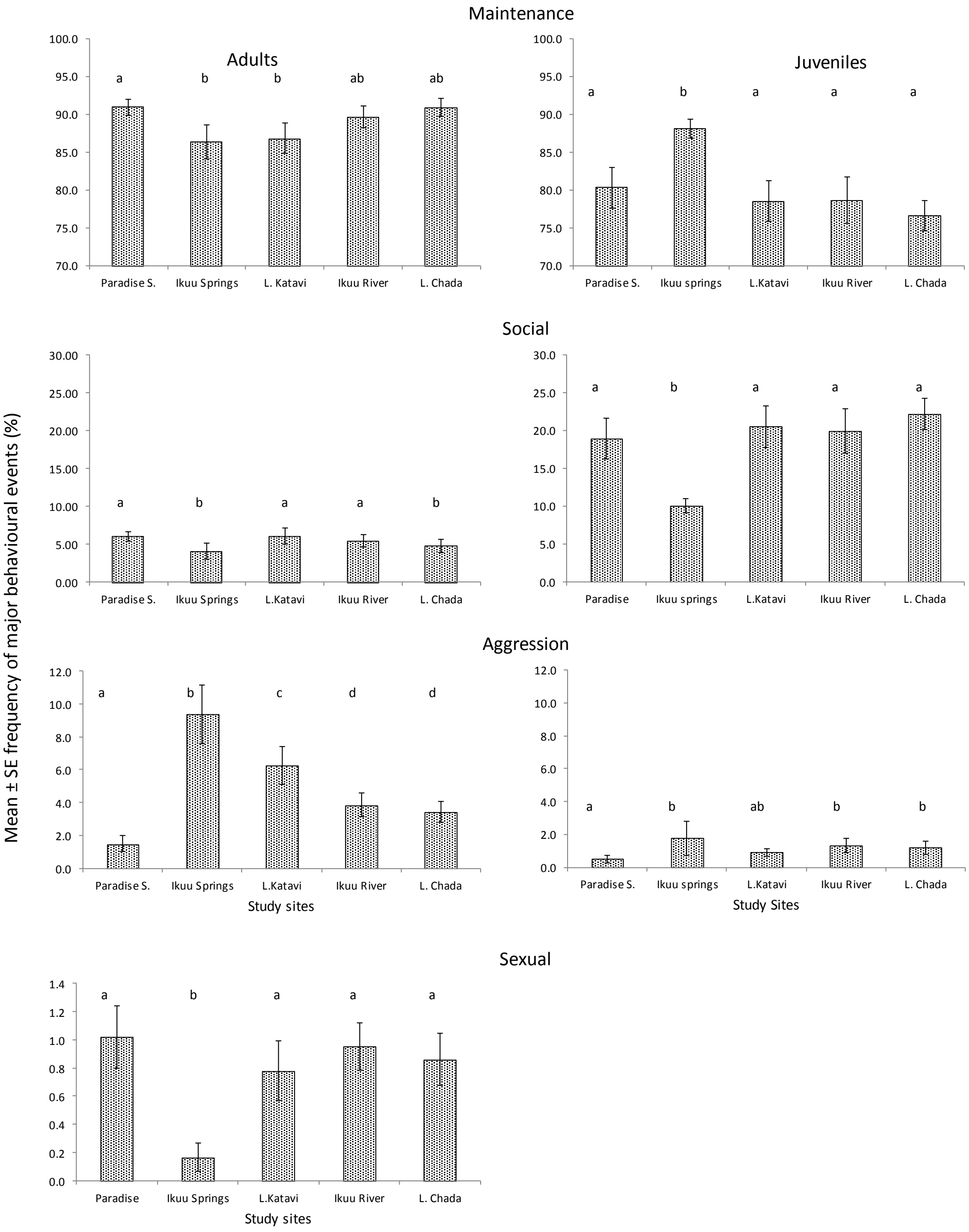


Fig. 8.11: Variations of major behavioural event category frequencies between the five study sites for adult and juvenile hippopotami in Katavi NP. Error bars are ±SE. Bars sharing the same letter are not significantly different at $p < 0.05$.

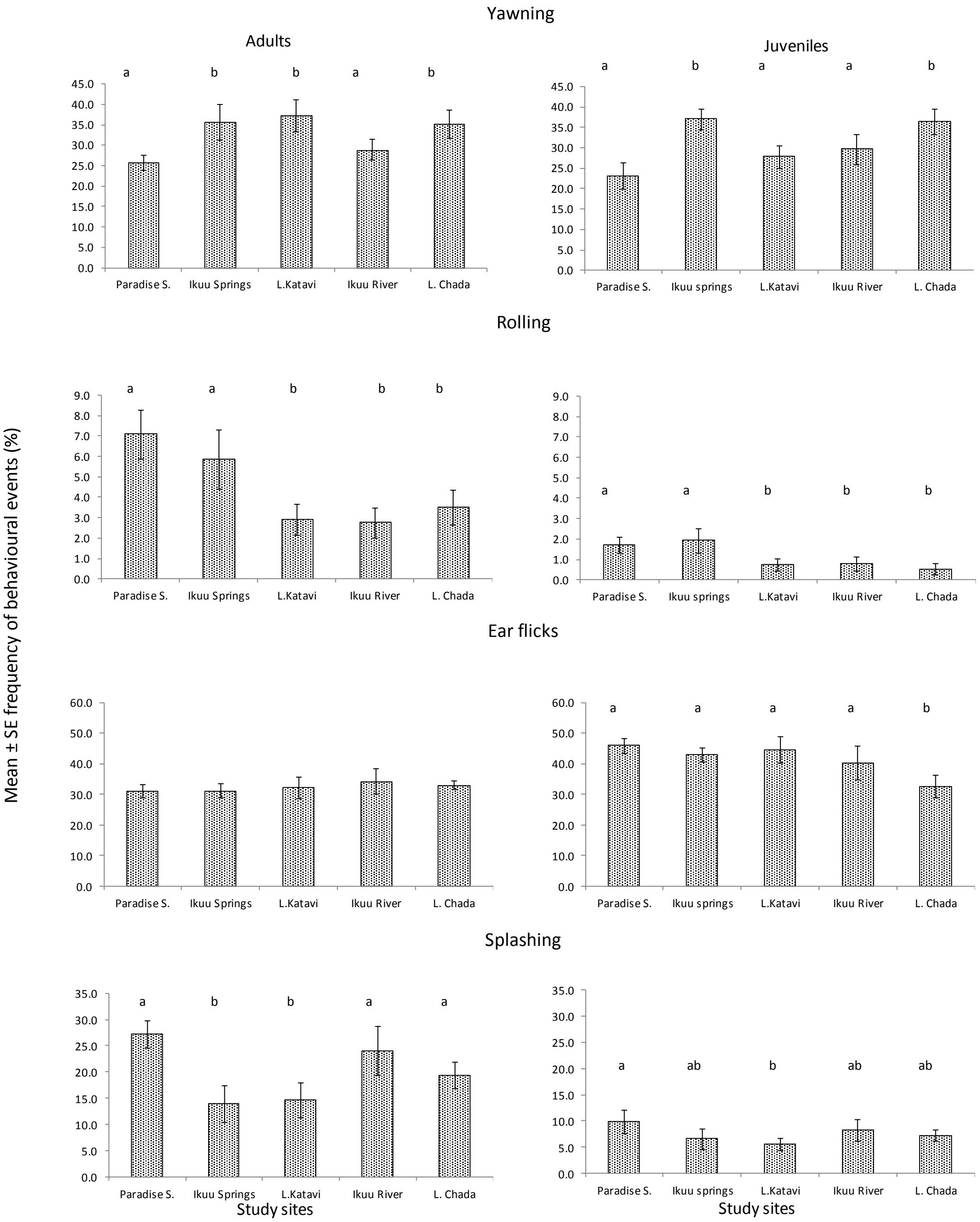


Fig. 8.12: Mean spatial variations in frequency of individual components of maintenance behavioural events for the five study sites in adult and juvenile hippopotami in Katavi NP, Tanzania. Error bars are ± SE around annual mean. Bars sharing the same letter are not significantly different at $p < 0.05$.

Ear flicking by adult hippopotami varied little between sites. However, there were more ear flicking events at Ikuu Bridge than in other sites with fewest at Paradise and Ikuu Springs (Fig. 8.12). Juveniles exhibited more ears flicking at Paradise Springs and least at Lake Chada (Fig. 8.12).

Water splashing onto the backs of adults was highest at Paradise Springs and least at Ikuu Springs and Lake Katavi (Fig. 8.12). Water splashing by juveniles was also more frequent at Paradise Springs and least at Lake Katavi (Fig. 8.12).

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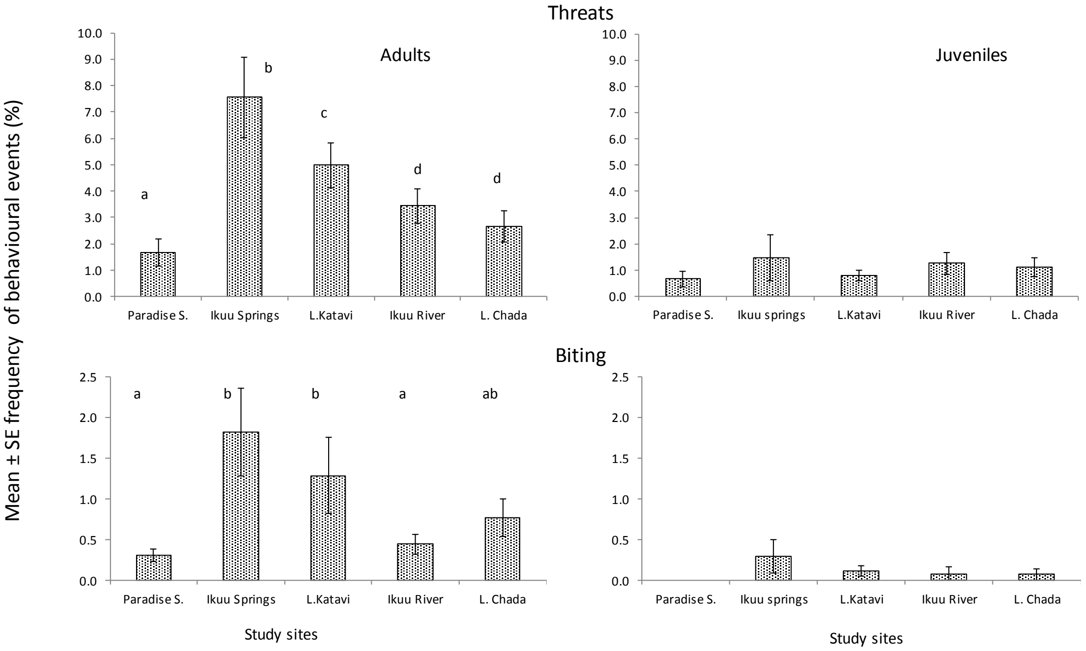


Fig. 8.13: Mean spatial variations in frequency of individual components of aggression behavioural events for the five study sites in adult and juvenile hippopotami in Katavi NP, Tanzania. Error bars are ± SE around annual mean. Bars sharing the same letter are not significantly different at $p < 0.05$.

3.5 Variations between times of the day

All event categories varied significantly with time of the day for adult hippopotami and most with the exception of threats and biting for juveniles. All other events varied significantly between times of the day (Table 8.4 and Fig. 8.14 - Fig.8.17).

Table 8.4: ANOVA results for variations in events between different sampling times for adult and juvenile hippopotami in Katavi NP

		Adults			Juveniles		
S/No	Factor	F-Value	df	p-value	F-Value	df	p-value
1	Threats	13.66	3, 258	0.0001	NS	NS	NS
2	Biting	4.34	3, 251	0.005	NS	NS	NS
3	Sexual	25.91	3, 259	0.0001	N/A	N/A	N/A
4	Social	8.63	3, 259	0.0001	3.34	3, 259	0.02
5	Yawning	43.7	3, 259	0.0001	19.37	3, 259	0.0001
6	Rolling	15.74	3, 259	0.0001	10.37	3, 259	0.0001
7	Ear flicks	8.47	3, 259	0.0001	5.71	3, 259	0.001
8	Splashing	24.26	3, 259	0.0001	14.25	3, 259	0.0001

Key: NS = Not significant, N/A = Not applicable

More threats and biting by adults were observed during the morning and mid morning between 8-11 am (Fig. 8.14). Social events for adults were mainly at mid-day while these were spread throughout the day in juveniles (Fig. 8.16). Sexual events were observed mainly during the time when animals had settled after coming back from feeding which was between 10 - 11 am and 1600 - 1700 hours (Fig. 8.16). Yawning was mainly observed during the morning as the animals were settling and during the late afternoon as they were about to move out of water for feeding. Rolling and water splashing increased as air temperatures increased. Ear flicks were spread throughout the day (Fig. 8.17).

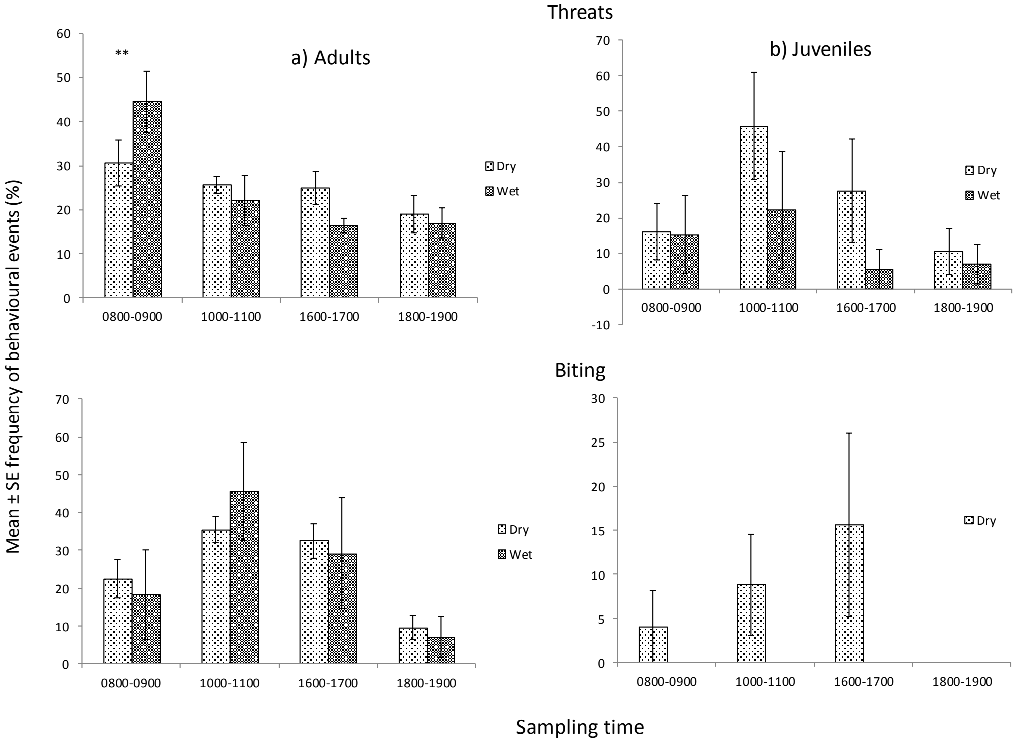


Fig. 8.14: Mean seasonal variations in individual aggression behavioural events between different times of the day in (a) adult and (b) juvenile hippopotami in Katavi NP, Tanzania. Error bars are ± SE around seasonal mean.

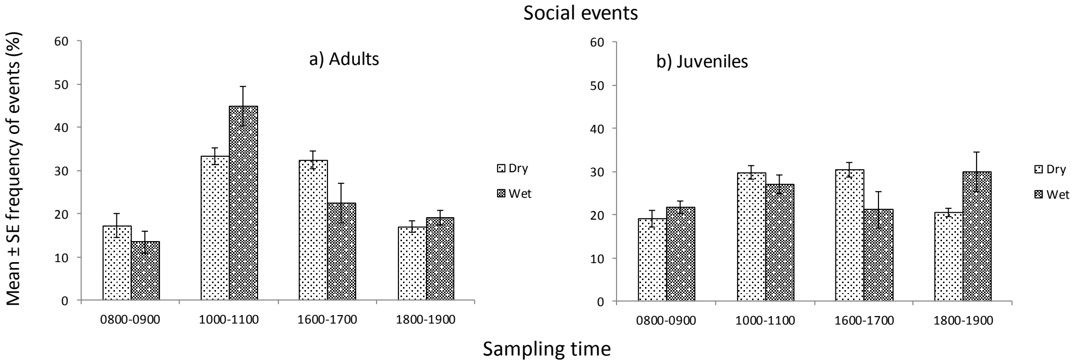


Fig. 8.15: Mean seasonal variations in social behavioural events between different times of the day (September 2009-September 2010) among (a) adult and (b) juvenile hippopotami in Katavi NP, Tanzania. Error bars are ± SE around annual mean.

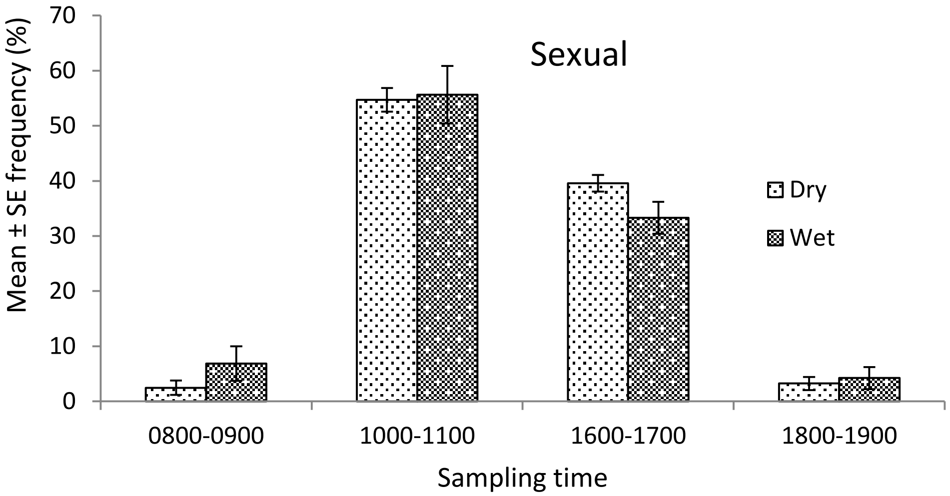


Fig. 8.16: Mean seasonal variations in sexual behavioural events between different times of the day in adult hippopotami in Katavi NP.

Rolling and water splashing by juvenile hippopotami were mainly observed at mid-day and after mid-day and decreased during the evening as the heat receded (Fig. 8.17). Ear flicks were almost equally spread out over the day. As with adult hippopotami, yawning was mostly recorded in the morning and late afternoon.

Threats were mainly observed during the morning, mainly in the wet season. Isolated incidences of biting during this season were mostly during mid-morning (Fig. 8.17). Most of the sexual events observed during the wet season were between mid-morning and afternoon. During the dry season, they were much reduced in the morning. Yawning during the wet season was most frequent during the morning and late evening. In the dry season yawning was more frequent in the late afternoon (Fig. 8.17).

Few and scattered incidences of water splashing and rolling were spread throughout the day during the wet season but were concentrated in the middle of the day during the dry season (Fig. 8.17).

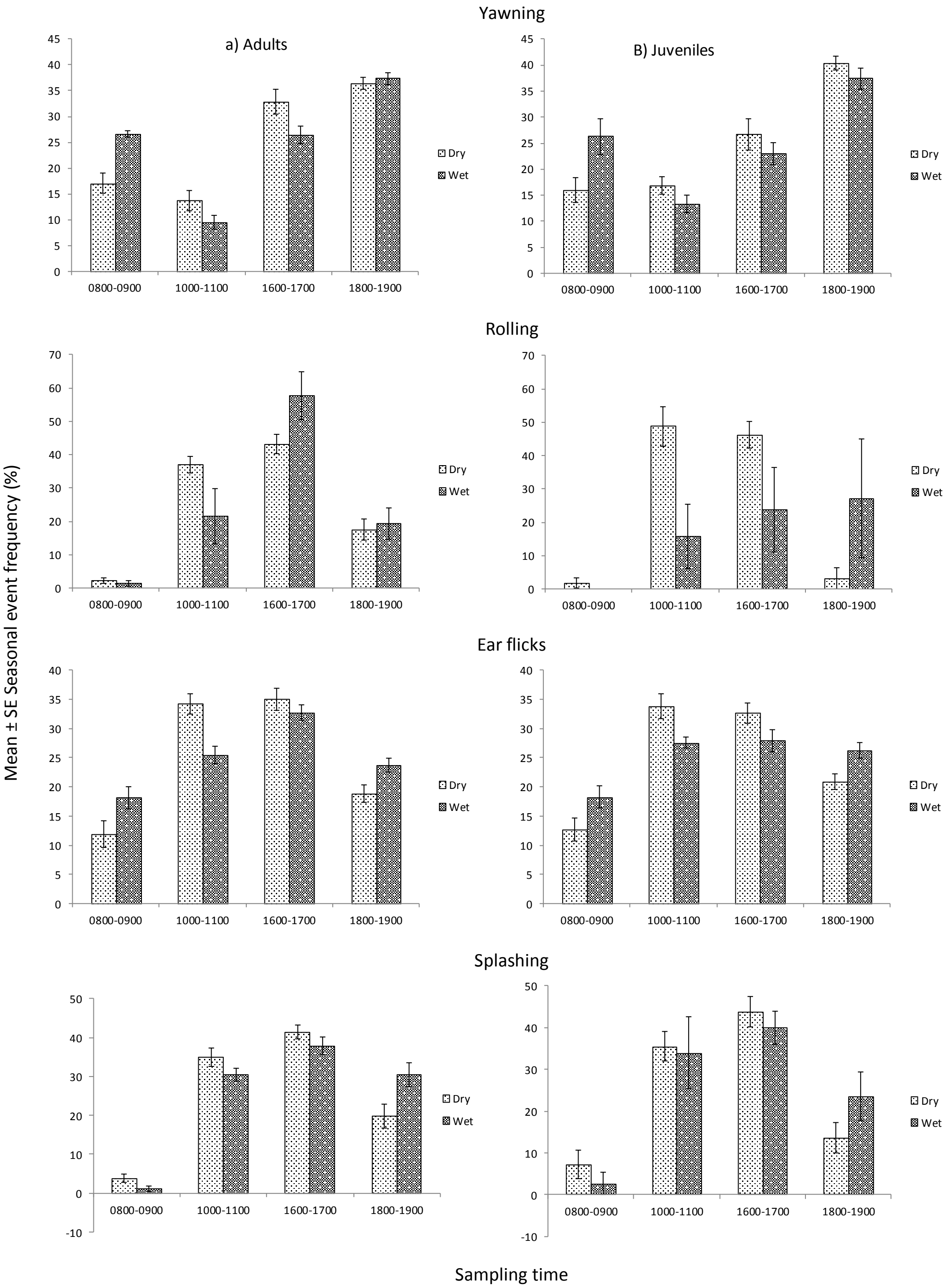


Fig.8.17: Mean seasonal variations in individual maintenance behavioural events between different times of the day in adult and juvenile hippopotami in Katavi NP, Tanzania. Error bars are ± SE around seasonal mean.

4. Discussion

4.1 Comparison of behavioural events between age classes

While resting, the commonest events were ear flicking and water splashing. Yawning was more frequent in the early morning when the animals were entering their resting sites and during the evening time when they were about to begin their feeding trips. Although exact functions of yawning are not clear, it is associated with body maintenance or social and agonistic displays.

Yawning was frequent event among both adult and juvenile hippopotami. This was more frequent when sites still had plenty of water. As water receded during the dry season less yawning were observed. The availability of water alone cannot be ruled as the factor for the occurrence because Paradise Springs with more water recorded the least, although Lake Katavi which had the highest also had more water than Lake Chada.

Yawning in vertebrates is the involuntary opening of mouth while taking a deep breath of air (Provine, 2005) as a result of fatigue or drowsiness. It is also a response to oxygen deprivation and is said to be unstoppable. It happens as a result of tiredness, stress, overwork, boredom or lack of stimulation. Yawning is also thought to help keep the brain cool. In humans and non-human primates, yawning has been found to be contagious (Norscia & Palagi, 2011; Miller *et al*., 2012). It is also frequent in humans and carnivores (Fureix *et al*., 2011). Socially contagious behaviours such as yawning are thought to occur in highly social vertebrates (Miller *et al*., 2012). Emotional contexts of yawning such as agonistic social interactions in primates, potential heat stress in budgerigars and general body stress are all triggers of yawning (Fureix *et al*., 2011). In animals such as baboon and guinea pigs; yawning serves as a warning signal. These triggers and functions of yawning may help to explain why most of yawning was observed during the morning and before the animals left for feeding trips.

Some events changed seasonally and were probably triggered by the changing seasons. Heat stress, for example, is linked to behavioural responses by dipping into water by hippopotami (Noirard *et al*., 2008). Social events are also affected as many hippopotami particularly males leave their dry season groups during the wet season for new resting sites (Olivier and Laurie, 1974; Blowers *et al*., 2008). Some events such as those related to sexual activity were found to be performed in watery conditions hence suggesting that without watery environments, such events may not be performed. Synchrony in birth among many ungulates is linked to resource availability, mainly food and water (Sinclair, 1974; Sinclair *et al*., 2000; Mduma *et al*., 1999; Sinclair, 2008a; Sinclair, 2008b). With such behavioural responses to resources, it is thought that they also played a part in the observed patterns in Katavi. Events were performed based on water availability as the seasons changed. More sexual events during the wet season might be a strategy for timing of such synchrony (Sinclair *et al*., 2000). Evidence of variations in events between seasons, months and sites indicate the central role of water to the behaviour of hippopotami.

4.2 Seasonal comparison in events

Hippopotami have a stable body core temperature of around 35.4 ± 0.7 ^{o}C (Luck and Wright, 1959; 1963; Cena, 1964; Noirard *et al*., 2008) and maintain their temperatures with no 24-hr or diurnal variations. Behavioural patterns are therefore thought to be adaptive response to thermoregulation constraints (Luck and Wright, 1963; Wright, 1964; Eltringham, 1999). They normally move into water for cooling (Eltringham, 1999) while basking when cold (Luck and Wright, 1963). In Lundi River, Gonarezhou NP in Zimbabwe, hippopotami were often seen basking during cold weather by displacing crocodiles from their sites (Kofron, 1993). It is likely that they cannot tolerate a very wider range of air temperatures. However, their thermal tolerance may be variable. In Niger, behavioural thermoregulation varied with seasons (Noirard *et al*., 2008) because air temperatures varied between 25-50^{o}C while water temperatures varied between 22 and 31^{o}C. Hippopotami bathed more frequently during the hot days when temperatures were higher in the dry season.

In a study of heat loss using infrared cameras, it was found that at ambient temperature of about 17 ^{o}C most of the hippopotami body parts were similar to air temperatures. At 21 ^{o}C thermal windows became visible (Schneider and Kolter, 2009). Thermal windows are brought about by local blood flows to the body surface for the purpose of cooling, at 28 ^{o}C numerous thermal windows fused. This suggests that temperatures well above 30 ^{o}C may be stressful for hippopotami. Schneider and Kolter (2009) further found that thermal windows in bigger males occurred more rapidly than in the younger males and females. This may indicate variation in thermal tolerance among individuals. In a study of the rate of evaporation from skin surface, Luck & Wright (1963) found that at air temperature between 32-39 ^{o}C live hippopotami lose water at between 9.1-16.4 mg. /5 cm^{2}/10 min. The rates for dead hippopotami were between 11.3-22.4 mg. /5 cm^{2}/10 min. It is therefore essential to dip into water to prevent further water loss. The thick oily pink fluid which acts as sweat and helps to keep their skin moist (Eltringham, 1999; Saikawa *et al*., 2004) might be among the factors which enable hippopotami to withstand variations in temperatures. Nevertheless, cooling by oily secretions is likely to be unsustainable over prolonged periods of drought without also cooling in water.

Although the animals may cool their bodies and brains by surface water evaporation, respiration and behavioural responses (Xue & Liu, 2011), larger animals, such as hippopotami experience more challenges in regulating their body temperatures. This might be one of the reasons for yawning as it is also thought to function as a way of cooling the brain (Provine, 2005). However, water for hippopotami remains the major and efficient mode for cooling.

In order to reduce exposure of their bodies to excesses heat, some hippopotami are adopting new strategies in behaviour such as using tree shade to avoid heat stress when air temperatures were high particularly during the dry season. This happened as in some localities where there was no water for cooling hence the hippopotami had to seek cover. It is thought that as the water scarcity increases further, animals in more sites may adopt this kind of behavioural responses. Behavioural responses for thermoregulation are effective (Noirard *et al*., 2008; Xue & Liu, 2011).

Hippopotami were also seen trying to ‘expand’ the wet parts in the shrinking shelters when they were drying up in order to lie on wetter parts. Use of feet and trunks to search for water from the soft river beds is increasing among elephants in Ruaha NP (Kashaigili *et al*., 2006; Epaphras *et al*., 2008). This is deviating from the ‘usual’ behaviours of depending on surface waters (Douglas-Hamilton, 1973). With increasing drought hippopotami might increase their water ‘searching’ ability.

There were significant variations in events between the wet and dry season. More threats, biting, rolling and water splashing were recorded during the dry season. During the wet season there were more sexual, ear flicks and yawning events. It can be argued that all of the events which were more prominent during the dry season were triggered by water reduction. Rolling is mainly thought to function as a way of cooling the back. It also may function as a way of scratching of the body.

Aggression was more frequent and intense during the dry season when resting habitat was more crowded. This is also the time when attacks on calves occurred and carcasses were observed. They all had wounds suggesting cause of death to be attacks or fighting. This supports the findings of Estes (1992) that aggressions during the dry season are common among hippopotami. Infanticide, aggression, taking over territories and change in dominance among hippopotami occurs mainly when water resources are scarce (Oliver and Laurie, 1974; Lewison, 1998). This is supported by the observed increase in aggressive behavioural events during the dry season in Katavi. As a strategy to water deficit in their resting sites, some hippopotami sheltered under tree cover when air temperatures were high and no water for cooling was available. This was different from the usual behavioural patterns where they enter water when air temperatures are high (Noirard *et al*., 2008). Resting under tree cover would have been in an effort to maintain body core temperatures at optimum. This is likely to have increased aggressiveness of some hippopotami as they struggled to use ‘suitable tree cover’ instead of the usual water site. This study was conducted during a year which can be considered as an average rainfall year. The situation is likely to be more severe during dry years.

Ear flicking among adults was more frequent during the wet than dry season. Among adults, more ear flicks were observed after the head of the animal emerged from water. Hence, it is thought it was for the purpose of getting rid of water from the ears. However, during the dry season, ear flicks were also more prominent and were probably to get rid of flies. This was because twitching of the ears was observed even when animals were lying immobile or asleep, suggesting that it was in response to flies. Ear flicks were therefore essential for different purposes during different seasons.

4.3 Comparison of events between months

Animals show differential aggressiveness towards kin and non kin members (Waldman, 1988). Aggressive interactions can limit population growth (Watson & Moss, 1970), and is reported as among the factors limiting red grouse density (Watson *et al*., 1994). In hippopotami aggressiveness towards their own calves is common (Chen *et al*., 2010). It was observed that hippopotami in the dry sites were more aggressive than those in the wetter sites which displayed more social behaviours.

More aggressive events (threats and biting) were observed during the dry than wet season. This was in September to November before rains started. Similarly, rolling and water splashing were mainly observed during the dry season months. These were observed when and where some water was still available between July and November. Threats and biting were mainly associated with declining water resources. These events happened during attempts to occupy suitable and better places in the shelter sites. While feeding in the nearby sites, aggressive events were recorded. Reduced water levels therefore appear to be the main cause of aggressions observed. Aggression decreased as water depth or water levels increased during the wet season months.

Sexual events were observed more during the wet season months. However, other events including social, yawning and ear flicking did not show as markedly a trend between sampling months as aggression and behaviour aimed at cooling (mainly rolling and splashing). Despite significant monthly variations in social, yawning, and ear flicking, their monthly trends were less abrupt compared with other events.

Threat and biting events in the wet season were mainly by adult towards others mostly initiated by adults probably females with young. Females with calves are highly defensive (Estes, 1992). In some instances, two individuals were involved in threats against a third one approaching when the ‘pair’ had a calf. However, most threats and biting were displayed when a ‘new’ hippopotamus approached a settled group or an individual hippopotamus. This was mostly to defend a place from intruding conspecifics. Different levels of aggression against unfamiliar conspecifics have been reported in pigs, *Sus scrofa* (Bolhuis *et al*., 2005). Hippopotami have a confrontational approach towards intruders. This mostly took place as the dry season approached and hippopotami attempted to regain the resting positions they left during the wet season.

4.4 Spatial comparison of events

More sociable or non-confrontational events were observed in sites with more water while more confrontational events occurred in sites with limited water supply or during the dry season. More threats and biting were recorded at Ikuu Springs. Ikuu Springs was mainly used as a dry season refuge and thus was mostly occupied by hippopotami during the dry season when water was limiting in other places. It is therefore possible that most of the threats and biting were due to scarcity of resting sites. Dominant animals seek to occupy the best space available. During the wet season, the site hosted very few hippopotami and hence there were fewer aggressive events due to limited contact between individuals.

Ikuu Springs was mostly occupied by adult hippopotami. It is most probable that the site harboured more males than females, assumed because there were very few juveniles at this site. Males occupy and protect territories. This is the reason for more aggressiveness at the site because dominant individuals were looking for the best space. This type of aggregation is reported to be due to lack social structure (Blowers *et al*., 2008). Ikuu Spring was most probably comprised of individual hippopotami aggregated in response to water resources and not due to their relatedness. Despite the importance of sex determination for ecological and behavioural studies (Beckwitt *et al*., 2002); it proved difficult to accurately determine sex in the field particularly in water and for grouped individuals.

Hippopotami being social animals have more attractions towards related individuals in kinship or familiar members of the herd (Blowers *et al*., 2008). This can explain why individuals at Ikuu Springs were seen to have a loose relations or attractions. Non dominant males have a tendency of loose attachment to the other members of the herd (Olivier and Laurie, 1974). This was probably the explanation for more aggression at this site. Hippopotami at sites such as Paradise Spring might be closely related because they are less migratory and with more juveniles, indicating close relations with their mothers. Familiarity between animal group members is thought to be responsible for minimizing aggression among them (Griffiths *et al*., 2004).

Lack of water may restrict some behaviour since there was variation of events between sites. While Ikuu Springs was the site with more threats and biting, the much wetter Paradise Spring was the site with the least aggressive events. Instead, Paradise Spring and Ikuu Bridge were the sites with most sexual events of all the sites. Paradise had more water throughout the year while at Ikuu Bridge, the sustained water pool created conducive microhabitat which lasted throughout the year.

More social events occurred at Lake Katavi and Paradise Spring sites than at the other sites. Fewest social events occurred at Ikuu Springs. This is despite the higher abundance of hippopotami at Ikuu Springs than at other sites. This is linked to water scarcity in that animals occupied Ikuu Springs only as a refuge, hence limiting some behaviour that are performed under normal conditions.

There was more rolling and water splashing at Paradise than at other study sites. Least rolling occurred at Ikuu Bridge and Lake Katavi while least water splashing was observed at Ikuu Spring and Lake Katavi. Both rolling and water splashing were observed for the purpose of cooling the backs of animals when water was insufficient to immerse the whole body. This represents a behavioural strategy for thermoregulation.

Similar observations were recorded for tail paddling for splashing water over the backs of animals. At other sites such as Ikuu Springs, lack of water or soft mud led to hippopotami failing to paddle their tails when water levels were very low and animals crowded. At Paradise, despite decline in water levels, there was more water and space compared with other sites. This led to the observed differences. Water was the main limiting factor for some of the events to be performed.

4.5 Comparison of events between times of the day

Some behavioural events varied between times of the day for both adult and juvenile hippopotami. More threats and biting were observed during the morning time. This was the time when animals were re-arranging themselves before resting after return from feeding trips. Occupation of a suitable space was a major driving force for threats and biting as water resources receded.

Although isolated incidences of threats and biting were observed among juvenile hippopotami, they were not fierce but rather directed towards their age mates. It was likely to have been practice or social play possibly mimicking adults. These did not seem to inflict injury or any serious impact to the pair involved. At some times, it was seen as a form of defense against aggressive adults.

5. Conclusions and recommendations

Aggression was highest at the end of dry season, during the driest time of the year and more at drier sites. Social and sexual events were frequent between September and

February. Yawning and ear flicks peaked at the end of wet season when maintenance was at minimum.

There were variations in events within and between study sites which were mainly due to availability of water resources. More aggression was recorded during the dry season and in sites with less water. There is a need to monitor hippopotami distribution and abundance in more sites particularly in relation to water resources. This is because prolonged water scarcity may cause conflicts with human as are likely to migrate into crop fields or settlement.

Stress on hippopotamus populations by water shortage is likely to increase over the years because of competition for water outside the park. More and prolonged stress on hippopotami is likely to affect them through physiological constraints. Sexual events which are linked to population growth are likely to be highly affected in prolonged drought. This in turn will affect population growth.

More aggression brought about by water scarcity is likely to interfere with the usual behaviour of hippopotami. Increased aggression is likely to cause more stress among the animals.

Water plays a central role in behaviour among hippopotami. Variation in availability of water resources is likely to affect the hippopotami event patterns. Events linked with thermoregulation such as rolling and water splashing cost energy and hence increase stress for the hippopotami when shelters cannot provide space for rolling and splashing. This will increase heat stress and hence physiological interferences.

Water remains the major driving force in most of hippopotami behaviours. Variation in the availability of water at their resting sites is likely to have a significant effect on hippopotami behaviour as partly observed during this study.

Chapter 8: Relationships between hippopotami, food and water resources

1. Introduction

Hippopotamus are under pressure from habitat degradation and hunting (Lewison, 2007; Lewison & Oliver, 2008; Kendall, 2011). The way in which they can adjust their behaviours contributes to their survival and reproduction (McFarland, 2006), and is important.

The ecology and behaviour of hippopotami respond to environmental variables, particularly food and water resources. Hippopotami live in habitats that are prone to human and natural impacts. Impacts are likely to change the way hippopotami respond at different sites. Anthropogenic and environmental factors have been reported to affect hippopotami abundance and behaviour in various ways. Anthropogenic factors such has hunting have been reported to cause hippopotami to avoid suitable habitats in the Okavango Delta, Botswana (McCarthy *et al*., 1998), and increase their aggressiveness (Patterson, 1976). Hunting has also been reported to make mammals more prone to disturbance (Caro, 1999b).

The major determinant of suitability of habitat is its quality. Habitat quality has been defined as the ability to provide conditions appropriate for individual or population persistence (Hall *et al*., 1997). Hippopotami respond to the resource availability in their environment. Resources are all things used by an organism (Tillman, 1982). These include food, water, cover, space and mates (Fulbright & Alfonso Ortega-S, 2006).

During dry seasons, grazing for ruminants becomes less available, with reduced biomass and of low quality (Manteca & Smith, 1994). Among adaptations to these changes are behavioral responses such as increasing feeding time and wider dispersion (Manteca & Smith, 1994). Food is the major limiting factor for hippopotami after water (Harrison *et al*., 2007). In habitats where hippopotami are found, poor availability of daytime sheltering space during the dry season can regulate their abundance (Olivier & Laurie, 1974; Tembo, 1987; Harrison *et al*., 2007).

Apart from restricted food resources, water scarcity and higher temperatures occur during the dry season (Manteca & Smith, 1994) and are likely to influence hippopotami distribution, abundance and behaviour.

The hippopotamus is the most water dependent mammal in Katavi, and is the most likely species to be affected by extreme water conditions (Lewison, 1998). Large body size and a tendency for large aggregations in turn may have an effect on water conditions.

This Chapter is about the relationships between abundance and behaviour of hippopotami and environmental impacts mainly food and water resources. Among anthropogenic impacts in tropical regions, habitat loss and disturbance have been reported as detrimental to biodiversity (Maclean *et al*., 2006). Impacts include harvesting of forest or woody products, burning and habitat fragmentation. Near Katavi, harvesting mainly for timber products and fragmentation through agriculture and settlement occurs adjacent to the Park, while burning occurs both within and around the park. Consequences to hippopotami have been reduced duration of river flow and water levels leading to earlier drying of water sources in the Park. These are discussed in Chapter 3 of this study and have also been reported by Lewison (1996; 1998), Meyer *et al*. (2005), Caro *et al*. (2011).

Water is among the key resources for hippopotami (Harrison *et al*., 2007). Seasonal variations in water levels within tropical swamps are a common feature (Boar, 2006). Variations in water flow regimes lead to variations in vegetation regimes particularly with respect to availability, quantity and nutritional quality.

Variations in resource availability affect animals and hence their activity patterns (Manteca & Smith, 1994). Distance travelled to and from the feeding grounds influences foraging behaviour including selectivity and intake (Lewison & Carter, 2004). This study was aimed at understanding how spatial and temporal variations in abundance of hippopotami respond to water and vegetation in the Park through immigration and emigration. It was also aimed at studying whether and how these variations in resources affect behavioural traits.

1.1 Aims and hypotheses

This was aimed at understanding how water regimes impact on hippopotami in Katavi. Emphasis was on the following aspects:

- Temporal and spatial changes in abundance in relation to changes in water and food resources
- Spatial and temporal changes in immigration and emigration
- Seasonal and spatial variations in aggregation
- Seasonal changes in behaviour traits in relations to resources.

The study therefore tested the following hypotheses

H_1: Hippopotami abundance is linked to water quantity and vegetation resources.

H_2: The extent to which hippopotami aggregate is related to seasonal variations in water quantity and vegetation resources.

H_3: Rates of immigration and emigration of hippopotami are related to seasonal variations in water quantity and vegetation resources.

H_4: Behavioral traits of hippopotami are linked to seasonal variations in water quantity and vegetation resources.

2. Methods

2.1 Study sites

The same five sites used for behaviour and abundance observations are used here. These are described in Chapters 5, 6 and 7. Water and vegetation data were obtained from studies reported in Chapter 3 and 4. The study sites are described in Chapter 2.

2.2 Data recording

Data recording and recording methods (sampling and recording rules) were conducted as described in Chapters 5, 6 and 7 on behaviour traits following rules according to Lehner (1996) and Martin and Bateson (2007). Abundance and water quantity was recorded from May 2009-September 2010, a total of 17 (n=17) sampling months.

2.3 Data analysis

Data used for analysis and correlating hippopotami and environmental variables are described in Chapters 3, 4, 5, 6 and 7.

Correlations and analyses of variance (ANOVA) were performed using the SPSS statistics package software (PASW Statistics 18) by IBM.

3. Results

3.1 Abundance and density

There were no significant correlations between either adult or juvenile hippopotami abundance and rainfall in all study sites.

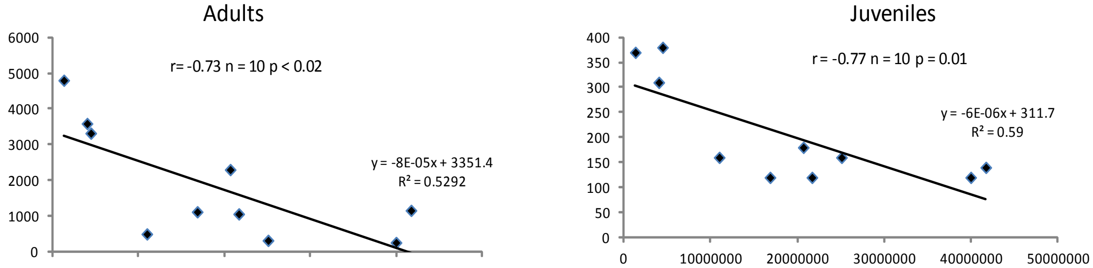
Total monthly river discharge was inversely correlated with adult hippopotami density at Lake Katavi and Ikuu Springs (Table 9.1, Fig. 9.3(a)), and juvenile hippopotami density correlated inversely with river discharge at Ikuu Bridge, Lake Chada and Lake Katavi sites (Table 9.1, Fig. 9.3(b)).

Table 9.1: Summary of Pearson correlations between water variables and hippopotami density in the five study sites in Katavi NP, Tanzania

Site name	Water variable	Adults			Juveniles		
R-discharge		**(r)**	**(n)**	**Probability**	**(r)**	**(n)**	**Probability**
Ikuu Bridge		-0.59	10	*NS*	-0.70	10	0.05
Lake Chada		-0.57	10	*NS*	-0.77	10	0.01
Lake Katavi		-0.7	10	0.05	-0.65	10	0.05
Paradise Springs		-0.52	10	*NS*	-0.17	10	*NS*
Ikuu Springs		-0.73	10	0.02	-0.39	10	*NS*
River depth							
Ikuu Bridge		-0.44	17	*NS*	-0.38	17	*NS*
Lake Chada		-0.39	17	*NS*	-0.52	17	0.05
Lake Katavi		-0.58	17	0.02	-0.56	17	0.02
Paradise Springs		-0.27	17	*NS*	0.2	17	*NS*
Ikuu Springs		-0.72	17	0.01	-0.72	17	0.01
Swamp extent							
Ikuu Bridge		-0.47	17	*NS*	-0.51	17	0.05
Lake Chada		-0.59	17	0.02	-0.73	17	0.001
Lake Katavi		-0.65	17	0.01	-0.65	17	0.01
Paradise Springs		-0.56	14	0.02	-0.50	14	0.05
Ikuu Springs		-0.75	17	0.001	-0.67	17	0.01
U-Water table							
Ikuu Bridge		-0.83	11	0.01	-0.81	11	0.01
Lake Chada		-0.80	11	0.01	-0.92	11	0.001
Lake Katavi		-0.76	11	0.01	-0.79	11	0.01
Paradise Springs		-0.39	11	*NS*	0.37	11	*NS*
Ikuu Springs		-0.76	11	0.01	-0.83	11	0.01

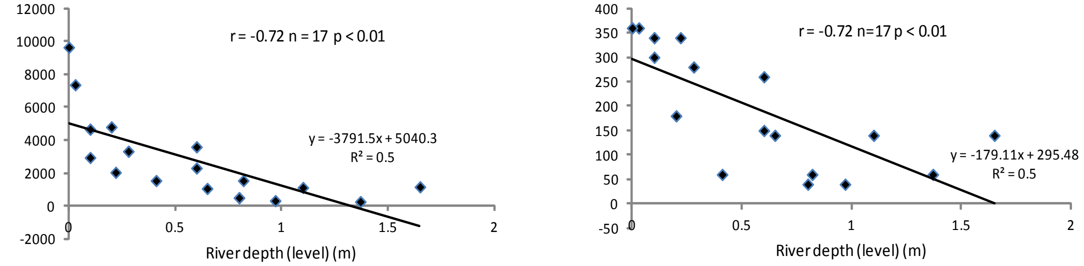
Key: Only significant probability values are shown at a site.

R-discharge= River discharge and U-Water table = Underground water table.



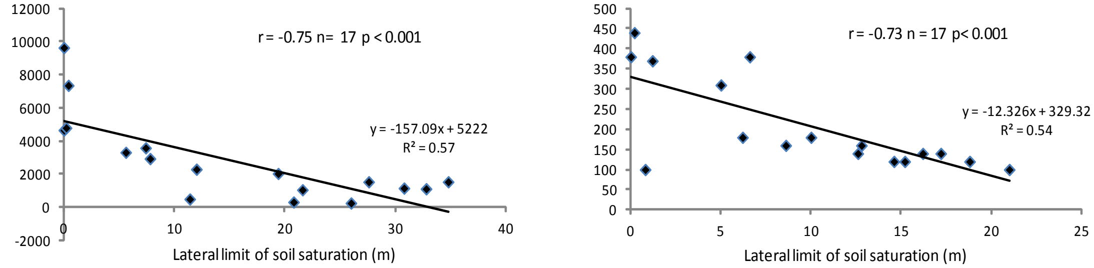
a: Correlation between adult hippopotami density and river discharge at Ikuu Springs site, Katavi NP, Tanzania

b: Correlation between juvenile hippopotami density and river discharge at Lake Chada site, Katavi NP, Tanzania



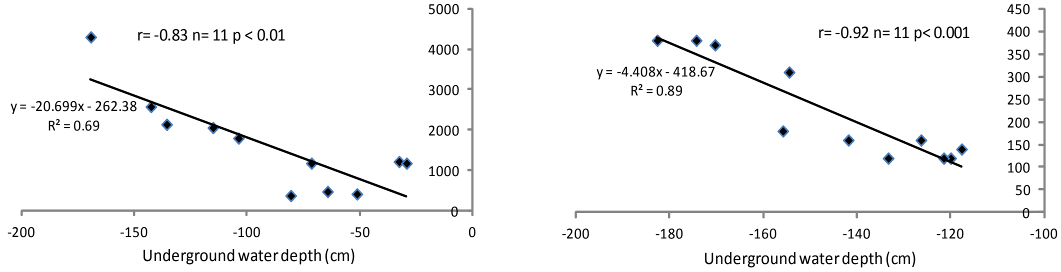
c: Correlation between adult hippopotami density and river depth at Ikuu Springs site, Katavi NP, Tanzania

d: Correlation between juvenile hippopotami density and river depth at Ikuu Springs site, Katavi NP, Tanzania



e: Correlation between adult hippopotami density and swamp extent at Ikuu Springs site, Katavi NP, Tanzania

f: Correlation between juvenile hippopotami density and swamp extent at Lake Chada site, Katavi NP, Tanzania



g: Correlation between underground water depth and adult hippopotami density at Ikuu River site, Katavi NP, Tanzania

h: Correlation between underground water depth and juvenile hippopotami density at Lake Chada site, Katavi NP, Tanzania

Fig. 9.3: Correlations between water variables and hippopotami density (May 2009-September 2010) at selected study sites in Katavi NP, Tanzania.

Note: Values in both x and y axes are different due to variations between measurements and between age group.

Adult hippopotami density correlated inversely with river depth only at Lake Katavi and Ikuu Springs, density decreased with river depth (Table 1; Fig. 9.3c and Fig. 9.4). At a river depth of about 1.5 m, abundance was at its lowest. Density among juvenile hippopotami correlated inversely with river depth at Lake Chada, Lake Katavi and Ikuu Springs (Table 9.1; Fig. 9.3d and Fig. 9.5).

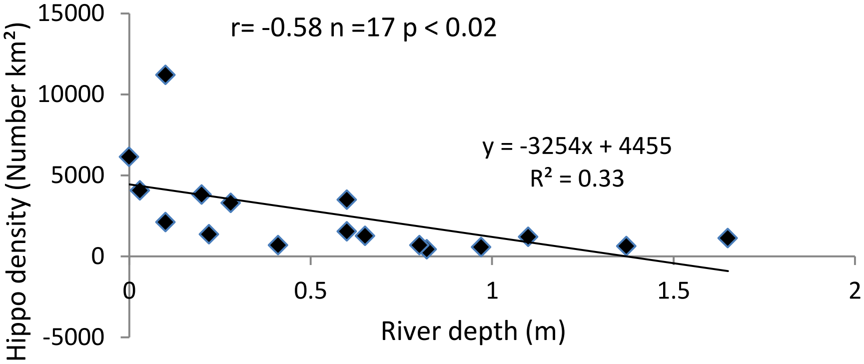


Fig. 9.4: River level and adult hippopotami density correlations at Lake Katavi in Katavi NP, Tanzania. n=number of sampling months

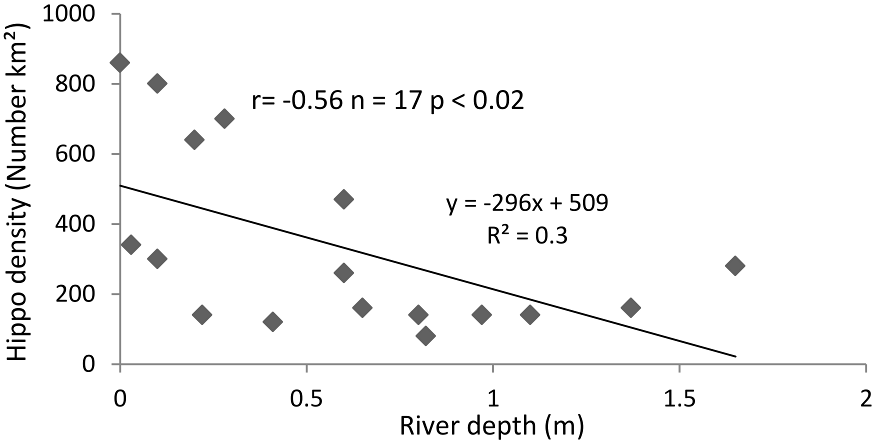


Fig. 9.5: River levels and juvenile hippopotami density correlations at Lake Katavi in Katavi NP, Tanzania

Adult hippopotami density correlated inversely with swamp extent (which is the lateral limit of soil saturation) at Lake Chada, Lake Katavi, Paradise Springs and Ikuu Springs. Ikuu Bridge was the only site where adult density did not correlate with swamp extent (Table 9.1, Fig. 9.3(e)). Density of juvenile hippopotami correlated with the areal extent of swamp at all the five study sites (Table 9.1, Fig. 9.3(f)).

Hippopotami density correlated with underground water depth at 80% of the study sites. With exception of Paradise Springs, both adult and juvenile hippopotami density correlated inversely with depth of underground water table (Table 9.1, Fig. 9.3g and Fig. 9.3h). Rise in water depth coincided with decreasing hippopotami density at the site and *vice versa*.

When individual sites results were pooled together to obtain overall Katavi results, there were significant correlations between adult and juvenile hippopotami and density with water quantity variables (Table 9.2). Quantity of water in the study sites estimated through river discharge, river depth, extent of swamps and underground water depth correlated with both adult and juvenile hippopotami density (Table 9.2). Increase in water quantity at the study sites was followed by decrease in hippopotami density at the site. The only exception was at Paradise Springs where only swamp extent correlated with density and hence density did not change between the dry and wet seasons.

Table 9.2: Correlations between hippopotami densities with water variables

	Adults			**Juveniles**		
Water variable	**R-value**	**n-value**	**P-value**	**R-value**	**n-value**	**P-value**
River discharge	-0.73	10	0.02	-0.77	10	0.01
River depth (levels)	-0.72	17	0.01	-0.72	17	0.01
Swamp extent (Lateral limit)	-0.75	17	0.001	-0.73	17	0.001
Underground water depth	-0.83	11	0.01	-0.92	11	0.001

3.2 Aggregation

There were inverse correlations between rainfall and mean inter-individual distances or aggregation in hippopotami at Paradise Springs (Fig. 9.6). Mean inter individual distances decreased as rainfall increased. However, there were no such correlations at the other four sites. At Paradise Springs, aggregations correlated with both the current month's rainfall, the previous month's rainfall and even when the two months rainfall were combined (r = -0.74, r = -0.75 and r = -0.85 respectively with n =17 and $p < 0.001$). This was not the case for the other four sites.

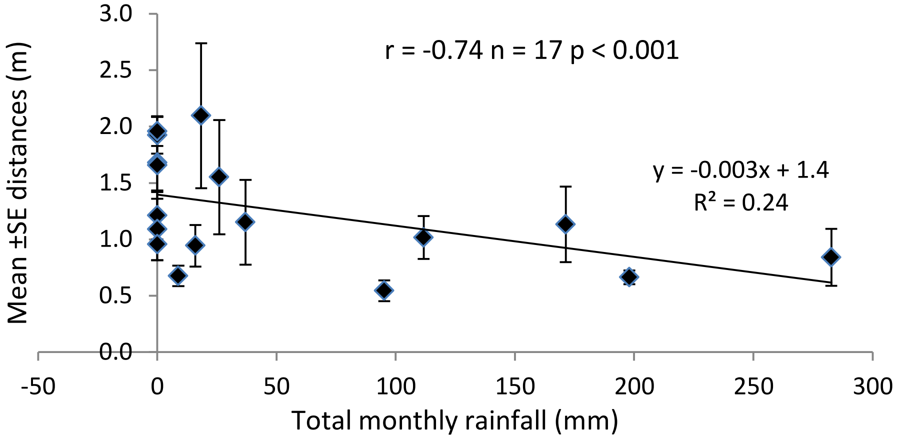


Fig. 9.6: Correlation between rainfall and mean inter-individual distances (aggregation) among hippopotami at Paradise Springs, Katavi NP, Tanzania

Aggregation did not correlate with river discharge at any of the study sites. However, there were correlations between river depth and aggregation at Ikuu Bridge (r = 0.54 n = 17 $p < 0.05$) and Ikuu Springs (r = 0.63 n = 17 $p < 0.01$) (Fig. 9.7 and Fig. 9.8). No correlations were observed between river depth and hippopotami aggregation at the other three sites.

The extent of swamps and underground water depth did not show any correlations with hippopotami aggregation at any of the five study sites.

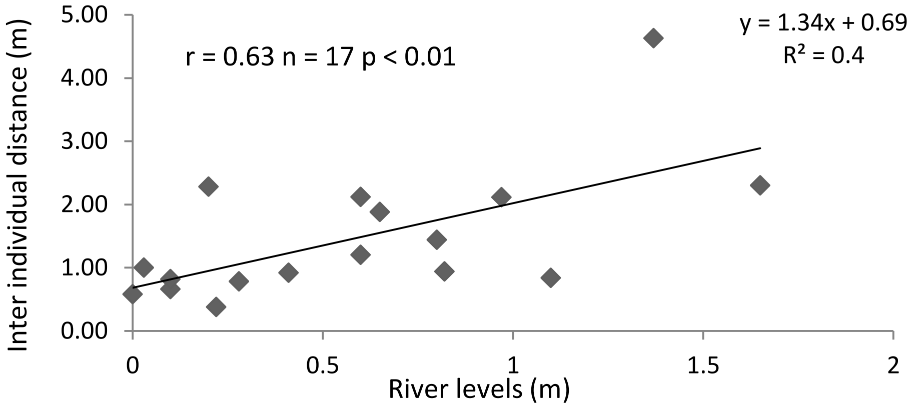


Fig. 9.7: Correlations between river levels and hippopotami aggregation at Ikuu Springs in Katavi NP, Tanzania

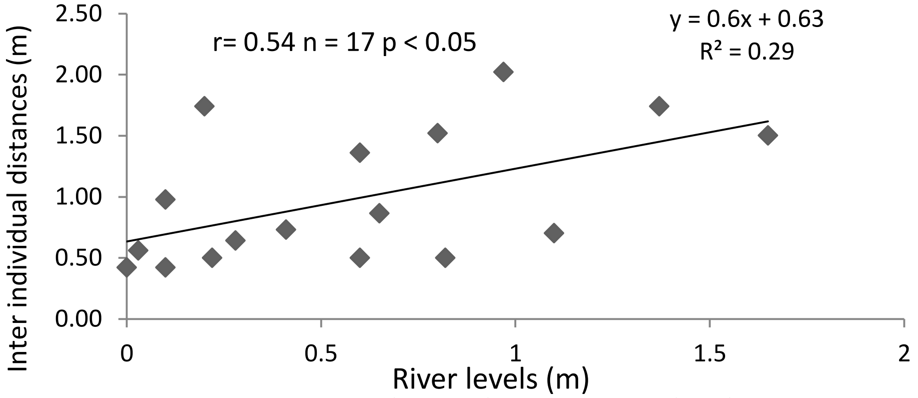


Fig. 9.8: Correlations between river levels and hippopotami aggregations at Ikuu Bridge in Katavi NP, Tanzania

3.3 Immigration and emigration

There were no correlations between rates of immigration and emigration and rainfall in Katavi for both adults and juveniles at any of the five sites.

There were no correlations between hippopotami immigration and emigration and river discharge, river depth or underground water depth at any of the five sites for either adult or juvenile hippopotami.

Immigration and emigration of adult hippopotami at Ikuu Bridge correlated inversely with changes in the extent of swamps ($r = -0.52$ $n = 17$ $p < 0.05$). Immigration and emigration at the other four sites did not show any significant correlations. Similarly, juvenile hippopotami at Ikuu Bridge were the only ones where immigration and emigration correlated with seasonal variations in the size of swamps ($r = 0.53$ $n= 17$ $p < 0.05$). The rest of the sites did not show any correlations.

3.4 Behavioural traits correlations

Resting by adults at Lake Katavi ($r = 0.70$ $n = 13$ $p < 0.01$), adult touching at Ikuu Springs ($r = -0.57$ $n = 13$ $p < 0.05$) and adult feeding at Ikuu Springs ($r = 0.64$ $n = 13$ $p = 0.02$) correlated significantly with rainfall using current and previous month's rainfall combined.

Juvenile touching at Lake Chada ($r = -0.73$ $n = 13$ $p = 0.01$) and Ikuu Bridge ($r = 0.56$ $n = 13$ $p < 0.05$) and resting at Lake Katavi ($r = 0.93$ $n =13$ $p = 0.001$) correlated significantly with rainfall using current and previous month's rainfall combined.

Changes in underground water depth, river depth and size of swamps were the only variations in water quantity that had significant effects on hippopotami behaviour at the study sites. River discharge had limited impacts on walking, feeding, standing and resting at some study sites.

Walking, feeding, standing, resting and touching by adults correlated with underground water depth in the study sites (Table 9.3). Walking, standing and resting by juveniles correlated with underground water depth at Paradise Springs and Lake Katavi (Table 9.3).

Table 9.3: Pearson correlation between underground water levels and behavioural activities among adult and juvenile hippopotami September 2009- September 2010 in Katavi NP, Tanzania

		Adults			Juveniles		
Behavioural activity	**Study site**	r	n	p	r	n	p
Walking	Ikuu River	-0.67	11	0.05			
Walking	Paradise Spings	-0.75	10	0.02	-0.76	10	0.02
Feeding	Ikuu River	0.88	11	0.001			
Standing	Paradise Spings	-0.81	10	0.01	-0.79	10	0.01
Resting	Lake Katavi	0.94	11	0.001	0.73	11	0.02
Resting	Paradise Spings	0.95	10	0.001	0.76	10	0.02
Touching	Ikuu River	-0.7	11	0.02			
Touching	Lake Chada	-0.65	11	0.02			
Touching	Lake Katavi	-0.76	11	0.01			
Touching	Paradise Spings	0.67	10	0.05			

River water depth was the other water quantity parameter that had significant impact and correlated with behaviour traits in the study sites. Walking, feeding, standing, resting and touching by adult hippopotami correlated with water depth (Table 9.4). Walking, feeding and standing among juveniles correlated with river depth.

Table 9.4: Pearson correlation between river water depth and behavioural activities among adult and juvenile hippopotami September 2009- September 2010 in Katavi NP, Tanzania

		Adults			Juveniles		
Behavioural activity	**Study site**	r	n	p	r	n	p
Walking	Ikuu River	-0.73	13	0.01			
Walking	Lake Katavi	-0.68	13	0.01			
Walking	Paradise Springs	-0.71	10	0.05	-0.71	10	0.05
Walking	Ikuu Springs	-0.55	13	0.05			
Feeding	Ikuu River	0.79	13	0.01	0.62	13	0.05
Feeding	Ikuu Springs	0.72	13	0.01			
Feeding	Paradise Springs				0.62	10	0.05
Standing	Lake Katavi	-0.62	13	0.05	-0.65	13	0.02
Resting	Lake Katavi	0.63	13	0.02			
Touching	Ikuu River	-0.71	13	0.01			
Touching	Lake Chada	-0.67	13	0.02			
Touching	Lake Katavi	-0.6	13	0.05			

The size of swamp correlated with walking, feeding, standing, resting and touching among adult hippopotami at some sites (Table 9.5). Feeding, standing, resting and touching among juveniles correlated with swamp extent at Paradise, Lake Katavi and Lake Chada.

Table 9.5: Pearson correlation between extent of swamp and behavioural activities among adult and juvenile hippopotami September 2009- September 2010 in Katavi NP, Tanzania

		Adults			**Juveniles**		
Behavioural activity	**Study site**	r	n	p	r	n	p
Walking	Ikuu River	-0.73	13	0.01			
Walking	Lake Katavi	-0.63	13	0.02			
Feeding	Ikuu River	0.64	13	0.02			
Feeding	Ikuu Springs	0.69	13	0.01			
Feeding	Paradise Springs				0.69	10	0.05
Standing	Lake Chada	-0.59	13	0.05			
Standing	Lake Katavi	-0.64	13	0.02	-0.69	13	0.01
Resting	Paradise Springs	0.78	10	0.01	0.7	10	0.01
Touching	Ikuu River	-0.72	13	0.01			
Touching	Lake Chada	-0.71	13	0.01	-0.55	13	0.05
Touching	Lake Katavi	-0.58	13	0.05			

River discharge correlated with walking, feeding, standing and resting by adults at four sites (Table 9.6). There were no correlation between river discharge and juvenile behavioural traits.

Table 9.6: Pearson correlation between river water discharge and behavioural activities among adult hippopotami September 2009- September 2010 in Katavi NP, Tanzania

		Adults		
Behavioural activity	**Study site**	r	n	p
Walking	Ikuu River	-0.77	10	0.01
Feeding	Ikuu Springs	-0.68	10	0.05
Standing	Lake Katavi	-0.64	10	0.05
Resting	Lake Chada	-0.81	10	0.01

3.5 Correlations between hippopotami and vegetation variables

There were significant inverse correlations between adult and juvenile hippopotami density and vegetation variables (sward height, greenness and cover) as summarised in Table 9.7. However, hippopotami density did not vary with seasonal variations in plant mass (biomass and standing dead mass).

Table 9.7: Pearson correlations between hippopotami density and vegetation variables

	Adults			Juveniles		
Vegetation variable	**R-value**	**n-value**	**P-value**	**R-value**	**n-value**	**P-value**
Vegetation sward height	-0.521	57	0.0001	-0.539	57	0.0001
Vegetation greenness	-0.517	57	0.0001	-0.564	57	0.0001
Vegetation cover	-0.504	57	0.0001	-0.544	57	0.0001
Sampling months	-0.381	57	0.003	****	*57*	*NS*

Key: **= Not significant

There were significant inverse correlations between adult and juvenile hippopotami immigration and emigration with vegetation variables, sward height, greenness and cover as summarised in Table 9.8. There were no correlations between hippopotami immigration and emigration with plant mass per unit area.

Table 9.8: Pearson correlations between vegetation variables and combined adult and juvenile hippopotami immigration rates in Katavi NP, Tanzania

	Adults			Juveniles		
Vegetation variable	**R-value**	**n-value**	**P-value**	**R-value**	**n-value**	**P-value**
Vegetation sward height	-0.395	57	0.002	-0.413	57	0.001
Vegetation greenness	-0.487	57	0.0001	-0.543	57	0.0001
Vegetation cover	-0.45	57	0.0001	-0.513	57	0.0001

There were no correlations between vegetation variables and hippopotami aggregation. Also, aggregation did not vary with seasonal variations in plant mass.

There were no correlations between adult hippopotami feeding and any vegetation variables. However, feeding in juvenile hippopotami correlated with vegetation variables as summarised in Table 9.9. Feeding in adult and juvenile hippopotami varied between study sites ($F_{4, 56} = 7.245$, $p < 0.0001$ and $F_{4, 56} = 5.065$, $p < 0.002$ respectively).

Table 9.9: Correlations between vegetation variables and juvenile hippopotami feeding activities

	Juveniles		
Vegetation variable	**R-value**	**n-value**	**P-value**
Vegetation sward height	0.289	57	0.03
Vegetation greenness	0.315	57	0.02
Vegetation cover	0.302	57	0.02

4. Discussion

4.1 Abundance and density

Forage availability for herbivores varies over time (Mduma *et al*., 1999; Fryxell *et al*., 2005) and space (Fryxell *et al*., 2005). Spatial variations in forage quality and quantity is due to varying abiotic factors such as rainfall, elevation or altitude, slope, soils and soil nutrients (Drescher *et al*., 2006) and biotic factors, such as interactions with other plants and animals (McNaughton *et al*., 1997; Drescher *et al*., 2006).Due to variations in abundance, nutritive value and distribution of forage, grazing animals have to decide on how to obtain adequate forage to meet their demands (Griffiths & Gordon, 2003), including where and how to facilitate rates of food intake.

Fire is another factor causing variations in forage quality and quantity, structure, composition and distribution in the savannah (Stander *et al*., 1993; Parr & Chown, 2003). The effects of it is yet to be fully explored (Smith *et al*., 2005; Hassan *et al*., 2007). In the Serengeti NP, fire is used to improve forage quality for large herbivores (Hassan *et al*., 2007). It is also used to prevent accidental hot fires during the dry season. Similar practice is in place in Katavi. It temporarily affects food availability while facilitating the emergence of new green shoots which become available to the grazers. It helps to replace the ageing forage by newer quality forage. However, other studies propose that fire does not have major effects on properties of grassland except slight stimulation of productivity (McNaughton, 1985).

Resource concentration is often regarded as the best predictor of population density in animals (Connor *et al*., 2000) as summarised in the resource concentration hypothesis (Root, 1973). Hippopotami as with other organisms live in the environment in which various resources are likely to influence them. The amount of day living space and productivity of food plants have been reported as among the most essential factors (Olivier and Laurie, 1974). The two are reported as essential in hippopotami habitat utilization and may limit population increase.

Day living space or sheltering sites are mainly associated with provision of water for hippopotami. Water and vegetation are therefore the major environmental resources likely to affect hippopotami in their environment.

Water availability to wild animals in Tanzania has been left for nature to determine except for human intervention in river discharge (Epaphras *et al*., 2008). Due to this, water available from the underground water table and on the river bed plus surface water is crucial to the survival of animals, particularly hippopotami during the dry season. This can determine their abundance, movements and distribution and in the driest sites, appears to have done this in Katavi National Park.

In the Serengeti, variations in grazing animal density and abundance correlated with grassland productivity rather than rainfall (McNaughton, 1985). This might also be the reason why there were no correlations between rainfall and hippopotami density and seasonal movements. The effect of rainfall rather than rainfall itself is responsible for the seasonal animal movements in and out of resting sites in Katavi. In the Serengeti study (McNaughton, 1985), rainfall triggered green forage hence grassland productivity and hence grazing animal density and abundance.

Lake Katavi which was located in riverine swamp and connected to the river by several channels and Ikuu Springs, also next to the river, showed some correlations with river discharge. This was possibly due to the rapid spillover effects of water discharged from the river which attracted hippopotami movement in and out of their sites, hence affecting abundance. The two sites harboured many hippopotami during the dry season.

On the other hand, at Ikuu Bridge, river discharge did not have an impact on hippopotami density. This was mainly due to an artificial water pool that retained water and later in the dry season became a muddy pool. The pool retained about the same number of hippopotami as in the wet season. Direct impacts of river discharge during the rainy season therefore did not significantly alter hippopotami density, but instead, local impacts related to site topography had an overriding effect. Some river discharge events lasted only for a few days but swamps retained water for much longer. River depth, size of swamp and underground water depth were more sustained and their impacts were felt by the rising depth of water at the hippopotami resting sites.

Paradise Springs was somewhat different to the rest of the sites because its dual sources of water were more perennial and the site therefore had more water than the other four sites. The impact of rise and decline in underground water was less obvious in the hippopotami at the site.

There were inverse correlations between vegetation sward height and hippopotami density. Increase in hippopotami density was associated with decrease in sward height. This was in agreement with earlier observations that hippopotami select patches with shorter swards (McCarthy *et al*., 1998; Harrison *et al*., 2007). However, this is not necessarily a cause and effect relationship. Increase in sward height which in turn corresponded with increase in greenness and cover, had similar inverse correlations with density. Therefore, the two had similar effects to the abundance as sward height.

Nevertheless, hippopotami density and abundance did not vary with seasonal variations in plant mass per unit area. This was contrary to observations by Chansa *et al*. (2011b), who reported that hippopotami responded to the foraging or grazing intensity in the river or surrounding grassland in Luangwa River in Zambia. However, it might have been due to response to the sward height.

Hippopotami select short grass with the height of about 15 cm (Lock, 1972; Olivier and Laurie, 1974, Harrison *et al*., 2007). This means that variations in sward height are likely to affect their distribution and abundance. Availability of nearby feeding grounds is crucial because hippopotami travel only short distances from water to feeding grounds (O’Connor & Campbell, 1986; Viljoen & Biggs, 1998). Chansa *et al*. (2011b) reported hippopotami travelling up to five kilometers in search for food.

In order to estimate preferred foraging sward height, Lock (1972) during examination of hippopotami tracks found that they graze in areas of short grass less than 15 cm. This led to the suggestion that this sward height might be optimal as their canine and incisors are not designed for grazing. Their teeth are simple, blunt, cusped and bunodont hence are incapable of chopping and grinding as effectively as other grazers (Spinage, 2012). Instead, hippopotami use their sharp edged, horny lips to grasp the grass and pull it off by jerking the head (Lock, 1972; Spinage, 2012). Pulling attempts often results in uprooting loosely rooted grass. However, it is not explained in Lock (1972) how sward height was measured. Also, sward height estimation was made based on the area where hippopotami tracks ended, but did not actually measure them foraging at 15 cm. Harrison *et al*. (2007) in Liwonde NP in Malawi used visual estimation to record sward height. Study by Lock (1972) formed the basis for the optimal sward height of 15 cm being referred to by several authors (McCarthy *et al*., 1998; Harrison *et al.,* 2007; Spinage, 2012). The present study used the standardized method of sward stick. Use of different methods for estimating sward height might be a source of variation. In measuring sward height using sward stick, several factors may influence results. These include height, density and strength of the stem. Sward structure may vary in terms of sward chemistry, architecture and species composition (Drescher *et al*., 2006). During the present study in Katavi, variations in forage species between study sites were relatively small as represented by a number of species for each site.

Although 15 cm has been reported as optimal foraging sward height for hippopotami, in Liwonde NP in Malawi, feeding by hippopotami was also recorded in the sward between 15 and 50 cm although grazing intensity was lower when compared with that of sward height around 15 cm (Harrison *et al*., 2007). In Katavi, actual feeding and signs were recorded in the sward height of up to 30 cm at foraging and shelter sites. In Malawi, grazing intensity decreased as distance increased from the river, being higher near the river (Harrison *et al*., 2007). This tends to agree with the central place foraging theory for hippopotami (Lewison and Carter, 2004) which is the special case of the marginal value theorem (Charnov, 1976) in which distance from the river influenced hippopotami foraging decisions of the energetically most effective feeding site. As per optimal foraging theory (Pyke *et al*., 1977; Allaby, 2004), animals tend to maximize intake of forage per unit time especially for hippopotami which faces temporal constraints in their feeding. Equally, the theory proposes that foraging decisions are influenced by physical and environmental constraints which are food intake or availability constraints and digestibility or processing constraint (Fryxell, 1991; Wilmshurst *et al*., 1994; Bergman *et al*., 2001). When foraging farther from the river, they increases intake which is the most effective in terms of net energy and searching effectiveness (Lewison & Carter, 2004). In such instances, hippopotami may become less selective and may feed on slightly longer swards.

In hippopotami, however, morphological constraints remain an important reason for preferring short swards. In Queen Elizabeth NP, Uganda, hippopotami were relatively common in most areas with varying sward heights (Field & Laws, 1970). This may signal that they may be feeding on slightly different sward heights.

In a study on foraging behaviour of Brent geese (Riddington *et al*., 1997; Hassall *et al*., 2001), captive geese took larger bites and had higher intake rates when feeding on 6 cm swards than on shorter ones. Similarly, in the field they preferred 6 cm sward to longer or shorter swards. This supported the forage maturation hypothesis. Bos *et al*. (2005) found that intake rates in Brent geese increased exponentially with sward height preferring plots with highest nitrogen contents. They concluded that forage quality was an important factor determining patch choice.

Hippopotami foraging on shorter swards might be due to trading off between availability of shorter, high quality and longer, low quality swards. Due to their morphology and ineffective chopping and grinding, shorter, higher quality swards are beneficial. Energy gains may be optimized by selecting patches with intermediate vegetation biomass and height (Wilmshurst *et al*., 1994; Durant *et al*., 2004). Hippopotami are effective in fermenting their forage due to their long food retention time. According to Lewison & Carter (2004), daily intake and gut capacity per body weight is lower than other herbivores of similar size due to long gut retention time and good assimilation (Arman & Field, 1973). Despite lack of rumination, fermentative digestion in hippopotamus is effective (Spinage, 2012). Low biomass swards are effectively processed although intake rates are low, unlike high biomass swards where intake rates are high but processing efficiency is low (Hassall *et al*., 2001). However, very short swards may be limiting particularly during the dry season. In Katavi, very short swards led to hippopotami consuming short swards with sand during the dry season (Meyer *et al*., 2005). Size and structure of grass stems affects rates of foraging and may affect foraging behaviour (Drescher *et al*., 2006b). Size and quality of forage varies as the result of grazing (Agreil *et al*., 2005), and may lead to less selectivity in consumption as observed by Meyer *et al*. (2005). In a study of sheep, as vegetation size and structure declined due to grazing, they increasingly took larger bites in compensating nutritive values (Agreil *et al*., 2005). In such a situation, animals like hippopotami are likely to feed unselectively in short mixed swards. However, the foraging areas which are used by hippopotami are also used by other herbivores. There are effects of various herbivores using the same resources (McNaughton, 1985) as they utilize resources differently often preferring different sward heights and different times of the day so partitioning resources (Schoener, 1974). Short swards created by hippopotami attract smaller antelopes (Field and Laws, 1970; Lock, 1972), hence decreasing the height further.

Increased sward height can indirectly indicate increase in the amount of food available, although higher sward heights can have a limiting impact on feeding by hippopotami. This is because the sward becomes morphologically inaccessible to the feeding hippopotami. Reported preferred sward height becomes a limiting factor as the hippopotami cannot easily access such a longer sward. This might have been the reason for the observed correlations between sward height and abundance and aggregation.

McNaughton (1985) reported that grazing animals in the Serengeti adjusted their densities in relations to grassland productivity. Productivity was estimated in terms of biomass and that actual productivity was found to be closely related to grazing intensity. This might help to explain the inverse correlations between hippopotami density and vegetation variables observed during this study in Katavi NP.

4.2 Aggregation

Aggregation is common among mammals (Blowers, *et al*., 2010). It involves a balance between both pros and cons of living in a group (Krebs & Davies, 1993). These may include reducing risk of predation, lowering thermoregulation energetic costs and joint care of young (Blowers *et al*., 2008).

Paradise Springs was the only site where there were correlations between rainfall and the size of hippopotami aggregations. Lack of correlations between rainfall and aggregation at the other four sites might have been because the impacts of rainfall at a particular site were not felt at that site but further downstream or indirectly because of local topography.

However, at Paradise Springs, rainfall was measured immediately upstream and it is very probable that the impact was felt at the study site which, contributing to the correlations between rainfall and aggregation at Paradise Springs. Similarly, availability of more water at Paradise Springs than the other sites might have explained the observed correlations. It is probable that impacts of water at the site concealed rainfall effects. At Paradise Springs, water levels responded to rainfall more quickly than on other sites because soils were already likely to be saturated by spring water.

Increases in river depth near Ikuu Springs corresponded with increase in inter-individual distances between hippopotami at the site. At a river depth of about 1.5 m, least aggregation was recorded. This coincided with the period when most hippopotami were dispersing to other resting sites during the rainy season. The most crowding occurred when river depth was lowest during the dry season. Rise in water level in Mara River in the Serengeti leads to dispersal of the hippopotamus population and decreased group size (Olivier and Laurie, 1974).

A similar aggregation pattern to Ikuu Springs was observed at Ikuu Bridge. However, during the dry season, hippopotami congregated at a large water pool along the river which remained throughout the year. This was unlike Ikuu Springs where perennial water springs provided wetter shelter for hippopotami during the dry season. The rest of the river ran dry with the exception of water pools which remained along several sections of the river bed; however, their sizes were much smaller than the pool at Ikuu Bridge.

There were observed correlations between river depth and aggregation at Ikuu Bridge and Ikuu Springs. This was probably due to the way the sites depended on the main Katuma River for water. Ikuu Bridge depends on the river only for its water. Ikuu Springs depends on the springs and indirectly on the river which is nearby. However, the effects of the Katuma may quickly be felt by hippopotami at Ikuu Springs. Rise of river level is likely to trigger hippopotami to disperse from Ikuu Springs.

Hippopotami spend most of their day time in water (Olivier & Laurie, 1974; McCarthy *et al*., 1998; Eltringham, 1999). Day living space has been discussed as important and is probably a limiting factor on abundance (Olivier & Laurie, 1974). Hippopotami also select water where they can submerge or shallow waters where they can move through or raft. River bends, lagoons, river mouths and open grassland plains with hippopotami food such as *Cynodon* and *Echinocloa* grass species have been reported to be favorable habitats (Wilbroad & Milanzi, 2011). These environmental relationships are essential to hippopotami.

4.3 Immigration and emigration

Rates of immigration and emigration among adult hippopotami did not correlate with rainfall. This might be because of distances to rain gauges and the extent of local soil saturation as already discussed.

4.4 Behaviour traits

From the observations recorded during this study, it seems most of the hippopotami responded to seasonal change in the extent of swamps, underground water table and river depth. These factors had a direct influence on behaviour, abundance and movements. River discharge tended to have indirect effects. This is probably because the impact of river discharge was mediated by local variations in the physical size and topography of resting sites and the extent of soil saturation by ground water.

4.5 Correlations between hippopotami and vegetation variables.

Although differences in vegetation might be expected between years, vegetation greenness as measured by satellite imagery in Katavi was relatively stable (Pelkey, Stoner & Caro, 2000; Stoner *et al*., 2006), and is reported to have increased only slightly during the time frame that surveys were conducted during the early to the mid-2000.

Vegetation variables have impacts on spatial variation in hippopotamus abundance and distribution. In Luangwa River in Zambia, abundance and distribution was influenced by diversity of grass species, grass biomass and grazing capacity (Chansa *et al*., 2011b; Wilbroad and Milanzi, 2010). Harrison *et al*. (2007) reported hippopotamus abundance was related to vegetation types in Malawi.

Grasslands have temporal and spatial variation in both quality expressed as protein content or digestibility and quantity measured as mass per unit area (Fryxell, 1991; Drescher *et al.,* 2006). Forage quality of grasses decreases with its age (Hassall *et al*., 2001; Drescher *et al.,* 2006). As the grasses mature, tensile strength increases correlated with a decline in their digestibility (Hassall *et al*., 2001). Equally, nitrogen contents in the swards decreases as sward height increases (Hassall *et al*., 2001). Temporal dynamics of forage quantity and quality of grasslands is best explained by forage maturation hypothesis (Fryxell, 1991; Drescher *et al*., 2006). The hypothesis states that net absorption rates are maximized on patches of intermediate plant biomass. This can help to explain the preference of hippopotami for the short swards and repeated grazing on the same pasture. Grazing stimulates productivity of grasses with intermediate grazing being more effective (McNaughton, 1985). This can also help to explain why hippopotami were resting more during the dry season, probably in an attempt to keep on digesting forage ingested during the previous night as during the dry season digestibility declines. During the wet season, while in their resting ground they fed more frequently during the day time as digestion was much faster and temperature much cooler.

Some vegetation variables (sward height, greenness and ground cover) were found to correlate inversely with hippopotami density, immigration and emigration. More hippopotami were recorded when sward heights and cover by vegetation were low compared to months when sward heights and vegetation cover were higher. Similarly, immigration and emigration of hippopotami were linked to sward heights (Table 5.8 and 5.9). This is a further confirmation of the effects of sward height on the feeding preferences of hippopotami. Seasonal variations in intensities of herbivory in South Africa (Shackleton, 1992) with the dry season having higher rates were linked with maturation of the sward. Similar conditions are thought to have influenced Katavi because hippopotami selected short swards. Raiding of short crops in Ruaha NP, Tanzania during the wet season (Kendall, 2011) is consistent with hippopotami avoidance of tall swards in the Park. Short swards have higher biomass (Shackleton, 1990) and are likely to have been the major feeding resource for hippopotami during the time when swards heights were above optimum. This might be similar to observations by O'Connor and Campbell (1986) in Zimbabwe where hippopotami used different areas for grazing during different times of the year, probably due to sward height and condition. These observations are also in line with those by Harrison *et al*. (2007) in Malawi where hippopotami changed their foraging areas following sward heights as the seasons changed. These correlations tend to further support observations in Section 4.2 that at some point, vegetation variables had influence on hippopotami abundance, immigration and emigration.

6.0 Conclusions

Availability of water at resting sites affected hippopotami abundance, movements and behaviours. During the wet months for example, more hippopotami were foraging than during the dry season months. This was because rainfall controls much of forage and directly or indirectly, water availability. Distribution of hippopotami was largely determined by the availability of the two resources.

Sward height, greenness and vegetation cover had correlated with seasonal hippopotami density, immigration and emigration. This indicates the importance of these measurements to hippopotami behavioural study as they are thought to have a causal relationship.

It can be concluded that water and vegetation variables had effects on hippopotami abundance, aggregation, immigration and emigration. These affected the animals in various ways and magnitude.

This study has provided preliminary insights for both management and conservation of hippopotami and its habitat in Katavi. It is hoped that it will form part of monitoring for the Park.

Chapter 9: Overall Discussion

The overall aim of this thesis has been to investigate the behavioural and ecological responses of the common hippopotamus, *Hippopotamus amphibious* L. to varying water resources in Katavi National Park, Tanzania. In this final discussion I synthesise results from the previous chapters interpreting them in relation to closely related studies elsewhere to identify possible threats to hippopotami in Katavi National Park. I conclude by briefly discussing possible ways of alleviating such threats. It has become increasingly obvious that the ecology of Katavi, as of many other National Parks in Africa, can only be appropriately understood in the context of the topography, ecology and land use of the whole catchment area in which the park is located. Key mitigation strategies are not therefore necessarily within the jurisdiction of Park authority alone.

I will first review how variation in water availability affects the basic physiological, behavioural and ecological aspects of hippopotami biology. This leads to consideration of the major anthropogenic factors of global climate change and of land and water use in the wider catchment area and how they might cause changes in water availability in the park concluding that the future of hippopotami in Katavi National Park has political implications as well as being a biological and hydrological issue.

9.1 Effects of Reduced Water on the Biology of Hippopotami.

All forms of life in the known universe require water to extents that vary with life stage and according to the hydrological properties of environments to which the life form has adapted. Hippopotami require water for several reasons. Firstly as for most large mammals living in hot tropical environments, they need it to drink and so maintain internal osmotic and ionic homeostasis. Secondly unlike most other large mammals in Africa, they also need it to maintain thermal homeostasis. They achieve this partly by perspiring to achieve evaporative cooling but to a much greater extent than most other African terrestrial mammals, they also need water for conductive cooling. Access to aquatic shelter sites in which to take refuge from high ambient air temperatures is a vital requirement for their thermoregulation (Louw & Seely, 1982; Noirard *et al*., 2008). This results in a core body temperature of about 36°C (Luck and Wright, 1963; Cena, 1964; Noirard *et al*., 2008). Immersion in water is also used to reduce the effects of exposure to direct solar radiation (Eltringham, 1999; Noirard *et al*., 2008). When exposed to higher temperatures out of water, hippopotami lose water rapidly at about 7.2 - 9.9 mg/5 cm^2/10 minutes (Luck and Wright, 1963), become less active and in extreme cases may die from dehydration. Because of these stringent thermoregulatory requirements hippopotami spend most of the day in aquatic shelters and forage predominantly during cooler nights. When hippopotami in the River Niger in Niger were exposed to air temperatures up to 50°C they spent less time exposed (Noirard *et al*., 2008) with ecological as well as behavioural consequences (Manteca and Smith, 1994).

In Katavi NP, as shelter sites dried out after the rainy season, hippopotami in the remaining wet shelters changes their behaviour, most conspicuously by immigrating into these more permanent water bodies from surrounding areas that were submerged during the rainy season but progressively dried out as the dry season progressed. A reverse emigration occurred soon after the start of the next wet season. There was thus an annual cycle in the dispersion pattern of hippopotami in Katavi NP with the populations being most dispersed during the wet season from December to April then exhibiting a consistent trend of increased aggregation as most of the wet areas dried out between July and December. In the permanent water bodies this change in water availability was mirrored by an increase in the distance between individuals during the wet season, followed by a progressive decrease in inter-individual distance in the shelters as more animals immigrated into them during the dry season.

The more crowded conditions during the dry season were accompanied by higher levels of aggression, as indicated by increased frequency of threats and biting behaviour in the dry season, especially in the drier study sites such as Ikuu Springs compared with wetter ones such as Paradise Springs. Such increased aggressiveness can result in serious fights, potentially leading to injury or even death (Estes, 1992; Lewison, 2007). In the drier sites the hippopotami also spent more time on maintenance behaviours such as splashing and rolling and less time on diurnal feeding, as they did at all sites at drier times of the year.

Reproductive behaviour can also be affected by typically severe reductions in water availability. In this study reproductive behaviour, including courtship and mating, was less frequent during the dry season at most sites, except at the wettest site at Paradise Springs where these behaviours continued throughout the dry season. As mating and calving mostly take place in water, reductions in its availability can result in decreased natality rates. During low rainfall and drought years the proportion of females likely to conceive can drop from 30% to only 5%, with the consequence that a hippopotamus population can crash because of this , together with abrupt increases in mortality (Lewison, 2007).

9.2 Indirect Effects of Water Reduction Mediated Via Changes in the Quantity and Quality of Food.

Quantity of Foods and the Mechanics of Feeding by Hippopotami

All large grazing animals ingest different sized bites and hence have different foraging efficiencies, when feeding on swards of different lengths, reflecting the constraints of their mandibular morphology. Hippopotami resemble avian grazers such as geese and ducks in that they use their hard, toughened lips to first grip a part of the sward, then pull by lifting the head to break it (Lock, 1972; Spinage, 2012). They are thus unlike other African Artiodactyla (e.g. antelopes) which have teeth only on the lower jaw, or perissodactyla (e.g. zebra with teeth on both mandibles). The result of these mechanical constraints is that hippopotami have a strong preference for swards of from 15cm (Lock, 1972) to 30 cm (Harrison *et al*., 2007) so are sometimes referred to as “short grass grazing specialists” (Dudley, 1998). It is important to note that there is considerable inconsistency and sometimes rather qualitative methodologies used for measuring sward height. In this study a standard design of dropped disc sward stick was used to measure temporal variation in sward height (Sharrow, 1984; Stewart *et al*., 2001) as discussed in Chapter 4. Analyses of these data showed that in the dry season mean ward height of swards hippopotami were known to graze, varied from 3 - 7 cm at the end of the dry season to 60 - 70 cm at the end of the wet season. Both heights were well outside the range preferred by hippopotami, suggesting that their feeding could be constrained for opposite reasons in the two seasons. During the dry season swards were at times too short for effective bite size, potentially resulting in nutrient deficiencies, while towards the end of the wet season biting efficiency could potentially be reduced by being unable to crop such long swards effectively as a result of not having teeth suitable for biting such long tough fibrous tissues.

Wildebeest, zebra and other large herbivores in the Serengeti, have evolved behaviours to overcome this difficulty by creating grazing lawns (McNaughton, 1985) as they have evolved spatially specific grazing patterns to prevent selected swards from growing higher than the optimal length by grazing the lawns to the preferred length in a regular temporal sequence to prevent them from becoming too long. There is some evidence that hippopotami similarly “manage” the length of selected feeding grounds as “lawns” at around 15 cm (Lock, 1972; Oliver and Laurie, 1974). Drought at such sites can constrain plant growth resulting in swards shorter than at the preferred length leading to less efficient grazing and reduced food intake rates. The difficulty hippopotami can experience when feeding on longer than optimal length swards is evidenced by hippopotami in Ruaha NP, Tanzania, in the wet season, raiding crops instead of feeding on long swards within the park when these grew above 30cm (Kendall, 2011). Whether the choice to feed outside the Park was driven by being more deterred by above optimal height swards within the Park or by attraction to crops at a particularly favourable stage of their life cycle outside the park, is not clear. Most crop damage occurred in relatively short swards, suggesting that sward height was a more important criterion for selecting feeding sites than species of plant (Kendall, 2011).

Rainfall determines the amount of available forage for many ungulates in East Africa (McNaughton, 1985; Sinclair, 2008). The observed relative stability of hippopotamus populations at Katavi between 1980s and 2010 might be associated with relatively stable forage availability which reflects consistent trends in rainfall during this period.

9.3 Sward Quality

Food quality, which can only be defined in terms of the performance of the species of herbivore concerned (Crawley, 1983) is often a more important driver of herbivore feeding behaviour than is the quantity of food available. Quality which represents nutrition is central to most aspects of ecology of animals (Parker *et al*., 2009). There is now extensive evidence supporting the “nitrogen hypothesis”, as reviewed by White (1983b). This is relevant to the present study because differences in forage quality with increases in maturity (and height) underpin the “Foliage Maturation Hypothesis” (Fryxell *et al*., 2004). This postulates that vertebrate grazers face a trade-off between higher intake rates on longer swards and both higher digestibility and higher nitrogen content of shorter swards, resulting in an inverted concave relationship between herbivore assimilation rates and sward maturation. Such a relationship has also been found for avian herbivores such as Brent geese (Hassall *et al*., 2001), wapiti (Wilmshurst *et al*., 1994) and grazing mammals in the Serengeti (McNaughton, 1985; Sinclair, 2001) It may also underpin the preference by hippopotami for a restricted range of sward heights.

Growth and development of ground layer plants, which determine food quality for hippopotami, are very sensitive to annual changes in soil moisture, which in turn is strongly influenced by variations in the intensity and periodicity of rainfall. Although the total annual rainfall in Katavi has remained relatively stable since 1950s, there have been some significant deviations both in total and timing of rainfall which can directly cause changes in mortality as in 2004 (Meyer *et al*., 2005) where a prolonged drought caused a significant increase in mortality of hippopotami, it can also cause reductions in both quality and quantity of food to the extent that death by starvation has been recorded in different parks in Africa.

Major natural demographic incidences among ungulates in Sub-Saharan Africa have been associated with drought and hence food scarcity. Examples include hippopotami death in Kruger NP, South Africa in 1991/2 (Viljoen & Biggs, 1998), wildebeest deaths during 1993/4 in the Serengeti (Mduma *et al*., 1999) and hippopotami in Katavi (Meyer *et al*., 2005). Mortality of adult buffaloes in Serengeti was caused by drought resulting in under-nutrition as the result of food shortage (Sinclair, 2008). A decline in hippopotami between 1983 and 1997 in Gonarezhou NP in Zimbabwe was attributed primarily to drought together with siltation and persecution in adjacent communal areas (Zisadza *et al*., 2010).

9.4 Trade-offs

Trade-offs occurs when two fitness correlates, which may be for example physiological, behavioural or life history traits, are negatively correlated with each other. Hippopotami are subject to a number of trade-offs which can be influenced by the availability of water. For example hippopotami forage within zones of, on average, 3.2 km diameter around their shelters (Viljoen & Biggs, 1998; Chansa *et al*., 2011b; Lock, 1972; O’Connor & Campbell, 1986) but this varies with water availability. In the dry season longer foraging journeys are made (O’Connor & Campbell, 1986). The normal life cycles of ground layer plants involves senescence and die back under adverse meteorological conditions such as when reduced soil moisture restricts new growth. Grazing herbivores further deplete the height and biomass of senescing swards, in the case of hippopotami as central place foragers (Lewison & Carter, 2004), in a gradient of decreasing severity with distance from their day time shelters. Therefore the distance travelled to feeding grounds varies between seasons with longer distances travelled in the dry season which are most difficult for females leading easily tired offspring. This leads to a behavioural trade-off between reduced ingestion rates and higher travel costs, both in time and energy. On swards nearer the shelters, ingestion is constrained by swards being of sub-optimal height but compensated for by low travel costs compared with feeding at more distant feeding grounds with higher travel costs but closer to optimal length swards, resulting in higher ingestion rates. Male hippopotami in Uganda have found a way of solving this dilemma by creating temporary wallows during the dry season in order to reduce the distance travelled (Field & Laws, 1963; Lock, 1972; Eltringham, 1999). Having to find alternative but sub-optimal, shelter sites nearer the forage grounds can increase conflicts with other groups of hippopotami or even with humans.

Hippopotami experience another potential trade-off that is even more obviously influenced by variations in water availability. This is the trade-off, which occurs as the dry season progresses, between aggregating in more permanent aquatic shelters with costs of increased crowding, more aggressive behaviours, higher depletion of foraging grounds, increased intra-specific competition for both space in the shelter and for food and increased transmission rates of diseases but very significant thermoregulatory and hence survivorship benefits. The alternative being staying more widely dispersed in temporary wet season shelters, with increased risk of overheating as the wet season shelters dry out and of higher mortality due to desiccation but with the benefits of less competition, aggression, and a lower risk of disease transmission (Turnbull *et al*., 1991; Viljoen, 1995; Viljoen & Biggs, 1998; Lembo *et al*., 2011).

Evidence for such a trade-off comes from comparing the most highly aggregated group in the two driest of the five study sites, Ikuu Springs and Lake Katavi sites, where there was significantly more fighting compared with the more widely spaced group in the less crowded wettest site at Paradise Springs where the animals fought less. The decision of when to move into wetter, more permanent, shelters will be strongly determined by the timing and extent of variations in river levels. Exceptional droughts can have a potentially catastrophic effect when they result in a large proportion of usually permanent shelter sites drying earlier in the year, as happened at Katavi in

2004 when rivers ran dry in August with consequently higher than average mortality of hippopotami.

9.5 Potential Future Changes in Supply of and Demand for Water by Hippopotami.

This study demonstrates the importance of both adopting a catchment wide perspective on what appear superficially to be more localised conservation issues and also of placing these in the context of global environmental change. Two of the biggest environmental challenges to society in the 21st Century are global climate change and world food security. Both are relevant to this study.

9.6 Possible Consequences of Predicted Changes in Global Climate

According to the IPCC (2001; 2007), climate change is likely to result in increased global temperatures and decrease predictability of rainfall. Africa will be highly affected (UNEP, 2010). Increase in precipitation intensities in the tropics are predicted due to warming of the atmosphere (IAH, 2012). However, evapotranspiration is also expected to increase by 5-10% due to increased temperatures. Although wildlife may respond to global climate change by acclimatization, evolutionary adaptation and moving into refuges (Wright *et al*., 2009), this would only be possible for hippopotami provided that adequate water was available for cooling. Although absolute annual totals of rainfall may remain the same or increase, projected changes in temporal distribution of rainfall are likely to result in more variable river discharge, soil moisture and shortages of fresh water IAH (2012).

Uncertainty in climatic driving processes (Hulme *et al*., 2005; APF, 2007; Collier *et al*., 2008; Toulmin, 2009) presents challenges in accurately predicting how climate change, particularly of rainfall, is going to affect Africa. Average temperatures for the whole of Africa are predicted to increase by 2°C by 2100 when compared with temperatures in the 1990s. Some parts of the continent are expected to experience an increase between 3 - 6°C by 2100 (APF, 2007; IPCC, 2007). In eastern Africa the predicted increase in temperature is by 1.5 to 4°C. Currently, drier sub-tropical regions, northern and southern Africa are becoming increasingly drier with increasingly variable and unpredictable rainfall and storms (APF, 2007; IPCC, 2007; Collier *et al*., 2008). Eastern Africa is predicted to get wetter due to increase in rainfall by up to 15 % or more by 2100 from 1990s rainfall (IPCC, 2007; UNEP, 2008; Collier *et al*., 2008) The whole continent is expected to experience increased frequency and intensity of drought and flooding (Collier *et al*., 2008). Between 1970 and 2000 East Africa has faced at least one major drought a decade (UNEP, 2008).

Global climate change could affect animals in Katavi NP in several ways. The convective rainfall which dominates the Katavi region is predicted to increase (IPCC, 2007). This increase will however be largely offset by simultaneous increases in evapotranspiration, resulting in predictions of no net change in the current annual water balance. If in the Katavi region the predicted increase in variance of rainfall resulted in some years in there being a shorter wet season with heavier rainfall events the consequence would be to increase the length of the dry season causing extended drought conditions which would not only affect availability of drinking water for many animals, including hippopotami, but would also for them, pose additional thermoregulatory problems which they might not be able to meet. This could result in drought induced reductions in natality and increased mortality, so potentially changing their long term population dynamics.

Such adverse effects could be made more severe by the predicted increase in *average* air temperature. These are unlikely to be in the form of a uniform increase in all daily temperatures but more probably will occur as increases, by e.g. 5 to 6^{o}C, on some days and little or no increase on others. Such temperature rises could potentially cause animals to reach, or exceed, their physiological thermal tolerance limits, potentially resulting in thermally induced mortality (Thuiller *et al*., 2006). The importance of considering changes in variance of meteorological conditions is reinforced by the possibility that extreme rainfall and temperature stresses could act simultaneously, potentially with multiplicative consequences.

9.7 Potential Indirect Effects of Predicted Global Climate Change on Hippopotami

Changes in patterns of rainfall will also affect hippopotami indirectly if they influence the availability of food resources (Thuiller *et al*., 2006). Increases in rainfall are predicted to occur within the wet season, so would not alleviate the indirect problems of reduced availability encountered during the dry season. This is because forage in East Africa depends mainly on rainfall (McNaughton, 1985)

9.8 Changes in Land and Water Use at a Catchment Area Scale

Changes in land and water use in the upper parts of the catchment area of the rivers flowing into Katavi NP reflect recent changes in agricultural practices implemented by communities in the upstream part of the Katuma catchment area. If these changes were to reduce the flow of water into the park all the potential direct adverse effects of increased aggregation discussed could be intensified. The risks of such problems caused by changes in land and water use outside the National Park could be further exacerbated by global climate change.

Human disturbances to the catchment area by clearing vegetation and removal of debris from river beds has resulted in altered flow patterns and severe changes to river structure and function (Brierley *et al.,* 1999). Use of water upstream and clearance of forest in the catchment area may result in Katavi NP and its wildlife experiencing water at levels lower than required for hippopotami to thermoregulate effectively. The recent reductions in river flow are partly caused by reduced soil water holding capacity brought by clearing woodland from parts of the catchment area and partly due to changes in farming practices. As a result of both these processes river flow levels and duration are declining significantly, rendering hippopotami more susceptible to prolonged droughts which naturally would be expected to occur about once a decade. The increased risk of critical reductions in river flows are likely to be exacerbated by climate change because the predicted increase in temperature would increase evaporation rates and thereby decrease surface water runoff.

Forest clearance is occurring despite forest conservation being a priority for many conservation efforts in Tanzania (Banda *et al*., 2006). These processes started in the Katavi catchments within the last two decades with clear impacts on reduced river flow which led to proposals for protection of downstream ecosystems (Appan, 1989; Callow *et al*., 1990).

Various possibilities have been considered to mitigate effects of the recorded reductions in river flow from 2004 – 2009 caused by changes in farming practice involving diversion of water upstream of the Park to irrigate recently constructed rice paddies deleteriously altering the water balance of Katavi NP Surface reservoirs have been tested by Park authorities without success. The use of wind powered bore holes was not considered due to discontinuity of supply resulting from variable wind speeds, problems of attracting non-target species and concentrated depletion of forage in large areas round the bore hole.

9.9 Management and Policy Implications

Indirect Effects of Predicted Climate Change on Food Availability

If as a result of increased variance of rainfall events, signs of feeding grounds becoming excessively depleted were detected, some manipulation of both quantity and quality of forage could potentially be achieved using controlled burning. There is a need of monitoring the length of hippopotamus foraging tracks to detect whether they had become longer than the maximum of 10 km (Estes, 1992; Eltringham, 1999) at which starvation and death from unsustainable foraging travel costs may occur. Burning savannah as a management practice is currently used extensively in Katavi to reduce the fuel load and hence the temperature and incidence of fires later in the dry season. This management tactic is employed just after the end of the rainy season, usually in May and June, when swards are at their highest and in least preferred upper height range selected by hippopotami. If changes in rainfall patterns started to reduce availability of forage within the optimal range, then potentially prioritising burning to target hippopotamus feeding grounds within 3.5 km of known shelter sites could be increasing favourability of their habitat during the rest of the dry season without detrimental effects on other species in the Park. Fire is known to rejuvenate swards and encourage new shoots. Burning of early dry season foraging near shelter sites could alter the ingestion rate-travel costs trade-off thereby increasing foraging efficiency of the hippopotami.

Changes in Other Parts of the Catchment Area

It is now apparent that changes in land and water use elsewhere in the catchment are central to recent changes in hydrology and hence the behaviour and ecology of hippopotami in Katavi NP. A system of governance is therefore required which can potentially address problems caused by the reduction in water flow at source. As the upper catchment area of the Katuma is not within the jurisdiction of the National Park authorities they cannot interfere directly with the communities damning the river. In 2010, there was some reversal of the recent trend of reduced flows as a result of efforts by National Park and authorities of the Rukwa regional government to inspect and reduce the number of illegal diversion dams on the river Katuma upstream of the Park, constructed to supply irrigation water. Diverting river flow in this way is illegal in Tanzania according to National Water Policy 2002 and Water Resources Management Act 2009 (URT, 2002; URT, 2009a; 2009b). Implementation of the act in the upper Katuma catchment area resulted in a resumption of significantly higher river levels in the Park during the wet season in 2010 but future such lobbying may become less effective as a result of repetition.

While it is desirable that the Katavi National Park should continue to lobby the Rukwa regional government to persuade local governments to continue enforcing the national Water Use Act it is recognised that this may not be a sustainable solution to the problem. Breaches of National Law which reduce starvation and increase well-being of the communities that benefit from diverting water from a river for crops may in time be overlooked on economical and humanitarian grounds.

The problem of diverting river flows upstream of National Parks is widespread in Africa where about 85 % of water is used in agriculture (Downing *et al*., 1997) On a very localized scale such diversion of upstream river flows could be regarded as helping in a very small way to mitigating problems of world scale food security. African National Parks which depend on water from beyond their boundaries include Ruaha NP (Epaphras *et al*., 2007; 2008), Serengeti (Gereta *et al*., 2003), Tarangire (Gereta, *et al*., 2004a), Kruger NP- South Africa (Viljoen, 1995; Viljoen & Biggs, 1998) and Liwonde NP-Malawi (Harrison *et al*., 2007). Most of the parks facing such catchment area challenges were created to protect big game rather than the whole ecosystem being given priority (TANAPA, 2008). Many national parks in Africa depend on water the sources located in public lands outside their boundaries. Use of water in Africa is projected to increase sharply over the coming decades (MacDonald *et al*., 2012). In the Serengeti in Tanzania, the Mara River is the main river but depends on water from neighbouring Kenya (Gereta *et al*., 2003). Use of water upstream is increasing challenges in managing the Serengeti because political solutions to the problem would require international agreements.

Similar catchment area problems exist within Tanzania. In Ruaha NP the catchment area and sections of the main Ruaha River above the Park are under human pressure leading to drying of this “life line” river (Epaphras *et al*., 2008). In Northern Tanzania Tarangire NP, which depends on waters form the main Tarangire River, is also faced by similar challenges during the dry season as the source of the river is outside the park and under human pressure (Gereta *et al*., 2004b). Conflicts over fresh water are increasing and are likely to continue as human population increases rapidly (Arthington *et al*., 2006).

A theoretically possible solution to the problem in Katavi could be to provide alternative sources of water for the animals. As a matter of policy however, Tanzania National Parks Authorities do not provide artificial water holes for wildlife (Peterson, 1973; Epaphras *et al*., 2008) as is practiced in Tsavo NP in Kenya because of the problems discussed in Section 9.8 Surface reservoirs have been tested during pilot studies in Katavi by Park authorities in 2005 but proved impracticable.

Conservation of whole catchment areas by involving communities might be an affordable alternative approach. Community based conservation outside the protected areas has been regarded as a possible cornerstone of currently acceptable forms of protection (Weladji & Tchamba, 2003; Hilborn *et al*., 2006). I propose that a local community based conservation approach could result in a more sustainable solution to the problems in Katavi NP.

9.10 Overall Conclusions

This study has increased our understanding of how the behaviour and ecology of hippopotami respond to changes in the availability of water. It provides more informed insights into hippopotamus responses to reduced water availability at several levels of biological organisation. These insights can assist when deciding priorities for the management and conservation of hippopotami in Katavi. Although this study was restricted to only one year, the data collected can form a base line for future monitoring in the Park. A key conclusion from this study is that adopting a catchment area basis for water management is absolutely essential for the conservation of hippopotami in Katavi National Park. Maintaining year round river flows is one of the most important tasks required to ensure the future wellbeing of this flag ship population of hippopotami in Tanzania.

World food security problems are nowhere more obvious than in Africa where millions of people die of malnutrition and associated illnesses annually. Any change in agricultural practice which results in higher productivity is therefore potentially favoured politically. Rice is not an indigenous food plant in Africa but can provide higher yields than traditional food plants. However this increased productivity comes with an increased aquatic cost to other land uses further downstream because changes in agricultural practice can potentially conflict with their water requirements. In Katavi NP these include water needed for conservation of a species that is the most sensitive to changes in river flow, the hippopotamus. It can be argued that conservation of such a charismatic member of the continent's megafauna could increase the quality of life for visitors to the park both from elsewhere in Tanzania but also from overseas. Others could however oppose such arguments by arguing that the survival of people is a higher priority than increasing the quality of life of others.

This poses a moral dilemma. There is good evidence that flow rates of the Katuma River have decreased since 1990 in response to increased diversion of river flow to irrigate rice crops. Effects of a natural drought, exacerbated by upstream river depletion, in 2004 resulted in increased numbers of hippopotamus deaths in the Park (Meyer *et al.*, 2005). This interpretation was confirmed by the increase in river levels in 2010, when lobbying by the Park Authorities at Regional government level led to firmer imposition by local government officials, of national laws on water use. The analyses presented in this thesis of responses by hippopotami to reduced water availability indicate that continuation of recent trends in increased diversion of water upstream of the Park could potentially jeopardize the long term sustainability of viable hippopotamus populations in the Park

Because protecting lives is a higher political priority than increasing the quality of lives, the lobbying approach used in 2010 cannot be relied upon indefinitely. Another form of compromise, possibly involving persuading upstream communities to switch back to less water dependent crops, better adapted to predicted future variability in rainfall, probably combined with providing economic compensation for changes in their cropping practices can be more effective. However, fund for such subsidies are unlikely to be provided by the Tanzanian Government.

A theoretically possible solution would be to generate more income within the local catchment area by increasing revenue from increased numbers of visitors to Katavi NP. At present this is limited by infra-structural constraints of transport to and accommodation within the Park. If access to the Park were increased for overseas visitors, it may be possible to persuade overseas donors to invest the initial capital to “pump prime” such a green tourism scheme and have a more user friendly and sustainable approach where water use can be balanced between outside users and in the park.

Application of the principle that consumers pay for goods, services and facilities they require, including opportunities for viewing hippopotami, would suggest that this might be the fairest solution to a conflict of interest between the two ecosystem services: those of biodiversity and food production. Such a moral dilemma is faced not only by the Katavi National Park authorities but also managers of many other national parks in East Africa, and in various guises, by conservationists worldwide.

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APPENDIX 1

Water quality

List of Tables

List of Figures

1.0 Introduction

Chapter 3 of this study on water quantity has shown that there have been no significant long-term changes in rainfall in Katavi over the past 60 years. However, there have been some reductions in water levels and duration of flow in the Katuma River. Among the possible causes for reduction is alteration of river flow, hence reduced flow duration. This chapter documents some basic water qualities that whilst not linked directly to hippopotami behaviour, might help to indicate possible sources of water, and hence their inclusion in this study. Information on interactions between ground and surface waters is generally very scarce in East and Central Africa (Owor, 2010). Katavi is thought to receive the majority of its surface water *via* rainfall on the surface drainage catchment (Lewison, 1996; 1998; Meyer *et al*., 2005). However, contributions from groundwater should not be neglected since these have the potential for sustaining dry season flows and dry season sheltering, wallowing and resting habitat for hippopotami.

The parameters chosen were pH, electrical conductivity and the relationship between air temperature and water temperature. These parameters were measured in many of the water bodies in the Park because deviations from general geographical or seasonal patterns might be indications of significant contributions of groundwater to surface water.

Ground waters have higher total dissolved salts (TDS) and hence conductivity than surface waters and so a sudden increase in electrical conductivity along the river may indicate the presence of springs or seeps originating from a calcareous aquifer. Conductivity values in the rivers and streams reflect primarily a combination of watershed sources of salts and the hydrology of the system (Bruckner, 2011). Underlying geology (rock types) determines the chemistry of the catchment soil and ultimately its streams and lakes. Apart from geology, conductivity is controlled and influenced by size of the drainage catchment, anthropogenic influences, evaporation of water from the surfaces, flow volumes, temperature and bacterial metabolism.

Water pH depends upon geology, additional water from other sources or other environmental factors such as pollution. Importantly, pH also determines the solubility and biological availability of chemical constituents. As all waters have particular pH ranges, any sudden deviations from normal ranges predicted from catchment geology may indicate additional sources of water. Measurements of pH can therefore help in detecting if there are any obvious deviation (hotspots) which may indicate springs output and hence, its inclusion in this study.

Ground water in the eastern Africa rift valley region has generally higher temperature than surface waters (Geijskes, 1942; Wolanski & Gereta, 2001; Gereta *et al*., 2004). Close to the river catchment source, water is cooler than surface drainage water further downstream. As ground water mixes with surface water and is warmed by air, water and air temperatures vary together more closely. Departures between water and air temperature may therefore reveal sources of ground water.

The water quality part of the study was not designed or intended to detect pollution although catchment land use in the upper catchment (discussed in Chapter 3) is likely to cause anthropogenic impacts on water quality. Agricultural activity in the catchment above the Park has been increasing (Lewison, 1996; 1998; Meyer *et al*., 2005) and along with mining for gold, such changes in land use bring potential impacts on water quality in the Park. Impacts may be direct or indirect but will always be difficult to detect over the natural ecosystem processes that occur in the seasonal wetlands of the Park. Low water quality may affect wildlife health but direct effects of low water quality on wildlife are not well documented (Wolanski and Gereta, 2001). Wolanski and Gereta (2001) and Gereta *et al*. (2004) found that increases in water hardness and salinity in the dry season coincided with migration of wildebeest and zebra. Any direct effects of increasing salinity of water on hippopotami immigration and emigration are unknown. Water quality may change seasonally and on a very local scale, for example in the dry season, animals may congregate in remaining watering areas and their excreta may cause nutrient enrichment and oxygen depletion

(Wolanski and Gereta, 2001). Detection and differentiation of larger-scale human influence on water quality from more local ecosystem processes is a challenge beyond the scope of this thesis.

Katavi National Park has in place a water quality monitoring program where the basic parameters of pH, electrical conductivity, dissolved oxygen, temperature and turbidity are monitored monthly. The program records time series for these parameters and any departures from seasonal patterns are examined by the managers of the Park as a possible indication of changes in the water environment that might require management intervention.

As part of the work presented here, the water quality program increased the number of sites monitored by the Park from eight to 26 and monitored twice per month from August 2009- September 2010. Additional sites included known sources, such as boreholes and springs to give reference values for these sources.

1.1 Aims and hypotheses.

Data from the monitoring program were used to test the following hypotheses:

Hypothesis$_1$: Increase or decrease of water temperature indicates possible additional ground to surface water flow.

Hypothesis$_2$: pH reflects strongly to catchment geology chemistry.

Hypothesis$_3$: Conductivity increases downstream in the Katuma River.

Hypothesis$_4$: Downstream variations in conductivity relate predominantly to the diluting or concentrating effects of variations in river discharge.

2. Methods

2.1 Site selection

Twenty six stations were selected (Fig. 4.1). These were taken to represent the range of water bodies in the Park and the sources of flow that contribute to the main Katuma River, or were close to the major hippopotami feeding/resting ground/shelters. Positions were marked using a Garmin hand-held GPS map 60CSx (Fig. 4.1).

The stations were divided as follows:

Boreholes Four stations were boreholes. These include one at Sitalike HQ, Ikuu Spring, new Ikuu Spring at Flycatcher camp and a village borehole near the Park HQ. These are shown in Fig. 4.1 and GPS coordinates are shown in Appendix 4.1.

Springs Three stations were springs contributing their waters to the main Katuma River and its associated swamps. These include Kasima Springs (discharging into Katisunga plains), Ikuu springs (discharging into Katuma River) and Paradise springs (discharging into Kapapa River). These are shown in Fig. 4.1 and GPS coordinates are shown in Appendix 4.1.

Tributaries Four sites were tributaries of the main Katuma River. The sites are shown in Fig.4.1 and GPS locations are presented in Appendix 4.1.

The Main River: Fifteen stations along the main Katuma River including the upper catchment above the Park, sites within the Park before and downstream of three major water bodies (Lake Katavi, Katisunga plains and Lake Chada) and the main river at its outflow from the Park (Kavuu-Katavi Outflow). The sites are shown in Fig.4.1 and GPS locations are presented in Appendix 4.1.

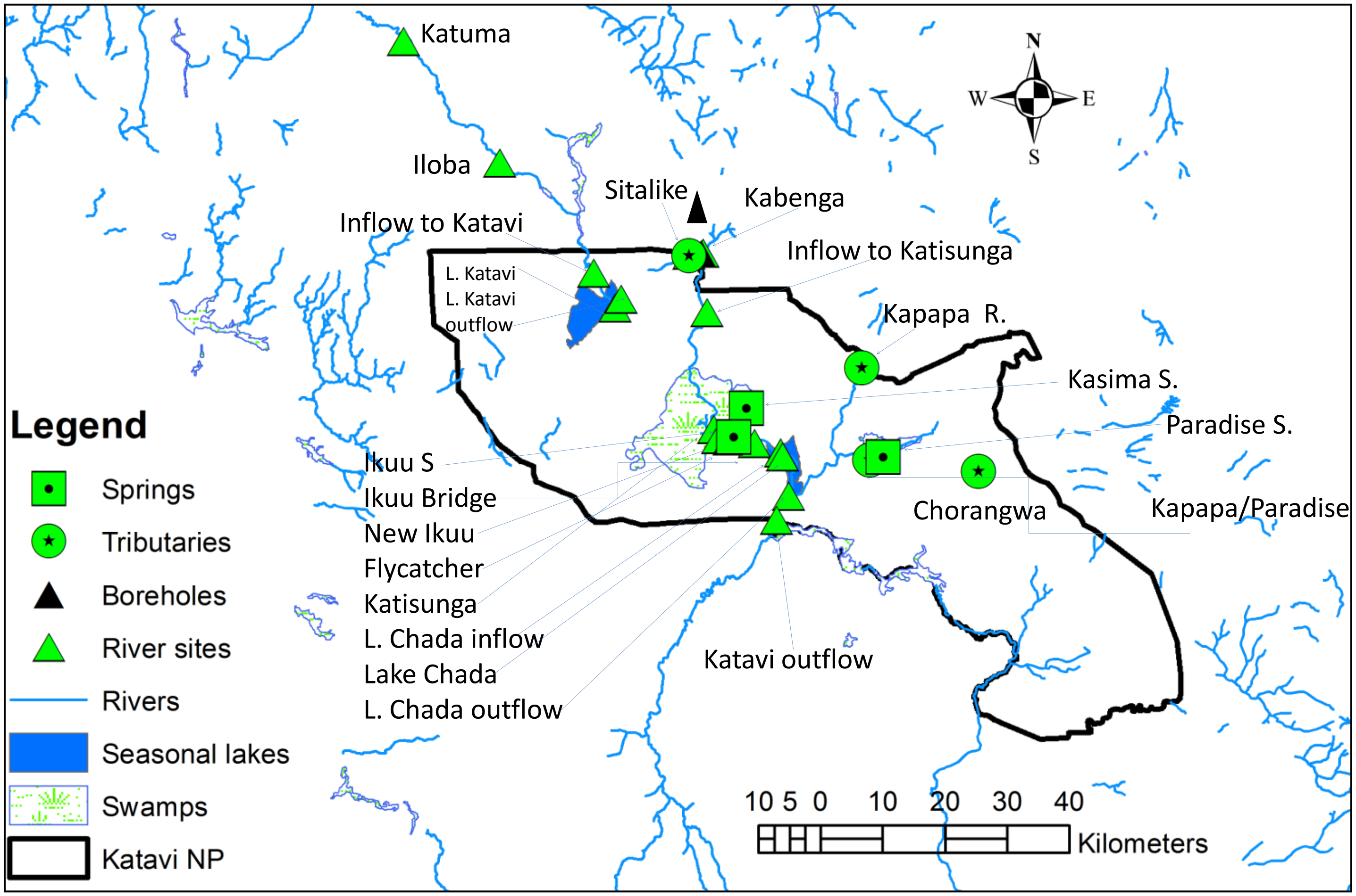


Fig. 4.1: Location of water quality study sites in Katavi NP, Tanzania. Data source: Katavi NP and GPS data collected during this study. NP=National Park, R= River, S= spring.

A longitudinal profile of Katuma River showing the altitude of water sampling sites is shown in Fig. 4.2. The two sites above 1000 m.a.s.l. (Katuma Village and Iloba Village) are both in the upper catchment above the Park boundary.

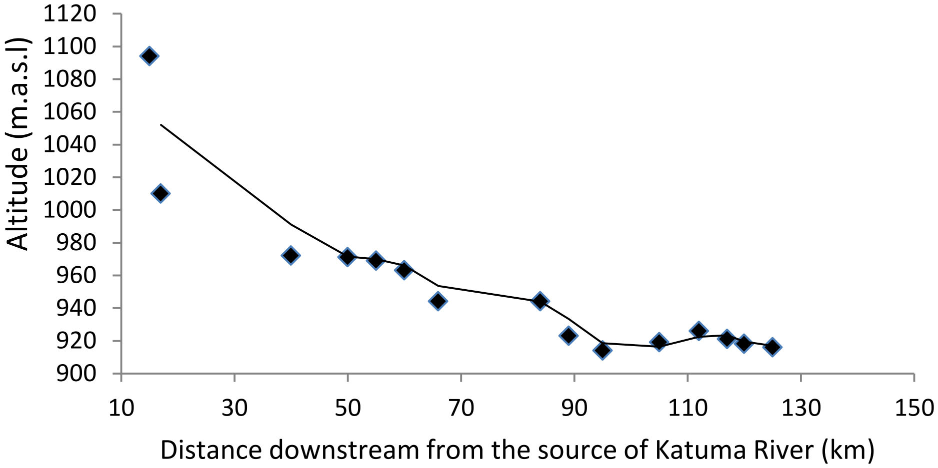


Fig. 4.2: Longitudinal profile of the Katuma River showing the altitude of water sampling points and therefore gradient of the river channel.

2.2 Water quality parameters

Air temperature and water temperature just below the surface were measured in all sites at two week intervals over the twelve months from October 2009 to September 2010. Measurements were made using an Extech DO600 meter. The DO600 meter calibrates automatically when it is fully powered. The DO600 features automated adjustable altitude compensation from 0-6096 m in 305 m increments as well as automated adjustable salinity compensation from 0-50 ppt. The DO600 has a basic accuracy of ± 2% full scale. Sufficient time was allowed for the temperature of the probe to reach the temperature of the sample before taking a reading. This was indicated by a stable temperature reading on the display.

Conductivity and pH were measured using an Extech EC500 pH/conductivity meter. The meter uses one electrode. The Extech EC500 pH/conductivity meter has an adjustable conductivity to TDS ratio from 0.4 to 1.0 and a 0.5 fixed salinity ratio so TDS and salinity data are not presented separately since they are both a simple function of conductivity. The Extech EC500 ‘renew’ feature alerts users when recalibration is required or when the electrode needs replacement. The probe was immersed in water and moved constantly before taking a reading. Readings were taken when the reading on the meter was relatively stable.

For all measurements, probes were immersed directly in the water body only when conditions were safe. In unsafe circumstances, water was sampled with minimum stirring using a cup attached to a rod and measurements taken within one minute of sampling. If there were delays in measuring, another water sample was taken and measured. After each measurement, the probes were cleaned and stored before the next measurement or storage.

2.3 Data analysis

Data were analysed using SPSS statistical software PASW 18 and the Microsoft Excel data analysis tool. Results were summarised as means with their standard errors, correlations were performed using Pearson correlations and differences between sites or groups of sites were analysed using one way ANOVA.

3. Results

3.1 Temperature

Air temperature

Annual mean air temperature over the study area varied between 27 ± 0.8°C (in the Park at Sitalike Bridge) and 31 ± 0.7°C (in the upper catchment at Iloba Village) (Fig. 4.3). Mean monthly air temperatures varied from about 26°C in August to about 31°C in September and October 2010. Maximum temperatures of 35°Cwere recorded in September, October and November

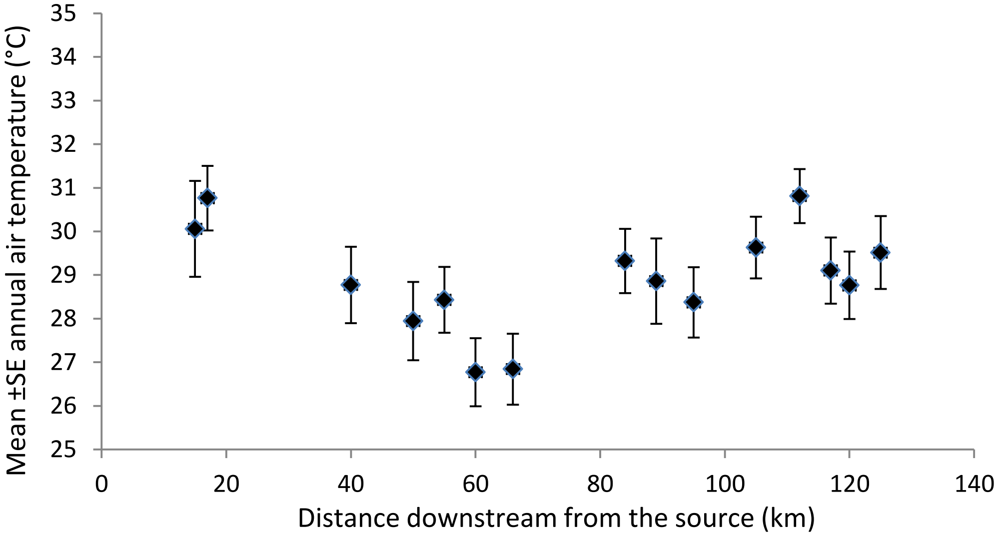
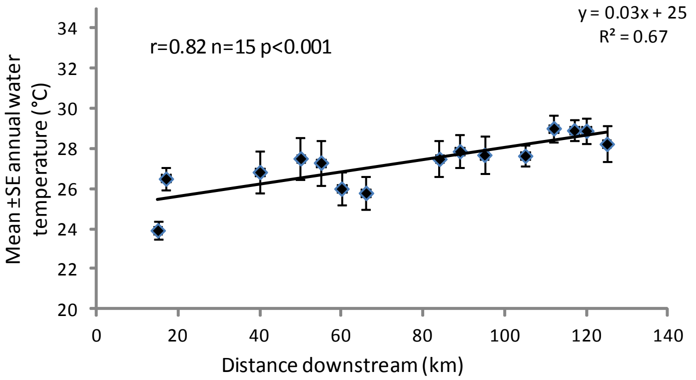


Fig. 4.3: Mean annual air temperature downstream relationship for Katuma River (October 2009-September 2010), Katavi NP, Tanzania.

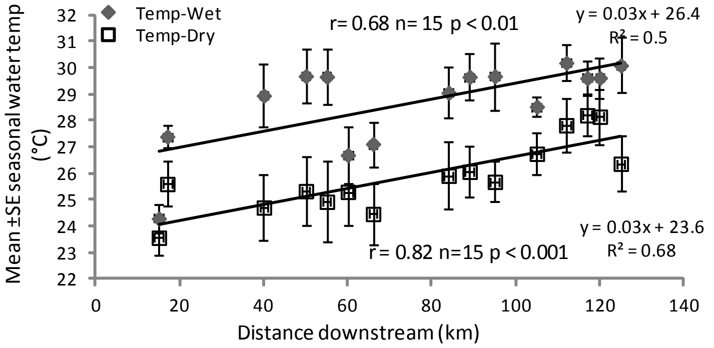
Water temperature

Annual mean water temperature varied between 24 ± 0.4°C (in the upper catchment at Katuma Village) and 29 ± 0.7°C further downstream in the Park. Water temperature increased with distance downstream from the source of the Katuma River ($r = 0.82$ $n = 15$ $p < 0.001$) (Fig. 4.4a).

a) Annual water temperature



b) Seasonal water temperature



c) Water and air temperature

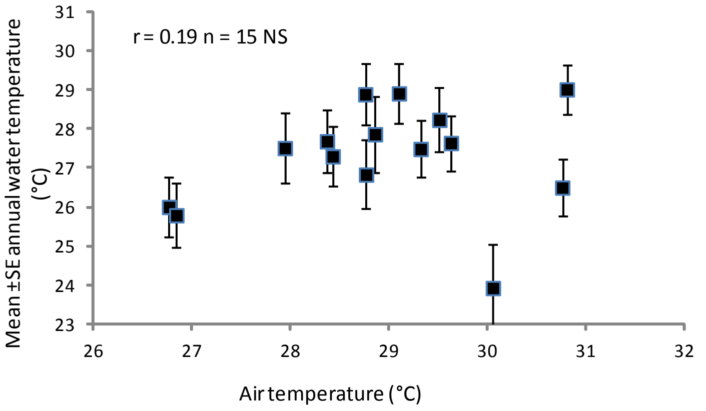


Fig. 4.4: Plots showing (a) mean annual temperature with distance downstream; (b) mean wet and dry season temperature with distance downstream and (c) air-water temperature relationship for Katuma River October 2009-September 2010 in Katavi NP, Tanzania. Error bars are ± SE around annual and seasonal means.

Wet season mean water temperatures varied between 24 ± 0.5^{o}C (at Katuma Village) to 30 ± 1.0^{o}C at eight other sites. Water temperature during the dry season varied from 24 ± 0.7^{o}C at Katuma Village to 28 ± 1.0^{o}C at Lake Chada (Fig. 4.4b), and were consistently lower in the dry season. Water temperature in both the wet ($r = 0.68$ $n = 15$ $p < 0.01$) and the dry ($r = 0.82$ $n = 15$ $p < 0.001$) season increased with distance downstream (Fig. 4.4b).

Air vs. water temperature

There was not a significant correlation between water temperature and air temperature ($r = 0.19$ $n = 15$ NS) (Fig. 4.4c). The upper catchment (Katuma Village and Iloba Village) had lower water temperatures in relation to air temperature than further downstream. The Katuma Village site, where the lowest mean water temperature of 24 ± 0.4^{o}C was recorded, appears as an 'outlier' in Fig. 4.4c.

There were significant differences in mean water temperatures between study sites ($F_{2,\ 25} = 7.56$, $p = 0.003$), with tributary rivers having significantly lower mean water temperatures than the main river, springs and boreholes (Table 4.1). The main Katuma River, springs and boreholes did not show significant differences between them.

Table 4.1: Mean water temperatures for study sites along the main river, springs and boreholes and river tributaries in Katavi NP, Tanzania

Main River		**Springs and boreholes**		**Tributaries**	
	Mean Water temp		**Mean Water temp**		**Mean Water temp**
Site	**(^{o}C)**	**Site**	**(^{o}C)**	**Site**	**(^{o}C)**
Katuma Village	23.5	Paradise Spring	26.8	Chorangwa	22.8
Iloba Village	26.0	Kasima Spring	27.8	Kabenga	25.3
Katavi Inflow	26.7	New Ikuu borehole	28.4	Kapapa	24.7
Lake Katavi	27.2	Ikuu spring	28.0	Kapapa/Paradise Confl.	26.4
Lake Katavi exit	26.9	Ikuu borehole	28.1		
Airstrip	25.6	HQ borehole	27.1		
Sitalike Bridge	25.9	Village borehole	27.4		
Inflow to Katisunga	27.5				
Katsunga Plains	27.5				
Flycatcher Camp	27.4				
Ikuu Bridge	27.3				
Lake Chada Inflow	28.3				
lake Chada	28.4				
Lake Chada exit	28.5				
Kavuu outflow	27.9				
Mean Temperature (^{o}C)	**27.0**		**27.7**		**24.8**

3.2 Water pH

Spatial variations of pH in the main river, tributaries, springs and boreholes

Mean annual water pH varied between 7.4 ± 0.2 and 8.2 ± 0.2 (at Lake Katavi outflow and Katisunga Plains) and pH was therefore slightly to moderately alkaline. The pH for named sampling sites on the main river is given in Table 4.2.

Table 4.2: Mean annual pH (October 2009 – September 2010) measured in the Katuma River and its tributaries, associated springs and boreholes, Katavi, Tanzania.

Site	Estimated Distance Downstream (km)	Mean annual pH	± SE
Katuma River:			
Katuma village	15	7.8	0.1
Iloba Village	17	7.5	0.1
Katavi inflow	40	7.6	0.2
Lake Katavi	50	7.6	0.2
Lake Katavi exit	55	7.4	0.2
Airstrip	60	7.6	0.1
Sitalike Bridge	66	7.5	0.1
Inflow to Katisunga	84	8.1	0.3
Katisunga Plains	89	8.2	0.2
Flycatcher camp	95	8.0	0.1
Ikuu Bridge	105	7.8	0.1
Lake Chada Inflow	112	8.0	0.1
Lake Chada	117	8.0	0.3
Lake Chada exit	120	7.7	0.2
Kavuu (Katavi) Corner	125	7.6	0.2
Tributaries:			
Kabenga		8.8	0.1
Kapapa		7.8	0.1
Chorangwa		7.7	0.1
Kapapa/Paradise confluence		8.4	0.3
Springs:			
Ikuu Spring		7.5	0.1
Kasima Spring		7.4	0.1
Paradise Spring		7.5	0.2
Boreholes:			
Ikuu Spring borehole		6.9	0.2
Sitalike HQ borehole		7.3	0.1
Flycatcher borehole		8.5	0.1
Village borehole		7.3	0.1

There were significant differences between sampling sites on the main river ($F_{14,\ 179}$ = 2.175 p < 0.011). Although the five sites on the main river that had a pH of ≥ 8.0 were all downstream, there was no correlation between annual mean pH and distance downstream (r = 0.45, n = 15 NS) (Fig. 4.5).

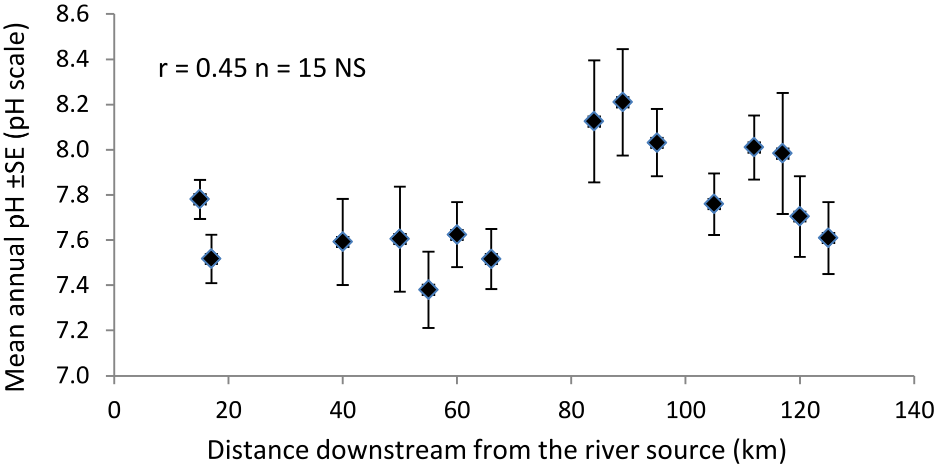


Fig. 4.5: Mean annual pH downstream Katuma River, October 2009 - September 2010 in Katavi NP, Tanzania. Error bars are ± SE around annual mean.

The mean annual pH of underground waters from boreholes and springs varied between 6.9 ± 0.2 at Ikuu Spring borehole to 8.5 ± 0.1 at New Ikuu borehole (Fig. 4.6). All other boreholes and springs were within the same neutral to slightly alkaline range as the Katuma River. The New Ikuu borehole was the only site that had a pH above that of Katuma River. At 6.9 ± 0.2, water from Ikuu Springs had a significantly lower pH than the more alkaline water from the neighboring Ikuu Spring borehole.

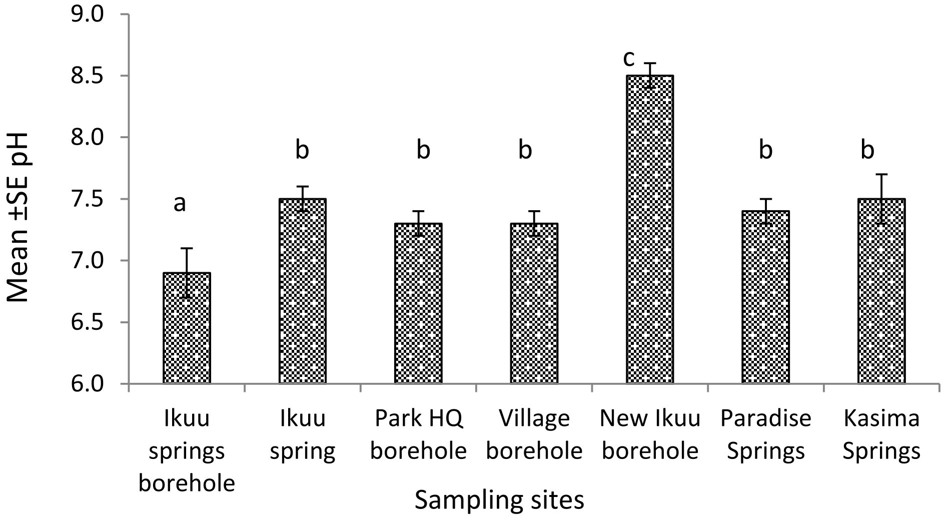


Fig. 4.6: Mean annual pH of boreholes and springs in Katavi NP, Tanzania. Error bars are ± SE around annual mean.

Mean annual pH of tributaries varied from 7.7 ± 0.1 at Chorangwa River to 8.8 ± 0.1 in the Kabenga tributary (Fig. 4.7). The only sites where pH was above that of the main Katuma River were at the confluence of waters from Kapapa River and Paradise Spring and the Kabenga tributary. The remaining sites were slightly alkaline and within the range of the main Katuma River.

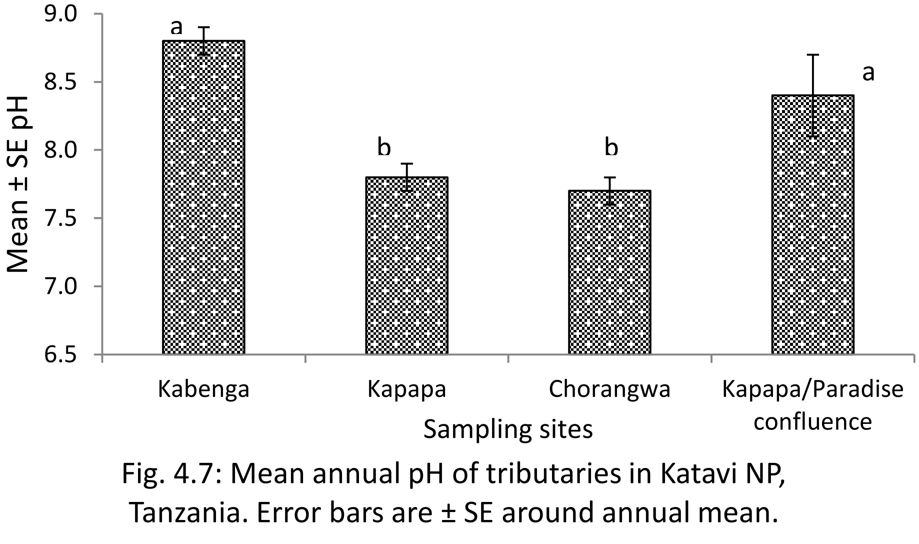


Fig. 4.7: Mean annual pH of tributaries in Katavi NP, Tanzania. Error bars are ± SE around annual mean.

Seasonal variation in pH

Water pH varied significantly between sampling months ($F_{11,\ 179}$ = 13.966 $p < 0.001$). Fig. 4.8 gives an example of how pH changed over the study period at Ikuu Bridge, a river used intensively by hippopotami, especially in the dry season. Here, mean monthly, pH varied between 6.89 ± 0.03 in April 2010 and 8.44 ± 0.03 in July 2010. Major variations within a single month were observed in June 2010.

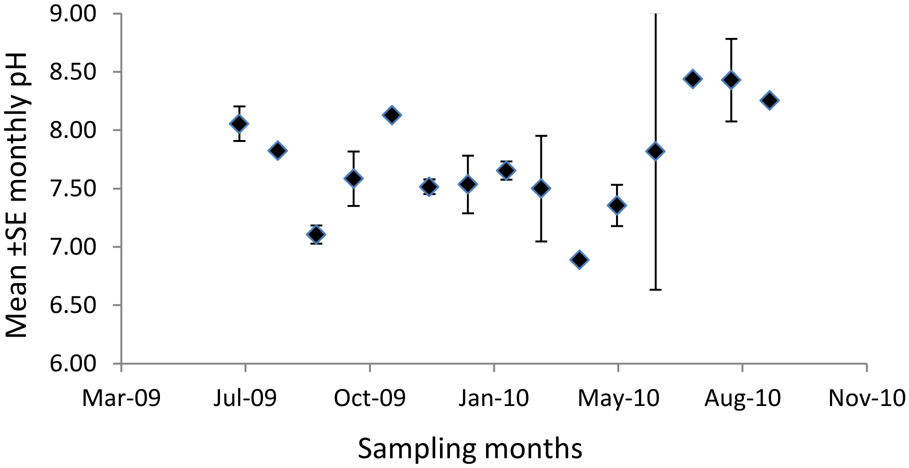


Fig. 4.8: Mean monthly water pH at Ikuu River Bridge site July 2009-September 2010 in Katavi NP, Tanzania.

In general, surface water pH was lower in the wet season months than in the dry season. Wet season mean pH ranged from 7.0 ± 0.1 to 7.8 ± 0.1 (Fig. 4.9). Sites with relatively low pH included Katavi Park inflow, Kavuu (Katavi) outflow, Sitalike Bridge and Lake Chada outflow. More alkaline waters were at Katuma Village, Katisunga Plains and Lake Chada inflow. There was no correlation between wet season pH and distance downstream ($r = 0.03$ $n = 15$ NS) (Fig. 4.9).

Mean dry season water pH ranged from 7.6 ± 0.2 in the upper catchment (at Iloba Village) to 8.8 ± 0.3 lower in the Park in the Katisunga Plains (Fig. 4.9) with an overall direct correlation between dry season pH and distance downstream ($r = 0.58$ $n = 15$ $p < 0.05$) (Fig.4.9).

There was more variation between sites during the dry season, with a range of 1.2 pH units compared with a range of 0.8 units during the wet season.

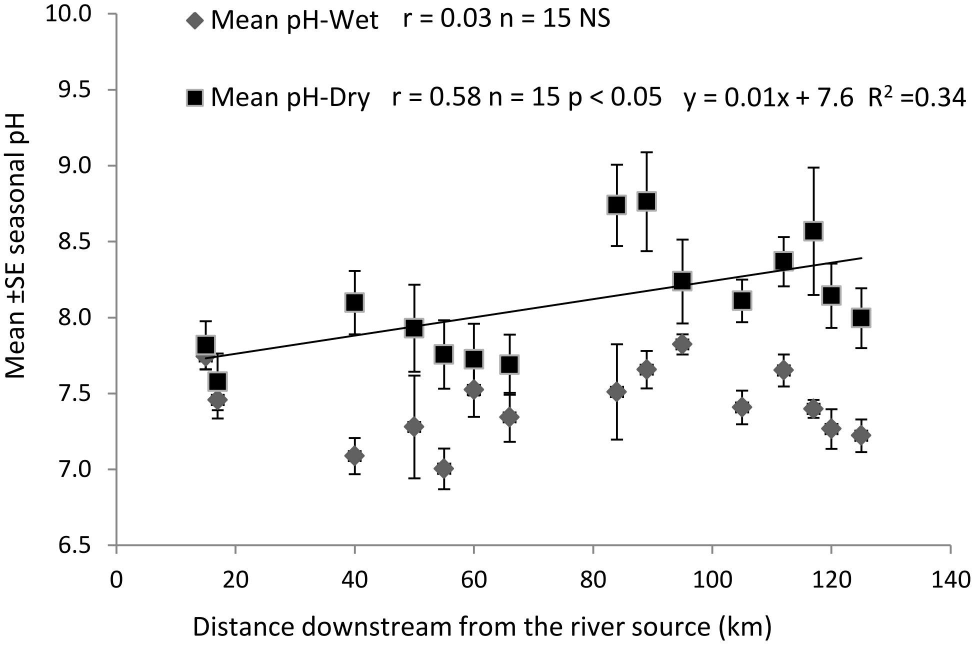


Fig. 4.9: Mean seasonal water pH variations at study sites downstream Katuma River (2009-2010) in Katavi NP, Tanzania. Error bars are ± SE around seasonal mean.

3.3 Electrical conductivity

Spatial variations of conductivity in the main river, tributaries, springs and boreholes

Annual mean conductivity of water varied significantly between river sites ($F_{14,\ 179}$ = 5.223 $p < 0.0001$) and ranged between the very low values of 76 ± 4.7 µS cm^{-1} in the upper catchment to its maximum value of 392 ± 80.8 µS cm^{-1} in the Park at the inflow to Lake Chada (Table 4.3).

Table 4.3: Annual mean (October 2009 – September 2010) electrical conductivity (Ec) measured in the Katuma River and its tributaries, associated springs and boreholes, Katavi, Tanzania.

Site	**Estimated Distance Downstream (km)**	**Annual mean Ec (μS cm^{-1})**	**± SE**
Katuma River			
Katuma village	15	76	4.7
Iloba Village	17	120	5.9
Katavi inflow	40	184	22.6
Lake Katavi	50	290	54.8
Lake Katavi exit	55	243	42.0
Airstrip	60	195	22.5
Sitalike Bridge	66	195	22.6
Inflow to Katisunga	84	246	39.0
Katisunga Plains	89	356	29.7
Flycatcher camp	95	300	36.7
Ikuu Bridge	105	338	67.0
Lake Chada Inflow	112	392	80.8
Lake Chada	117	276	36.4
Lake Chada exit	120	211	20.6
Kavuu (Katavi) Corner	125	192	19.2
Tributaries:			
Kabenga		606	97
Kapapa		90	4
Chorangwa		14	1
Kapapa/Paradise confluence		120	5
Springs:			
Ikuu Spring		168	12
Kasima Spring		306	18
Paradise Spring		104	18
Boreholes:			
Ikuu Spring borehole		140	27
Park HQ borehole		310	40
New Ikuu borehole		1971	29
Village borehole		622	5

Conductivity increased with distance downstream the Katuma River ($r = 0.63$ $n = 15$ $p < 0.05$) (Fig. 4.10).

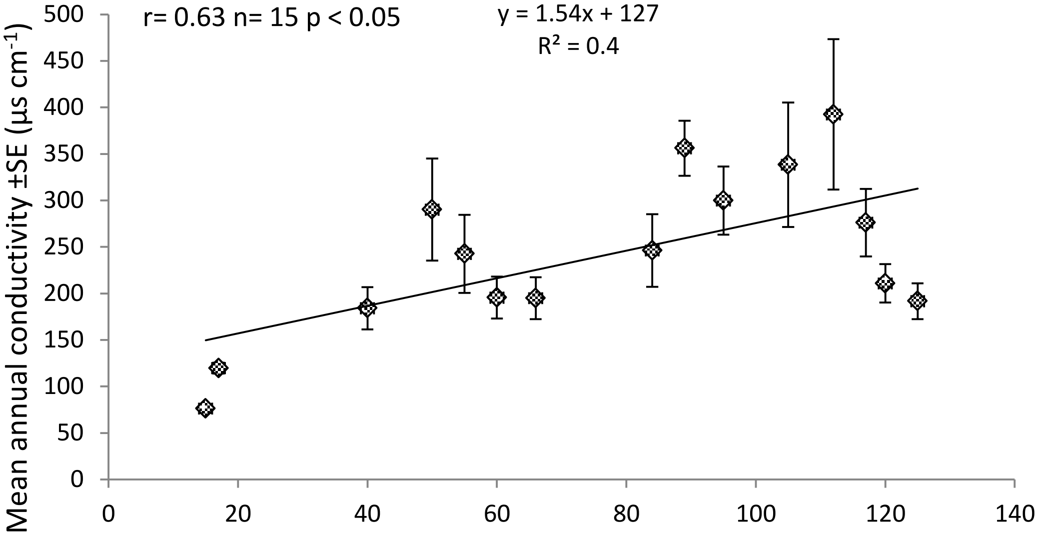


Fig. 4.10: Mean annual electrical conductivity downstream Katuma River from October 2009-September 2010 in Katavi, Tanzania. Error bars are ± SE around annual mean

Mean annual water electrical conductivity in spring outcrops and ground water pumped from boreholes varied between 104 ± 18 µS cm^{-1} at Paradise Springs to 1971 ± 29 µS cm^{-1} at the New Ikuu borehole (Fig. 4.11). Water from the New Ikuu borehole had a much higher conductivity than any of the other sites although conductivity was also high in water pumped from a borehole in Sitalike Village. Spring outcrops had conductivity values within the range recorded along Katuma River (Fig. 4.11).

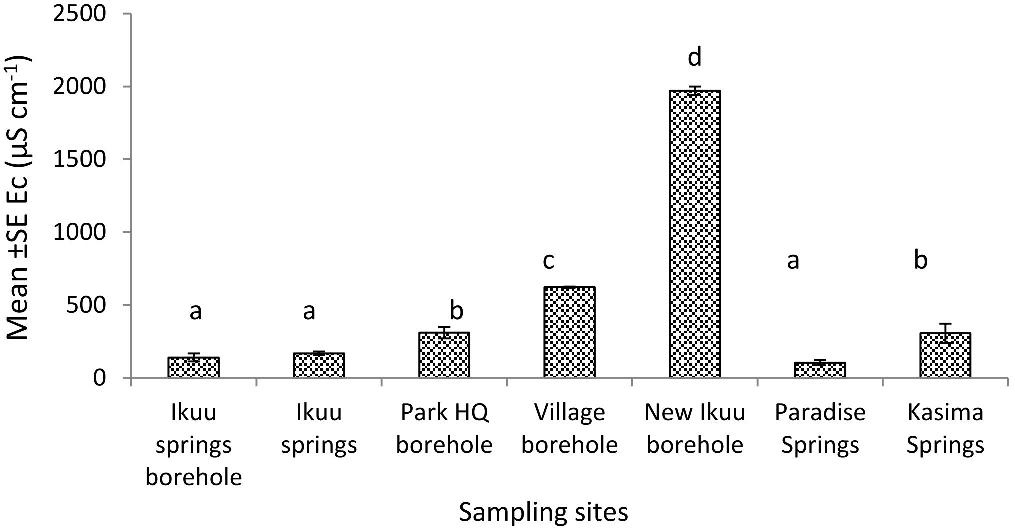


Fig. 4.11: Mean annual electrical conductivity (µS cm^{-1}) of ground water (boreholes and springs) in Katavi NP, Tanzania. Error bars are ± SE around annual mean

Mean annual electrical conductivity in tributaries varied between 14 ± 1.0 in the Chorangwa River to 606 ± 97 in the Kabenga (Fig. 4.12). Kabenga River had higher values than the main Katuma River and Chorangwa River water much less conductive than water from any of the other sites in Katavi.

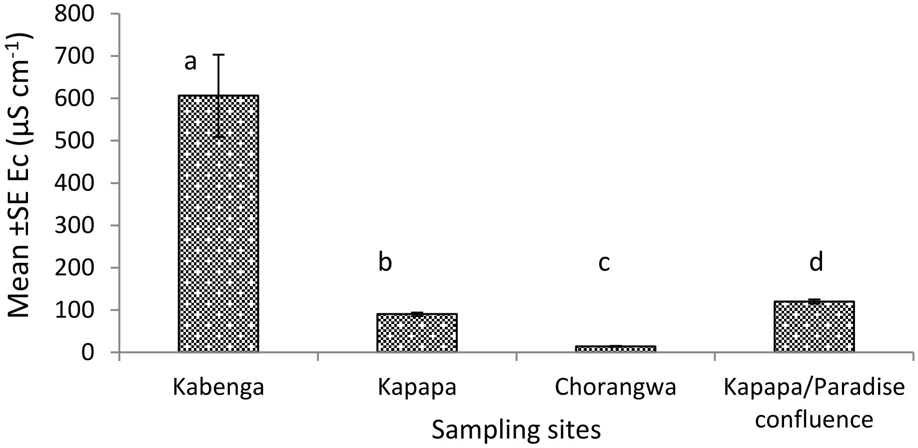


Fig. 4.12: Mean annual electrical conductivity (µS cm^{-1}) of surface waters from tributary rivers in Katavi NP, Tanzania. Error bars are ± SE around annual mean.

Seasonal variation in conductivity

Conductivity varied between sampling months ($F_{11,\ 179}$ = 7.603 $p < 0.0001$), with dry season months having higher conductivity than wet season months (Fig.4.13).

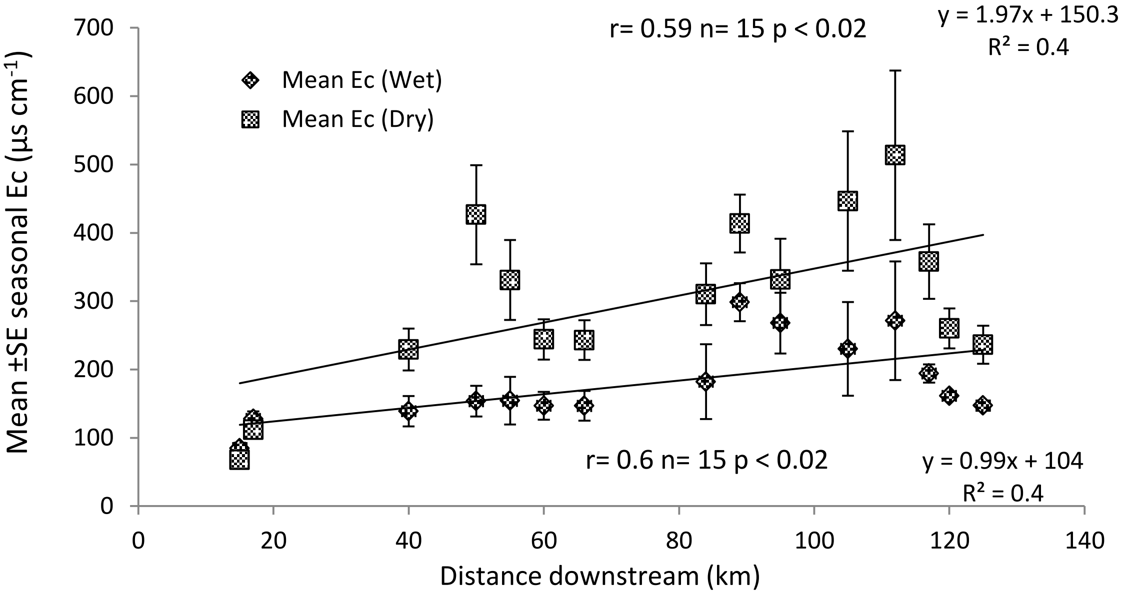


Fig. 4.13: Seasonal variations in electrical conductivity downstream Katuma River from October 2009-September 2010 in Katavi, Tanzania. Error bars are ± SE around seasonal mean

During the wet season, mean electrical conductivity varied between 85 ± 7.9 µs cm^{-1} at Katuma Village and 299 ± 27.7 µs cm^{-1} in the Katisunga Plains. There was a positive correlation between wet season electrical conductivity and distance downstream (r = 0.6 n = 15 $p < 0.02$), (Fig.4.13).

Dry season conductivity varied between 68 ± 2.2 µs cm^{-1} at Katuma Village to 514 ± 123.9 µs cm^{-1} at the inflow to Lake Chada (Fig.4.13) with increasing conductivity with distance downstream (r = 0.59 n = 15 $p < 0.02$) (Fig.4.13).

4.0 Discussion

4.1 Temperature

Water temperatures increased downstream from the source of the Katuma River. Water temperatures varied between 24°C and 30°C which is typical for tropical rivers (Geijskes, 1942; Wolanski & Gereta, 2001; Gereta *et al*., 2004; Epaphras *et al*., 2008). In Ruaha NP, Tanzania, which has a similar climate to Katavi, water temperatures varied between 20°C and 33°C along the Great Ruaha River and associated waterholes (Epaphras *et al*., 2008).

Several factors may influence values for water temperature particularly the depth at which water is sampled. In the Serengeti, Wolanski & Gereta (1999) found a marked difference between surface water and underlying water temperatures with a decrease of up to 2°C per 0.9 m difference in depth. For uniformity, water in Katavi was all sampled at the same depth. Katuma River is less than 2 m deep even during the wet season and at its maximum depth, there was little evidence of temperature variations with depth. It is therefore thought that the water column was well mixed.

Diurnal variations may also affect results. For example, in the Seronera River, Serengeti, diurnal variation in water temperature is up to 6°C (Wolanski & Gereta, 1999). This range is greater or equal to the variation between all the sampling sites in Katavi measured over a distance of over 120 km. Although the exact time of sampling each site did vary between months, effort was made to keep to morning time sampling throughout the study period.

Environmental factors that may affect water temperatures include altitude, vegetation cover and openness of the area, shading and the time of sampling (Geijskes, 1942; Gereta & Wolanski, 1999; Wolanski & Gereta, 2001). These influences, particularly altitude and shading by trees are thought to explain the lower water temperatures in the upper forested catchment at Katuma Village. Downstream increases in water temperature were probably due to decreasing altitude, increasing openness of the river environment and longer opportunity for daytime warming of water. Highest water temperatures were recorded in the open plains with low or no tree cover. Similar observations by Gereta *et al*., (2004b) showed increasing downstream temperatures in the Serengeti due lack of shading by trees and other vegetation.

The reason for presenting temperature data as part of this work is to detect anomalies in the relationship between water and air temperature that might be due to additions of warmer ground water. With exception of Katuma Village where shading seemed to explain the lower than expected water temperature, any impacts of ground water on temperature were not detectable. This is because there was no unexplained variation in the relationship between air and water temperature over the study area.

Seasonal variation in water temperature was expected but was not detected. During the dry season, water volumes and flows in the river were lower than in wetter months and temperatures were therefore expected to rise more quickly and to a higher temperature during the day (and cool more quickly overnight) than in the wet season. Ground water inputs would make a higher proportionate contribution to water volume in the dry than in the wet season so locally higher than expected water temperatures would occur in the dry season although were not observed.

Seasonal variations in water temperature broadly corresponded to air temperature. Minimum monthly mean air temperature was recorded in August during the dry season while the highest was recorded in December. December is at the start of wet season. Water temperature therefore reflected the prevailing air temperatures and Hypothesis 1 is therefore rejected.

4.2 Water pH

Most of the Park and its neighboring areas are underlain by metamorphic rocks of Palaeproterozoic age, gneisses and metamorphic grades of the Ubendian super group. These have been intruded by several phases of granitic rocks (Waltert *et al*., 2008; Meyer *et al*., 2007; Rukwa, 2011). The pH of natural waters is therefore predicted to be neutral to slightly acidic.

Katavi waters were neutral or slightly to moderately alkaline with values similar to those recorded in Katavi by Lewison (1996) where pH varied between 6.9 to 7.7 in Lakes Katavi and Chada and the Katuma River.

Shallow rift valley wetlands and lakes in East Africa are typically more alkaline than their geology predicts because of salt input from ground water and hot springs (Yuretich, 1982) and high evaporative water loss (Peterson, 1973; Rodgers, 1982; Shorrocks, 2007; Wilhelm 1993 as quoted in Meyer *et al*., 2005; Yuretich, 1982). Katavi waters were generally less alkaline than in rift valley lakes of East Africa. In Kenya, Olago *et al*. (2009) found that rift lakes had pH values ranging from 7.7 to 10.7. The Ruaha River with its associated natural springs and watering holes also appears more alkaline than Katavi with pH varying between 7.2 and 9.4 (Epaphras *et al*., 2008). In the Serengeti, pH in the rivers and swamps ranged from 5.9 to 10 (Wolanski & Gereta, 2001) and thus spanned a wider range than in Katavi. There were spatial and temporal variations in pH within the Serengeti with alkaline conditions (pH > 10) in the plains and acidic conditions (pH = 5.9) in the wooded areas (Gereta, 2004). In Tarangire NP, Tanzania, pH varied between 7 and > 11 with higher pH during the dry than wet season (Gereta *et al*., 2004b). In both Tarangire and Serengeti, data were collected over more than one year. High pH in other East African waters may be seasonal and relate to their higher fertility and the effects of intense photosynthesis by algae on the alkalinity and hence pH of water. The generally low conductivity of waters in Katavi suggests that the nutrient status of water in Katavi is relatively low compared to waters elsewhere.

Water pH varied significantly between study sites and months and was more site specific than other variables, with no overall downstream trend. Some large variations were very local, for example, in the river site at Ikuu. Ikuu is one of the animal recording sites and large pH variations in June 2010 may have been linked to increasing hippopotamus abundance over the transition between the wet and dry season. Any effects of additions of groundwater on pH would have been hidden by the probably much larger influences of drying, disturbance of the sediment and nutrient enrichment by dung.

Several other sites had higher than average pH. These were Paradise Springs, the New Ikuu borehole and the Kabenga tributary. High alkalinity at Paradise Springs and in water pumped from the New Ikuu borehole is likely to be linked to ground water from locally calcareous geology. The Kabenga may also be fed by calcareous ground water but may also be influenced by human activity outside the Park boundary since the tributary through human settlement and farmed land outside the Park boundary.

Apart from the three sites discussed above, there is little detectable evidence of any significant point sources of ground water to the Katuma River or its associated swamps and lakes. The range of values between sites was generally small and this also suggests that the runoff from the surface catchment is the major source of water for the Park. This is broadly similar to the Ruaha NP where Epaphras *et al.* (2008) found no significant differences between the pH of river water, springs or artificial watering holes. There is thus no evidence from this part of the study to suppose that the open waters of Katavi are any different from other Rift Valley lakes in that their major sources of water are rainfall, perennial/ephemeral streams and un-channeled runoff (Olago *et al*., 2009). This is consistent with the drying of the Katuma River in 2004; flow would have been sustained had significant perennial ground water originating in the Park contributed to flow.

The starting hypothesis is not accepted because although pH largely reflected the metamorphic geology of the catchment area, it did not reflect geology alone. pH also varied locally perhaps because local ecological processes increased the alkalinity of more fertile water.

4.3 Electrical conductivity

There are very many influences on the total ion concentration in natural waters. These include larger-scale influences such as climate and bedrock geology, more local influences such soils, plants and animals, and anthropogenic influences such as land use (Bruckner, 2011). Flow volumes, run-off, ground water inflows, temperature, evaporation and dilution may also add, concentrate or dilute ions in water.

Conductivities of between 0-800 µS cm^{-1} are usual in freshwaters with values of up to 800-1600 µS cm^{-1} in river margins (Suttar, 1990). The electrical conductivity of waters in Katavi National Park was within the range expected in fresh water environments with very low conductivities in the upper catchment indicating base poor water arising from the metamorphic or granitic bedrock. Conductivity was also low in the Chorangwa and Kapapa tributaries that both flow from an upper granitic escarpment. A general pattern of increasing conductivity downstream indicates ion accumulation due to transport of weathered materials from the catchment to the river and the indirect ecological effects of accumulation of organic matter in the lower alluvial plains. Hypothesis 3 was thus largely supported.

Dry season conductivities in Katavi were higher than in the wet season suggesting an important overall influence of evaporation in the dry season and dilution in the wet season. The seasonal patterns support Hypothesis 4. In this work, however, the effect of evaporation cannot be separated from any increased proportion of ground water in low dry-season flows.

Ground water in the region has a higher conductivity than surface water (Bruckner, 2011). Epaphras *et al*. (2008) found that electrical conductivity in the Great Ruaha River and its associated waterholes and springs varied between 302 µS cm^{-1} and 1990 µS cm^{-1}. Most of the stations in Great Ruaha had much higher conductivity than in Katavi. Of the 27 stations sampled, only six had conductivity below 450 µS cm^{-1}. Relatively high conductivities could have been explained in the Ruaha by inputs from natural springs, but this explanation was discounted because springs there were not considered deep enough. Lack of any significance differences in conductivity in the river, natural springs or artificial waterholes was observed and this suggested that conductivity was mainly influenced by the uniform catchment geology. The same argument may be relevant for Katavi where there were also no convincing differences between river and spring water.

Waters with conductivity between 1600 and 4800 µS $cm^{-1}$are considered brackish. Only one borehole site (the New Ikuu borehole) in Katavi had usually high conductivity at 1990 µS cm^{-1}. This was likely to have been saline ground water pumped from the Parks deepest borehole. Several boreholes exist in Katavi to serve accommodation for Park staff, an administrative office and tourist camps and all are more shallow and 'fresh' than at New Ikuu. Generally low conductivities elsewhere suggest that groundwater contributions to surface flow are small.

Ecological processes can also affect conductivity. In Katavi, higher conductivities were recorded in alluvial swamps (Lake Katavi, Katisunga plains, Lake Chada) and where flow velocity decreased at bridges (e.g. at Ikuu Bridge) and where the river left or entered swamps (Flycatcher camp and Lake Chada inflow). Ion accumulation in swamps perhaps linked to mineralization of organic matter was probably occurring and reduced oxygen concentration in swamp sediments may have retained ammonium and increased the solubility of some elements such as phosphorus and iron which would then have diffused into the water column and contributed to conductivity. This observation is consistent with Estevez & Nogueira (1995) who found that shallow lakes and flood plains influenced water chemistry and functioned as nutrient storage compartments when rivers flow through them. Similar observations were made by Boar (2006) for swamps that intercepted and transformed materials as they moved from catchment to receiving water. In contrast to the present study, Lewison (1996) found that Katuma River water had higher conductivities than Lakes Katavi and Chada. Work by Lewison was conducted over five months mainly in the wet season when dilution would have affected and reduced conductivity so the differences between the two studies give some additional support for Hypothesis 4.

5.0 Conclusions

Temperature measurements made in Katavi waters have shown little deviation from the expected patterns in relation to air temperature and gave little or no evidence of significant addition of ground water to the Katuma River. The usefulness of water temperature is, however, in doubt because of the overriding local effects of shading and because there was little consistent difference between the temperature of water from the river and from the deepest borehole (the New Ikuu borehole) and from spring-fed sites. Only the tributaries showed variations with the rest.

With the exception of one borehole, the pH and electrical conductivity of the main river, its tributaries, boreholes and springs varied little between sites within the Park and downstream changes were predictable. This gave little evidence of groundwater contribution to the main river.

pH was generally slightly higher than that predicted from catchment geology. Strong ecological processes particularly in seasonal swamps are likely to have had local effects on conductivity and perhaps pH that superimposed on the background influence of catchment geology.

Predictable downstream increases in conductivity (with few anomalies) suggest that ions are transported by runoff from the surface drainage catchment with catchment area increasing with distance downstream. Lower wet season conductivities indicate dilution of ions in larger flow volumes and higher dry-season values suggest concentration through evaporation. Dilution, concentration and mixing all confound conductivity as an indicator of groundwater.

None of the three parameters used provided any convincing evidence of significant groundwater contributions to the flow in the Katuma River. This conclusion is consistent with the drying of the river in 2004; flow would have been sustained had perennial ground water originating in the Park contributed base flow. Water was slightly more alkaline in some of the spring-fed sites which are consistent with groundwater contributions. These spring-fed areas are thus major dry-season wildlife refuges.

A main conclusion of this Chapter is therefore that the Katuma River is highly dependent on runoff from its surface drainage catchment, much of which is above the Park's northern boundary. Since Katuma River is the Park's major water resource, any upstream impacts on its flow volume and duration will have rapid, major and very damaging effects on the Park.

Appendix II

Table 2.1: GPS locations of water quantity and quality study sites and their estimated distance downstream Katuma River in Katavi NP, Tanzania.

S/No	Site Name	Est. distance downstream (km)	GPS location
1	Katuma Village	15	36M 0246800 UTM 9301464 *Alt* 1094 m
2	Iloba Village	18	36M 0261919 UTM 9281260 *Alt* 1010 m
3	Katavi inflow to park	40	36M 0277024 UTM 9263437 *Alt* 972 m
4	Lake Katavi	50	36M 0280131 UTM 9257676 *Alt* 971 m
5	Lake Katavi exit	55	36M 0281481 UTM 9259279 *Alt* 969 m
6	Airstrip	60	36M 0292490 UTM 9266421 *Alt* 963 m
7	Sitalike Bridge	66	36M 0294723 UTM 9266730 *Alt* 944 m
8	Katisunga entrance	84	36M 0295326 UTM 9257106 *Alt* 944 m
9	Katisunga plains	89	39M 0296440 UTM 9238346 *Alt* 923 m
10	Flycatcher Camp	95	36M 0297039 UTM 9236711 *Alt* 914 m
11	Ikuu Bridge	105	36M 0303007 UTM 9236110 *Alt* 919 m
12	Lake Chada inflow	112	36M 0305582 UTM 9235693 *Alt* 926 m
13	Lake Chada	117	36M 0307464 UTM 9233962 *Alt* 921 m
14	Lake Chada exit	120	36M 0308492 UTM 9227622 *Alt* 918 m
15	Kavuu (Katavi) outflow	125	36M 0306553 UTM 9223665 *Alt* 916 m
1	Kasima Springs	Springs	36M 0301732 UTM 9241805 *Alt* 926 m
2	Ikuu Springs	Springs	36M 0299625 UTM 9237125 *Alt* 924 m
3	Paradise Springs	Springs	36M 0323694 UTM 9233964 *Alt* 925 m
1	Kabenga Tributary	Tributary	36M 0292490 UTM 9266421 *Alt* 963 m
2	Kapapa Tributary	Tributary	36M 0320294 UTM 9248365 *Alt* 961 m
3	Paradise-Kapapa confluence	Tributary	36M 0321600 UTM 9233438 *Alt* 925 m
4	Chorangwa	Tributary	36M 0339063 UTM 9231668 *Alt* 913 m

Appendix III

Table 3.1: Summarised abundance table for hippopotami in the five study sites in Katavi NP, Tanzania (May 2009 – September 2010)

	Paradise Springs		**Ikuu Springs**		**Lake Katavi**		**Ikuu Bridge**		**Lake Chada**	
Months	***Ads.***	***Juv.***	***Ads.***	***Juv.***	***Ads.***	***Juv.***	***Ads.***	***Juv.***	***Ads.***	***Juv.***
May'09	53	7	77	3	21	4	9	2	16	5
Jun'09	55	7	77	3	34	6	11	2	25	7
Jul'09	56	8	102	17	68	7	14	3	25	7
Aug'09	52	4	147	15	105	15	18	3	30	9
Sep'09	63	11	368	18	203	17	60	11	31	5
Oct'09	104	24	482	18	307	43	214	36	98	22
Nov'09	104	26	233	17	560	40	215	35	96	19
Dec'09	105	25	166	14	165	35	129	21	96	19
Jan'10	81	17	115	13	77	13	103	17	84	9
Feb'10	-	-	53	7	63	8	59	8	51	6
Mar'10	-	-	56	7	60	7	61	13	53	6
Apr'10	-	-	58	7	56	14	59	13	53	7
May'10	67	24	13	3	31	8	21	6	15	6
Jun'10	67	27	16	2	28	7	24	5	15	8
Jul'10	73	32	25	2	34	7	19	9	17	8
Aug'10	119	31	180	8	175	24	90	24	70	16
Sep'10	127	37	240	9	190	32	107	32	94	19
Total	**1126**	**280**	**2408**	**163**	**2177**	**287**	**1213**	**240**	**868**	**177**
Mean	**80**	**20**	**142**	**10**	**128**	**17**	**71**	**14**	**51**	**10**
SE	**6.99**	**2.89**	**31.27**	**1.46**	**33.26**	**3.14**	**15.89**	**2.81**	**7.83**	**1.41**

Key: Ads=Adults Juv. =Juveniles

Appendix IV

Table 4.1: Mean monthly frequencies (%) for adult and juvenile hippopotami activity budget in Katavi NP, Tanzania. Errors are ± SE around monthly mean.

Months	Resting		Standing		Walking		Feeding		Touching	
	Adult	Juveniles	Adult	Juveniles	Adult	Juveniles	Adult	Juveniles	Adult	Juveniles
Sep-09	39.5 ± 6.5	29.5 ± 2.5	10.1 ± 2.5	12.7 ± 3.3	26.3 ± 2.5	29.8 ± 5.0	16.9 ± 2.8	14.2 ± 3.1	7.2 ± 1.5	13.7 ± 3.1
Oct-09	52.2 ± 2.9	50.3 ± 4.5	9.0 ± 1.0	9.2 ± 2.2	23.1 ± 1.9	18.6 ± 3.2	9.3 ± 2.6	11.0 ± 3.1	6.4 ± 1.0	10.9 ± 2.2
Nov-09	40.1 ± 5.4	35.7 ± 2.2	11.6 ± 2.1	13.0 ± 3.3	20.6 ± 2.4	19.1 ± 3.9	20.3 ± 2.9	15.4 ± 2.3	7.3 ± 1.1	16.8 ± 2.6
Dec-09	41.3 ± 2.6	39.1 ± 3.0	10.3 ± 1.3	14.3 ± 1.7	23.7 ± 2.2	17.4 ± 0.6	19.1 ± 3.2	17.7 ± 1.9	5.5 ± 1.2	11.5 ± 1.6
Jan-10	44.2 ± 2.3	32.5 ± 4.4	10.9 ± 1.2	13.0 ± 1.6	20.0 ± 0.5	17.9 ± 2.3	21.2 ± 2.4	20.8 ± 2.0	3.7 ± 0.8	15.8 ± 2.1
Feb-10	51.3 ± 4.3	44.4 ± 2.0	10.0 ± 2.0	12.4 ± 2.2	16.0 ± 2.2	15.5 ± 2.1	20.8 ± 2.8	18.1 ± 2.3	2.0 ± 0.7	9.6 ± 1.7
Mar-10	52.7 ± 2.4	43.4 ± 2.9	7.1 ± 1.0	11.7 ± 2.4	17.1 ± 1.2	16.9 ± 0.6	22.0 ± 1.9	19.4 ± 1.5	1.3 ± 0.1	8.6 ± 2.3
Apr-10	51.1 ± 1.8	45.1 ± 1.8	7.5 ± 1.5	10.1 ± 2.1	18.3 ± 1.1	16.5 ± 0.5	22.2 ± 1.9	21.3 ± 1.2	1.0 ± 0.1	7.2 ± 1.6
May-10	51.6 ± 3.2	46.0 ± 4.1	7.5 ± 1.1	7.2 ± 1.5	15.1 ± 2.8	15.3 ± 3.3	22.0 ± 1.2	18.0 ± 2.0	3.9 ± 0.4	13.5 ± 1.5
Jun-10	47.3 ± 2.6	37.5 ± 2.3	7.6 ± 1.6	7.2 ± 1.0	13.5 ± 1.2	13.4 ± 3.2	26.9 ± 3.5	20.9 ± 3.3	4.7 ± 0.4	21.0 ± 1.6
Jul-10	48.2 ± 3.8	37.8 ± 2.0	8.4 ± 0.7	9.9 ± 0.8	12.7 ± 1.3	12.8 ± 1.6	26.7 ± 3.1	21.6 ± 3.1	4.0 ± 1.3	18.0 ± 2.3
Aug-10	46.5 ± 5.2	38.7 ± 3.3	7.7 ± 1.4	11.1 ± 2.3	18.8 ± 1.9	15.6 ± 2.2	23.3 ± 4.5	20.2 ± 5.0	3.7 ± 0.7	14.4 ± 2.1
Sep-10	43.0 ± 5.4	36.8 ± 4.8	9.9 ± 2.0	13.9 ± 3.5	22.8 ± 1.3	22.3 ± 2.3	18.8 ± 2.4	13.7 ± 1.8	5.5 ± 1.3	13.3 ± 2.4

Table 4.2: Spatial variations in frequencies (%) of activity budget for adult and juvenile hippopotami in Katavi NP, Tanzania. Errors are ±SE around annual mean.

	Ikuu River		Lake Chada		Lake Katavi		Paradise Springs		Ikuu springs	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Resting	51.2 ± 1.3	44.7 ± 2.1	41.4 ± 2.1	35.7 ± 2.4	40.6 ± 2.6	37.0 ± 2.2	43.5 ± 2.7	39.8 ± 3.5	55.7 ± 1.4	40.5 ± 1.8
Standing	9.1 ± 0.9	8.9 ± 0.9	10.1 ± 0.7	13.1 ± 1.3	8.2 ± 1.1	11.2 ± 1.8	9.1 ± 1.2	10.1 ± 1.6	8.9 ± 1.1	12.5 ± 1.3
Walking	18.2 ± 1.5	16.5 ± 1.2	20.9 ± 1.4	17.2 ± 1.3	21.4 ± 1.6	17.9 ± 1.7	17.1 ± 1.6	17.0 ± 2.8	17.8 ± 1.6	20.5 ± 2.8
Feeding	17.3 ± 1.6	14.3 ± 1.3	22.6 ± 1.3	18.3 ± 1.3	25.6 ± 2.2	22.1 ± 1.9	24.0 ± 1.7	20.0 ± 2.3	14.6 ± 1.5	14.7 ± 1.5
Touching	4.1 ± 0.8	15.6 ± 1.1	5.1 ± 0.7	15.7 ± 1.6	4.2 ± 0.7	11.8 ± 1.7	6.3 ± 0.9	13.1 ± 1.1	3.0 ± 0.5	11.9 ± 2.0