Chapter one
General Introduction and Study Rationale
Introduction

Many countries in sub-Saharan Africa host large and world-famous conservation estates some of which are hotspots of unique biodiversity and ecosystem processes and offer excellent opportunities for ecotourism. Nonetheless, numerous changes have markedly modified both protected and non-protected areas in many of these countries in recent decades with significant consequences for biodiversity conservation and human well-being. Marked increases in human populations, shifts in cultural traditions and land tenure arrangements and rising demand for land for human settlements, crop and livestock production and other uses have fundamentally altered land use patterns (Meyer and Turner 1994; Foley et al. 2005). The impacts of these land use changes are further compounded by climatic changes due to global warming, thereby posing major challenges to efforts to conserve and sustain biodiversity, key ecosystem processes and services in protected and non-protected areas, especially in dryland savannas (Ogutu and Owen-Smith 2003, Holmgren et al. 2006; Li et al. 2006). These changes often have asymmetrical effects on neighboring protected and non-protected ecosystems and thus alter the nature and strength of critical ecosystem connectors and flows.

Marked impacts of land use changes are evident in Kenyan ecosystems regardless of their conservation status and include loss of wildlife habitats in savanna rangelands, degradation, fragmentation and loss of wildlife migratory corridors, restricted access to water, spiraling human-wildlife conflicts, loss of biodiversity and declining wildlife abundance (Prins 1992; Verlinden 1997; Homewood et al. 2001; Serneels and Lambin 2001). The Masai Mara Region of Kenya (Mara), which forms the northernmost part of the Serengeti-Mara Ecosystem, exemplifies savanna rangelands experiencing major perturbations in recent decades. Although the Maasai and their livestock have long coexisted harmoniously with wildlife in the Mara; that harmony is now being increasingly threatened by human population growth and expansion of settlements, diversification of livelihood options, privatization of formerly communally owned lands, among other changes (Lamprey and Reid 2004; Ogutu et al. 2009). The changing land tenure has encouraged cultivation, permanent settlements, including development of urban centers, and intensification of land use with the result that traditional wildlife habitats have contracted and wildlife numbers and diversity declined (Thompson and Homewood 2002; Ottichilo et al. 2001; Serneels and Lambin 2001).

African savannas support diverse assemblages of indigenous large herbivores supplemented by livestock (Skarpe 1991) whose grazing and browsing activities shape many ecosystem processes, including creating and maintaining spatial heterogeneity in landscapes (McNaughton 1984, 1985; Illius and O’Connor 2000; Ogutu et al. 2010). Human activities and location of water sources additionally influence ecosystem structure and function, in particular the spatial and temporal
distribution of wild herbivores and livestock (Western 1975; Verlinden 1997, de Leeuw et al. 2001; Redfern et al. 2003; Ogutu et al. 2010). This is especially true for the Mara, in which water availability becomes progressively limited and water sources become points of contacts and conflicts between wild herbivores, the pastoral Maasai and their livestock during the dry season. However, although the Serengeti-Mara is the most well studied savanna ecosystem in Africa in both its ecological and human dimensions, with detailed background knowledge available on community and ecosystem processes, the ongoing sentinalization of the pastoral Maasai and increased livestock concentrations, especially around water sources, have exposed glaring gaps in our knowledge and understanding of how these processes alter biodiversity, particularly in riparian-edge habitats, that are key resources zones during dry seasons.

Within the riparian habitats of the Mara, the common hippopotamus *Hippopotamus amphibious* Linnaeus 1758 and livestock are the main resident grazers. Due to their strong water dependence, both hippos and livestock heavily utilize the riparian habitats year-round and so have the potential to compete for grazing resources. Furthermore, because hippo and livestock grazing can differentially modify vegetation structure, they may have contrasting effects on plants and other herbivore species (Lock 1972; Walker et al. 1987; Harrington et al. 1999; Eltringham 1999; Fleischner 1994; Thrash 2000).

I thus undertook this study to analyze (1) human-hippo conflicts in Kenya over the 12-year period covering 1997-2008, (2) hippo population dynamics in the Mara during 1958-2006 and (3) the pattern and consequences of hippo and livestock grazing in the riparian habitats of the Mara on vegetation structure, species richness and composition and herbivore abundance and diversity under protection in the Masai Mara National Reserve and traditional pastoralism in the adjoining pastoral ranches.

**Mara Region**

The riparian habitats that formed the main focus of this study are part of the Mara River Basin that covers some 13,750 km², and is located between 37.78°E and 0.43°S in southwestern Kenya and 33.78°E and 1.48°S in northern Tanzania. The basin is shared between Kenya and Tanzania, with an upper basin area of about 8,941 km² (65%) in Kenya and a lower basin area of about 4,809 km² (35%) in Tanzania (WREM 2008). The basin is the catchment area for the Mara River and is also an important habitat for people and wildlife (Fig. 1.1). The basin is characterized by a diversity of land use patterns ranging from natural forests in the upper reaches to large-scale mechanized farms, smallholder subsistence farms, communal pastoral grazing lands, protected open savanna grasslands and wetlands. The upper
reaches of the basin is at about 2,915 m asl, and comprises escarpments that constitute the Mau Forests in Kenya, receiving an average of 1,400 mm of rainwater annually. This rainwater infiltrate through the soil into Enapuyapui swamp to form the Nyangores and Amala rivers, that are the source and only perennial tributaries of the Mara River (WREM 2008; Fig. 1.1). The Mara River meanders through Maasai pastoral ranches and the Masai Mara National Reserve (MMNR). In the MMNR, two other main but seasonal tributaries, the Talek and the Sand Rivers, join the Mara River. The mainstream Mara River continues flowing through the savannah grasslands of the northern Serengeti National Park (SNP) before entering the Mara Swamp and discharging into Lake Victoria (Fig. 1.1). Thus, the Mara River is part of the Lake Victoria drainage system and the greater Nile River Basin.

The lowlands and wooded savannah grasslands that form the Maasai pastoral ranches, MMNR and northern SNP receive an average annual rainfall ranging from about 500 mm in the southeast to 1200 mm in the northwest (Norton-Griffith et al. 1975), hence the flow of Mara River provides the only permanent source of surface water for the Maasai pastoralists, their livestock and wildlife. In addition, the Mara River sustains one of the greatest spectacles of the natural world; the annual
The focal species

The common hippopotamus, commonly referred to as hippo, is an unmistakable species, with a barrel-shaped, almost hairless body weighing about 1500 to 3000 kg (Kingdon 1982; Eltringham 1999). It is adapted to semi-aquatic habitats, and therefore it is never found far from water. Hippos have featured in human affairs since at least the time of Pharaohs, where they were venerated as gods and have been portrayed in art down the ages (Eltringham 1999). Therefore, it is surprising that in an intensely studied savanna like the Serengeti-Mara ecosystem, the hippo has largely been overlooked (see Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995; Sinclair et al. 2008). Nonetheless, the hippo is an exceptional megaherbivore (Owen-Smith 1988) within the Mara River Basin, and it differs from other megaherbivores in having a dual requirement of a shelter and day-living space in water and an open grazing range often visited at night (Eltringham 1999).

In coining the term megaherbivore, Owen-Smith (1988) grouped together all terrestrial large herbivores with an adult body weight greater than 1000 kg. Other megaherbivores within the Mara include the African Elephant *Loxodonta africana* Blumenbach 1797, Black Rhino *Diceros bicornis* Drummond 1826 and giraffe *Giraffa camelopardalis* Linnaeus 1758. Owen-Smith (1988) emphasized that the large body size of megaherbivores renders them largely immune to non-human predation and they can generally tolerate food of a lower quality than that required by other herbivores. Owen-Smith (1988) further suggested that megaherbivores
would therefore be less affected by predation or environmental fluctuations like drought and that their populations would be maintained at high densities causing heavy sustained impacts upon their environments. Nevertheless, hippos maintain short grazing lawns in areas that they graze, suggesting that they also enjoy high quality food. In addition, hippos can be vastly affected by environmental fluctuations especially prolonged droughts and above-average rainfall (Marshall and Sayer 1976; Smuts and Whyte 1981).

Historically, hippos were found throughout sub-Saharan Africa, but most populations have greatly declined in size while others have disappeared, with the largest populations remaining in East Africa (Eltringham 1999; Lewison and Oliver 2008). Although not strictly nocturnal, hippos typically forage for food at night, and spend the day digesting their food, sleeping and socializing (Klingel 1991). Hippos have a chambered stomach and are referred to as ‘pseudo-ruminants’, and their digestive system can effectively ferment grasses and other low quality foods (Eltringham 1999). Various studies claim that their diet consists predominantly, or solely, of grasses (Field 1970; Oliver and Laurie 1974; Mackie 1976; Scotcher et al. 1978; Kingdon 1982; Eltringham 1999) but recent studies have challenged this assumption and described their diet as variable (Mugangu and Hunter 1992; Boisserie et al. 2005; Cerling et al. 2008), with a few incidences of scavenging on carcasses reported (Dudley 1996). The primary threats to hippos are loss of essential grazing lands to cultivation and encroaching human settlement, unregulated or illegal hunting (Weiller et al. 1994; Eltringham 1999; Williamson 2004; Conservation 2006; Lewison and Oliver 2008) and the growing pressure on fresh water resources across Africa (WWC 2003) that has often resulted in loss of their habitats. Due to increasing human population and agricultural expansion and development in and around wetlands, hippos often run into frequent conflict with people. In addition, hippos have notorious crop-raiding tendencies and can extensively damage the range through grazing and trampling when they occur at high densities (Lock 1972; Thornton 1971; Mkanda and Kumchedwa 1997; Eltringham 1999). The protection of riparian and wetland habitats is currently therefore a pressing priority for hippopotamus conservation, including measures to prevent the drying-up of water courses and loss of riparian-edge grazing ground.

Hippos are important to the ecology of permanent wetlands in Africa and exert significant environmental impacts (Olivier and Laurie 1974). Their regular movements from water pools used during the day to adjacent grazing areas utilized at night create trails, modify river channel geomorphology, and assist in developing micro-topography (Naiman and Rogers 1997; McCarthy et al. 1998; Deocampo 2002), with consequences for other organisms. Their trampling and grazing impacts directly or indirectly control the availability of resources for other organisms along the riparian habitats, through physical modification, maintenance, or creation of micro-habitats. At moderate densities, hippos can be beneficial to the ecology of an
area through their maintenance of habitat mosaics while at high densities they can cause intense grazing, soil erosion and may decrease plant and other wildlife abundance and diversity (Field 1970; Thornton 1971; Lock 1972; Olivier and Laurie 1974; Eltringham 1999; Arsenault and Owen-Smith 2002). In addition, the short, hippo-grazed grasses along the riparian habitats create biological barriers to fire, further influencing biodiversity of riparian communities.

Hippos pond and create water pools that are important refugia for aquatic organisms. They stir the water, prevent development of anoxic conditions, while their dung fertilizes water, and alter the dynamics of nutrients and particulate matter, promoting primary production, especially fish life which in turn feed crocodiles and birds and numerous other aquatic organisms (Naiman and Rogers 1997; Gereta and Wolanski 1998; Wolanski and Gereta 1999; Mosepele et al. 2009). Thus even though they are less studied in the Serengeti-Mara ecosystem, hippos may have significant non-trophic impacts on the structure, function and biodiversity of this ecosystem.

The creation and modification of riparian habitat structures by hippos is an important mechanism generating landscape-scale heterogeneity and is synonymous with physical ecosystem engineering (Jones et al. 1994, 1997; Write et al. 2002). However, there has been little recognition of the importance of hippos and their influence in shaping the riparian habitat mosaics and environments across Africa (but see Olivier and Laurie 1974). Here I present a study on the grazing and trampling effects of hippos within a savanna riparian community and explore the feedback from the abiotic environment along rivers to hippo grazing, the responses of plants and other herbivore species to the changed abiotic conditions, in the protected reserve and the adjacent pastoral system in the Mara Region of Kenya. I assess differences in patterns of responses of plant and herbivore species abundance and richness to hippo and livestock grazing and how these patterns are modified by protection versus pastoralism.

**Research Hypotheses**

**H₁:** Vegetation height and cover will increase with distance from water in response to declining grazing intensities

This hypothesis predicts that vegetation height and cover will increase with increasing distance from water sources, due to declining grazing intensities from water (Fig. 1.2). The consequences of this hypothesis are that hippopotamus grazing will further contribute directly to patchiness in grasslands through defoliation and trampling within a restricted strip along the riparian zone, aiding spatial heterogeneity of landscapes at intermediate distances from rivers.
H2: Plant species richness will increase with distance from rivers in response to declining grazing intensities

This hypothesis predicts that plant species richness will increase with increasing distance from rivers in response to declining grazing and trampling intensity. The heavily grazed and trampled areas close to river banks will have low plant species richness except for forb species. The distribution and abundance of forbs is expected to respond positively to grazing intensity and the species abundance and richness of forbs to decline with distance from rivers (Fig. 1.3). Grass species will increase with distance from rivers as grazing intensity declines while shrub species will establish in areas of high grazing intensity and decline with distance from rivers as grazing intensity declines.

Figure 1.2 Hypothesized response of vegetation cover components, grass <10 cm high, grass 10–30 cm, grass >30 cm and forbs and shrubs to distance from rivers as a function of declining grazing intensity.

Figure 1.3 Hypothesized response of plant species, forbs, grass and shrubs with distance from rivers as a function of declining grazing intensity.
**H₃:** Herbivore abundance and species richness will increase with increasing distance away from rivers due to a corresponding increase in forage availability

This hypothesis predicts spatial variation in herbivore abundance and distribution with distance from rivers and along the distance-to-river gradient. Hippo grazing along riparian areas will facilitate some herbivore species and cause competitions with others. In addition, hippo grazing will influence predation risk for herbivores, as the cover of tall vegetation increases with distance from rivers, with varying effects on different herbivore foraging guilds. The dry seasons will further force herbivores to congregate close to rivers, amplifying habitat stress especially in the pastoral ranches grazed heavily by livestock. Herbivore use of the riparian habitats in the pastoral ranches will be constrained by human presence and livestock herding. Herbivores that are more water dependent and require high food quality will decline with distance from rivers. Herbivores that are bulk feeders will increase with distance from rivers. Herbivores that are less water dependent will be uniformly distributed relative to distance to rivers. In general, a humped distribution will describe the distribution of the abundance of most herbivores along the distance-to-river gradient (Fig. 1.4; Ogutu et al. 2010).

![Figure 1.4](image_url)

**Figure 1.4** Hypothesized response of herbivores that are, water dependent and sensitive to food quality, bulk feeders, and water independent and generalized herbivore response along grazing gradients from rivers.

**Research Questions**

I attempted to find answers to the following three questions. (1) How does the pattern of human-hippo conflicts throughout Kenya vary over time and what does this variation imply for the future of hippo conservation in Kenya? (2) How do
long-term hippo population dynamics respond to changing land use and climatic variability and compare with the dynamics of other megaherbivores in Kenya? (3) What are the impacts of hippo grazing on vegetation and other herbivores and how are these impacts modified by land use? In particular, how does the impact of hippopotamus grazing and trampling on (1) bare ground cover, (2) vegetation cover and height, (3) plant species richness and composition, (4) herbivore abundance and species richness vary along the distance-to-river gradient and with protection and pastoralism?

**Thesis outline**
This thesis is organized in 6 chapters as follows. Chapter 1 serves as an introduction and provides brief background information on anthropogenic effects on the distribution and abundance of herbivores in savannah ecosystems. The chapter also provides background information on the Mara River Basin that is the focus landscape for most of this study. This chapter also highlights the ecological importance of hippos in African wetlands. Finally, the chapter presents the three main hypotheses and research questions explored in greater detail in subsequent chapters of this thesis. Chapters 2 and 3 cover the conservation and management of hippopotamus in Kenya. Chapter 2 presents an analysis of human-hippo conflicts throughout Kenya during 1997 to 2008. Very few studies have directly addressed the problem of human-hippo conflicts in Kenya, thus, there has been major gaps in information on this topic. Given the importance that the Kenya Wildlife Service (KWS) attaches to wetlands and threatened species conservation, analysis of the long term monitoring data that KWS collects on human-hippo conflicts in Kenya is clearly useful. This chapter thus examines key management issues on human-hippo conflicts, identifying the extent, severity and distribution (spatial and temporal) of hippo-related damages to crops and how retaliatory killings of hippos are threatening and undermining hippo conservation efforts in Kenya. This chapter highlights the fact that conflicts between people and hippopotamus in Kenya probably cannot be entirely eliminated but can be mitigated, by discouraging agricultural activities associated with high human density on lands bordering riparian habitats and promoting conservation and sustainable use of wetlands.

Chapter 3 explores the population status and conservation of hippopotamus at one of Kenya’s important conservation area, the Masai Mara. Despite its imposing size and formerly large abundance, the common hippopotamus has been much less studied in Kenya compared to other Megaherbivores. Thus, this chapter also fills this important gap in our knowledge. The chapter reveals how hippopotamus populations can increase rapidly and expand their range even in a context of considerable climatic variability and against a background of deteriorating habitat conditions. Increased anthropogenic activities, especially land-use changes and livestock herding are predicted to adversely affect hippopotamus conservation.
efforts, with significant spill over effects on other mammalian grazers dependent on hippo grazing impacts on vegetation along riparian habitats.

The ecological implications of hippopotamus grazing and trampling activities and their relations with the environment are covered in Chapters 4 and 5. Although herbivore grazing is an important evolutionary force shaping vegetation biodiversity and structure in African savanna ecosystems, most studies have generalized herbivore grazing effects, with few studying the effects of specific herbivore species, and especially along sensitive riparian habitats. Chapter 4 explores the interactive effects of hippopotamus and livestock grazing on vegetation structure, herbaceous plant species composition and richness along a riparian habitat in protected and pastoral systems of Masai Mara, and demonstrates the important engineering impacts of hippopotamus that enables establishment and co-existence of plant species, culminating in increased species richness in areas experiencing intermediate grazing levels, especially within protected areas. Chapter 5 documents the facilitative role of hippopotamus grazing on habitat use by other wild herbivores along the Mara riparian habitat, demonstrating that hippopotamus grazing activities led to a shifting mosaic of patches that differ in vegetation structure, that enhance structural heterogeneity of vegetation and attract a diverse and abundant herbivore assemblage at intermediate distances from rivers. Lastly, chapter 6 synthesizes the results from chapters 2 to 5 and concludes that hippopotamus are keystone ecosystem engineers able to profoundly modify ecosystems and facilitate other herbivores in the Mara River Basin but the future of their conservation is threatened by dramatic land use changes in the basin, water abstraction from the Mara River, and rising levels of conflict with people throughout Kenyan wetlands. This chapter recommends urgent preparation of a species management plan for Kenyan hippos that aims to reduce human-hippo conflicts and promote peaceful interactions between hippos and local communities.

I have tried to make these chapters as independent of each other as possible so that each can be read essentially independently of the others, while retaining a sequence from the very general to the very particular, in what I consider to be a natural order for this thesis.