The impact of climate variability on the ecology of a lion (Panthera leo Linnaeus 1758) population and lion livestock conflicts in the Amboseli ecosystem – Kenya

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Introduction

1.1 The importance of conserving large carnivores and lion as a species

Carnivores are an important component of many ecological systems and they play a vital role in maintaining ecosystem health (Terborgh et al., 1999; Terborgh et al., 2002; Ray et al., 2005). Being at the top of the food chain, carnivores have important ecological impacts, such as the regulation of mesopredators and prey numbers present in an area (Terborgh et al., 1999). Important cascading trophic effects, caused by population changes of their prey or of sympatric mesopredators, may result when some of these large carnivores are extirpated from ecosystems. Unexpected effects of trophic cascades on various taxa and processes include changes to other vertebrates and herpetofaunal abundance or diversity. It could also have indirect effects and altered disease dynamics; carbon sequestration; modified stream morphology; and crop damage (Ray, 2005). Therefore, promoting tolerance and coexistence with large carnivores is a more crucial societal challenge now than ever before.

The removal of top predators from ecosystems commonly results in dramatic changes in biodiversity and community structure, and as a result these areas can have severe consequences for the functioning of ecosystems (Berger et al., 2001; Terborgh et al., 1999).

An absence of carnivores can have significant effects on herbivore – vegetation interactions, for example, species such as the African buffalo (*Syncerus caffer*), plain zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) exert more pressure on the vegetation when their abundance increases (Mills et al., 1995). However, the effect of top predators on the prey community is not always direct (killing prey). Other, indirect effects also play an important role in shaping ecosystem structure (Roemer et al., 2009; Oswald et al., 2014). For example, fear of predation can affect prey species' activity patterns, habitat use, group size, and response to predators (Altendof et al., 2001). These indirect effects of predation can cause prey to make a choice and neglect food in certain areas for their safety as they shift activities toward safer areas with less food, or they may increase vigilance at the expense of feeding efficiency. These alterations can ultimately affect the prey community (Lima & Dill, 1990).

Large carnivores are an important tool for conservation planning because they are often used as indicator species, umbrella species, flagship species or keystone species (Ray et al., 2005). An indicator species refers to a species whose characteristics (such as population density and reproductive success) are used as an index of attributes that are too difficult, inconvenient or expensive to measure for other species and/or for the environment in question (Simberloff, 1998). Umbrella species are those species that need large tracts of habitat. Therefore by conserving such species many other species are automatically preserved (Simberloff, 1998). Large carnivores such as lions are often used as umbrella species (Beier, 1993). Flagship species are usually charismatic, large vertebrates that are used to engage public interest in promoting the conservation of reserves, promote connectivity, corridors or enlarge existing reserves, thereby conserving other species (Sergio et al., 2008; Maes, 2004). The idea behind this is that, because large carnivores require extensive and intact habitats to survive, their conservation also protects other species found within their range or habitat (Ray et al., 2005). In addition to their value in conservation planning, top predators are also often charismatic and can have direct economic benefits. This is particularly important in developing countries, where revenues are generated by trophy hunting (Child, 2000; Baldus & Cauldwell, 2005; Lindsey et al., 2007), or by non-extractive viewing and photographic tourism (Treves & Karanth, 2003). Carnivores also often have socio-cultural values; in some societies, animal products such as skin, claws and teeth are used in traditional medicine (Toledo et al., 2011; Ripple et al., 2010; Ripple et al., 2014).

1.2 Protected areas and their importance for the conservation of lion and other large carnivores

Historically, the conservation of biodiversity throughout the world has been facilitated by the designation of protected areas (PAs) (Chape et al., 2005; Pimm et al., 1995). These are areas set aside principally for the protection and maintenance of biological diversity and of their natural and associated cultural resources. According to the International Union for Conservation of Nature (IUCN), protected areas (PAs) are managed through national legal systems or in some cases through other effective frameworks (IUCN, 1994). Most PAs have strict rules that exclude human activities and this enables them to provide better protection for many species that would otherwise have difficulties due to human activities (Salafsky & Wollenberg, 2000). PAs are therefore well recognized as important 'core' units for *in situ* conservation (Brandon et al., 1998; Bruner et al., 2001; Balmford et al., 2001; Chape et al., 2005; Gorenflo & Brandon, 2006). Nevertheless, PAs alone cannot provide a long term solution for the conservation of certain species such as large carnivores, because many of these PAs are too small to maintain viable populations. An example is Amboseli NP in Southern Kenya. This is because large carnivores such as lions (*Panthera leo*) usually have large home ranges and therefore only large PAs can provide full protection (Tuqa et al., 2014). Moreover, many wildlife species disperse outside PAs at certain times of the year and come into contact with humans (Tuqa et al., 2014; Geldmann et al., 2013), making their survival difficult due to human activities. Furthermore, effective management of PAs requires sufficient human and financial resources and law enforcement, which are lacking in many developing countries (Salafsky & Wollenberg, 2000)

1.3 Conservation status: effects of land use and climate change on populations of lions and other carnivores

It is widely accepted that global biodiversity is changing at an alarming rate (Millennium Ecosystem Assessment, 2005), and that much of this change in biodiversity is induced by human activities (Pimm et al., 1995). Ecologists are increasingly aware of the importance of environmental variability in natural systems. Variability is a critical environmental factor that may have consequences for vital population dynamics. Organisms are subject to selection imposed by both the mean and the range of environmental variation experienced by their ancestors. Overall extreme climate fluctuations are more relevant than mean values over a longer time span. Environmental variation and climate change are important for generalist, wide-ranging species, at the slow end of the slow-fast continuum of life histories, with broad implications for population regulation (Marion et al., 2010). Of all human impacts on biodiversity, land use change has been singled out as the greatest immediate threat to terrestrial biodiversity, because it results in fragmentation and loss of habitats (Vitousek et al., 1997; Jetz et al., 2007). Such changes may lead to the restriction of animal movements as well as a decline in species richness and abundance. There are many anthropogenic factors that drive land use change. The most important ones include the need for human settlements, cultivation of crops and other economic activities (Geist & Lambin, 2002). The impacts of these drivers of land use change on biodiversity vary because they differ in the extent to which they modify the quality of habitats (Forman, 1995). However, land use change due to agricultural expansion is often cited as one of the major threats to biodiversity.

Existing evidence shows that land use change has a negative impact on species. For example, predictions of the impact of tropical forest clearance show that approximately 50,000 species may become extinct by 2060 (Pimm & Raven, 2000). Similarly, the 'human footprint' study by Sanderson et al. (2002) suggests that anthropogenic land transformation is the single greatest threat to biodiversity. Furthermore, it is also estimated that 86% of globally threatened mammals on Earth are at risk of extinction from habitat change (Baillie et al., 2004).

Large carnivores are particularly vulnerable to habitat loss because they have large home ranges and require extensive, intact habitats to survive (Sillero-Zubiri & Laurenson, 2001). For example, loss of habitat is cited as the main threat to cheetah (*Acinonyx jubatus*) (Caro, 1994). This is in part because the cheetah is more vulnerable to spatial fragmentation, as heterogeneity in habitat is also required for successful protection of prey-kill from other predators (Durant, 1998). Furthermore, habitat loss may affect carnivores indirectly by reducing the availability of prey. Carbone & Gittleman (2002) showed that the abundance and distribution of carnivores is strongly related to the population density of their prey species. The impact of loss of habitat may be more severe for some species than for others, yet to date there are no comprehensive studies that have investigated the impact of habitat loss on carnivore biodiversity, especially in areas which have rich carnivore community such as Kenya.

It is clear from the above that the conservation of large carnivore biodiversity throughout the world is extremely challenging due to expanding human populations and the associated impacts on wildlife. These challenges are particularly acute in Sub-Saharan African countries, which are currently characterised by a rapid increase in human populations (Ceballos & Ehrlich, 2006). Unfortunately, in Sub-Saharan Africa, scientific information for conservation planning is often scarce (Rodriguez & Delibes, 2003).

These challenges are especially acute for carnivores because populations of many species are declining rapidly due to loss of habitat, hunting, depletion of prey, diseases and trade in body parts as well as conflict with humans (Novaro et al., 2000; Sillero-Zubiri & Laurenson, 2001). These declines are also accelerated by inherent biological factors that make carnivores more vulnerable to environmental change, such as their low densities (Cardillo et al., 2004; Cardillo et al., 2005). Large carnivores are usually at the top of the food chain, which means that they will always be less abundant than their herbivore prey, and therefore have lower densities and are more vulnerable to extinction (Noss et al., 1996, Sillero-Zubiri & Laurenson, 2001).

Consequently, large carnivores such as lions tend to suffer first when human populations expand into untouched habitats (Muntifering et al., 2006). In places where lions still occur outside protected areas, they are often intentionally or accidentally killed by humans (Woodroffe & Ginsberg, 1998; Graham et al., 2005; Woodroffe & Frank, 2005). Currently, lion populations are restricted to Sub-Saharan Africa and India (Schaller, 1972; Nowell & Jackson, 1996; Bauer & van der Merwe, 2004), African lions are considered genetically monotypic (Dubach et al., 2005). The IUCN Cat specialist group, however, has identified two sub-species, *Panthera leo leo* in Africa and *Panthera leo persica* in Asia. Several recent publications have identified the lion in West and Central Africa to be genetically distinct from the lion in East and Southern Africa, while this group would cluster with the Asiatic lion (Bertola et al., 2011; Dubach et al., 2005, Dubach et al., 2013; Barnett et al., 2006a, Barnett et al., 2006b, Barnett et al., 2014). There is need to conserve and protect the remaining lion populations by making an inventory of their numbers, species habitats, threats and prey populations and with the support of policies that enhance their conservation. There is, however, great local and international variation in current wildlife policies and laws regarding predator conservation and management throughout Africa. Lions are regulated for international trade under Annex II of the Convention for International Trade in Threatened Species (CITES). The African lion is classified as 'Vulnerable' on the IUCN Red List but 'Regionally Endangered' in West and Central Africa (Tumenta, 2012). Estimations of the lion population in Africa about 20 years ago rangeed from 30,000 to 100,000 individuals (Nowell & Jackson, 1996). More recently, these numbers have been estimated at 16,500 to 23,000 (Bauer & Van der Merwe, 2004), of which half of the population (8,000-18,000) lives in Tanzania (Bauer & Van der Merwe, 2004). Riggio et al. (2013) indicated a total population estimate of 32,000 lions in Africa.

Lions have suffered from dramatic reductions of home ranges and population sizes (Patterson et al., 2004). This is largely due to conflict with humans over livestock losses. Lions in particular suffer from conflicts with humans, as their psychological impact on people is often greater than their actual economic impact. On the other hand, the impact of disease and drought on livestock mortality is often much larger than the impact of livestock raiding by lions (Frank et al., 2005). Increasing conflict and lion retaliatory killing are often also a result of habitat loss and a reduction of prey numbers, brought about by an ever-growing human- and livestock population (Woodroffe et al., 1998). However, lions and other large predators have survived and persisted in pastoralist-dominated landscapes for centuries. Despite the fact that predation does happen, local people have always used traditional control methods such as livestock herding, '*boma*' fencing and keeping dogs to prevent livestock predation by large predators (Tumenta, 2012). Because of the existence of these traditional control methods, large carnivores and pastoralists have probably co-existed for a very long time (Frank et al., 2005). The other side of the coin is that lions provide income to the human communities they interact with, through non-consumptive use. Many lion conservation programmes today are dedicated towards finding the correct balance between the cost of living with lions, and the benefit realized (Maclennan et al., 2009; Hazzah et al., 2009). Raffaelli (2004) observed that most of the large carnivore species, including leopard, lion, cheetah and spotted hyena can be observed in the Amboseli Ecosystem in Kenya. These large carnivores rank high as a tourist attraction in Amboseli National Park and the adjacent areas.

1.4 Current lion population status in Kenya and in the Amboseli Ecosystem

Most large carnivore declines in Africa have occurred in West and Central Africa (Henschel et al., 2010). However some East African countries, particularly Kenya, have also lost a large proportion of their lions in the recent years (Kenya Wildlife Service, 2010). Of the species spectrum of large carnivores, lions are thought to have suffered most. In Kenya, lions have suffered dramatic reductions of population size over the past decades, from

7,000 in the 1990s to 2,000 in 2010 (Patterson et al., 2004; Bauer & Van der Merwe, 2004). The decrease in lion numbers is mainly due to habitat loss and conflicts with pastoralists. Approximately 825 lions may be left in Kenyan Maasailand (Kajiado and Narok Districts) an area regarded as lion strong hold in Kenya (Bauer & Van der Merwe, 2004; Frank et al., 2005; Dolreny, 2013). The challenge faced when conserving lions is that they can have large negative impacts on the livelihoods of the human communities with which they interact. Increasing human populations combined with the fact that lions require large areas to sustain viable populations means that interactions between humans and lions are only likely to intensify. From an alternative perspective, the interaction between lions and human communities can also lead to the generation of income through non-consumptive use, such as with tourism. Many lion conservation programmes today are dedicated to finding the correct balance between the cost of living with lions, and the benefit realized – it is the focus of this study to contribute to finding this balance.

1.5 Conservation of lions in the Amboseli Ecosystem

Like elsewhere in Kenya, increasing human encroachment into predator ranges is displacing prey species, resulting in increased livestock-predator interactions and resulting predation incidents (Dolreny, 2013). Livestock predation is therefore the main reason why locals kill predators in the Amboseli Ecosystem (AE). In addition, factors contributing to reduced carnivore populations, particularly lions, are attributed to diseases such as canine distemper virus and feline immunodeficiency virus, which have killed a substantial number of lions in the recent past (Packer et al., 1988).

The lion population in the AE has declined, with only small populations remaining in the Amboseli National Park (ANP) and in the Mbirikani-Chyulu area (Tuqa et al., 2014). In the early 1990s, the entire Amboseli lion population was destroyed through poisoning and killing, but dispersal into the ANP from surrounding lands ensured that a new population re-established itself (Cynthia Moss, personal communication). That reservoir population has been nearly exhausted, and at the current rate of killing, ANP may soon have no lions, and no source of replacements (Dolreny, 2013). Maclennan et al. (2009) reported that as a consequence of livestock raiding by large carnivores, Maasai perform retaliation killings. Limited data from the AE indicate that approximately 108 lions were killed in the region between 2001 and 2006, in spite of a generous compensation programme that pays people for livestock lost to predators (Maclennan et al., 2009; Dolreny, 2013). Most of the killings were through poisoning and spearing, both in retaliation for livestock killed by lions and for traditional *Olamayio* (the ritual whereby young men prove their manhood). Maasai are also known to hunt lions traditionally; this habit is in expression of manhood and bravery (Maclennan et al., 2009). Without a strong and immediate response, lions may become locally extinct.

1.6 Problem statement and justification

Increasing human population, land tenure and land use change are mainly responsible for the loss or fragmentation of wildlife habitats affecting both carnivores and their prey in the Amboseli Ecosystem. Climate change and especially recurrent droughts have also changed the movement patterns of wildlife, as animals have to migrate widely in search of forage and water.

The lion population in the AE has declined greatly in the past decade with only small populations remaining in the Amboseli NP and a few in the Amboseli areas neighbouring the park. Increasing human encroachment into predator ranges, land use changes, climate variability and environmental stochasticity is displacing prey species, resulting in increased frequency of livestock-predator interactions. Livestock predation is therefore the main reason why local livestock owners kill large carnivores such as lion, leopard, cheetah and jackal in the Amboseli Ecosystem. To ensure carnivore survival, it is critical to analyse the nature, extent and trends of human/carnivore conflict, from monitoring to support and management. This study aims to enhance carnivore conservation by gaining knowledge of the lion population structure and density, lion-prey relations, ranging patterns and spatial and temporal distribution of livestock predation. It also investigates, the attitude of the local community around the park, before and after an extreme drought and uses it to design mitigation measures aimed at developing viable local conservation strategies. Indiscriminate killing, the key threat to the survival of large carnivores in the Amboseli ecosystem, is driven by depletion of their prey and habitat due to human activities such as settlements, agriculture and livestock production.

The knowledge so generated can be used to determine wildlife corridors and dispersal areas. This information is also used to identify potential conflict hotspots and conservation zones. It will also be used to develop outreach materials to educate communities on the importance of co-existence with large carnivores to foster Community Partnership and Education Programmes.

1.7 Research design and conceptual framework

To study the effects of drought and climate change (variability) on lion populations, I developed three conceptual framework, including; 1) Natural Climate variability, 2) Bio-physical environment and 3) Human environment. Using this, I investigated how lions responded to climatic variability in terms of lion population structure, prey and diet, and movement and home range to enhance their survival before, during and after the severe drought that occurred in 2009.

1.7.1 Natural climate variability

Climate variability is one of the greatest challenges of the 21st century. Drought and climate change produce a complex web of impacts that spans many sectors of life on Earth. Anthropogenic activities are exerting additional pressure on biodiversity. Climate variability are expected to exacerbate climate-mediated biodiversity loss through fragmentation of wildlife habitats, and the spread of alien invasive species (Jeltsch et al., 2011). The impact of climate variability is generally compounded by environmental degradation. A dwindling natural resource based on the loss of biodiversity as a result of rangelands deterioration and diminishing grazing lands to support wildlife. The displacement of animals and increasing migrations due to pastoralists activities also increases the frequency of drought and scarcity of water resources, finally resulting in increased human-wildlife conflicts.

The Amboseli basin, a semi-arid, open savannah area of Southern Kenya, has experienced extensive changes in habitat since the early 1960s (Western & van Praet, 1973; Altmann & Roy, 2002). These include a dramatic loss of trees and shrub cover and concomitant changes in the populations of large mammals. Rainfall in the Amboseli Ecosystem exhibited a pattern of high variability across the months and between years (Altmann & Roy, 2002). June to late October, usually referred to as the long dry season, was consistently a dry period. The remaining months were more variable. In some years, rain fell in the pattern typically described for the area, in which one rainy season occurs in November and December and a second occurs in March or April through May. Often, however, the long, dry season was preceded by the failure of one or both of the previous rainy seasons (Altmann et al., 2002). At the other extreme, significant quantities of rain fell, in which one rainy season occurs in March or April through to May.

In the Amboseli Ecosystem, the drought of 2009 was thought to be the most severe of the last few decades (Wangai et al., 2013). The drought had a devastating effect on wildlife and livestock. Heavy losses affected herbivores such as wildebeest (reduction of 70%), zebras (reduction of 60%), buffaloes (reduction of 70%) and elephants were widely observed (personal communication Charles Musyoki). The precipitous drop of herbivore numbers is expected to have affected the carnivore population, particularly lions, causing additional pressure to the local livelihood, due to a sharp rise in livestock predation.

The impact of drought on large carnivores has not been studied in ANP in the past (Dolreny, 2013). It was expected that the drought may have had a serious impact on both herbivore and large carnivore populations, particularly lions. This study therefore used a methodological approach to analyse the likely impact of an extreme drought, with climate change as the main driving force behind climate variability. In my study, I analysed ecological and human variables, their interactions, and their effects on a lion population in Amboseli National Park.

1.7.2 Bio-physical environment

In African savanna environments, vegetation growth and hence food production for herbivores depends strongly on rainfall during a wet season (Festa-Bianchet, 1988). Determining biological and environmental factors that limit the distribution and abundance of organisms is central to our understanding of the dynamics of animal populations. This is crucial for predicting how species may respond to large-scale environmental change, such as drought (short term) and climate change (long term) (Sinclair et al., 2008; Walker & Noy-Meir, 1982). Wildlife populations may increase or decrease dynamically depending on rainfall (Ogutu & Owen-Smith, 2003). Plenty of rainfall may lead to an increase in an animal population, as improved range conditions result from the growth of forage and from the abundant water necessary for various physiological functions. Large mammal communities are ultimately limited by their food supply through mortality and reproductive stress (Sinclair et al., 2008; Coe et al., 1999). Rainfall has been seen as the single most important environmental variable affecting the abundance of large savanna herbivores as it determines the amount of food available, particularly in the dry season (Coe et al., 1999; Sinclair et al., 2008). Droughts have disruptive effects on the vegetation, affecting animals through direct behavioral and phyisiological selection. The direct effects of drought on vegetation by a lowered primary production affects food availability too (Sinclair et al., 1985).

Changes in rainfall patterns thus influence vegetation dynamics and hence ungulate populations (Ottichilo et al., 2000). Predator populations generally follow the dynamics of prey populations (Sinclair et al., 2008). The movement of animals in response to rainfall and food supply has been well documented and reviewed for the Serengeti-Mara ecosystem (Mwalyosi, 1991; Sinclair et al., 2008; Ottichilo et al., 2000), where wildebeest and other ungulates (e.g., Burchell's zebra and Thomson's gazelle) migrate between their dry season and wet season ranges in Kenya and Tanzania. Differences in migratory movement patterns can be related to differences in the food requirements of animals. Herbivores, particularly wildebeest, zebra and buffalo, are the preferred prey of lions (Schaller, 1972). In ANP, lion population size, density, and their movement patterns and distribution are expected to correlate with densities and dynamics of prey species. The lion populations are expected to oscillate following the abundance of populations of the main prey species (Ogutu & Owen-Smith, 2005). The prevailing density of the ungulate population may also modify the effective food availability (Ogutu & Owen-Smith, 2005), and may influence the selection of alternative prey species by lions (Mills & Biggs, 1993). Climate, in interaction with the bio-physical environment, therefore sets the conditions for the dynamics of the lion population in Amboseli ecosystem.

1.7.3 Human environment

Disturbance by human activities, such as encroachment of cultivation and settlements (Figure 1.2) causes a decline in the area of natural habitats and reduces space for grazing by wild herbivores (Sinclair et al., 1995; Ottichilo et al., 2000; Veldkamp & Lambin, 2001; Ogutu et al., 2009). Loss of the habitat and habitat fragmentation are considered the most important factors influencing the level of threat of species extinction (Bailie et al., 2004). Livestock may alter the composition and physiognomy of range vegetation communities at the expense of wildlife (Ogutu & Owen-Smith, 2003). Some plants decrease with grazing, whereas other non-palatable ones increase.

One of the major challenges facing wildlife conservation in rangelands is the increasing loss of dispersal areas due to farming and settlement, which is exacerbated by the ongoing subdivision of communally owned group ranches (Western & Nightingale, 2005). The rangelands are being increasingly fragmented as wildlife corridors are cut off by development. These developments could lead to a concentration of wildlife in the protected areas and subsequent ecological degradation. For instance, the dispersal areas south of the Amboseli National Park, a link to Tsavo ecosystem and the Kitenden wildlife corridor linking Amboseli to Kilimanjaro forest, are threatened by increased settlement.

The above factors largely contribute to a high frequency of lion-livestock encounters in the areas neighbouring group ranches and often result in depredation affecting local livelihoods (Dolrenry, 2013). Livestock owners, in retaliation, often use poison and other methods to kill lions. The killing of lions by local people in combination with habitat fragmentation is considered the main contributing factor to the decline of lion populations in the Amboseli Ecosystem (Dolrenry, 2013). The reduction in lion numbers has both negative ecological and economic effects. The lion is a flagship species for the tourism business. If lions were to disappear from Amboseli, it is expected that the number of tourists visiting the ANP would soon decline, affecting the revenue base both for the Kenya Wildlife Service park and as well as lodge owners and other entrepreneurs.

Based on the conceptual framework four main items in response to severe drought can be predicted for the lion population.

- a Lion population characteristics and social structure will change to its survival advantage to cope with severe climate variability.
- b Lions will have expanded home ranges and unpredictable movement patterns.
- c Lions will change their predation patterns thus become less selective.
- d Livestock predation rate and intensity by lions and other carnivores will increase and this will affect local community attitude and perceptions towards lions and other carnivores

This conceptual framework shows a realistic interplay of lion-prey response to extreme drought. This flow chart can be used to predict the response of lion populations in terms of movements, seasonal home range variation, habitat use, interaction with wild prey and livestock in and around Amboseli National Park (Figure 1.1).

1.8 Conceptual framework

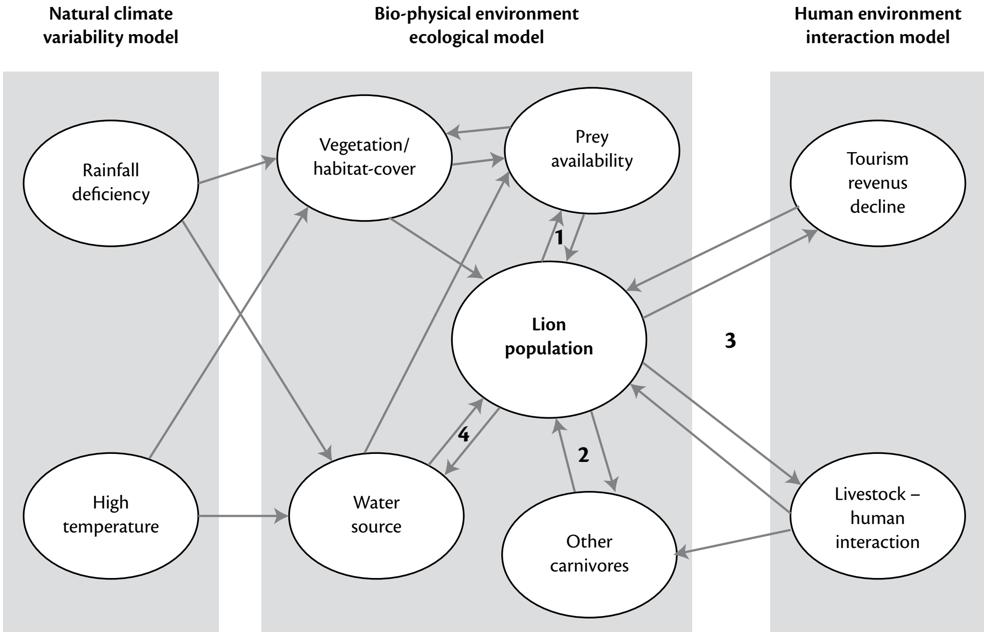

Figure 1.1
Conceptual framework processes; (1) Lion-prey interaction (2) Lion habitat use and movement (3) Lion-livestock interaction

1.9 Hypotheses

Based on the conceptual scenarios described above, I hypothesize that a severe drought would have a significant short-term effect on the lion population structure, ranging pattern, diet and livestock interactions in the Amboseli Ecosystem. I expect significant changes after the drought, but also signs of resilience of the lion population several years after the drought.

1.10 Main objective

The main aim of my research was to analyse the response of lion populations to severe climate variability (drought) and their persistence in a high conflict zone with pastoralists in an African savannah, with a view to contributing to improved conservation and management of the species. My research focused on the lion population in Amboseli National Park and the surrounding communal group ranches.

Scientific information on lion population status, ranging behaviour, interaction with their prey and with livestock, can be useful to the park management for decision making and for better management of the lion population of the Amboseli Ecosystem. My research covered the following research questions:

1 What is the impact of severe drought and human-induced mortality on the lion population structure in the Amboseli Ecosystem?
2 What are the effects of climate variability on lion home range and movement patterns in the Amboseli Ecosystem?
3 What is the effect of severe drought on prey abundance and lions' diet?
4 What are the large carnivore – livestock predation rates and community attitudes and perception towards large carnivores around Amboseli National Park?
5 Finally what is the scope for recovery of the lion population after the drought as synthesis?

The Amboseli National Park and adjoining communal group ranches, plus the distant conservation areas such as Tsavo, Chyulu and Kilimanjaro constitute important wildlife conservation units within what is known as the Amboseli Ecosystem. The ANP has received attention in recent years, with researchers such as elephants, as well as other long-term research on ecology and on primates (Maclennan et al., 2009). Field work for the present research started in July, 2007 and ended in December, 2012.

1.11 Study assumptions

In my research, I assumed that the lion population and behaviour of individual lions varied in a detectable and measurable way in response to prey abundance in relation to climate fluctuations as well as to anthropogenic pressures. A reduction in the carrying capacity of the ANP as a result of the 2009 drought was expected to result in increased mortality in the lion population in 2010 and thereafter.

1.12 Study area: Amboseli National Park and ecosystem description

Amboseli is situated in the foothills of the Kilimanjaro Mountain. The rainfall pattern is bi-modal, with a short dry period during February-March and a longer dry period during June-September (Figure 1.2)

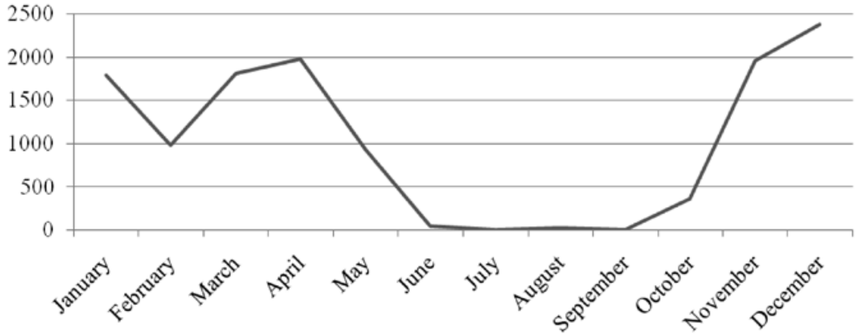

Figure 1.2
Mean monthly rainfall for Amboseli National Park over a 35-year period, 1977-2012) (KWS meteorological station Amboseli headquarters and meteorological station baboon project at Tortilis Camp Amboseli).

The Amboseli Ecosystem covers an area of approximately 5,700 km^2, stretching between Mt. Kilimanjaro, Chyulu Hills, Tsavo West National Park and the Kenya/Tanzania border. The area is generally arid to semi-arid with a very small variation in its agro-ecological zones. It is more suitable for pastoralism than cultivation and has a high potential for conservation of wildlife and tourism enterprises. Administratively, the AE consists of the ANP and six surrounding group ranches. The group ranches, namely; Kimana/Tikondo, Olgulului/Olararashi, Selengei, Mbirikani, Kuku, and Rombo, cover an area of about 506,329 hectares in Loitokitok District. It also includes the former 48 individual ranches located in the foothills of Kilimanjaro, which are now under rain-fed crop production.

As described by Moss et al. (2011), the Amboseli Ecosystem is unique. No other place in Africa combines the special hydrological, topographical, geological and cultural history of Amboseli. The area has modest rainfall, a greatly rolling bush land surrounded by a system of swamps fed by underground rivers from snow-capped Kilimanjaro mountain forest catchment, and supports an array of mammals and other flora and fauna. At the heart of this ecosystem is one of the oldest traditional Maasai nomadic pastoralist societies, whose culture and pride is steadfast and closely linked with livestock, wildlife and nature in the midst of rapidly changing socio-economic development. Amboseli National Park is situated in the centre of the AE, which for decades has been a major biodiversity, wildlife and tourism epicenter.

In order to place the ecology, ranging pattern, population dynamics, and social structure of Amboseli lions into the perspective of their habitat over the course of the study, in this section we describe:

- The variable and dynamic Amboseli ecosystem in general and
- The broad habitat changes that have taken place over the past five decades (1957-2010), including an assessment of changes in numbers of wildlife species.

Since the 1950s and 1960s, swamps have grown in size, the amount of standing water has increased, and some acacia woodlands (*Acacia xanthophloea*, the yellow-barked "fever tree") have changed dramatically (Dolrenry, 2013). The designation "Amboseli basin" is commonly used to refer to the area containing the dry lakebed, ANP, and immediate surroundings.

The changes underway today are precedented; they are driven by large-scale fluctuations in water flow from the Kilimanjaro watershed, which is driven in turn by regional rainfall as well as man-made alterations to water capture, holding delivery characteristics of the catchment zones. Annual rainfall data from local meteorological stations show considerable inter-annual variation but no clear pattern (Altmann et al., 2002), suggesting that basic ecosystem drivers are a constant flux. A more clearly directional change is occurring at the scale of the global climate (Smith et al., 2007), evidenced locally by the rapid shrinking of Kilimanjaro glaciers.

1.13 Location

The Amboseli ecosystem is located in the southern Kajiado District, a 22,000 km^2 administrative unit that stretches from just outside the capital of Nairobi, south to the Tanzanian border. For administrative reasons, the former Kajiado District has now been split and the AE largely falls under the Loitoktok District of Olkejuado County. The area has marked geographical features, such as faults of the great Rift Valley, that create four distinct ecological zones as defined by geomorphology, topography and vegetation, namely the Athi-Kapiti plains, the Rift Valley, the Central Hills and, Ilksongo (Moss et al., 2011).

The Kenyan portion of the Amboseli Ecosystem is defined by a commonality of soil and vegetation types, a local rainfall regime, a distinct drainage system, and the presence of a large herbivore population consisting of both residents and locally seasonal migrants. When migratory species make up a large proportion of the animals in an area, the limits of their annual movements may be taken as operational ecosystem boundaries (Gittleman, 1985). The ecosystem has been well described elsewhere (Western & Van Praet, 1973), and the general account that follows will paraphrase freely from those sources.

The Amboseli Ecosystem is a roughly 8,000 km^2 area that straddles the Kenya-Tanzania boundary, reposing at 1,100 m as a broad basin between the northern slopes of Kilimanjaro, the late (post-Pleistocene) volcanic Chyulu Hills (2,200 m) to the east, a motley range of broken basement-rock hills to the north, and scattered granitic outcrops and earlier volcanic cones to the west and south west, the largest of which, Oldonyo Orok, is 2,400 m. The most recent eruption of Kilimanjaro, about 1.5 million years ago, blocked the ancient Pangani River that flowed northwest to southeast and thus created a closed central basin and a lake with no outlet: the lacustraine silts that have accumulated over the years reflect starkly white on satellite imagery.

1.14 Geology and soil

Quaternary volcanic soils predominate on the northeastern Kilimanjaro slope, encouraging rain-fed agriculture around the town of Oloitoktok; basement rock soils cover most of the rest of Ilkisongo, making only pastoralism possible. These dark-red to reddish-brown sandy clay soils are low in fertility, despite the rapid growth of grass on them in the early rains. Darker brown-to-black (“black cotton”) alluvial clays accumulate along seasonal runoff lines and low-lying areas of impended drainage, where they trap nutrients and support grass growth for a while after the rains.

In general, even where volcanic soils are present, soil fertility in the ecosystem is a tenuous matter, underlaid as it is with nutrient–impoverished basement quartzite, crystalline limestone, schist, and gneiss. The soil in and around the Pleistocene lakebed are a mix of saline accumulations that form calcrete pavements, support only a meagre seasonal grass growth, and produce an intense albedo, the energy of which is believed to repel clouds and delay the onset of the rains compared with the surrounding areas (Dolrenry, 2013). The soil chemistry in the immediate vicinity of the springs and swamps is less saline due to dilution by groundwater and percolation of salts to the margins of the groundwater zone.

1.15 Land use

It is acknowledged that land users in the ecosystem will only adopt or invest in a particular land use depending on the extent to which they feel the land use is beneficial to them, either as individuals or as a community. As such, based on environmental and socio-economic considerations, the ecosystem has been divided into three broad zones, arable agriculture, livestock production, and wildlife tourism.

The arable agriculture zone comprises the individually owned land at the foothills of Kilimanjaro and the irrigation schemes in the ecosystem where crop production is the best land use option (Dolrenry, 2013). In this zone, returns from crop farming are comparatively higher than returns from other competing uses such as pastoralism and tourism. The wildlife tourism zone comprises the Amboseli National Park and both the existing and proposed wildlife concession areas. This zone is characterized by high densities of wildlife, which makes wildlife tourism a preferred land use option. The zone also falls in areas where the mean annual rainfall is about 400 mm, which does not favour arable farming. The rest of the ecosystem is categorised as livestock production zone with traditional pastoralism, which is the mainstay of the local community in the ecosystem.

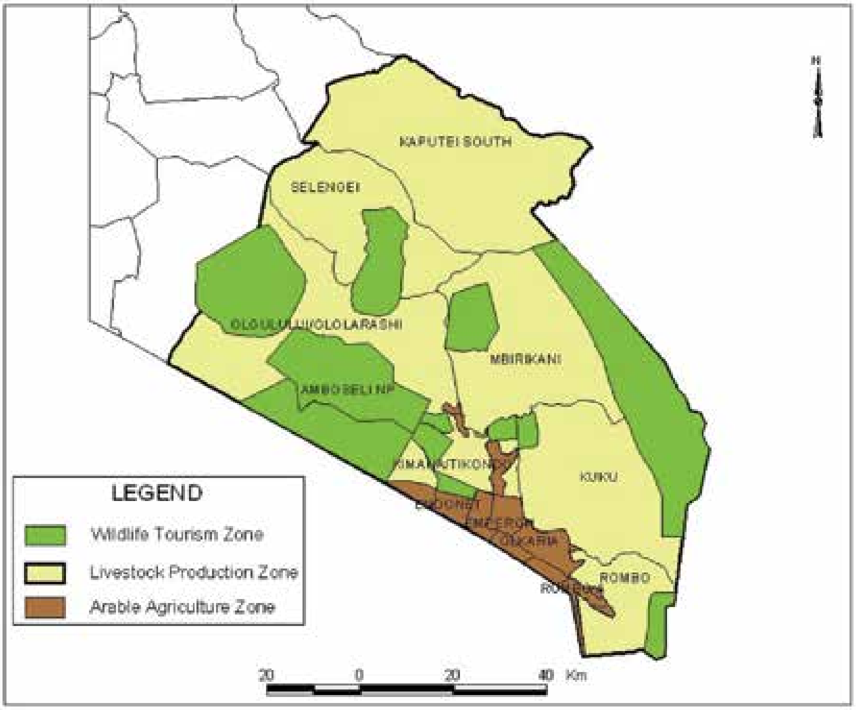

Figure 1.3
A summary of the land use zones in the Amboseli ecosystem

1.16 Thesis organization

Wildlife monitoring records and incidences of retaliatory killing by livestock owners provide evidence that the lion population in the rangelands of southern Kenya has been shrinking both in size and distribution. It is not clear, however, how the lion population is affected in the face of climatic fluctuations and changes in abundance of their preferred prey species. Chapter 2 shows how severe climate variability affects lion population density and social structure. The influence of climate variability on lion home range and movement patterns is covered in chapter 3. This chapter also attempts to elucidate how the lions are adjusting their behaviour to cope with changing prey composition. Chapter 4 highlights the impact of severe climate variability on prey abundance and selection by lions. Chapter 5 covers the livestock predation trends and local community knowledge and attitudes towards large carnivores. Moreover, there are certain aspects of livestock predation by lions that are still not well understood. For instance, it is not known whether livestock in Amboseli is habitually killed by the same individuals, or killed by various lions. The final chapter 6 covers a synthesis of the different chapters and a discussion on the main results of my research. Information on the direct and indirect impacts of climate variability on the lion population, ranging behaviour of individuals as well as lion interactions with their natural prey and with livestock, is valuable for better management of the lion population in the Amboseli Ecosystem in general. This study sought to shed light on those issues and propose sustainable conservation interventions.

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