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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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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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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

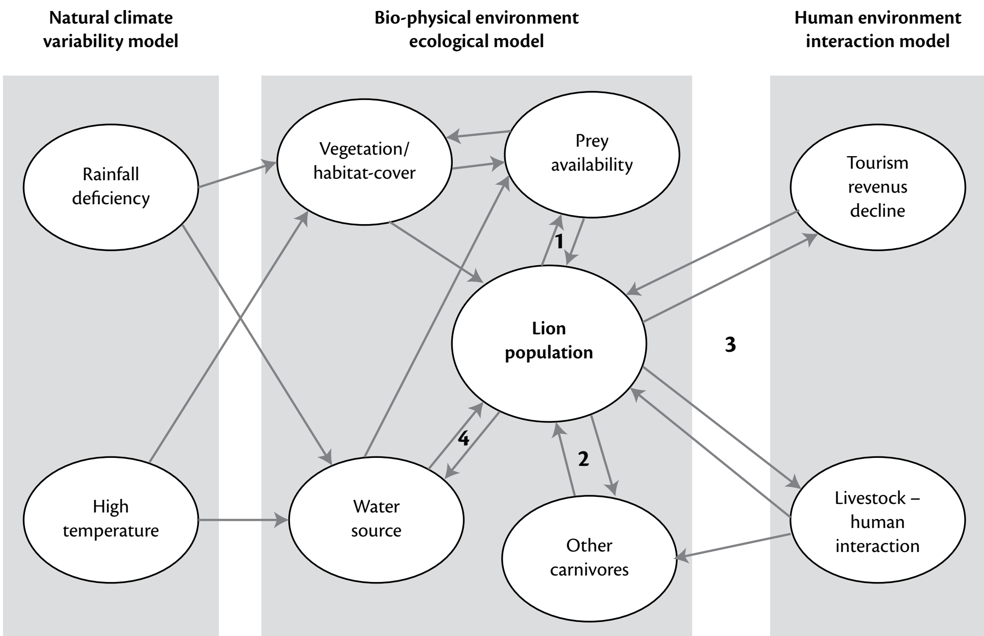

Figure 1.1
Conceptual framework processes; (1) Lion-prey interaction (2) Lion habitat use and movement (3) Lion-livestock interaction

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)

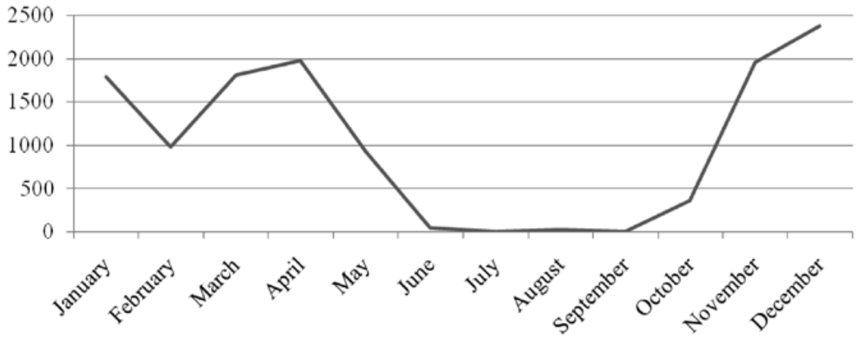

Figure 1.2
Mean monthly rainfall for Amboseli National Park over a 35-year period, 1977-2012) (KWS meteorological station Amboseli headquarters and meteorological station baboon project at Tortilis Camp Amboseli).

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.

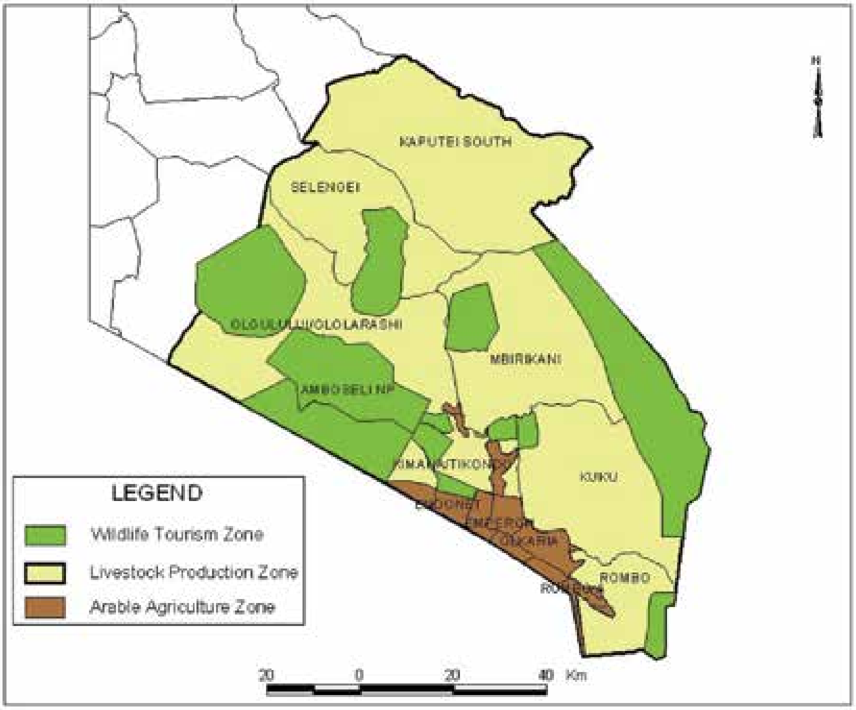

Figure 1.3
A summary of the land use zones in the Amboseli ecosystem

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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2

Impact of a Drought on the Social Structure of a Lion Population in the Amboseli Ecosystem, Kenya

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Abstract

This study looked at the impact of severe drought in 2009 on lion population density and social structure in Amboseli National Park. The covered a period of six years, three years before (2007-2009) and three years after the drought (2010-2012). We used Rainfall Variability, Drought Severity Index, Prey Abundance Index and human-induced mortality to assess lion vulnerability to the extreme drought. The Vulnerability Index (VI) indicates response of lion populations to drought in terms of social structure, diet and mortality. The VI was negative in 2010, the year directly following the drought. This negative VI coincided with a changes in lion social structure (sex ratio, adult: juvenile ratio and group size) and increased mortality. The VI was positive in 2011, this was the time the lion population showed signs of recovery, with high reproduction. We witnessed 28 lions being killed (15 in 2010 alone) around the park during the post-drought period 2010-2012, compared to 14 before and during the drought (2007-2009), among them five pride males. After the drought, the lion population showed a significant change in structure, with a decrease in male: female sex ratio (due to a decline of males), a significant increase in adult group size and a significant decline in juvenile to adult ratio (due to increase of juveniles). All these changes correspond to increased lion vulnerability in 2010. We noticed that during this period, male lions were targeted more than females by Maasai warriors (Moran), probably due to cultural practice (use of manes and claws). The increase of juveniles was probably a result of less competition between pride males and consequently less infanticide. While the reduced group size was probably a response to lower prey densities and a drought-resilience mechanism.

2.1 Introduction

Variability of climate such as extreme drought determines dryland productivity and its ecosystem services (Toxopeus, 1999; Reynolds et al., 2007). Climate variability and droughts can have a severe impact on the dynamics of animal populations (Altmann & Roy, 2002); particularly in semi-arid and arid environments where herbivore populations are strongly limited by resource availability, water and pasture (Ogutu et al., 2009). Climate also influences a variety of ecological processes, including variations in prey and water availability, which are important determinants for the survival of large carnivores such as the African lion (*Panthera leo leo*) (Elliot & Cowan, 1978; Van Orsdol et al., 1985; Packer et al., 1988; Macdonald, 1983). Increased drought intensity and rainfall variability are expected to reduce the viability of such populations, reducing their carrying capacity and driving species to extinction. Droughts are also a significant component of such climatic variability (Challinor 2009, Ogutu et al., 2008); Scheel and Packer (1991) also noted that reduction in herbivore prey is likely to decrease lion carrying capacity. When coupled with other factors, such as retaliatory killing, drought could have a devastating impact on lion populations.

The African lion is considered as 'Vulnerable' on the IUCN Red List of globally threatened species because a population decline of about 30% is believed to have occurred over the past two decades, which is a period of approximately three lion generations (IUCN, 2012). Of the 67 sub-populations of lions in Africa, only 10 sub-populations are so-called 'lion strongholds' (Riggio et al., 2013). In Kenya, lion numbers have declined from an estimated 2,700 in 2000 to an estimated 2,000 in 2010, primarily due to human-lion conflict (Kenya Wildlife Service, 2010).

Schaller (1972) defined a lion pride as "any resident lionesses with their cubs and attending males who share a pride area and interact peacefully". The lionesses of a pride are related and most young females become a part of their mother's pride (Heinsohn et al., 1996), thus female membership in a pride is relatively stable. When foraging in separate groups rather than as a whole lion pride may increase hunting success and limits competition while feeding (Scheel & Packer, 1991, Valeix et al., 2001). Prides can be considered fission-fusion units that consist of 2-18 females (Packer et al., 1988; Packer et al., 1990). Group size is defined as the number of adult lions observed together on an encounter, excluding cubs <2 years old (Grinnell et al., 1995; Scheel & Packer, 1991, Smuts, 1978). In contrast to females, males never stay with the same pride throughout their lives. Males associate with a pride to protect their offspring, typically staying in charge of a pride for about 2-2.5 years (Grinnell et al., 1995), the time a generation of cubs needs to reach sub-adulthood. During male takeovers, the new males may kill or evict all cubs and juveniles in a pride to increase their own reproductive output (Van Orsdol et al., 1985; Hanby & Bygott, 1987). Males are generally expelled from their natal pride around the age of 3-3.5 years and tend to become nomadic (Grinnell et al., 1995).

We hypothesised that, with the impact of human interventions and declining animal populations, stochastic events such as climate variability may have a severe impact on the dynamics of animal populations. The situation is even dire in semi-arid and arid environments where herbivore populations are strongly limited by resource availability, such as water and pasture (Ogutu et al., 2009). With the increased frequency of drought and shortening of its cycle and intensity, rainfall variability will have potentially significant effects; 1) On the short term they may benefit lion populations by increased availability of weakened prey animals and enhanced reproduction 2) On the long term they may reduce the viability of lion populations due to a decline in the abundance of prey animals' populations. With the observed declining trend of lion populations in Kenya, the long term impact of frequent droughts may increase the vulnerability of lion populations (Barrows et al., 2010). Few studies have showed the impact of extreme droughts on populations of carnivores and their prey. Since extreme droughts are considered a significant component of climatic variability and may have impacts over long periods of time (Carroll 2007, Challinor et al., 2009). Our study covers the event of an extreme drought during 2009 in southern Kenya. This severe drought strongly affected herbivore densities in Amboseli National Park and intensified lion-livestock predation by large carnivores, triggering retaliatory killing by local people. Here we used Rainfall Variability, Drought Severity Index, and Prey Abundance Index and human-induced mortality to determine the impact of the drought on the social structure (group size, pride size, and sex ratio) and density of the Amboseli lion population before and during (2007-2009) and after (2010-2012) the drought to ascertain lion vulnerability to the extreme drought.

2.2 Material and methods

2.2.1 Study area

The Amboseli ecosystem is situated across the border of Kenya and Tanzania near the foothills of Mt. Kilimanjaro. On the Kenyan side, the ecosystem covers an area of approximately 5,700 km^2, stretching between Mt. Kilimanjaro, Chyulu Hills, Tsavo West National Park and the Kenya/Tanzanian border (Figure 2.1). The area is generally arid to semi-arid, with an average rainfall of 340 mm per annum (Altmann & Roy, 2002, Moss et al., 2011). The area has bi-annual rainfall, short rains from November until December with longer rains in March-April (Moss et al., 2011). Within the ecosystem, there is little variation in agro-ecological zones and the area is more suitable for pastoralism than cultivation, with a high potential for conservation of wildlife and tourism enterprises (Moss et al., 2011). Administratively, the Amboseli ecosystem consists of Amboseli National Park (ANP) (392 km^2) and six surrounding Maasai group ranches namely: Kimana/Tikondo, Olgulului (North, East, South, and West), Selengei, Mbirikani, Kuku, and Rombo, which cover at total area of (5,063 km^2) in Kajiado County (Figure 2.1). Amboseli NP is a dry season grazing area for wildlife, which disperses widely to the adjacent group ranches during the wet seasons (November-December and March-April), when water and forage are plentiful. Although Amboseli NP is one of the leading tourist destinations in the country, with an average of 150,000 visitors per annum (Makonjo et al., 2009), its future is threatened by the loss of wildlife dispersal areas and corridors that are critical to ungulate populations (Toxopeus, 1999). Development activities around the park's edge have caused fragmentation of wildlife habitats, diminishing the dispersal areas and limiting the free movement of animals (Toxopeus, 1999).

2.2.2 Assessment of drought severity and prey abundance

To assess rainfall variability, we obtained 35 years of rainfall data (1977 to 2012) from two meteorological stations Kenya Wildlife Service [KWS] Amboseli NP and the Baboon research station at Tortilis tented camp situated inside and near the park, respectively. We used rainfall variability, and Amboseli NP annual prey counts as independent variables to assess the impact of severe drought on the local lion population. Because rainfall variability is high in drylands ecosystem, the months with a mean rainfall ≥ 10 mm were regarded as wet and those with ≤ 10 mm dry. Five transects (2×1 km) along

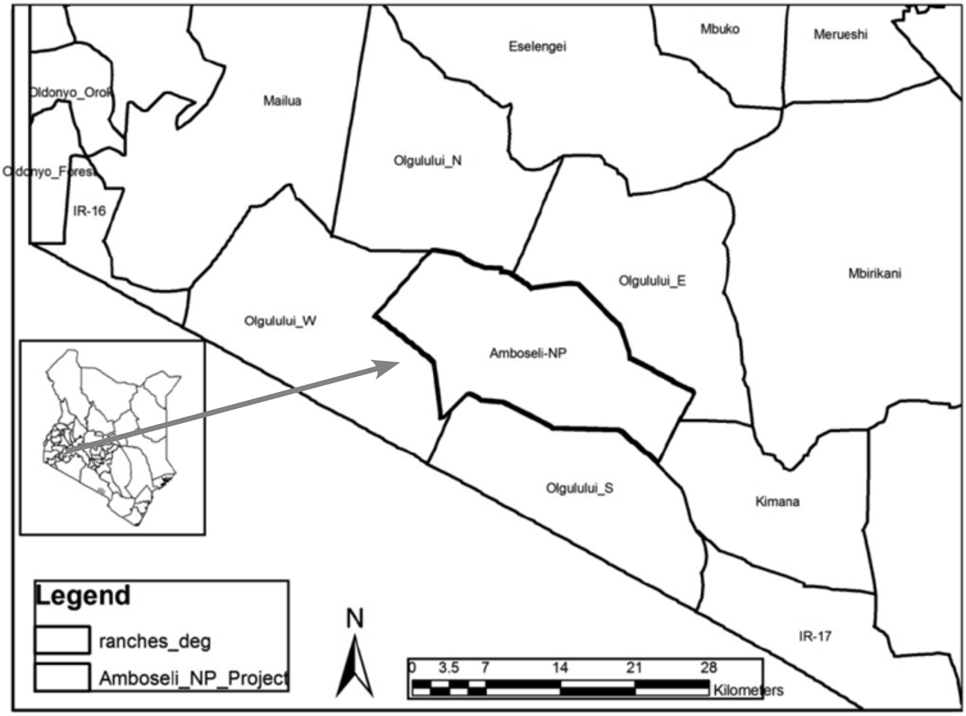

Figure 2.1
Map showing the location of Amboseli National Park and community group ranches.

a park track (500 m on each side) were semi-randomly selected to cover a number of habitats (Figure 2.2). These habitats included short and tall grasslands, alkaline plains, *Acacia* woodlands, Phoenix mixed woodlands and freshwater Papyrus swamps (Moss, 2011).The transects covered a total of 10 km^2, which were representative for the rest of the park (396 km^2).

The general trend of prey abundance within the park and neighbouring group ranches was established using distance measured in meters (Bushnell Yardage Pro Trophy Rangefinder) during the transect counts the exact distance of the herbivores was determined within the distance of 500 meter.

These transect counts were, conducted weekly every month, when possible, at the same time, alternating between 08:00-10:00 and 16:00-18:00 hours, both during the wet and dry season. These times were chosen so that animals seeking shade during the warmer periods of the day were not overlooked. All herbivores larger than ~5 kg were recorded. Additional data included numbers of neonates within the group, habitat type, and weather and grass conditions. Complementary data from counts conducted by the KWS and previous studies were added to assess the size of the wild prey population and how this changed over previous years. Transect counts were used to classify prey species in weight/size groups to estimate the available biomass of prey species in the national park (Hayward et al., 2007).

We also used ANP data from aerial and ground wildlife censuses which were carried out twice each year, in the wet and dry seasons. The aerial counts were done for the whole ecosystem while the ground total count was done within ANP. We used these data along with transect counts to evaluate animal seasonal abundance.

We calculated the Drought Severity Index (DSI) modified from Fraser et al., (2007), with DSI as average annual rainfall over 35 years divided by the average monthly rainfall in a particular year. The years with drought index >2 were categorised as "severe drought year", while those with the index >1.5 but <2 as "moderate drought year" and those with <1.5 were regarded as "high rainfall year".

We also calculated the Prey Abundance Index (PAI) for only preferred lion prey species: zebra, wildebeest and African buffalo (Hayward et al., 2007). PAI was calculated as the average prey numbers (2007-2012) divided by prey numbers in a particular year (only for zebra, wildebeest and buffalo). Amboseli has several other smaller prey species, but the PAI captures the bulk of food intake. Prey numbers were established through direct transect counts and taken from periodic KWS Park count data (Figure 2.2). Pearson et al. (2003) defined vulnerability as "the degree to which a species is susceptible to or unable to cope with, adverse effects of climate change, including climate variability and extremes" while climate vulnerability is defined as "the extent to which climate change may damage or harm a system". We considered lion vulnerability to drought as a function of rainfall and herbivore abundance (Pearson et al., 2003). Dependent variables were lion Vulnerability Index, lion densities, lion population structure (male-female ratio and juvenile-adult ratio) and the number of lion killing incidents by humans.

Finally, we assessed the Vulnerability Index (VI) as follows: VI=Log (DSI) × Log (PAI). Vulnerability is defined here as the response of lion populations in terms of social structure

(Sex ratio, juvenile: adult ratio, group size), lion diet, reproduction and mortality to extreme drought. Positive values of VI are expected to show low vulnerability (thus a low response of lion populations to drought), while negative values indicate high vulnerability (thus a high response of lion populations to drought). So in our results we then related the VI to social structure, diet, human induced lion mortality, reproduction of the lion population (group size, sex ratio and and juvenile: adult ratio) before/ during (2007-2009) and after the drought (2010-2012). We emphasise that VI may stand both for negative impact (mortality) and for positive impact (increased reproduction), depending on the parameter most affected by drought.

2.2.3 Field observations and sampling technique for lion population structure

We used direct individual identification, radio telemetry and calling stations to estimate lion densities and social structure in and around Amboseli NP during 2007-2012. Lions were identified using distinguishable marks such as (lack of) ear notches, facial scars and most importantly the whisker spot pattern, which was unique for each lion (Pennycuick & Rudnai, 1970). A whisker spot pattern was found on each side of a lion's face and consisted of two rows, a reference row and the identification spots. The reference row was the top complete row of whisker spots while the identification spots formed the incomplete row above the reference row. A Fujifilm S5600 (10x optical zoom) was used to take photographs in order to document these unique marks for each adult lion in the population. This lead to a photo database for most of the lion population in ANP.

In addition to distinguishable marks, information on the unidentified lion's age, sex, natal pride and family ties was gathered.

Ten lions (three males and seven females) were collared in four different prides with GPS – GSM – VHF collars (Hawk) of African Wildlife Tracking (S.A), and their movements monitored online and in the field from 2007 to 2012. In addition, during 2007-2012. We spent at least two weeks per month on transect observations of lions and their prey. For this we established five transects of each 1 km long (Figure 2.2). Sightings were also made via opportunistic encounters, through information received from tourists and tour guides. Photographs were taken for each animal and a database was established; individual identification (Pennycuik & Rudnai, 1970) was more appropriate than vocalization call-ups station, because of low response rates (Ogutu & Dublin, 1998). When no new individuals were observed, with reference to the Amboseli Lion Photo Data Base, we assumed that we had an accurate annual lion population estimate. Lion densities were calculated by dividing the annual lion population estimates by the surface area of Amboseli NP per 100 km^2. Lions were aged following (Whitman & Packer, 2006), with juveniles defined as <2 years, and sub-adults and adults >2years. We classified lions of adult size lacking juvenile spots as sub-adults and adults, while lions smaller than adult size having juvenile spots were considered juvenile (Schaller, 1972). The lion prides were named after the collared or dominant (alpha) female lion, resulting in Pride I (Amy-Jane), Pride II (Tato), Pride III (Belta) and Pride IV (Nane/nomad); Groups were determined as any aggregation of lions at a particular time (Schaller, 1972). Lion killing incidents before and after the drought were obtained from the KWS occurrence book (2007-2012) at park headquarters, this is where patrol units recorded any incident on a daily basis.

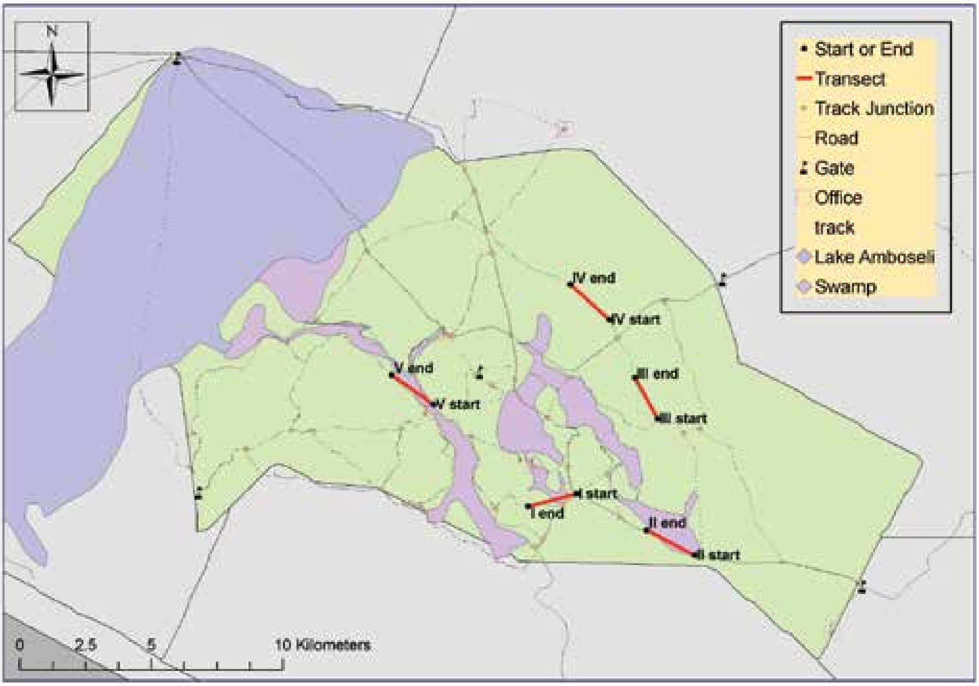

Figure 2.2
Transect count location in Amboseli National Park

2.2.4 Data analysis and statistics

Data obtained were analyzed using descriptive statistics in Excel and Statistical Package R (version 3.0). Data were tested for normal distribution using the Shapiro-Wilk test. We used Welch's two sample t-test and Bonferroni correction for the period before/during and after the drought in 2009 to assess differences in lion group size, sex ratio and density.

2.3 Results

The year 2009 had the highest drought severity index of 2.42 and was categorised as the most severe drought year in the last 35 years, while the year 2010, with a DSI of 0.60 was categorised as among the very high rainfall years (Figure 2.3).

Prey abundance showed a significant decrease after the drought (2010-2012) for three species used as indicators (wildebeest, buffalo and zebra) (Figure 2.4). The lion Vulnerability Index showed negative values in 2007, 2010 and to lesser extent in 2012, however, there were signs of recovery with positive values in 2011. Lion Vulnerability Index was highest in 2010, the year immediately following the drought (Figure 2.5).

There was no significant difference ($t = 0.3293$, $df = 2.42$, $P>0.05$) in adult lion density before/during compared with after the drought (Table 2.1).

A total of 42 lions were killed during 2007-2012, of which 14 were killed before the drought (2007-2009). The average number of lions present per annum in ANP were eight male lions and 13 females during this period. In the period between 2010 and 2012, 28 were killed. A total of 5 pride males were killed during the period after the drought, whereas no lions were killed during the actual drought year (Figure 2.6). The lion population in 2012 was estimated at 34 individuals, 19 adults (three males and 16 females) and 15 juveniles.

When excluding the two disturbed years with outliers in lion mortality (2009 and 2010), we found a significantly lower lion mortality in the period after the introduction of the consolation scheme (2007-2012) compared to the period before (2001-2006) (t-test, $p = 0.00284$). When excluding the two disturbed years with outliers (2009 and 2010), there was also no significant difference in mortality in the years after the start of the consolation scheme before the drought (2007 and 2008) and after the drought (2011, 2012), (t-test, p = 0.845).

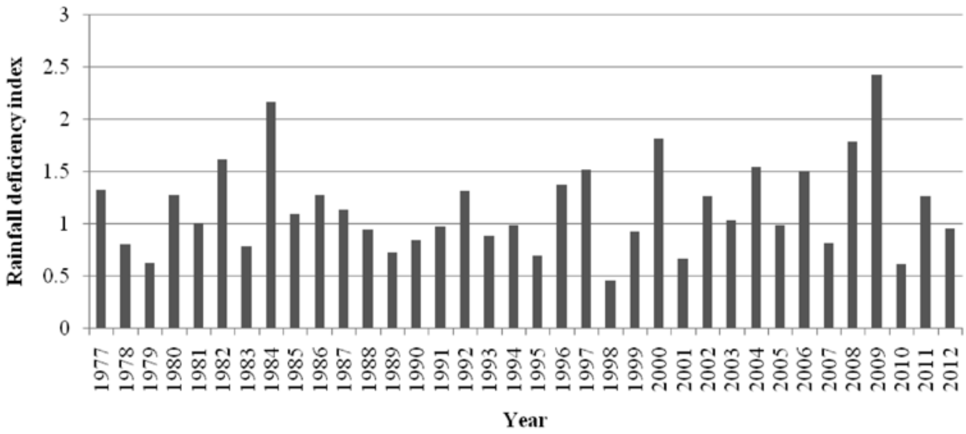

Figure 2.3
Amboseli area Drought Severity Index (1977-2012).

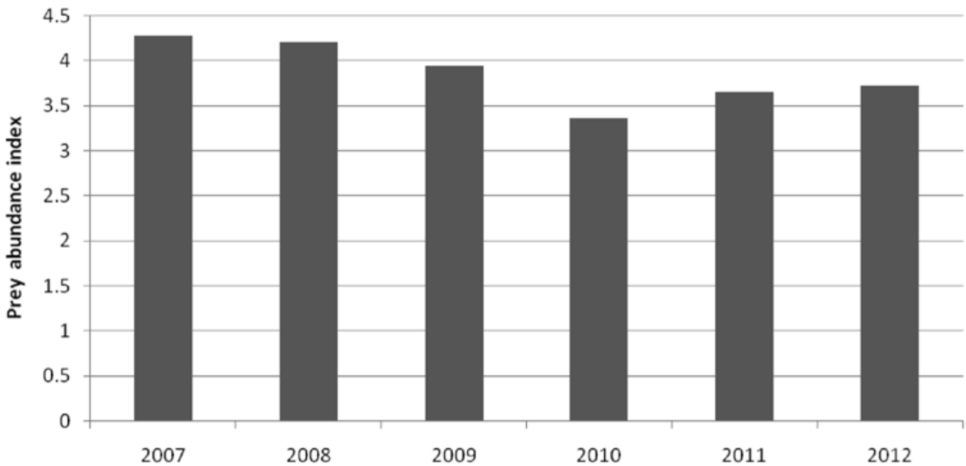

Figure 2.4
Change in annual wild prey abundance (index) for three species (Index based on log of Zebra, Wildebeest and Buffalo) 2007-2012. (Source: KWS; Amboseli NP).

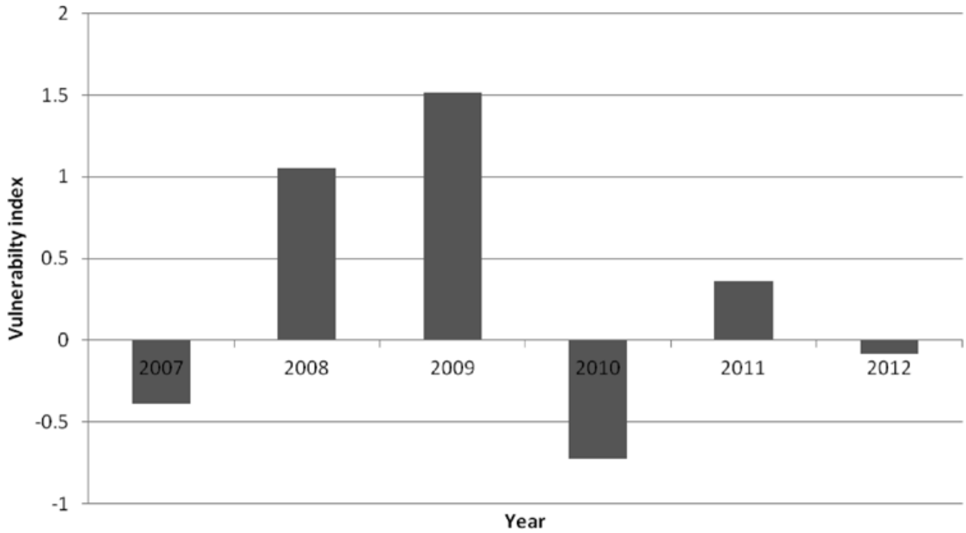

Figure 2.5
Amboseli lion Vulnerability Index to drought 2007-2012.

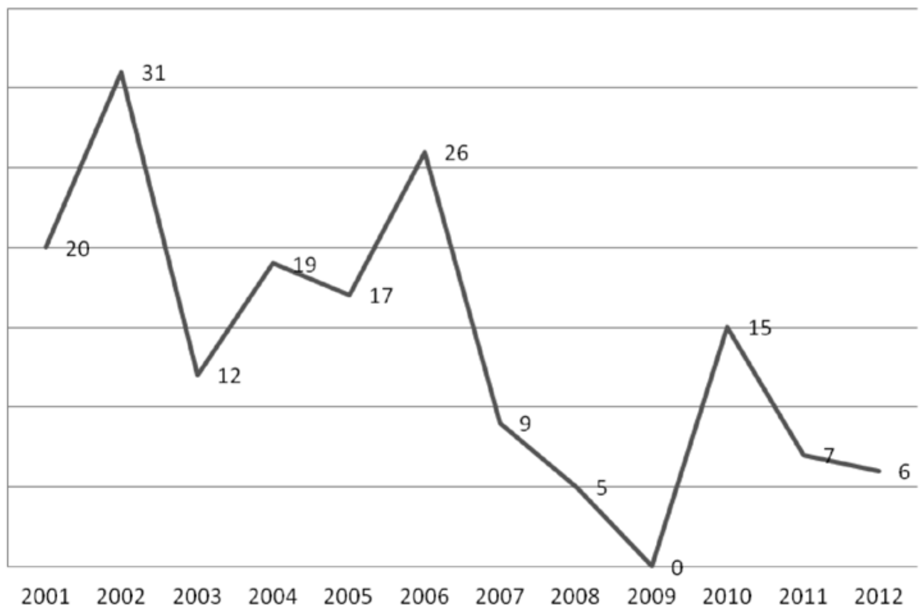

Figure 2.6
Retaliatory lion killing in Amboseli National Park and neighbouring community areas (Sources: KWS occurance report book 2001-2012)

The sex ratio (Male: Female) of the Amboseli NP lion population decreased significantly ($t = 4.24$, $df = 2.047$, $P < 0.05$) from 1:1.63 (± 5.23 SE) before/during the drought (2007-2009) to 1:4.26 (± 0.02 SE) after the drought (2010-2012) (Table 2.1). Similarly, the age ratio (Juvenile: Adult) increased significantly ($t = 3.53$, $df = 3.051$, $P < 0.05$) from 1: 3.07 (± 0.153 SE) before/during (2007-2009) the drought to 1: 1.64 (± 2.70 SE) after the drought (2010-2012) (Table 2.1).

The lion adult group size showed a significant ($t = 12.33$, $df = 3.275$, $P < 0.001$) decline from 3.75 (± 0.77 SE) before/during the drought (2007-2009) to 1.35 (± 1.28 SE) after the drought (2010-2012) (Table 2.1).

Table 2.1
Changes in lion population density (Total lions per km^2, Adult lions per 100 km^2), sex ratio (Male: Female) and sex ratio (Juvenile: Adult) and estimated lion pride size between 2007 and 2012 in Amboseli NP, ($P>0.05$) NS indicates non-significance.

Years	Total density	Adult density	Juvenile: Adult ratio	Male: Female ratio	Adult group size
2007	6.63	4.85	1:2.71	1:1.7	3.58
2008	6.63	4.85	1:2.71	1:1.7	3.58
2009	10.2	6.38	1:3.78	1:1.5	4.08
2010	8.16	5.35	1:1.9	1:3.2	1.25
2011	8.42	5.35	1:1.75	1:4.25	1.25
2012	8.67	4.85	1:1.27	1:5.33	1.55
Pre/during drought mean	7.31 s.d.:± 3.87	5.36 s.d.:±1.79	1: 3.07 s.d.:± 0.153	1:1.6 s.d.:± 0.08	3.75 s.d.:± 0.77
Post-drought mean	8.42 s.d.:± 1.65	5.18 s.d.:± 2.14	1: 1.64 s.d.: ± 2.70	1:4.26 s.d.:± 0.02	1.35 s.d.:± 1.28
	t = 1.596, df = 2.187, NS	t = 0.3293, df = .422, NS	t = 3.5303, df = 3.051, P <0.05	t = 4.2468, df = 2.047, P<0.05	t = 12.205, df = 3.3, P<0.001

Based on Table 2.1 there is no significant difference between lion population density (including juveniles) before (2007, 2008) and after the drought year (2010, 2011, 2012).

When taking into account lion densities including juveniles, the picture is different (see Table 2.1). The densities after the drought year is significantly higher compared to before the drought year (t-test, p=0.00902)

2.4 Discussion

2.4.1 Impact of drought severity, prey abundance and related lion retaliatory killing

The Drought Severity Index (DSI) showed 2009 to be the most 'severe drought' in the last 35 years. The Prey Abundance Index (PAI) showed a sharp decline during the years after the drought (2010-2012). The Vulnerability Index (VI) for lions was lowest (negative) in 2010, which means the response of the lion population in terms of social structure (sex ratio, juvenile: adult ratio and group size), diet, mortality and reproduction was highest in the year directly after the drought. In 2011 the VI was positive meaning a lower response in terms of social structure, diet, mortality and reproduction. The slight negative VI in 2012 indicates that the system was still unstable while on its way to recovery to the orginal parameters. It is clear that a negative VI does not necessarily mean a negative impact, since reproduction was very high shortly after the drought year.

We used the vulnerability index to demonstrate changes in population structure and diet but also increased mortality of males or increased reproduction of females on the short term. The results showed an increased mortality of male lions the year after the drought due to increased livestock raiding. We conclude that the extreme drought had negative effects on the lion population in terms of increased mortality, a change in sex ratio and a change in diet, but also positive effects, like an increase in reproduction. We observed a change from several pride males(coalitions) in the park, serving at least three prides, before the drought year to a single pride coalition (Ambogga and Shaka) serving all prides in the park. Also the high mortality of pride males in 2010 did not affect reproduction in a negative way, on the contrary, it may well be that lion populations have developed capacity to cope on the short term with extreme droughts by strong reproduction to compernsate for increased mortality.

When excluding the two disturbed years with outliers in lion mortality (2009 and 2010), we found a significantly lower lion mortality in the period after the introduction of the consolation scheme (2007- 2012) compared to the period before (2001-2006). When excluding the two disturbed years with outliers (2009 and 2010), there was no significant difference in mortality before the drought (2007 and 2008) and after the drought (2011, 2012).

Apparantly the introduction of the consolation scheme had a dominant impact on lion mortality figures and that, apart from the peak mortality in 2010, the extreme drought in 2009 had no long lasting impact on lion mortality. We realise that our sample size is very small, but it gives an indication.

Our study demonstrates that the year directly after the drought (2010) was crucial for lion survival and determined the outcome in terms of mortality and lion population structure. In terms of lion densities, 2009 showed an extremely high lion population density, probably due to immigration of lions resident outside Amboseli NP, but pre- and post drought densities did not show significant differences, when looking at adult lion density, but showed a higher density when we included juveniles. Our interpretation is that human-induced mortality and climatic variability had significant effects on lion pride organization and social structure. The drought affected lion prey availability, and as a result lion livestock predation increased, along with lion retaliatory killing. A total of 14 lions were killed before the drought and 28 lions were killed after the drought, of which 15 in 2010 alone. Our finding showed clearly from all data sets that mortality of male lions is very high one year after the drought (2010) because there is more livestock raiding due to changes in prey availability. In the years before the drought lion mortality went down from 26 in 2006, 9 in 2007, 5 in 2008 to 0 in 2009. This downward trend can be explained by the introduction of the consolation scheme in 2008. After the peak mortality in 2010 mortality went down and reproduction went up and the lion population and their prey start to recover.

We observed, that although drought also affected livestock, people moved with their livestock and returned after the rains. Other livestock owners restocked their farms with livestocks bought from else where. Our study found a serious problem in prey availability during the first wet season after the drought year (2010) showing changes in diet, sex ratio and group size as well as extremely high mortality. There may also be positive effects of drought for lion populations, shown by enhanced reproduction immediately after. Previous studies have established strong relationships between herbivore abundance and rainfall (Ottichilo et al., 2000) and showed that extreme drought had adverse impacts on predator biomass (Georgiadis et al., 2007). Rainfall variability, therefore, is considered important as it influences the dynamics of African ungulates and thereby may alter carnivore population structure and abundance.

2.4.2 Effect on lion sex ratio

The Male: Female sex ratio showed a significant decrease, possibly due to; i) Increased livestock predation by males as compared to females due to a collapse in pride structure that affect traditional hunting system, ii) increased offtake of males which appear to be preferentially targeted by Maasai livestock owners. This is probably because the law allows property defence, and due to cultural background, Maasai livestock owners have a preference for killing male lions. We also suggest that due to the fact that females often hunt in groups, and have lower energy requirements than males; therefore, females probably may cope better with altered prey communities of more smaller preferred prey than the males (Hayward, 2007). The skewed Male: Female sex ratio is comparable to the one reported for a lion population in the Luangwa Valley (Zambia) another male-depopulated area (Fryxell et al., 2007, Loveridge et al., 2006; Croes et al., 2011; Yamazaki, 1996) separately found that social structure and behaviour of prides was disrupted by removal of pride males by sport hunters, leaving gaps within the territorial structure. The high density in 2009 is directly related to the drought. In search of water also lion's resident outside Amboseli NP entered the park. During the whole study period lion density was not affected, but population structure (group size, ratio male: female and ratio adult: juvenile), diet and mortality showed changes.

The significant change in age structure (Juveniles: Adults) was an indication of a growing population with more juveniles than adults, a sign of rapid restoration and high resilience. This increase in reproduction was probably a response to the excessive mortality of male lions, which resulted in less competition between males and less infanticide.

2.4.3 Effect on lion social structure and group size

The changes in social structure, with smaller group size after the drought, are an indication of a disturbed social structure as a result of scarcity of food. The study found a serious problem in prey availability during the first wet season after the drought year (2010) showing changes in diet, sex ratio and group size as well as extremely high mortality. There may also be positive effects of drought for lion populations, like enhanced reproduction immediately after the drought.

Previous studies have shown that lion group size is correlated with prey sizes and prey density (Bauer et al., 2003) but in this study we found that even prey densities have significant effect. The lion group size in Amboseli NP before the drought (3.5) was closer to the lion group size found in the Serengeti ecosystem (2.8) (Schaller, 1972; Cooper, 1991).

We suggest that low prey density makes it necessary to hunt individually and reduce group size, as also found by (Bauer et al. 2003; Carbone & Gittleman, 2002). This reduced group size after the extreme drought (1.35) may be a survival strategy for lions and indicates resilience in coping with food shortage in the aftermath of the drought.

The final conclusion is that there is no long term negative effect and that indeed there is a positive effect of increased reproduction, the vulnerability index is not necessarily negative, only indicates the chance of change in structure (sex ratio and group size), diet and mortality. With a high proportion of juveniles, and with larger prey numbers, we expect that the lion population will ultimately be restored. The drought Vulnerability Index can be used to plan mitigation measures and identify drought coping- or adaptation mechanisms for lions in other areas.

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3

Impact of Severe Climate Variability on Lion Home Range and Movement Patterns in the Amboseli Ecosystem, Kenya

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Abstract

In this study, we were interested in understanding if droughts influence the home range of predators such as lions, and if it does, in what ways the droughts influenced lions to adjust their home range, in response to prey availability. We monitored movements of ten lions fitted with GPS-GSM collars in order to analyse their home range and movement patterns over a six year period (2007-2012). We assessed the impact of a severe drought on the lion home range and movement patterns in the Amboseli ecosystem. There was strong positive correlation between the home range size and distance moved in 24 hours before and during the drought (2007-2009), while after the drought there was a significant negative correlation. A weak positive correlation was evident between the lion home range and rainfall amounts (2010-2012). The male and female home ranges varied over the study period. The home range size and movement patterns coincided with permanent swamps and areas of high prey density inside the protected area. Over the course of the dry season and following the drought, the ranges initially shrank and then expanded in response to decreasing prey densities. The lions spent considerable time outside the park boundaries, particularly after the severe drought. We conclude that under fragmented habitats coupled with severe climate conditions create can new challenges for lion conservation due to its effects on prey availability and subsequent influences on carnivore species ranging patterns. Stochastic weather patterns can force wide-ranging species beyond current reserve boundaries, into areas where there will be greater conflicts with humans.

3.1 Introduction

African lions (Panthera *leo leo*) are threatened with extinction across their range, and have been classified as 'Vulnerable´ on the global IUCN Red List (Brooks et al., 2006). They are also currently under consideration for the Endangered Species Act, US Fissures and wildlife society (US-FWS) (Place et al., 2011). Several authors have described the declines in lion population due to factors related to human interference (trophy hunting, poaching, agricultural and urban development, habitat fragmentation and conflicts) while others relate it to natural factors related to environment-climate variability, cover, prey availability and topography (Bauer & Van der Merwe, 2004). There is, however, paucity of research on the impacts of stochastic drought on a lion population and their home ranges.

Conservation policy and habitat management based on scientific information is important for managing protected areas for large carnivores (Karanth & Chellam, 2009). However, climatic changes may modify the distribution and abundance of species and include some key variables that may have severe impact on ecosystems that adversely influence lions' natural habitat selections (Iverson & Prasad, 1998; Ohlemuller et al., 2006). Knowledge of a species' ranging behaviour is both fundamental to understanding its behavioral ecology and a prerequisite to planning its management. Rainfall determines habitat quality and structure through its influence on vegetation health, mediated through edaphic and topographic/catenary gradients (Bell & Jachmann, 2008; McNaughton et al., 1988) and can induce changes in habitat suitability, which is capable of substantially modifying predator-prey relations (Smuts, 1978; Whyte et al., 1995). Besides prey availability and vegetation cover, rainfall also affects the distribution of drinking water, thereby modulating the spatial-temporal distribution of water-dependent herbivores and carnivores (Hanby & Packer, 1995; Krebs & Dominique, 2006), "Similarly, climate affects the distribution and abundance of mammals" (Krebs & Dominique, 2006); Moreover, the impact of climate change and climatic variability show a spatially heterogeneous pattern and may have already resulted in several recent local species extinctions (Parmesan 2006). These changes raise concerns about the effectiveness of existing species protection strategies (Halpin, 1997; Hannah et al., 2002; Peter & Darling, 1985).

Species conservation relies predominately on fixed systems of protected areas. Furthermore, the mandated goals of many conservation agencies and institutions are to protect particular species assemblages and ecosystems within these systems (Lemieux & Scott, 2005). Of particular importance are the challenges associated with conservation of carnivores outside protected areas, including both anthropogenic and ecological factors (Dolrenry et al., 2014). The home range size of large carnivores is a good predictor of its extinction probability relative to the size of the neighbouring protected areas, where home ranges extend significantly into non-protected areas relative to the size of the neighbouring protected areas (Woodroffe & Ginsberg 1998; Woodroffe et al., 2001). Increased anthropogenic activities as a consequence of rapid human population growth has resulted in the reduction of natural habitats for lions (Riggio et al., 2013; Bauer et al., 2004) and increasing persecution (Tumenta et al., 2010).

Home-range analysis of large carnivores provides answers to many biological questions related to population dynamics, social interactions, and spacing patterns. Lions' home range size varies in relation to a wide range of factors, including prey availability, social interactions, habitat quality and reproductive status (Gittleman & Harvey, 1982; Van Orsdol et al., 1985; Spong, 2002; Bauer & De Iongh, 2005). Abundant food and high-quality habitat allow an animal to meet its biological requirements in a relatively small home range and vice versa (Gittleman & Harvey, 1982; MacDonald, 1983).

The home range area is used during an animal's normal activities of food gathering, mating and caring for its young. The core of its home range is defined as the most intensely used area within that animal's home range (Powell, 2000). In the case of lions, their home range is directly related to prey abundance and the presence of water, thus lower prey densities and low availability of water correspond with larger home ranges and vice versa (Celesia et al., 2009; Van Orsdol et al., 1985; Tumenta et al., 2013). However, other factors such as social status, sex, age, season, disturbance and the presence of livestock may influence home range (Schaller, 1972; Loveridge et al., 2007; Tumenta, 2013).

Group size and territoriality are social factors that also influence home range size (Packer et al., 1990). Home-range size increase therefore lead to group size (Van Orsdol et al., 1985). Larger group require more prey and therefore larger areas corresponding to prey biomass and density. The most important factor that influences lion home range size (Van Orsdol et al., 1985; Bauer & De Iongh, 2005), with lion home range size being negatively correlated with prey abundance (Van Orsdol et al., 1985; Bauer & De Iongh, 2005; Loveridge et al., 2007). Maintaining a pride home range is of great importance, as evidenced by the fact that fatalities are relatively common during intergroup encounters (McComb et al., 1994). Understanding the variation in animal home range size and identifying the factors that underlie this variation are fundamental to understanding the distribution and abundance of animals, and ultimately their population regulation (Wang & Grimm, 2007), habitat selection (Rhodes et al., 2005), community structure (Matias, 2013), as well as the management and conservation of ecosystems (Woodroffe & Ginsberg, 2000).

The present study is the first of its kind to analyse the effect of drought on lion movements, covering a period of three years before and during the drought period (2007-2009) as well as a three year period after the severe drought period (2010-2012). Our study investigated the impact of a severe drought on lion's home ranges size and movement patterns, in relation to variation in food resources (prey abundance) before and during versus after a severe drought period.

3.2 Materials and methods

3.2.1 Study area

The Amboseli ecosystem is situated in the south-west of Kenya, bordering Tanzania. The ecosystem covers an area of approximately 5,700 km^2 stretching between Chyulu Hills and Tsavo West National Parks South to Mt. Kilimanjaro in Tanzania (Figure 3.1). Administratively, the Amboseli ecosystem consists of Amboseli National Park (ANP; 392 km^2) and the six surrounding communally-owned Maasai group ranches. These group ranches cover an area of about 5,063 km^2 in Kajiado County (Figure 3.1). In the centre of the ecosystem, lies the Amboseli Basin, a Pleistocene lake bed. The basin provides a permanent source of water from Mt. Kilimanjaro that attracts high concentrations of migratory animals during the dry season.

The area is generally arid to semi-arid. Rainfall is bi-modal, with short rains coming in November and a long rain period in March-May (Altmann et al., 2002). An average of 340 mm rainfall per annum is expected (Moss et al., 2011), This rainfall deficiency makes the area suitable for conservation and tourism enterprises (Moss et al., 2011). The ANP is a dry season grazing area for wildlife that disperses widely to the adjacent group ranches during the wet season, when water and forage is plentiful (Groom & Harris, 2010; Muthiani & Wandera, 2000; Ntiati, 2002). Although ANP is one of the leading tourist destinations in the country, with an average of 150,000 visitors per annum due to high congregation of wildlife (Makonio et al., 2009), its future might be threatened by the increase of human development and livestock grazing- this is already indicated by increased human conflicts (Okello & Kioko, 2010). The development activities around the park have caused fragmentation of wildlife habitats, diminished the dispersal areas and limited the free movement of animals (Okello & Kioko, 2010, Moss et al., 2011).

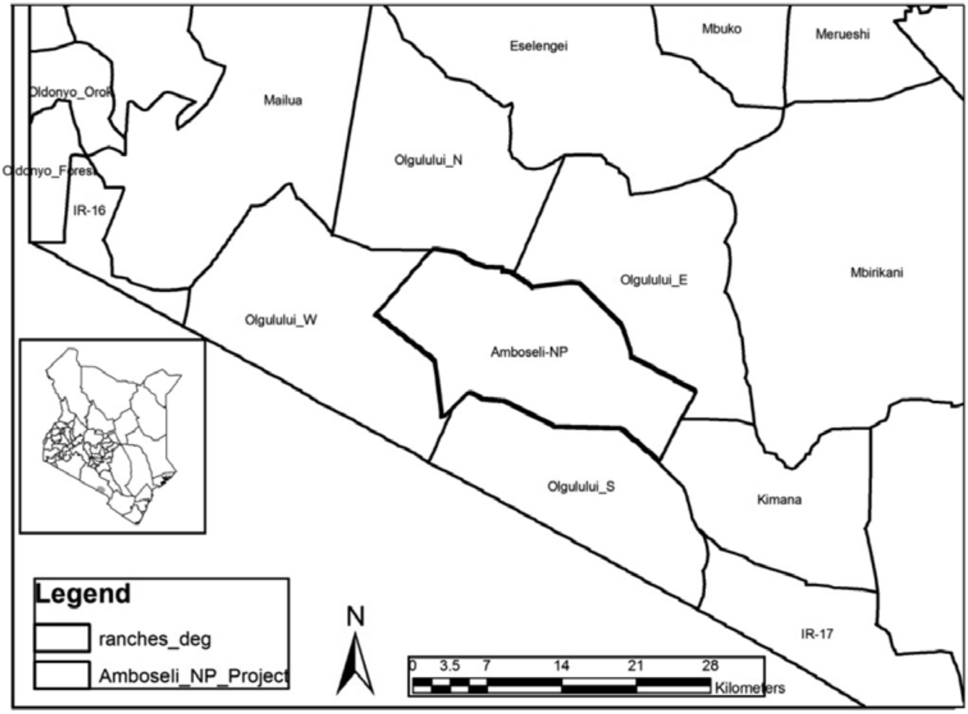

Figure 3.1
Amboseli National Park and surrounding group ranches which together from the Amboseli ecosystem.

3.2.2 Methods

To understand lion ranging patterns and seasonal movements, we immobilized and radio-collared ten lions between 2007 and 2009. The lions were captured by free darting (Bauer & De Iongh, 2005), after being attracted using a calling station set-up adapted from Ogutu & Dublin (1998). We used GPS-GSM collars from African Wildlife Tracking with an integrated VHF radio transmitter (Pretoria, SA). Characteristics of these collars have been described previously (Tomkiewicz et al., 2010; Schwartz & Arthur, 1999). The collars were programmed to attempt location of animals at either 3-hour or 30-minute intervals. The collars recorded date, time, latitude, longitude, and general cause of successful location fixes. Direct observations of individuals were made periodically using VHF radio tracking techniques, following White & Otis (1999). Table 3.1 presents details of the collared lions. The GPS coordinates of scheduled lion locations were downloaded from the Yrless website (www.yrless.co.za). The lion locations were subsequently processed in ArcMap (ArcGIS 9.3.1, ESRI, Redwood, CA, USA), using the Hawth's Tools extension packages Spatial Analyst and Animal Movement (Gitzen et al., 2006) to determine the home ranges, movement path parameter, and step length. We only used the functioning GPS/GSM continuously for more than one month (Table 3.1). A large number of fixes, 17,333 before and during the drought and 26,309 after the drought were obtained during the study period. To facilitate analysis and reduce the probability of autocorrelation, a three-hour selection was carried out on the data reducing the data size to six GPS points per day.

3.2.3 Home Range analysis

Home ranges were estimated using two methods, the minimum convex polygon (MCP) and the Kernel Density Estimator (KDE). The MCP method is the oldest one used among home range analysis methods (Burt, 1943), being the smallest convex polygon that encompasses all lion locations, either using all the locations (MCP 100%) or by first removing 5% of the outliers in the dataset (MCP 95%) (Powell, 2000). Some authors suggest that MCP is inefficient and highly sensitive to sample size and outliers (Börger et al., 2006), hence important to compare with KDE for accuracy. In contrast, the KDE method is remarkably efficient, robust and unbiased (Worton, 1989; Börger et al., 2006). This method uses the harmonic mean of the locations to assess the core density areas, with the areas defined as the boundaries of the lion's home range (KDE 95%), the core home range (KDE 50%) and the heart of the core area (KDE 5%). We used the KDE method to calculate home range metrics. We set the outer boundary at 95% and the core area at 50% (White & Otis, 1999). The smoothing factor was chosen using the least square cross validation (Garton & Horne 2006) of 0.02 for all our calculations. Ranges were analysed for each year during the study period. Home ranges, both MCP and KDE, for the different seasons were calculated and compared with other studies.

Table 3.1
Overview of Lion collarings in Amboseli NP during 2007-2012. Dates are in dd/mm/yy. Estimated year of birth is based on morphometrics and examination of nose pigmentation and canines during collaring. GPS fixes represent all fixes received from start of collaring until end of collaring or collar

Lion ID	Collar ID	Collar Frequency	Gender	Date collaring	End data-transmitter	Estimated year of birth	No. of months monitored	No. of GPS fixes
L1 **Amy Jane**	AS69, AS71	149.820 149.7067	F	9/7/2007 12/7//2008	12/7/2008 12/6/2010	2001	34	7134
L2 **Tato**	AS70 AS129	149.860 149.8607	F	10/7/2007 19/8//2009	2/2/2009 30/3/2010	1998	26	4514
L3 **Kip**	AS71 AS129 AG174 AG452	149.7067 149.8607 149.390 149.130	M	11/7//2007 11/7//2008 17/8/2009 3/7//2010	11/7/2008 17/8/2009 3/7/2010 24/8/2010	2004	37	5178
L4 **Shangiki**	AS72 AG513	149.7289 151.530	F	11/7//2007 9/11/2010	31/5/2010 8/3/2013	2003	63	16557
L5 **Ambogga**	AS73 AS128 AG369	149.9509 149.070 150.580	M	12/7//2007 13/7//2008 5/7//2010	23/3/2008 5/7/2010 29/11/2012	2004	60	12730
L6 **Willy**	AG175	149.620	F	17/8//2009	24/1/2012	2004	29	3456
L7 **Belta**	AG370	150.710	F	6/7//2010	25/5/2011	2006	10	2327
L8 **Amy**	AG451	149.050	F	6/7//2010	22/8/2012	2005	25	7730
L9 **Shaka**	AG452	149.130	M	12/10/2010	16/2/2013	2004	28	11023
L10 **Nane**	AG514	151.380	F	9/11/2011	28/9/2012	2004	22	5756

We used potential minimum distance, defined as the minimum distance travelled by a lion in a straight line, measured in kilometers, either in a 12-hour period, night (18:00 hours until 06:00 hours) or day (06:00 hours until 18:00 hours) or average potential minimum movement, measured over a 24-hour period. All were measured for the period before, during, and after the drought to assess the impact of severe drought on the lion movement pattern.

We also assessed use by lions of protected areas versus non-protected areas in relation to the drought by assessing the number of days that the lions spent exclusively inside the park, the number of days the lions they were both inside and outside the park, and number of days the lions spent exclusively outside the park. We determined overlap in home range and movement inside and outside ANP using ARC-GIS (ESRI, Redwood, CA, USA).

We analysed rainfall statistics during 1977-2012 obtained by the Amboseli Baboon Research Project following Altmann et al. (2002). We then determined the effect of rainfall variability and severe drought on lion home range by relating seasonal rainfall and lion home range in square kilometers and daily distance moved, in kilometers. We set annual mean monthly rainfall of 28.3 mm (Figure 3.2) as a cutoff point between the drought and wet period.

3.2.4 Statistical analysis

All statistical analysis were carried out in R 3.0 programme (R Development Team, Vienna, Austria). The dependent factors were home range and potential minimum movement per day. The independent factors were monthly rainfall and sex of lion. The regression of covariates on MCP was done using a generalized linear mixed effects model (GLM) with the Poisson link function. For the problem of fit of distribution to the KDE data, we did a linear mixed effects model for both KDE50 and KDE95 response variables.

The lions' home range and daily movements were compared to one another to test for significant differences according to social status and sex differences. A test on normal distribution was done with the Shapiro-Wilkes test. We found the distribution of home range data were non-normal, thus we log-transformed the data and applied a t-test. Furthermore, each lion's day and night movements were compared using one-sided Wilcoxon signed rank tests ($p<0.05$) since the samples were not normally distributed and the subsamples were paired. In order to test whether the lion's travelled distance changed between 2010 and 2011, a paired t-test ($p<0.05$) or a Wilcoxon signed rank test ($p<0.05$) were run. Difficulties with data analysis were attributable to unbalanced structures, nesting verses crossed structure, size of data and negativity of variance, as well as residual analysis and diagnostics due to assumptions on the residuals, among others. Restricted/Residual Maximum Likelihood Estimation (REML) is well-suited to handle the negativity of variance estimates, unlike ANOVA or Maximum Likelihood Estimation (MLE).

We compared several models before we decided on an optimal model for all home ranges MCPs and KDE on parameter interpretation. We considered a fixed effect factor as opposed to a random effect factor whose levels in the study are just a sample of all the other possible choices. In the mixed model, the multilevel structure contains factors that are considered fixed and others random. In such a mixed-model scenario, the key steps of mixed-model analysis involve estimating variance component parameters using Restricted Maximum Likelihood (REML), then estimating fixed effects parameters using Bayesian Information Criterion (Sclove, 1987), for lion home range. We carried out ANOVA on (model 1, 2 and 3) as follows:

Model 1, had the response variable as home range areas MCP in km^2 while the explanatory variables were: fixed effects of season, period of drought, sex, interactions between season and drought period and the interaction between period of drought and sex. Random effect was the individual lion.

Thus, Model 1 was constructed as follows:

> Area of MCP, KDE 95 and KDE 50 in km^2 ~ season * drought period_ * sex +
> (1 | LION_ID)

Model 2, had the response variable as home range area MCP in km^2 while the explanatory variables were: fixed effects of season, period of drought, sex, interactions between season and drought period, interaction between season and sex and the interaction between period of drought and sex. Random effect was the individual lion.

Model 2:

> Area of MCP, KDE 95 and KDE 50 in km^2 ~ season + drought period + sex +
> (1 | LION_ID) +; season: drought period + season: sex + drought period: sex

Model 3, the response variable was the area of the MCPs, KDE 95 and KDE 50 in km^2. The explanatory variables were the: fixed effects main effects of season, period of drought, sex, and up to three way interactions between season, drought period and sex. Again, the random effect was the individual lion.

Model 3:

Area of MCP, KDE 95 and KDE 50 in km^2 ~ season + drought period + sex + (1 | LION_ID) + season: drought period + drought period: sex

3.3 Results

3.3.1 Relationship between rainfall, home range and movement patterns

Our analysis of rainfall data during 1977-2012 showed high rainfall variability and severe recurrent droughts at varying annual intervals (Fig 3.2). For example, severe droughts occurred during 1984, 1992, 1999, 2003, and 2009. The lion home range data during 2007-2012 showed strong correlation between home range sizes and lion daily distance moved in 24 hours before (2007 and 2008; $r^2 = 0.401$) and during (2009; $r^2 = 0.359$) the drought. During the period that followed the drought (2010-2012), there was a non-significant correlation ($r^2 = 0.285$) between home range size and average daily distance movement by lions. There was also a significant negative correlation ($r^2 = -0.030$) between the amount of rainfall and the average potential minimum distance moved in 24 hours after the severe drought.

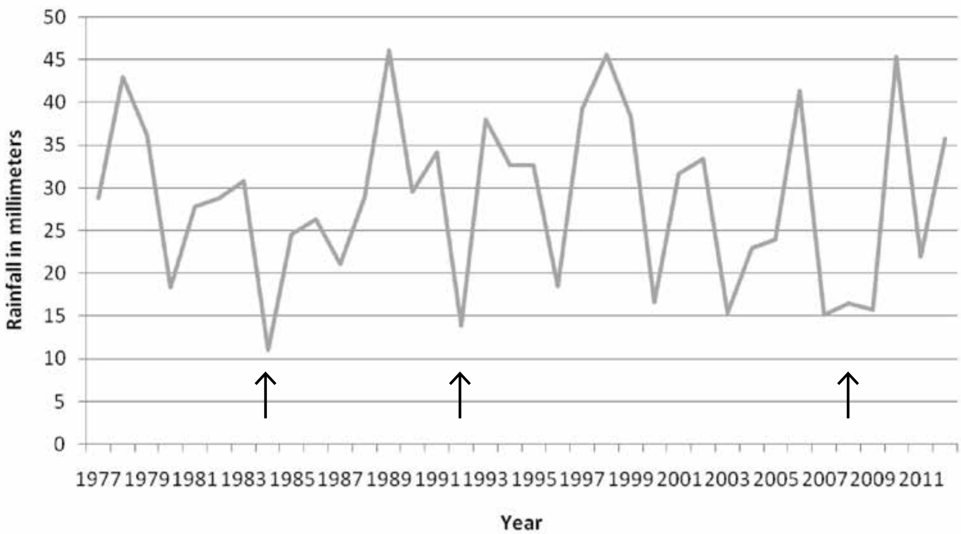

Figure 3.2
Mean annual monthly rainfall for the years 1977-2012 and severe drought period 2008-2009 in Amboseli Ecosystem (Source: Amboseli Baboon research). The arrow indicates drought which was comparable to 1984 and 1992 droughts and drought period which indicate worse drought in 35 years (2009).

We found a high mean seasonal (wet and dry) lion home range variability before and during (2008-2009) and after the drought (2010-2012) (Table 3.2). The mean home range seasonal variability was greater during post-drought. Our results showed expanded home ranges even during the dry season for the post-drought period, as compared with that of dry seasons of the pre-drought and actual drought period (Table 3.2). The mean overall home range was not significantly different for male and female lions however.

Table 3.2
Summary of dry and wet seasonal variation of lion home ranges (km^2) for MCP 100, KDE 95 and KDE 50, also indicating periods before/during and after the drought, for both male and female lions (T test, $p>0.05$).

Home range (km^2)	**Sex**			**Period before and during drought**		**Period after drought**	
		Sample size	s.d.	Dry season	Wet season	Dry season	Wet season
Mean range size MCP100	Female	7	0.33	121.70	34.91	262.43	187.98
	Male	3	-1	177.10	57.03	373.61	272.26
Mean range size KDE95	Female	7	0.33	23.93	46.15	63.98	73.28
	Male	3	-1	26.01	52.76	74.16	91.252
Mean core range size KDE50	Female	7	0.33	4.85	9.22	11.97	14.06
	Male	3	-1	9.56	4.52	11.59	14.95

There was a high variation in lion home range sizes for the period after the drought (2010-2012) compared to the period before and during the drought (2007-2009; Figures 3.3 and 3.4). Lions expanded their home range during the period after the drought, seeking new territories not covered before/during the drought.

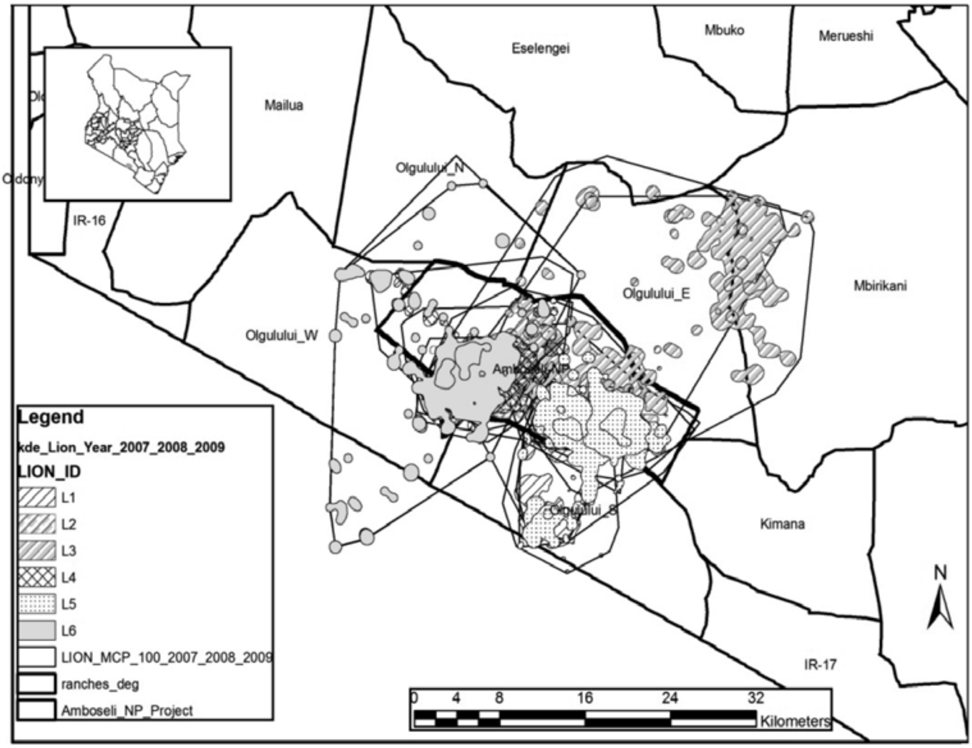

Figure 3.3
Lion home range sizes before and during the severe drought (2007-2009) measured in kilometer squared for MCP100, KDE95 and KDE50.

3.3.2 Mixed modeling and model comparisons

The results show that model 2 was the most optimal of the three models for MCP 100 (smallest BIC=19060), KDE95 (smallest BIC=2511), and KDE50 (smallest BIC=688.99). Similarly, the p-value shows that model 2 variables were significantly different (p=1.718), but model 1 was not significantly different from model 3 (p=0.375, >0.05). We therefore interpreted the output of model 2 for MCP100, KDE95 and KDE 50.

The results showed that all the variables considered in model 2 were significant (Table 3.3). We therefore did not need to remove any variables in the model before we ran the mixed-model analysis. The intercept in this case represented the average area in km^2 for MCP 100, KDE 95 and 50 for the following conditions: dry season, period after drought, female lion.

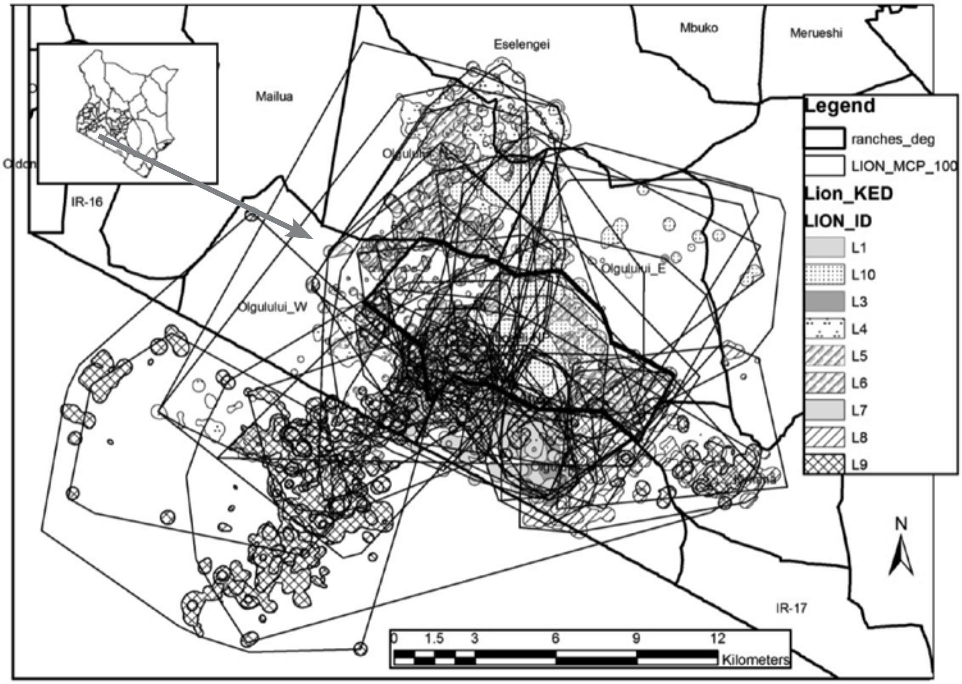

Figure 3.4
Lion home range sizes for the period after the drought (2010–2012) measured in km^2 for MCP100, KDE95 and KDE50.

Mixed *model (main effects)*

Holding other variables at their default, the mean MCP area in km^2 for male lions was greater by 0.89 km^2 compared to the mean MCP for female lions. The difference is statistically significant ($p=0.002$, <0.05). The MCP area for the period before drought was lower by 0.61 km^2 compared to the period after the drought. Similarly, the dry season MCP measurements were also lower by 0.385 km^2 compared to the wet season. Conversely, holding other variables at their default, the mean KDE95 area in km^2 for male lions was greater by 0.31 km^2 than the mean KDE95 for female lions. The difference was statistically significant ($p=0.017$, <0.05). The KDE95 area for the period before the drought was lower by 0.37 km^2 than the period after the drought, while the dry season also had lower KDE95 areas by 0.18 km^2 compared to the wet season. Similarly, holding other variables at their default, the mean KDE50 for male lions was higher by 0.08 km^2 than the mean KDE50 for female lions. However, the difference was not statistically significant ($p=0.604$, >0.05). The KDE50 area for the period before the drought was lower by 0.25 km^2 compared to the period after the drought while the dry season also had lower KDE50 by 0.22 km^2 compared to the wet season.

Mixed *effects (interaction terms)*

The interaction between season and period was significant ($p < 0.0001$). We observed that the period before the drought had a lower MCP than the period after the drought by 0.79 km^2 during the dry season. The interaction between season and period was significant ($p < 0.0001$). We observed that the period before the drought had a lower KDE95 than the period after the drought by 0.48331 km^2 during the dry season. The interaction between season and period was significant ($p<0.0001$). We observed that the period before the drought had a lower KDE50 than the period after the drought, by 0.44 km^2.

Table 3.3
Output of Fixed Effects of Mixed Modeling for lion home range indicating seasonal home range variation, before/during and after the drought, sex, and their interactions showing estimated standard error, Z-values and level of significance P<0.005 for MCP100, KDE 095 and KDE 50.

	Period	Estimated	Std. Error	Z-value	Pr(>|z|)
Model 1: Home range MCP100	(Intercept)	5.26893	0.15954	33.03	< 2e-16 ***
	Dry Season	-0.38578	0.01470	-26.25	< 2e-16 ***
	Before drought	-0.61415	0.02347	-26.16	< 2e-16 ***
	Sex: Male	0.88742	0.29099	3.05	0.00229 **
	Dry Season: Before drought	-0.78875	0.02492	-31.65	< 2e-16 ***
	Dry Season: Sex: Male	0.08383	0.01950	4.69	1.72e-05 ***
	Before drought Sex: Male	-0.65428	0.04373	-14.96	< 2e-16 ***
Model 3: Home range KDE95	(Intercept)	4.22476	0.06506	64.94	< 2e-16 ***
	Dry Season	-0.17830	0.02053	-8.68	< 2e-16 ***
	Before drought	-0.36607	0.03952	-9.26	< 2e-16 ***
	Sex: Male	0.30873	0.11609	2.66	0.00783 **
	Dry Season: Before drought	-0.48331	0.03967	-12.18	< 2e-16 ***
	Before drought Sex: Male	-0.28064	0.05881	-4.77	1.82e-06 ***

Model 2: Home range core KDE50	(Intercept)	2.55628	0.09153	27.927	< 2e-16 ***
	Dry Season	-0.22355	0.04886	-4.576	4.758e-06 ***
	Before drought	-0.25082	0.08782	-2.856	0.00429 **
	Sex: Male	0.07837	0.15118	0.518	0.604
	Season dry: Before drought	-0.44136	0.09131	-4.833	1.34e-06 ***
	Before drought Sex: Male	0.35531	0.08014	-4.434	9.26e-06 ***

Signifiance: *** p<0.001 ** p<0.01 '*' p<0.05 '.' P<0.1

Table 3.4 shows that there was no significant difference by sex (W=1680, p=0.102) in the number of days spent outside the park or by season (W=2420, p=0.114), but there was a significant difference between males and females in the number of days spent outside the park for the period before and during the drought and after the drought (W=1732.5, p=0.033). Clearly, the lions moved further outside of the protected area during the drought when prey became scarce.

Table 3.4
Lion daily, and seasonal movement before/during and after the drought, Wilcoxon – Paired sample t-test values and level of significance.

Parameters	Wilcoxon (W) test	P=values
Days outside by sex	1680	0.1022 - NS
Days outside by season	2420	0.1489 - NS
Days outside by period before and after drought	1732.5	0.03394*
Distance moved in 24hrs	4972	1.873e-07***
Distance moved in 24hrs by season	8576	0.007838***
Distance moved in 24hrs by periods before and after drought	14717	< 2.2e-16***

Significance: 0 '***' p<0.001 '**' p<0.01 '*' p<0.05 '.' P<0.1

3.4 Discussion

3.4.1 Home ranges and movement patterns

We found significant variation in lion home ranges and movement patterns by the lions before and during the drought versus after the drought. We also found variation in male and female home ranges over the study period (Table 3.2). This was not surprising, as female lions defend smaller areas that provide good resources and are suitable for raising their cubs, whereas male lions defend larger areas that may cover the ranges of two or more female prides (Funston et al., 2003). Interestingly, this variation was significantly different between the before/during period and the period after the drought (Table 3.2). Similar findings were reported for the lions in Cameroon by Tumenta et al. (2013).

During the wet season, when food is abundant due to the large herds of herbivores dispersing outside the park, the lions increased their home range. Permanent water sources in ANP would have drawn herds of prey animals into the ANP during the drought year, when the minimum observed lion home ranges varied between 28-37 km^2. A similar situation was observed in Waza National Park in Cameroon with larger home ranges recorded during the wet seasons, probably because the prey species disperse more (Tumenta et al., 2010). Due to the expansion and contraction of home ranges in response to prey availability, the total prey biomass within the home range may remain relatively constant.

MacDonald (1983) suggested that resources and especially food dispersion are the main factors determining the home range size of large carnivores. According to their findings, the home range size is mainly determined by how food is distributed in space, while group size is determined by the prey size and quality of food patches (Bauer & De Iongh, 2005). An understanding of an animal's ranging patterns provides an important insight on how it uses its resources. Climate events affected the habitat quality, food supply and access, which in turn, as our results show, influenced the lions' home-range and movement patterns.

Our study is the first extensive study on the impact of a severe drought on the movements and home ranges of lions as it has demonstrated dramatic changes before and after the drought that could be explained by changes in prey densities.

3.4.2 Lion movement and landscape connectivity

We found that the potential minimum distance travelled was significantly greater after the drought (2010-2012) than before or during the drought (2007-2009). The daily distance travelled represented a measure of space requirement that partly reflects the food resource needs and distribution (Carbone et al., 2005).

On several occasions, both the male and female collared lions moved far from the ANP into the surrounding communal group ranches as also found by Dolrenry (2013). Furthermore, one of the males collared in this study spent a greater amount of time in the neighbouring country of Tanzania, located south of the park. This indicates that the lion populations in ANP are not isolated, as wildlife corridors exist between the park and group ranches (and maybe further away) (Dolrenry, 2013). This ability to disperse and survive in the surrounding landscapes and possibly connect to other lion populations serves an important function in endurance of the lion population inside the ANP (Dolrenry et al., 2014).

To improve lion conservation in a small National Park such as Amboseli we need to improve landscape connectivity, which would allow species movement for effective adaptation to climate change. The expanded home ranges observed in this study depict that the wild prey populations are in decline, due to severe climatic conditions such as the drought that caused the death of a large number of key lion prey, including wildebeest, zebra and buffaloes (Zwaagstra et al., 2010). When resource availability varies in both the short and long term, it poses difficult challenges for the long-lived, territorial species whose range persists longer than the periodicity of change in resource availability. To restore the populations of prey species and thus reduce the vulnerability of the lions, there is a need for concerted efforts to implement measures such as establishing community conservancies, and linkage and corridors to other protected areas within the region.

We conclude that under conditions of fragmented habitats, severe climate conditions create new challenges for lion conservation due to their effects on prey availability and subsequent influences on carnivore species' ranging patterns. Stochastic weather patterns can force wide-ranging species beyond current reserve boundaries, into areas where there will be greater conflicts with humans.

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4

Effects of Stochastic Drought on Prey Abundance and Diet of Lions in the Amboseli National Park – Kenya

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Abstract

We investigated the impact of climate variability on prey availability and diet of a lion population in Amboseli National Park before, during and after a severe drought in 2009. We used Jacobs' indices to analyse the changing prey preferences and the implications this may have had on conservation of prey and predator species in the Park. Lion prey composition showed significant difference before/during and after the drought. The lions' preferred prey species were wildebeest and zebra before the drought. During the drought, the lions benefited from high concentration of herbivores attracted to the Amboseli National Park due to a permanent swamp water. The drought resulted in mass mortality among wildebeest and zebra, forcing the lions to shift prey selection towards smaller prey species (Thomson's gazelle, ostrich and warthogs) and larger prey species (giraffe and buffalo), in addition to livestock. We noticed some recovery in the lions' preferred diet in 2011 and 2012, when they shifted back to medium-sized prey such as zebra and wildebeest. We conclude that the short-term impact of drought on herbivore abundance and lion diets is significant, but there are signs of high resilience and recovery as they bounced back after a few years after the drought. We also suggest that the changing abundance of lions and the decline in prey species during periods of severe drought are likely to cause high livestock predation, also affecting the tourism industry in the short term. Due to high resilience and recovery, we expect the long-term impact of the drought to be limited in the case of Amboseli National Park.

4.1 Introduction

Studies of natural animal populations often ignore the background effects that impact their dynamics, in focusing mainly on biological and reproductive cycles, while ignoring such factors as prey availability and the role that climate variability plays in shifting prey selection. This study investigated whether climate variability caused shifts in prey selection or influenced in anyway the populations of a top African predators in the Amboseli Ecosystem, in Kenya. This investigation was motivated by arguments of others (e.g., Krebs & Berteau, 2006) that it is not known if there is a direct link between climate variability, prey abundance and shift in prey selection. Many animal populations are clearly affected by climatic variability (Börger et al., 2006). Relatively little is however known about the impact of climate variability on predator-prey interactions, in areas where rainfall is highly unpredictable (Noy-Meir, 1973). Knowledge of predator-prey interaction under conditions of climate variability contributes substantially to our understanding of how future climate changes would influence ecosystems such as protected wildlife reserves and parks, which today have among the greatest concentrations of prey and predators (Mills & Shenk, 1992). Kunkel et al. (1999) and Owen-Smith & Mills (2007) noted that in such dynamic ecosystems prey availability, activity patterns and spatial distribution of herbivores can influence the prey selection and hunting success of carnivores.

It is therefore well understood that prey biomass influences ecological and demographic parameters of lion populations (Elliot & Cowan, 1978; Hanby & Bygott, 1979; Van Orsdol et al., 1985; Packer et al., 1988). Lions are opportunistic and often capture incautious prey (Schaller, 1972). Lion prey preference and selection is influenced by prey size and prey abundance as well as prey vulnerability and distribution (Schallar, 1972; Hayward & Kerley, 2005). Optimal diet theory predicts that the inclusion of a prey type in the diet may depend on the encounter rate and profitability as well (Scheel, 1993). As long as a predator can increase its survival chances or reproductive success by hunting more efficiently, natural selection will favor efficient, optimally foraging predators (Scheel 1993). For lions (*Panthera leo leo*) this means preying upon a broad range of medium – and large-sized mammals (Hayward & Kerley, 2005; Funston et al., 1998).

To better understand how or why a predator selects a prey species, it is important to know the prey availability. If a prey species is killed more often than would be expected according to chance, it is considered a preferred prey species. Conversely, if the percentage of a prey species in the diet of a certain carnivore is less than would be expected according to the availability of the said prey, it is considered an avoided prey species (Hayward & Kerley, 2005). The size of a prey species influences the balance between energy gain and energy expenditure in a particular hunt. Studies show a correlation between predator size and mean prey size as well as between predator size and prey diversity (Van Orsdol et al., 1985). Therefore, a detailed understanding of the dietary composition of the lion's diet is fundamental to understanding this predator – prey interaction, under variable climates and drought conditions. Drought and climate fluctuation affect resource availability to carnivores in general and the lions in particular. Many predators have strong preferences for a certain prey type regardless of its abundance (i.e., they are specialists), while other predators consume a wide variety of prey, with changes in prey availability strongly affecting their patterns of selection (i.e., generalists or opportunistic hunters).

Our research was conducted in the Amboseli Ecosystem in southwestern Kenya between 2007-2009 (Pre-drought) and 2011 to 2012 (Post drought recovery years). We posed the following questions:

1. How does climate variability associated with droughts influence prey selection of lions in the Amboseli ecosystem?
2. How do severe stochastic droughts limit prey availability to lion populations and thereby affect lion ecology and feeding preferences?
3. What is the response of lions to extreme drought interms of diets and prey preferences?

4.2 Study area: The Amboseli Ecosystem

The Amboseli ecosystem is situated across the border of Kenya and Tanzania (Figure 4.1). The area is generally arid to semi-arid with an average of 340 mm rainfall per annum (Moss et al., 2011). The ecosystem has bi-annual rainfall, short rains starting in October-November and long rains in March until May. Within the ecosystem, there are variations in its agro-ecological zones. The ecosystem is more suitable for pastoralism and for conservation of wildlife and tourism enterprises than for crop farming (Moss et al., 2011). Administratively, the Amboseli ecosystem consists of Amboseli NP (392 km^2) and the surrounding six group ranches (6,000 km^2) namely; Kimana/Tikondo, Olgulului (North, East, South and West), Selenkei, Mbirikani, Kuku, and Rombo. These group ranches cover an area of about 5,063 km^2 in Kajiado County (Figure 4.1). The Amboseli ecosystem also includes the former 48 private ranches located in the foothills of Kilimanjaro, which are now under rain-fed crop production, and no longer utilized by wildlife.

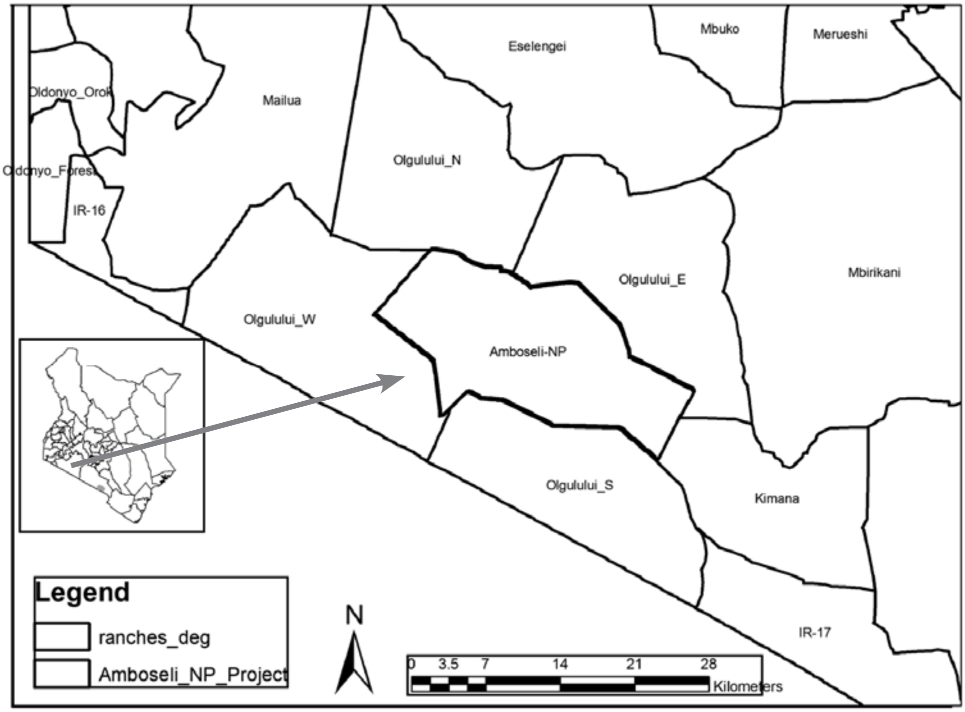


Figure 4.1
Amboseli National Park and surrounding group ranches which together form Amboseli ecosystem

4.3 Methods

4.3.1 Assessment of rainfall variability

Rainfall is seasonal, with bi-modal rainfall interrupted by dry months. The long rains (March-June) are when most plant growth is expected and prey and predators reproduce. The short rains (October-November) are often sporadic and extended periods of dryness are not unusual, disturbing both wild animals and domestic stock. For the Amboseli Ecosystem, we relied on the rainfall records kept at the baboon research station inside the park. We used 35 years of data on rainfall to calculate the deviations from the long-term mean. From the long-term rainfall deviations from the mean, we were interested mainly in the years 2007-2009 (which corresponded with severe droughts) and 2010-2012 (recovery years). The year was divided into wet and dry seasons of six months each. All prey killed by lion was recorded for each season and seasonal lion prey composition for each year was compared to find if there was any variation in prey composition.

4.3.2 Seasonal prey composition

In our sampling protocols we used five strategies. In the first strategy, we collared ten lions, three males and seven females, during 2007-2012 (Tuqa et al., 2014). We recorded hunting activities of collared lions and their pride members on a continuous basis and made at least weekly observations both during the wet and the dry season using car tracking with VHF telemetry (White & Otis, 1999; White & Garrott, 1990). Lion behavior related to hunting, feeding, mating and social aspects were recorded (Estes, 1991). Prey behavior as related to predator avoidance was recorded at the same time (Estes, 1991).

In the second strategy, in order to determine lion prey composition, we tracked collared lions weekly using a VHF radio tracking system throughout the day. More emphasis was given to early morning and late evening because lions are known to hunt actively at these times. When a collared lion was located, we conducted intensive searches in the vicinity of any prey carcass, without causing disturbances to the lion. We also deployed GPS-GSM collars identifying GPS clusters to locate lion prey carcasses in the field. Lion kills were uncommon during the day and most of the active hunting and feeding took place at dawn, dusk and at night from 18:00 to 06:00 hours. Several GPS locations, together (cluster points) were searched for carcasses if a collared lion stayed for more than 3 hours at the same location during the night.

The third sampling strategy consisted of counting carcasses of a kill if they were found within 200 meters of the GPS location and identifying lion claw and bite marks on the carcass, indicating a lion attack. Sample sizes of carcass counts were as follows; 2008 (n=19), 2009 (n=22), 2010 (n=76), 2011 (n=11), 2012 (n=20)

We also used the presence of scavengers such as hyenas and vultures to detect the lion at a prey kill.

In the fourth sampling strategy, we conducted 60 annual and seasonal transect prey counts (Table 4.1, Figure 4.2), to determine the distribution and density of potential lion prey. Five transects (2 × 1 km) along a park track (500 m on each side) were semi-randomly selected to cover a number of habitats, to include short and tall grasslands, alkaline plains, *Acacia* woodlands, Phoenix mixed woodlands and freshwater Papyrus swamps (Moss, 2011).The transects covered a total of 10 km^2, which were representative for the rest of the park (396 km^2). Their locations are marked in the map of Amboseli NP (Figure 4.2).

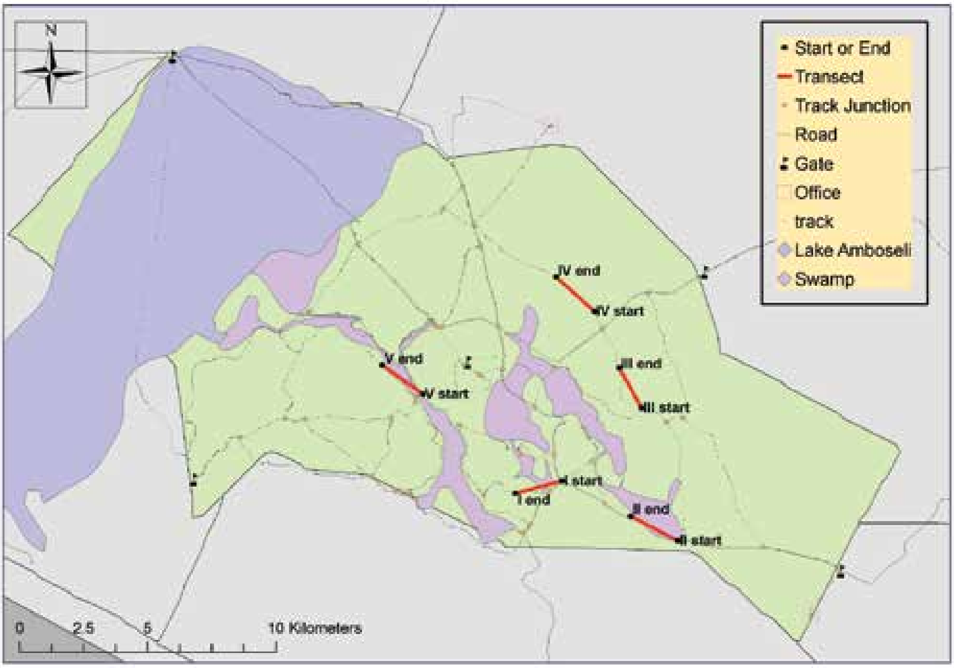


Figure 4.2
Transect locations inside Amboseli National Park

By using distance measured in meters (Bushnell Yardage Pro Trophy Rangefinder) during the transect counts the exact distance of the herbivores was determined within the distance of 500 meter. These transect counts were, conducted once every week, when possible at the same time, alternating between 08:00-10:00 and 16:00-18:00 hours, both during the wet and dry season. These times were chosen so that animals seeking shade during the warmer periods of the day were not overlooked. All herbivores larger than ~5 kg were recorded. Additional data included numbers of neonates within the group, habitat type, and weather and grass conditions. Complementary data from counts conducted by the KWS and previous studies were added to assess the size of the wild prey population and how this changed over previous years. Transect counts data were used to classify prey species in weight/size groups to estimate the available biomass of prey species in the national park (Hayward et al., 2005).

In the fifth method, aerial and ground wildlife censuses were carried out twice each year, in the wet and dry seasons. The aerial counts were done for the whole ecosystem while the ground total count was done within ANP. We used these data along with transect counts to evaluate the general trend of prey abundance within the park and neighbouring group ranches.

4.3.3 Scat analysis

Paralel to carcass counts, lion scats were collected from the field opportunistically, only in 2012 and by following lion sighting revisiting earlier sightings and by following GPS/GSM fixes of collared lions locations. Total number scat gathered in 2012 was n=61.

The field guide of Stuart & Stuart (2000) was used for identifying lion scat. After collection, the scats were transported in individual plastic bags and sundried (Breuer, 2005) for approximately two days and then soaked and washed through a 1mm sieve to collect hairs (Breuer, 2005). After washing the hairs in 95% alcohol they were stored in plastic zip lock bags to await further analysis. A minimum of 50 scats should be collected to estimate the lion diet and 20 hairs per scat viewed upon (Trites & Joy, 2005).

We used hair samples from known lion prey species from taxidermy (Hayward & Kerley, 2005) provided a reference hair collection (RHC) (Beveridge, 2013). These reference hairs were collected from different body locations on the hide of herbivores (neck, dorsal and ventral), to create a full image of the diversity of hairs within species. Part of the hair sampels where obtained from the collection of the National Biodiversity Collection Naturalis in Leiden part from carcasses in the field.

Hairs collected from scats and for the RHC were washed in acetone for 5 minutes, dehydrated for 5 minutes in 96% alcohol and dried on filter paper (Ramakrishnan et al., 1999). Imprints were made to view the cuticle pattern of the hairs. A solution consisting of 1.7 grams of gelatin (one sheet of Dr.

Oetker white) and 40 mL demi-water was left to soak for 5 minutes and then placed on a hot plate (65 °C) until the gelatin would be completely dissolved. A thin layer of gelatin was spread out over a microscope slide and left to harden for 5 minutes on room temperature. Individual hairs were placed on the gelatin layer and left there for the gelatin to completely dry up. The hairs were removed from the microscope slides and stored in individually labeled 1.5 mL Eppendorf tubes. Hair shape, size and color were analyzed using a stereo microscope and the scale patterns (cuticle imprints) were observed with a light microscope (Leitz Dialux 20 microscope). Additional photos for the RHC were created using the photographic software Cell^D (Olympus Soft Imaging Solutions) on a light microscope (Olympus Type BH2, series number 214351). By comparing hairs from the reference collection with those from the fecal material it was possible to determine the lion's diet.

All the lion kills were used to determine monthly lion diet for each year. The percentage contribution by each species to lion diet was then determined. Prey species were grouped into three categories (Bauer et al., 2008); small, medium and large prey, all the prey species above 200 kg was classified as large and those below 200 kg but above 100 kg were classified as medium and those below 100 kg were classified as small. The number of prey kills was used together with prey abundance from transect counts to calculate the lion prey preference index for the each year and seasons respectively.

4.3.4 Data management

Transect data were extrapolated to estimate the abundance of each species. Species number and weight class categories were estimated according to Estes (1991). To establish abundance of prey species from the transect counts, daily average animal density per km^2 was consolidated for all herbivore species counted in the whole park. We used this data to an average animal density per species per month for the five transects.

Animal densities of prey animals were calculated as follows:
1 Total Number of Transect Counts (TC) = 247
2 Months of observation = 30 months (approximately 3 years)
3 Total Transect Area (TA) per month = 5 transects * 2 count periods * 2km^2;
4 Total Month's Average Count (MAc) = Σ individual animals counted per month

5 Monthly Density = MAc / TA
6 Study Period Density = MAc TC * TA

Lion kills and scat analysis were used to determine monthly lion diet for each year. In the case of lion kills the percentage contribution of each species to lion diet was determined.

We used the Jacob's equation to find out if there was any preference or avoidance for a particular prey species (Jacobs, 1974). Dietary analysis was derived from results of both carcass counts and scat analyses. Prey species abundance from transect count data and game counts. These data were used to calculate the Jacobs' Index (the prey preference or avoidance in the diet) (Jacobs, 1974).

$$Jacobs'Index\ (D) = \frac{(r-p)}{(r+p-2rp)}$$

Where r is the proportion of how much a prey species contributes to the whole diet and p the proportional availability of that prey in the prey species abundance. Carcass counts and scat analysis determine the proportion of a species' r value in the diet. Transect counts determine the p value of a species. Values from the Jacobs' Index range between -1 and +1. A +1 index indicates preference and whereas -1 indicates avoidance.

The determination of lion prey diet fron scat analysis involved collection of lion fecal material and used hair sample taken for analysis to identify the prey species a lion had consumed. Lions generally eat one type of prey at a time, ingesting its hair as well, and excrete the hair after the flesh is digested.

4.3.5 Data analysis and statistics

We tested for differences in preference across the years and between seasons, as well as between periods (i.e., before, during and after drought). Log. transformation was done for Jacob index. Data was tested for normality distribution using Kolmogorou – Smirnof test. As the Jacob's Index values followed a non-normal distribution, a non-parametric Wilcoxon test was done. We carried out pairwise Wilcoxon test comparisons for any two pairs of years. Furthermore, a post hoc analysis for difference between any pairs of years (a factor with 5 levels) and between seasons (a factor with two levels) was conducted.

4.4 Results

4.4.1 Rainfall variability and severe drought

There was high annual and seasonal rainfall variability over the years, with 2009 (drought year) having the lowest total mean annual rainfall and seasonal deviations. This drought year had the lowest mean rainfall (1977-2012) over 35 years in Amboseli National Park (Figure 4.3),

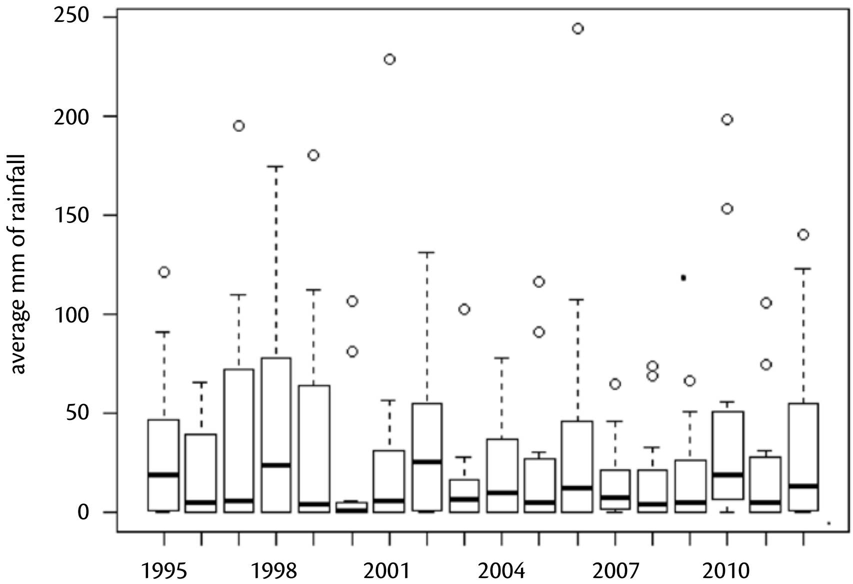


Figure 4.3
Summary of Mean annual rainfall variability in Amboseli National Park 1995-2012 (Source: Baboon Project, 2013).

4.4.2 Herbivore density and seasonal fluctuation

There were large differences in herbivore density in Amboseli National Park between the period before/during the drought (2008-2009) and after the drought (2010–2012). The fluctuations were both annual and seasonal (Table 4.1). There was a heavy decline in densities of wildebeest, zebra and buffalo populations during the severe drought in 2009. The estimated zebra population was significantly reduced from densities of 42.5 per kilometer in 2009 to densities of 9.54 per km^2 in 2010 and 0.2 per km^2 in 2012. The wildebeest population was found to show an extreme decline from densities of 73.9 per km^2 in 2009 to 9.87 per km^2 in 2010 and to 3.4 per km^2 in 2012.

Table 4.1
Ammboseli National Park herbivore transects counts from April to July 2012 and density (per km^2) from 2007 till 2012.

Herbivore (size class)	Density Apr-Jul 2012	Density Jul-Sept 2011	Density Jun-Aug 2010	Density Jan-May 2009	Density Oct 2007-Jan 2008
Baboon (s)	0	0	0.47	0	–
Cape buffalo (l)	0.14	1.45	0.67	8.01	5.15
Eland (l)	0	0.03	0	0.11	–
Elephant (l)	4.57	3.73	2.83	5.78	–
Gerenuk (s)	0	0.03	0	0	–
Giraffe (l)	0	0.65	0.03	0.14	0.08
Grant's gazelle (s)	0.03	3.00	1.71	1.81	–
Hartebeest (m)	0.01	0	0	0	–
Hippopotamus (l)	0.64	0.53	0.17	0.51	–
Impala (s)	0.58	0.18	0.09	0.32	0.22
Ostrich (m)	0.51	0.67	0.26	0	–
Reedbuck (s)	0	0	0	0.09	–
Thomson gazelle (s)	3.05	7.52	4.19	9.83	–
Warthog (s)	0.08	0.38	0.14	0.35	–
Waterbuck (m)	0.03	0.18	0	0.30	0.09
Wildebeest (m)	3.74	9.17	9.87	73.91	21.30
Zebra (m)	0.20	21.53	9.54	42.48	10.41
No. of transect counts	60	30	35	43	19

4.4.3 Lion prey composition

Lion prey composition and selectivity showed significant variation before/during (2008-2009) and after the drought (2010-2012). The lion prey kills from carcass counts and scat analysis of both showed showed similar pattern of variation, with a higher preference for medium size prey (Table 4.2). Lion prey size composition were 79-95% for medium prey before/during the drought and between 90-91% after the drought. There was a low percentage of small and large classes, before/during and after the drought. The year after the drought there was a slight increase of small prey (4%).

Table 4.2
Analysis of seasonal lion prey composition in wild herbivore weight categories (Small, medium and large) – class distribution 2007-2012.

Prey weight class	2007/2008 carcass	2009 carcass	2010 carcass	2011 carcass	2012 carcass	2012 scat
Small	0.021 (2.1%)	0.05 (5%)	0.14 (14%)	0 (0%)	0.05 (5%)	0.05 (5%)
Medium	0.79 (79%)	0.95 (95%)	0.86 (86%)	0.91 (91%)	0.90 (90)	0.895 (89.5%)
Large	0 (0%)	0 (0%)	0 (0%)	0.09 (9%)	0.05 (5%)	0.05 (5%)

4.4.4 Changes in diet composition

There was high seasonal variation in individual prey species included in the lion diets before/during (2007/2009) and period after the drought (Figures 4: I, II, III, IV V, and VI). Lions had ten different prey species included in their diet in the year 2010, while in 2008 and 2009 combined they had only six. In 2011 and 2012, the majority of the carcasses were wildebeest (55%) and Zebra (25%), followed by buffalo, ostrich, Thomson's gazelle and waterbuck, each contributed to 5% of the diet. Before and during the drought, however, 50% of lion diets consisted of wildebeest in both dry and wet seasons in 2008 and 2009, while in the year 2010 this was reduced to less than 20%. Zebra was the second-most prominent animal species in lion's the diet. Together zebra and wildebeest constituted between 70 and 90% of the lions diet in both dry and wet seasons for the period before/during the drought year. In the year after the drought (2010), these had been reduced significantly, with wildebeest contributing 15 and 16%, and zebra 28 and 20% in the wet and dry seasons, respectively.

The scat analysis showed a combination of hairs from a total of 65 different prey species. The origin of four samples (6%) remained unidentified. Collectively, blue wildebeest (51%), zebra (15%), waterbuck (9%), buffalo (5%), ostrich (3%), Grant's gazelle (3%) and impala (1%) comprised 87% of the diet. Domestic animals (donkey, sheep and goat) contributed to 6% of the diet in Amboseli NP.

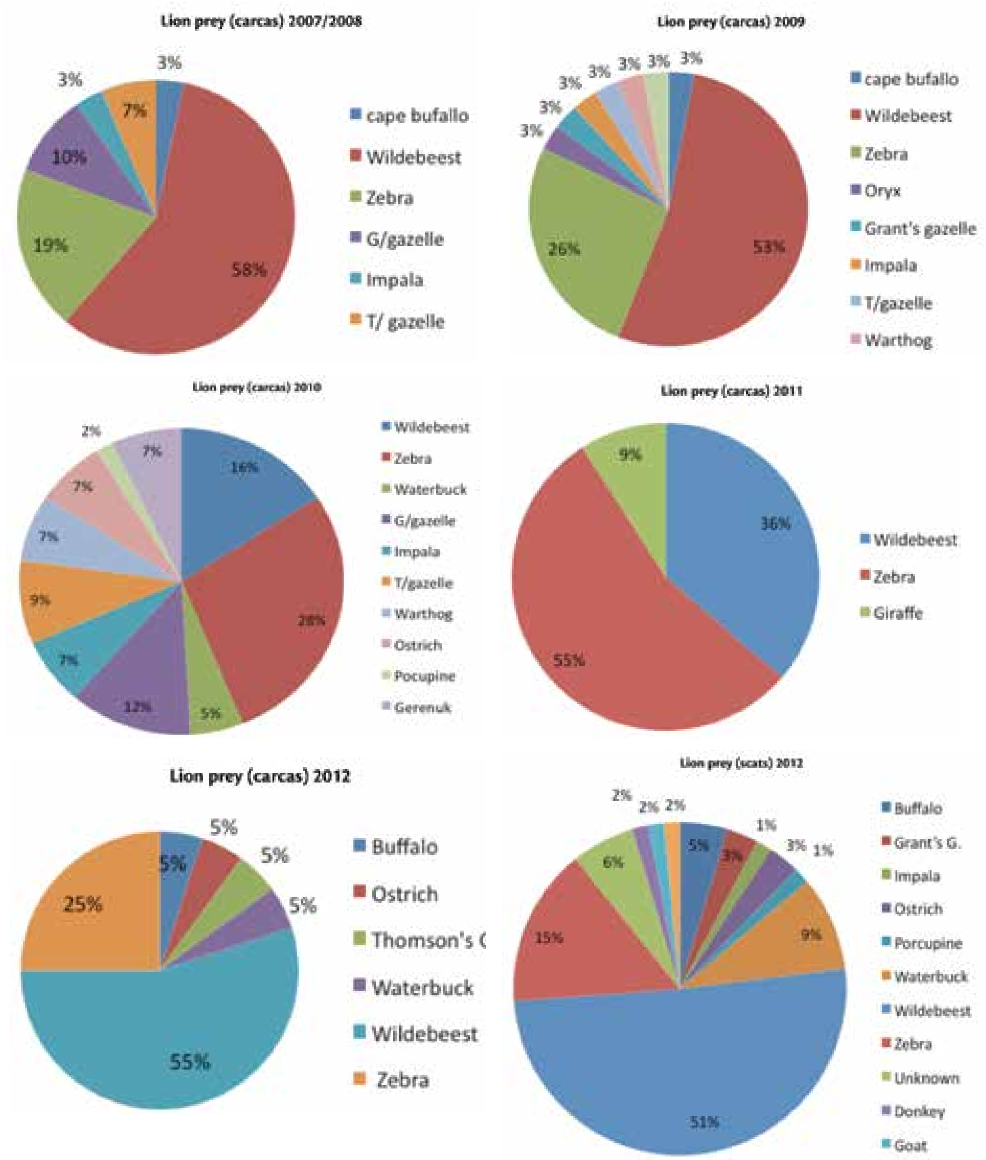


Figure 4.4
Analysis of seasonal lion prey kills from carcass and scat during continuous observation 2008-2012; (2008 (n=19), 2009 (n=22), 2010 (n=76), 2011 (n=11), 2012, n=20 2012 – (in scat n=61)

4.4.5 Prey preference and selectivity

The Jacobs index was analysed for different years and periods before or after drought. The Wilcoxon test on periods shows that there was a significant difference between feeding preference in the period before and after drought (p-value <2.2e-16). We conducted a pairwise Wilcoxon test on both years and period (Table 4.3). Table 4.3 shows that 2008 and 2009 are significantly different (p=0.0029). Similarly, year 2009 and 2010 are also significantly different (p=0.0264). We summarized the differences below, where years with the same letter are similar and years with different letters are significantly different in terms of lion feeding preference: 2008 ("a") 2009 ("b") 2010 ("a") 2011 ("ab") 2012 ("ab") 2007 ("a").

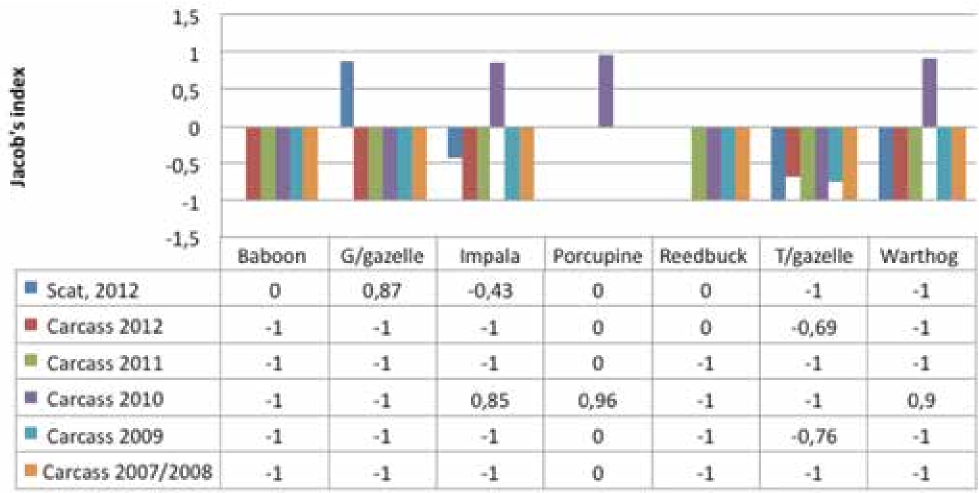
Table 4.3
Differences in lion annual feeding preference and selectivity based on Jacobs index 2007-2012 (P>0.005)

Year/number	2007/2008 (n=19)	2009 (n=22)	2010 (n=76)	2011 (n=11)	2012 (n=20)
2007/2008(n=19)	1.0000	–	–	–	–
2009(n=22)	0.0033	0.0029	–	–	–
2010(n=76)	1.0000	1.0000	0.0264	–	–
2011(n=11)	0.0567	0.0723	1.0000	0.532	–
2012(n=20)	1.0000	1.0000	1.0000	0.5624	1.0000

P value adjustment method: Bonferroni

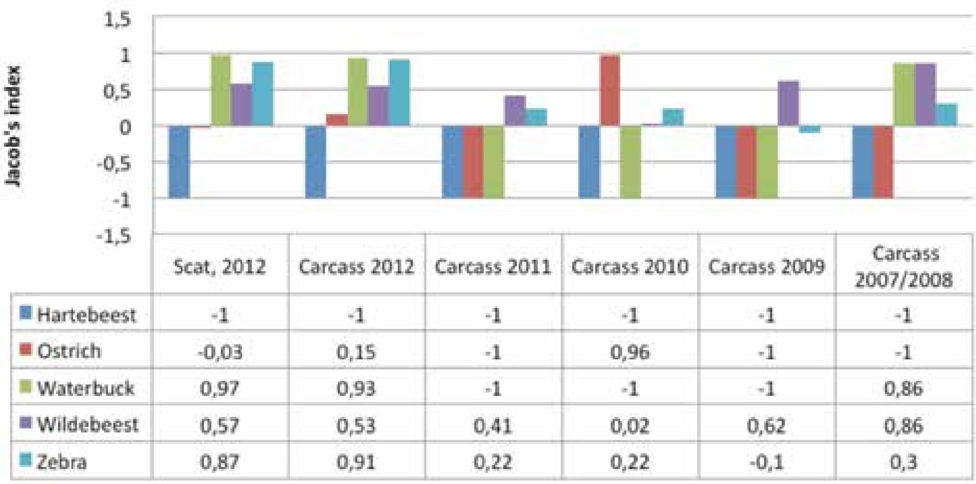
The overall Jacob's indices for the entire study period showed a preference of the Amboseli NP lions for wildebeest and zebra (figures 4.5a, 4.5b, & 4.5c), which are killed more often than any other prey, but not as much as would be expected from their proportional availability.

Based on figure 4.5b the preference for wildebeest declines during the years after the drought (2010-2012), compared to the period before/during the drought (2007-2009) (T test, p=0.06151), while the preference for zebra remained the same in the period after the drought (2010-2012) (T test, p=0.3373). In 2010 there was partial shift in Jacobs' selectivity indices towards smaller and larger prey animals.



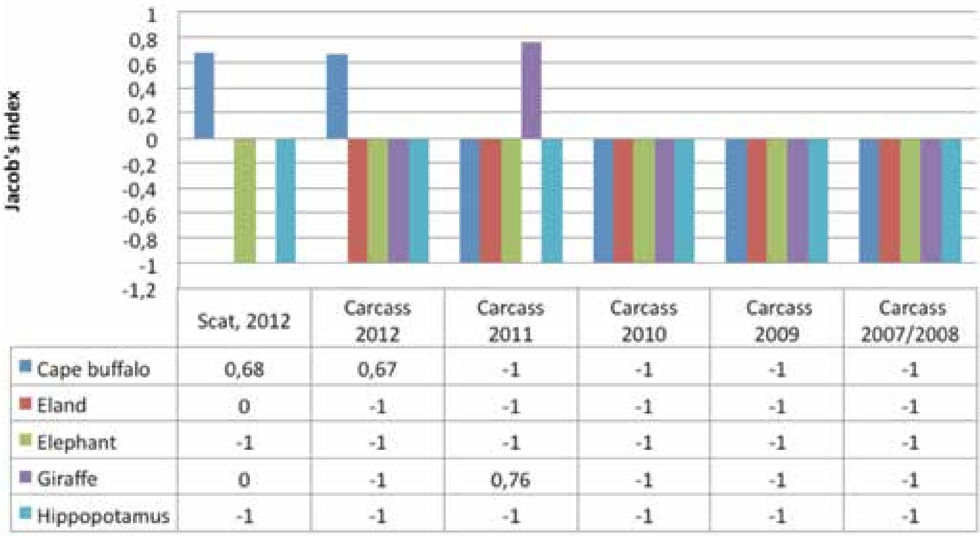
	Baboon	G/gazelle	Impala	Porcupine	Reedbuck	T/gazelle	Warthog
Scat, 2012	0	0,87	-0,43	0	0	-1	-1
Carcass 2012	-1	-1	-1	0	0	-0,69	-1
Carcass 2011	-1	-1	-1	0	-1	-1	-1
Carcass 2010	-1	-1	0,85	0,96	-1	-1	0,9
Carcass 2009	-1	-1	-1	0	-1	-0,76	-1
Carcass 2007/2008	-1	-1	-1	0	-1	-1	-1

Figure 4.5a
Small size herbivores lion prey preference index from carcass (2007-2012) and scat (2012) in Amboseli National Park.



	Scat, 2012	Carcass 2012	Carcass 2011	Carcass 2010	Carcass 2009	Carcass 2007/2008
Hartebeest	-1	-1	-1	-1	-1	-1
Ostrich	-0,03	0,15	-1	0,96	-1	-1
Waterbuck	0,97	0,93	-1	-1	-1	0,86
Wildebeest	0,57	0,53	0,41	0,02	0,62	0,86
Zebra	0,87	0,91	0,22	0,22	-0,1	0,3

Figure 4.5b
Medium size herbivores lion prey preference index from carcass (2007-2012) and scat (2012) in Amboseli National Park.



	Scat, 2012	Carcass 2012	Carcass 2011	Carcass 2010	Carcass 2009	Carcass 2007/2008
Cape buffalo	0,68	0,67	-1	-1	-1	-1
Eland	0	-1	-1	-1	-1	-1
Elephant	-1	-1	-1	-1	-1	-1
Giraffe	0	-1	0,76	-1	-1	-1
Hippopotamus	-1	-1	-1	-1	-1	-1

Figure 4.5c
Large size herbivores lion prey preference index from carcass (2007-2012) and scat (2012) in Amboseli National Park.

Our study investigated the impact of a severe stochastic drought on lion diet. We found significant variation in lion diets before/during the drought (2007-2009) compared with after the drought period (2010-2012). Lion diets were largely medium size prey such as wildebeest and zebra before/during the drought.

4.5 Discussion

Based on figure 4.4b, the preference for wildebeest declined during the years after the drought (2010-2012) while the preference for zebra increased in the period after the drought (2010-2012). This possibly reflects the impact of drought, which more severely affected wildebeest populations than zebra populations. In 2010 there was a partial shift in Jacobs' selectivity indices towards smaller and larger prey animals. In the aftermath of the drought, the diet composition indicated a partial shift to smaller prey such as ostrich, Thomson's gazelle and warthog as well as some larger prey species (giraffe and buffalo) and livestock. Our findings thus confirmed that lions are opportunistic feeders that are generally preffered to prey on small, medium-to-large sized ungulatesa wide niche breath that enable them to adapt to stochastic events such as drought by adapting their diet. This was also suggested by Hayward & Kerley (2005).

4.5.1 Impact of rainfall variability on prey densities

We found that in ANP, the density of large prey (buffalo, elephant, and giraffe) is in general much lower than that of medium sized prey (zebra, wildebeest). The densities of zebra and wildebeest peak in March, at the beginning of the short rainy season, coinciding with the calving season, and then decrease to levels much lower than during the dry periods (November to May and June to October). However, this scenario changed during and after the drought in 2009. Heavy losses occurred in wildebeest, zebra and buffalo populations after the drought, with a decrease of 95% for wildebeest and 60% for zebra populations in Amboseli NP and many elephant and hippos also died (African Conservation Centre, 2009). Overall losses to the large migratory herbivores were in excess of 75%. The precipitous drop in herbivore numbers was expected to affect the carnivore populations, causing additional pressure on remaining herbivores and a sharp rise in livestock predation. Similar findings of fluctuations in wildebeest population in Maasai Mara following rainfall patterns have been reported by Ottichilo et al. (2010).

4.5.2 Prey distribution and density

We found strong fluctuations in the density (per km^2) of the wildebeest and zebra population from 2007 till 2012, with a significant reduction in densities during 2010-2012.

In June 2009, the first effects of the drought were noticeable (e.g., a reduction in surface water and grass availability). The swamps in the Amboseli basin act as a permanent and only source of water during the dry season. The reduction of availability of water and grass in the surrounding ecosystem makes Amboseli NP a migratory destination for wildlife during the dry season. As the transect herbivore count data indicates in 2009, there was an increase in the number of herbivores present. This could be an indication that the effects of the drought in 2009 on the herbivore population were beginning to diminish and that a recovery to conditions prior to 2009 is possible (Van de Koppel & Rietkerk, 2000).

Although clearly before the drought (2009) wildebeest and zebra were preferred lion prey species, after the drought (2010-2012) lions expanded their diet and also fed more on smaller animals such as impala, warthog and porcupine. In addition in 2010 and 2011, there were some larger prey such as giraffe in the diet.

As for livestock in ANP, very little hard data were obtained from transect counts. This is due to the herds drinking and moving in and out of the park at times that did not coincide with the transects. The scat analysis showed some 9% of livestock in the diet, this is low compared to the 25% of livestock reported for lion in the Waza NP Cameroon (Tumenta et al., 2012).

4.5.3 Lion diet composition and preference

Normally, lions obtain the bulk of their diet from middle-sized (between 50 and 200 kg) and large herbivores (>200 kg, excluding adult elephant, giraffe and hippopotamus) (Schaller, 1972; Packer et al., 2005; Ogutu & Dublin, 2002; Hayward & Kerley, 2005). Being opportunistic feeders, however, they also regularly prey upon species as small as 50 kg or smaller (Bauer et al., 2008). Observations were made of a lioness in Waza NP surviving on birds such as owlets and marabu storks when she was ill (Wiggers, 2007). Pride females in particular have a preference for medium-sized ungulates such as wildebeest. In other studies, this prey preference was shown to overlap significantly with that of spotted hyenas (*Crocuta crocuta*), meaning that these two species are serious competitors for prey (Trinkel & Kastberger, 2005). As we did not include hyena diets in our study, we cannot draw conclusions on the overlap of diet for Amboseli. The lion's main prey species in East and Southern Africa include the migratory wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) and the non-migratory buffalo (*Syncerus caffer*), warthog (*Phacochoerus aethiopicus*), giraffe (*Giraffa camelopardalis*) and springbok (*Antidorcas marsupialis*) (Ogutu & Dublin, 2002; Funston et al., 1998; Stander, 1992; Hayward & Kerley, 2005). In our study, 55% of the diet consisted of wildebeest in 2007/2008 and 60% in 2009, this dropped to 16% in 2010 and 36% in 2011. In 2012 there was some recovery to 55% wildebeest in the diet. Wildebeest in particular are one of the most preferred species for lion, particularly in East and southern Africa (Hayward & Kerley, 2005). Two possible reasons may be 1) the animal's speed, similar to that of lions and slower than that of other prey, and 2) its decreased ability to detect predators compared to that of zebra and gazelles (Elliot & Cowan 1978). The wildebeest's high abundance after their migratory arrival (which increases their abundance by a factor of two or three) or during the calving period may be another reason for this preference (Ogutu & Dublin, 2002; Hayward & Kerley, 2005).

In our study, the Cape buffalo represented approximately 2% of the diet before and during the drought and it disappeared entirely from the diet after the drought in 2010 and 2011, and reappeared in the diet in 2012. We think the reason for this may have been the mass mortality among buffalo during the drought (African Conservation Centre, 2009). Whereas, it is particularly dangerous prey species, the buffalo's great body mass (400 kg, the heaviest ungulate after giraffes) provides enough energy returns to make it rewarding. Hayward & Kerley (2005) found that lions had a preference for this species above that expected from the buffalo's local density. In Kruger National Park male lions in particular nomadic ones, showed more preference for buffalo than do pride females (Funston et al., 1998).

There can be several reasons for the limited number of livestock carcasses we found in our study. It is possible that the lions stayed outside the park longer at night, moving out of the park just before dusk and coming back after sunrise. The time at which the lions hunt during the night has not changed (Schaller, 1972). It may be that most livestock is caught and eaten outside the park, explaining why we were unable to find livestock carcasses in the park. Also the scat analysis in 2012 showed a much larger range of species in the diet than did the carcass counts. It may well be that we missed carcasses of prey that were caught outside the park. Another explanation may be an increase in the hyenas population in the park, as compared to previous years, an observation that was also confirmed by the local Maasai community. Carcasses found in the morning had generally disappeared by afternoon, which may have been the result of hyenas and vultures feasting on and removing the carcasses. This also provides an explanation for the general lack of carcasses we observed in the morning, as they may have been removed by hyenas during the night.

The fact that the scat analysis showed a larger range of species in the lions' diets suggests that this method if used in combination with carcass appropriate compared to carcass counts alone. There are various methods for determining diets from scat analysis (Klare et al., 2001) and these methods can be classified as qualitative (frequency of occurrence per scat) or as quantitative (biomass calculations per scat). The qualitative methods overestimate the contribution in the diet of small-sized prey, compared to larger-sized prey, because the presence of both is weighed equally even though there are differences in surface area to volume ratio (Marker et al., 2003). A requirement for a successful quantitative method is to conduct feeding trails to convert the frequency of occurrence into relative biomass and number of individuals consumed (Breuer, 2005).

As a result of the low adult prey densities caused by the 2009 drought, the Amboseli lions showed a shift of prey preference. The Amboseli NP lion prey preference seems to be strong for wildebeest (both adult when present) and slight for Thomson's gazelle. These results are in line with both prey size and species preferences found in the literature, where wildebeest and zebra (or more generally medium prey) is listed as the top prey, with less preference for small and large sized prey (Heyward & Kerley, 2005).

Compared to other areas, the 90% medium-sized prey and less than 10% large-sized prey in the lions diet was very different from the diet of lions in similar habitats across Eastern and Southern Africa (20 and 80%, respectively; (Hayward & Kerley, 2005; Owen-Smith and Mills, 2008). The diet in East and Southern Africa is more skewed towards larger prey compared to West and Central Africa, where 66% of the lion's diet consist of medium prey and 34% of large prey.

Finally, the lion population in Amboseli National Park is under continuous pressure from natural climate variability that threaten their prey and anthropogenic influences such as land use changes. In order to gain a better understanding of the causes and effects of these influences, it is imperative that research in Amboseli National Park be continued. Determination of the proportional prey availability in relation to livestock predation can help to reduce retaliatory killing. Many prey animals move outside the park before dusk and come back in the morning. It would be interesting to investigate whether this is related to the hunting times of lions. It should be further noted, that the short term impact of extreme drought in 2009 on prey abundance and lions diet were significant, but that there was signs of high resilience and fast recovery. Therefore, we expect that the long term impact of such stochastic events will be limited, provided the drought periods do not last too long.

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5

Local Knowledge and Attitudes towards Livestock Predation by Large Carnivores in the Amboseli Ecosystem (Southern Kenya)

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Abstract

Our paper assesses if a severe drought that occurred in 2009 had any the impact on large carnivore livestock predation trends. We also studied the local knowledge of local communities (Maasai pastoralist) about large carnivores and how that influences the attititude towards them in residents of two communal group ranches of Olgulului/Oloolarash and Kimana, situated adjacent to Amboseli National Park, Kenya. We conducted interviews with the heads of 294 households in 2011. This was done while the effects of the drought were still fresh in the peoples mind, in order to assess their knowledge and attitudes in relation to large carnivores and factors that influenced predation levels. We used large-carnivore-livestock predation incident reports around Amboseli over a period of five years data, thus covering the period before/during (2008-2009) and the post-drought period (2010-2012), to quantify livestock predation trends. We also assessed if there was any relationship between rainfall variability, wild herbivore abundance and livestock predation trends.

We found that the 2009 drought was so severe and it had painful memories among the pastoralists in the Amboseli ecosystem. Livestock and wild herbivores in the region were severely affected too, which led to 75% of the wildebeest population and 60% of the zebra population perishing as a result of the drought.

Some 34.7% of respondents suggested that lions caused most problems, while 50.7% suggested that the spotted hyena caused most problems, in terms of loss of livestock. The fact that lions are less perceived as causing problems can be explained by the compensation scheme that reduced losses related to predation. We found that there was an increase in carnivore predation and risk of repeated attacks when a livestock carcass was taken for human consumption after a kill.

Livestock predation predation was very high, with 4553 head of livestock killed over a five-year period, 2008-2012. In total, 3497 of the kills consisted of sheep and goats, 742 of cattle and 295 of donkeys. Livestock predation incidences for both the periods before and after the drought were higher during the wet season except during the drought year (2009). We also found that herbivore abundance within the park had a significant effect on livestock predation trends. Livestock predation increased exponentially during and after the drought, when wild herbivore abundance was low.

5.1 Introduction

Protected areas in Africa are important for the conservation of biodiversity. In spite of the presence of a protected area network, many of these areas have experienced a decline in large carnivore species (Weber & Rabinowitz, 1996; Geldmanna et al., 2013). During the last decades, natural resource management policies have changed dramatically from a pure preservationist model or a "fences and fines" approach, to more decentralized approaches (Gibson & Marks, 1995; Hulme & Murphree, 2001; Songorwa, 1999). Brüner et al. (2001) suggested that direct benefits for local communities would contribute to biodiversity conservation in national parks. Benefit sharing has been a popular strategy designed to offset conservation costs and motivate local people to support conservation (Archabald & Naughton-Treves, 2002; Brockington, 2006). This is done by aligning communities with conservation goals through the benefits they receive from the protected areas, which can be provided as a share of the park fees or in kind (Borrini-Feyerabend et al., 2012; Gibson & Marks, 1995; Hulme & Murphree, 2001; Brockington et al., 2006; Newmark & Hough, 2000). Several approaches are used, therefore, with the intention of creating good relationships by influencing local peoples' attitudes and perceptions to engender support for biodiversity conservation. Large carnivores, humans and their livestock have coexisted for millennia, but recent decades have seen dramatic increase in the frequency of human-carnivore conflict. The exponential increase in the human population and an expansion of the use of natural resources, which has resulted in encroachment on the habitats of large carnivores (Woodroffe, 2000; Treves & Karanth, 2003). Although habitat conversion, declining natural prey populations, and commercial exploitation have contributed to carnivore losses, active persecution and retaliatory killing by humans, based on real or perceived threats to themselves and their livestock, appears to be the most important factor in observed declines (Woodroffe, 2001). For example, many large carnivores tend to move beyond the boundaries of protected areas, triggering conflicts with people (Gusset et al., 2009; Patterson et al., 2004). These conflicts are a major source of mortality for large carnivores (Woodroffe & Ginsberg, 1998; Woodroffe, 2000). Retaliatory killing of carnivores occurs in many cases, in community areas surrounding protected areas, which have become population sinks, especially for species with a large range home range in relation to the size of the protected areas (Marker et al., 2008; Woodroffe & Ginsberg, 1998).

Protected areas are becoming the last refuge for many large African predators, all of which have experienced significant declines in recent times (Riggio et al., 2013; Woodroffe & Ginsberg, 1998; Linnell et al., 2001; Woodroffe, 2000). It is widely understood that even within protected areas, humans often remain the main source of mortality for large carnivores (Woodroffe and Ginsberg, 1998). The situation is rather serious in smaller protected areas surrounded by dense human populations (Brashares et al., 2001; Parks & Harcourt, 2002). In this context, the unprotected buffer zones become an important part of predator home ranges, and variations in habitat quality of the surroundings of a protected area could affect the dynamics of populations (Tuqa et al., 2014). Few of Africa's existing reserves are large enough to maintain viable populations of wide-ranging predators. Therefore conservation of large carnivores depends on networks of smaller reserves and private and communal lands. In these areas successful conservation is closely linked to the ability of people to resolve human-carnivore conflicts and minimize numbers of carnivores killed by people (Brashares et al., 2001; Woodroffe, 2001). Therefore park managers, biologists and indigenous people should coordinate efforts to understand the circumstances surrounding carnivore – livestock conflict. They should combine empirical data with local experience to define appropriate solutions (Tumenta et al., 2013; Treves & Karanth, 2003). Although much work has been done on large carnivore-livestock predation and mitigation thereof, there has been limited research on the role of climate variability and severe droughts on trends in carnivore-livestock predation over a period of several years.

Our study focused on livestock predation trends in the group ranches surounding Amboseli NP over a period of five years (2008-2012) before, during and after a severe drought in 2009. We covered seasonal patterns of predation, spatial distribution of predators, relationship between predation and wild prey abundance and finally we looked at community attitudes and local knowledge. The results of our research will be used by Amboseli NP management to develop large carnivore management strategies and conflict-mitigation measures within the Amboseli ecosystem.

5.2 Study area: the Amboseli Ecosystem

The Amboseli ecosystem covers approximately 6,000 km^2 and is situated across the border of Kenya and Tanzania (Figure 5.1). The area is generally arid to semi-arid with an average rainfall of 340 mm per annum (Moss et al., 2011). The ecosystem is more suitable for pastoralism and conservation of wildlife and tourism enterprises than for crop farming (Moss et al., 2011). Administratively, the Amboseli ecosystem consists of Amboseli National Park (Amboseli NP) (392 km^2) and the surrounding six group ranches, namely; Kimana/Tikondo, Olgulului/Olararashi (North, East, South and West), Selenkei, Mbirikani, Kuku, and Rombo. These group ranches cover an area of 5,063 km^2 in Kajiado County (Figure 5.1). It also includes the former 48 individual ranches located in the foothills of Kilimanjaro, which are now under rain-fed crop production and no longer utilized by wildlife. All six Group Ranches are owned by Maasai communities who have been pastoralists and relied primarily on cattle, goats and sheep for their livelihood. Much of the landscape is arid and semi-arid and rainfall is scarce and unpredictable. Under these conditions livestock herding is an efficient form of land use.

Livestock for beef production is the dominant socio-cultural and economic activity in this ecosystem and centers around cattle, goat and sheep. This is at both subsistence and commercial level. Crop farming is becoming an economic activity in the dispersal area, particularly in the eastern part of ANP, where irrigated agriculture is practiced along the swamps and rivers. Very limited commercial agriculture takes place along the slopes of the Kilimanjaro (Campbella et al., 2000). Some members of the local Maasai community are changing their lifestyles from nomadic pastoralism to sedentary subsistence and mixed farming. The diversity of the ecosystems enables the utilization of a wide variety of natural resources. The major activities are related to the area's geographical location or geological characteristics.

In the Amboseli ecosystem, prey dispersal and abundance is subject to rainfall (Western & Nightingale, 2005; Altman, et al., 2002). For the migratory grazing species, such as zebra and wildebeest, the distribution and densities differ during the dry and the wet season. In the dry season, both species concentrate inside the park and densities are high, while there is a much wider dispersal and overall lower densities during the wet season. This implies a lower availability of the preferred prey species during the wet season.

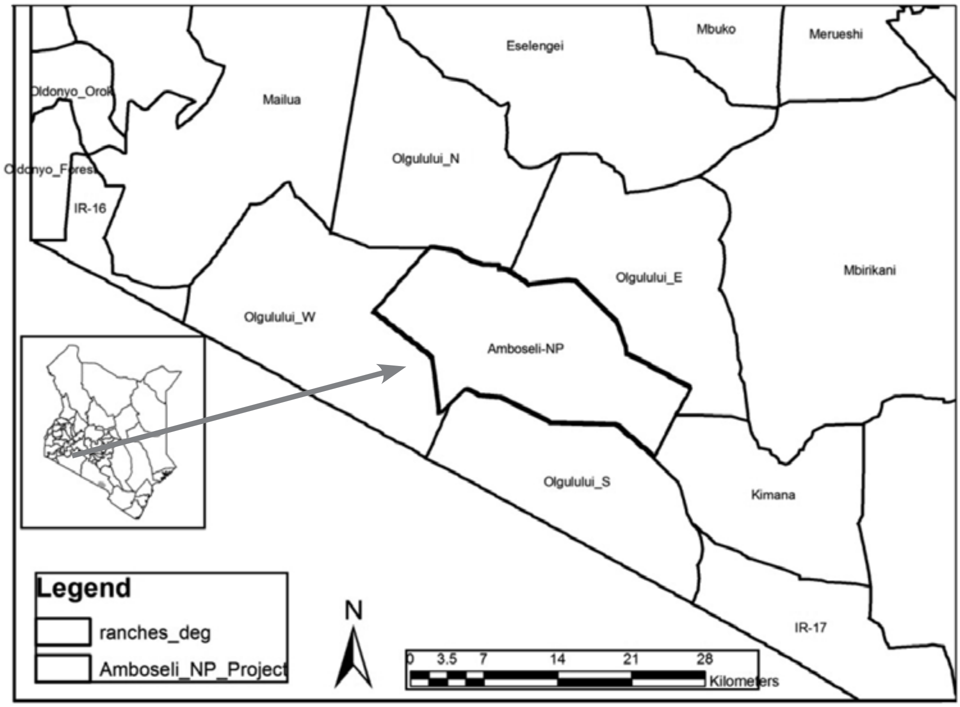


Figure 5.1
Amboseli National Park and surrounding group ranches which together form Amboseli ecosystem.

5.3 Methods

5.3.1 Assessment of livestock predation trends

All incidences of human-carnivore conflict (attack of large carnivores on livestock) occurring in the two group ranches, adjacent to Amboseli NP, Olgulului and Kimana were investigated jointly and separately this researcher, by the Kenya Wildlife Service (KWS) problem-animal control unit and staff of the Ogulului predator compensation scheme. All data on carnivore-livestock predation were entered in the KWS patrol register and occurrence Book (OB) for future reference. The following details were recorded; date and time of occurrence, livestock owner, Place name/GPS coordinates, livestock type(s) and age, predator species involved. Because Olgulului is very large, it has been sub-divided into four administrative zones (Olgulului North, Olgulului West, Olgului South and Olgulului East); conflict data were collected and analysed for each zone.

5.3.2 Wild herbivore abundance measure

The general trend of prey abundance within the park and neighbouring group ranches was established using distance measured in meters (Bushnell Yardage Pro Trophy Rangefinder) during the transect counts. The exact distance of the herbivores was determined within the distance of 500 meter. We conducted 60 annual and seasonal transect prey counts , to determine the distribution and density of potential lion prey. Five transects (2 × 1 km) along a park track (500 m on each side) were semi-randomly selected to cover a number of habitats, to include short and tall grasslands, alkaline plains, *Acacia* woodlands, Phoenix mixed woodlands and freshwater Papyrus swamps (Moss, 2011). The transects covered a total of 10 km^2, which were representative for the rest of the park (396 km^2).

These transect counts were conducted once every week, when possible at the same time, alternating between 08:00-10:00 and 16:00-18:00 hours, both during the wet and dry season. These times were chosen so that animals seeking shade during the warmer periods of the day were not overlooked. All herbivores larger than ~5 kg were recorded. Additional data included numbers of neonates within the group, habitat type, and weather and grass conditions. Complementary data from counts conducted by the KWS and previous studies were added to assess the size of the wild prey population and how this changed over previous years. Transect counts were used to classify prey species in weight/size groups to estimate the available biomass of prey species in the national park.

We also used ANP data from aerial and ground wildlife censuses which were carried out twice each year, in the wet and dry seasons. The aerial counts are done for the whole ecosystem while the ground total count was done within ANP. We used these data along with transect counts to evaluate animal seasonal abundance.

5.3.3 Survey on attitudes

We conducted semi-structured interviews with a total of 294 respondents in the two group ranches surrounding Amboseli NP during 2011. The information we gathered, mostly from heads of households, was to assess local community attitudes, knowledge and practices in relation to wildlife conflict, drought and the impact of the predator consolation scheme.

The target population of this study consisted of all households in Kimana/Tikondo and Olgulului group ranches. We considered the head of the household as the unit of analysis. Deliberate sampling was used to draw the sample of 294 households in total, based on place of residence. Only adult men and women, ranging in age from 18 to 68 years, were selected to participate as they traditionally make the livestock, pasture - and social decisions. The respondents were 85.4% men and 14.6% female.

5.3.4 Methods of data collection

The semi-structured interviews were conducted with the help of a local research assistant and translator fluent in the local language. The interviews were either conducted in English or in the traditional Maa language, depending on the participant's preference and comfort level. Supplementary sources of data included in-depth discussions with key informants, direct observations, and participation in local meetings with community members and local non-governmental conservation organizations.

5.3.5 Data analysis

Data collected were statistically summarized and presented using frequency tables in Excel and charts in Word. For the descriptive data, descriptive statistics were used for analysis utilizing frequency distributions, percentages and mean scores.

Data involving livestock losses, characteristics of attacks and attitudes were summarized using SPSS, IBM 2.0 proportions. Normal distribution was checked with a Shapiro-Wilkes test. Relationships between ecological variables and monthly attack frequencies were investigated using Pearson's χ^2 non-parametric test. To identify whether large carnivore spatial and temporal predation patterns were associated with rainfall, settlement patterns (Maasai Boma) or prey abundance. For association between spatial predation patterns and seasonality we used monthly rainfall index to classify rainfall into wet-month and dry-month categories. The months of May–October was classified as dry months while November – April was wet months. All tests were considered statistically significant at $P< 0.05$. Finaly we applied principal component analys to get derterminant factors.

5.4 Results

5.4.1 Part I: Seasonal incidence of livestock and the influence of severe drought on livestock attacks

We found significant differences when we compared the number of livestock attacks per predator species, during the year before the drought (2008), the drought year (2009), the year immediately after drought (2010), the recovery year (2011) and the post-recovery year (2012) (Pearson χ^2 (16) = 796.1733, P< = 0.000; Table 5.2). Livestock predation was significantly higher during the severe drought than in other years for lion, spotted hyena, cheetah and jackal, with a total of 1543 livestock kills in 2009. The year before the drought (2008) and the post recovery year (2012) experienced lower predation incidence.

Table 5.2
Annual predation trends before/during the drought (2008-2009) and after the drought (2010-2012) and as per predator species.

Carnivore species	Before drought (2008)	During drought (2009)	Immediately after drought (2010)	Recovery after drought (2011)	Post recovery after drought (2012)	Total
Lion	32	91	243	134	125	625
Cheetah	37	240	122	145	125	669
Hyena	204	1014	337	426	348	2329
Jackal	98	176	137	221	172	804
Leopard	68	22	7	3	0	100
Total	439	1543	845	929	770	4526

All predator species had the highest livestock predation rates during the drought and lower predation rates during post-recovery and before the drought period, except for lions which had low predation rates during the drought (Table 5.2). The data showed the highest predation rates for lions during the period immediately after drought (2010) but also showed lower predation rates during the post recovery year (2011-2012) and before the drought period (2008).

There was a significant seasonal difference in predator species on livestock (Pearson χ^2 (4) = 51.2001, P< 0.000) for dry and wet season. Livestock predation was higher during dry season for all large carnivores except for lion and leopard (Table 5.3).

Table 5.3
Seasonal livestock predation incidences by large carnivores around Amboseli NP

Season	Cheetah	Hyena	Jackal	Leopard	Lion	Total
Dry season	358	1336	525	47	299	2565
Wet Season	311	993	279	53	326	1962
Total	669	2329	804	100	625	4527

Influence *of drought on specific livestock predation in relation to wild prey* abundance *and rainfall*
The numbers of livestock species killed by the various large carnivores in the years 2008-2012 are indicated in (Figure 5.2).

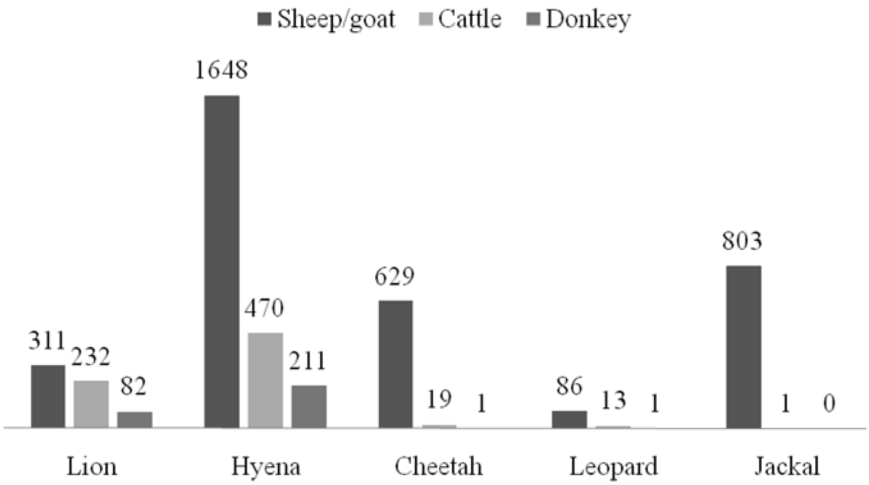
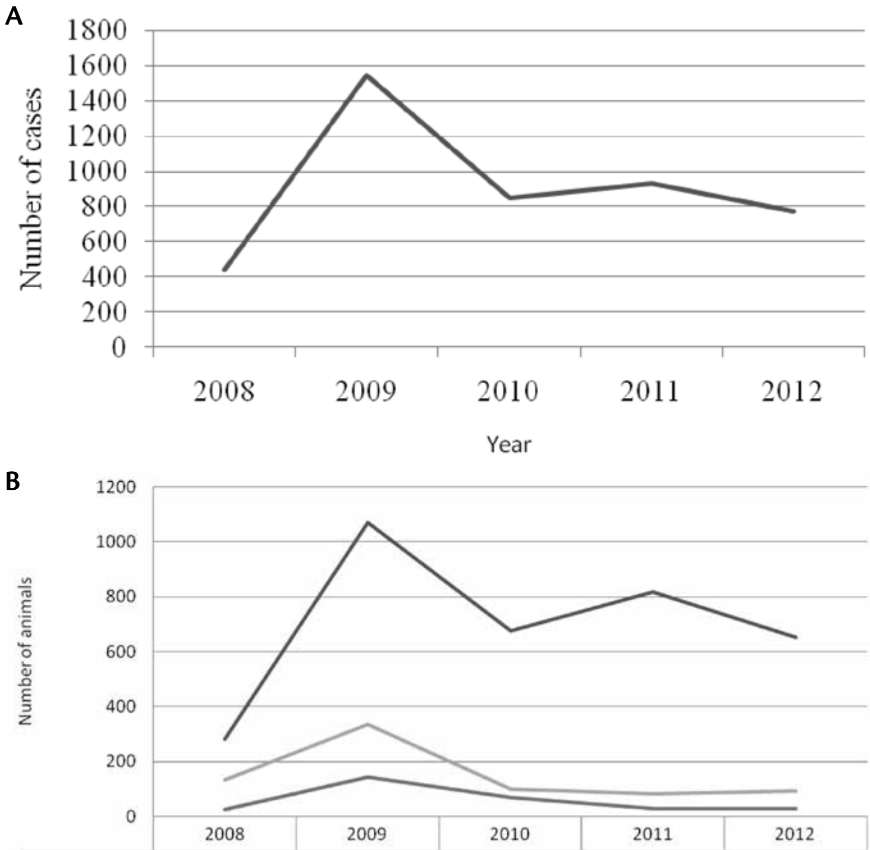


Figure 5.2
Livestock species killed by specific large carnivore species

A comparison was made of all the livestock killed by predators per year (Figure 5.3).



	2008	2009	2010	2011	2012
Shee/goat	282	1070	677	817	651
Cattle	133	335	100	82	91
Donkey	25	142	68	30	30

Figure 5.3
Actual number of livestock species killed by large carnivores in the Amboseli Ecosystem during 2008-2012: Number of annual livestock kills divided according to sheep/goats, cattle and donkies.

After a peak in 2009, the number of attacks decline to similar levels after the drought (2010-2012) compared to the pre-drought year (2008). All attacks occurred in the group ranches surrounding Amboseli NP and this pattern was consistent during the years.

There was a significant decline in herbivore number during 2009 (Figure 5.4) due to effects of drought particularly for wildebeest and zebras.

A

B

C

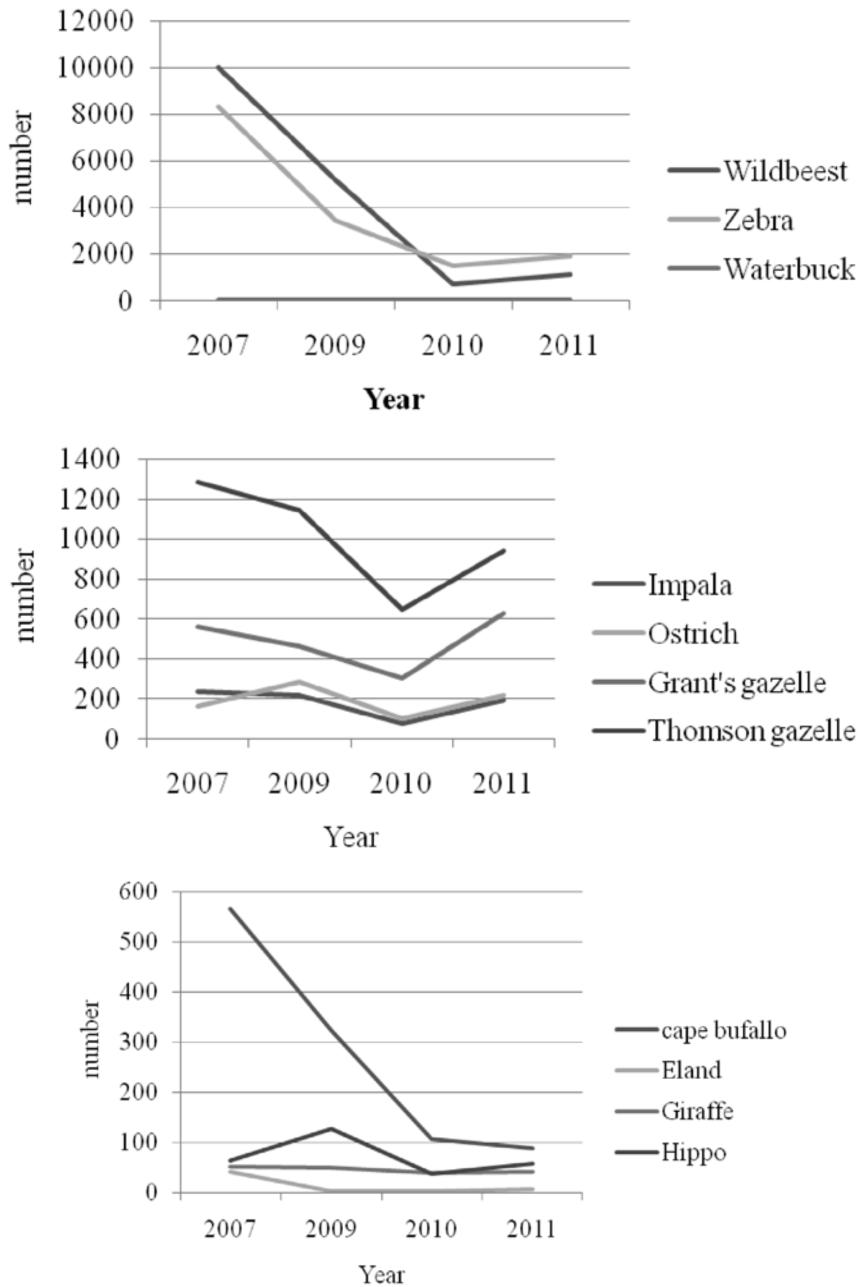
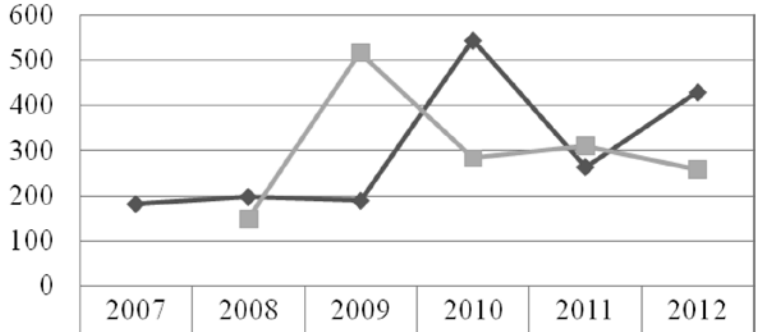


Figure 5.4
Annual herbivore population trends in Amboseli National Park 2007-2009 (pre-drought and drought period) and 2010-2011 (post drought) of medium-sized herbivores (A), small-sized herbivores (B) and large-sized herbivores (C). Small size was <50 kg body mass, medium size was between 50 kg and 200 kg body mass and large was >200 kg body mass (Estes 1995).

There was no direct relationship between mean annual rainfall and mean annual predation rates both before and after the drought (Figure 5.5)



	2007	2008	2009	2010	2011	2012
Rainfall	181.7	197.5	189.1	544.4	263.7	429.4
Predation		147	516	282	310	257

Figure 5.5
Pattern of rainfall in mm and yearly livestock predation for the period 2008-2012 in the Amboseli ecosystem.

5.4.2 Part II: Community attitudes

There was convergence in the result from community attitude and knowledge and the predation monitoring results with both indicated similar pattern of high livestock predation aspects.

Major *sources of livelihoods*
Most of the residents were livestock keepers, atotal of 83.3% of the respondents kept livestock, 8.2% were involved in trade, and 4.8% practiced some form of agriculture and 3.7% of the respondents held paying jobs (Figure 5.6).

Some 46.9% of the respondents keep sheep and goats, 44.6% of the respondents keep cattle and 8.5% of the respondents keep donkeys (Figure 5.7).

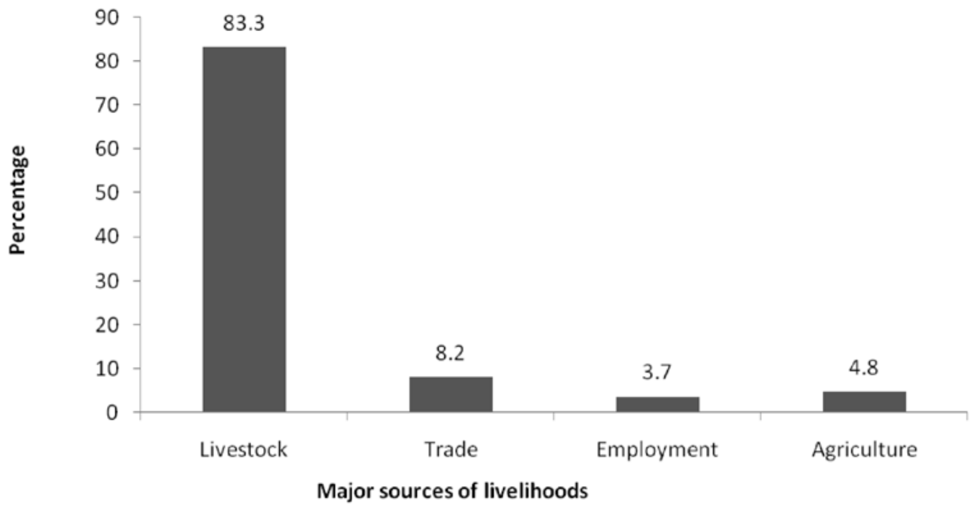


Figure 5.6
Major sources of livelihoods of respondents

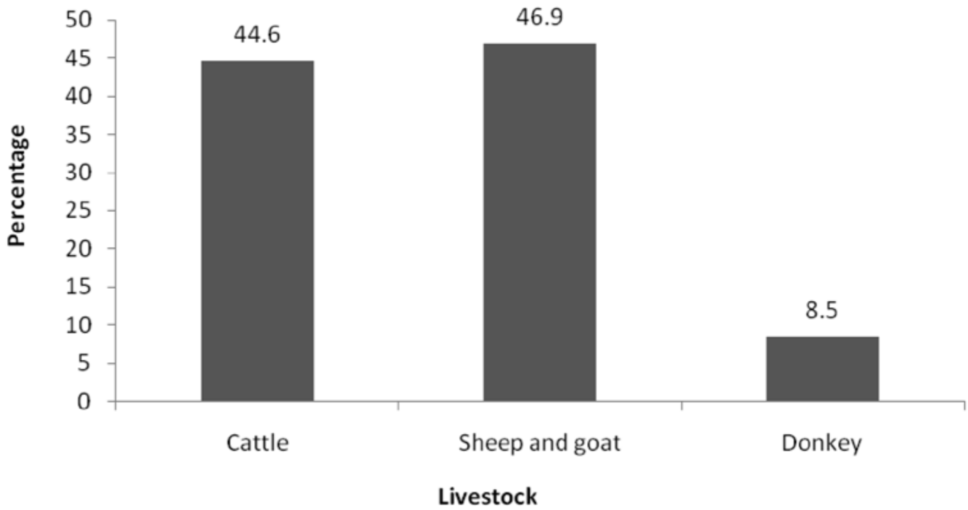


Figure 5.7
Percentage of respondents who keep cattle, sheep and goat or donkey

Problems *with wild carnivores*

All respondents indicated that they have problems with wild carnivores. The major problem mentioned was predation on livestock, while human injury/death and general threat to human life were also seen as causes of conflicts (Table 5.4).

Table 5.4
Main problem concerning wild carnivores according to respondents

Problems mentioned	No. of respondents	Percentage
Predation on livestock	236	80.3
Cause human injury/death	46	15.6
Threat to human life	12	4.1
Total	294	100

Carnivores *species that often causes problems.*

Table 5.5 shows that the spotted hyena was seen as most problematic of the predators, with lions taking a second place and other carnivores having smaller roles in conflicts. The respondents further explained that destruction of property during the night is common, and restrictions in movement of school-going children in the morning and evening restriction for those attending social gatherings is worrying.

Table 5.5
Carnivore species that often cause problems according to respondents

Carnivores causing problems	No. of respondents	Percentage
Hyenas	149	50.7
Lions	102	34.7
Leopards & Jackal	32	10.9
Cheetah	11	3.7
Total	294	100

Season *when problems are more prevalent*

A majority of the respondents indicated the predation problem is more prevalent during wet season as opposed to the dry season throughout the year (Table 5.7).

Table 5.7
Season when predation problem is more prevalent according to respondents

Seasonal livestock predation	No. of respondents	Percentage
Wet season	173	58.8
Dry season	65	22.1
The same throughout the year	56	19.0
Total	294	100

Major *benefits of living next to Amboseli National Park*

Respondents indicated that there are some benefits to living next to Amboseli National Park, such as the fact that the park attracts tourists, the park provides bursaries for schools, employment, social projects grazing and water for livestock (Table 5.8).

Table 5.8
Major benefits of living next to Amboseli National Park according to respondents

Benefits of living next to ANP	No. of respondents	Percentage
Attracts tourists/ foreign exchange earner	112	38.1
Provide bursary for schools	55	18.7
Employment	48	16.3
Provide social projects	30	10.2
Livestock/grazing and watering	29	9.9
No benefits	20	6.8
Total	294	100

Major *problems of living next to Amboseli National Park*

There were varied responses on the part of respondents on what they perceived as the main problem associated with living next to Amboseli NP, such as attacks by problem animals, restricted movements, rarrest/harassment by rangers, and 4 loss of grazing land (Table 5.9).

Table 5.9
Major problems associated with living next to Amboseli National Park according to respondents.

Problems of living next to ANP	No. of respondents	Percentage
Problem animals	227	77.2
Restricted movements	36	12.2
Rangers arrest/harassment	17	5.8
Loss of grazing land	14	4.8
Total	294	100

Disposal *of carcass/meat or predators kills*

Nearly all respondents (94.6%) indicated that they eat livestock killed by predators, while only 5.4% of the respondents' indicated other forms of disposal of livestock kills.

Patterns *and circumstances of repeat predator attacks*

According to respondents, there was a variety of circumstances under which repeated predator attacks on livestock took place. Table 5.10 shows that a majority of the respondents (46.6%) indicated that immediate attacks by predators happen when predators are chased, shortly after they started feeding on livestock kills, 40.1% of the respondents indicated that a repeated attack happens when predators are chased away immediately after killing livestock before they are able to feed, 7.1% indicated that repeated attacks happen when predators are chased away after they started feeding, but before they were fully fed and 6.1% indicated that repeated attacks happen when predators are chased after being fully fed.

Table 5.10
Circumstances under which respondents experience repeated predator attacks

Circumstances of immediate predator repeat attack	No. of respondents	Percentage
Predators chased away shortly after they started feeding on killed livestock	137	46.6
Predators chased away immediately after killing livestock, before feeding	118	40.1
Predators chased away after they started feeding but before fully fed	21	7.1
Predators chased when fully fed	18	6.1
Total	294	100

Major *obstacles to pastoralism in the future*

A majority of respondents (62.6%) consider drought to be major obstacle for pastoralism in the future; 13.3% of the respondents indicated predation by animals, 9.9% of the respondents indicated diseases, and 7.8% of the respondents indicated lack of pasture and 6.5% of the respondents indicated climate change as the major obstacles for pastoralism in future

Actions *taken in case of serious drought*

Table 5.11 summarizes that the respondents mentioned several options in case of serious drought: 66.3% would migrate to other areas in search for pasture for their livestock, 23.5% indicated that they would sell off their livestock, while 10.2% indicated they would diversify to other income-generating activities (Table 5.12). Some of the respondents further said they buy hay for their animals during periods of drought.

Table 5.11
Actions taken in case of serious drought by respondents

Actions to be taken in case of serious drought	No. of respondents	Percentage
Migrate	195	66.3
Sell livestock	69	23.5
Diversification to other income-generating activities	30	10.2
Total	294	100

5.5 Discussion

5.5.1 Livestock predation trends

Our results show a significant variation in livestock predation figures when we compare the year before the drought with the drought year (2009) and the years immediately after the drought per predator species. All attacks occurred in the group ranches surrounding Amboseli NP and this pattern was consistent in all the years. We had no data on wether attacks occurred within boma's or during grazing outside boma's. Livestock predation was significantly higher during the severe drought in 2009 than in the years before and after the drought. Our findings are confirmed by several other studies which have demonstrated that livestock depredation is more common in areas with low prey abundance (Sillero-Zubiri & Laurenson, 2001; Polisar et al., 2003; Treves et al., 2004; Rabinowitz, 2005; Bagchi & Mishra, 2006; De Iongh & Bauer, 2008). Many studies have suggested that local environmental conditions such as rainfall correlate with increased livestock predation during the wet season (Patterson et al., 2004; Woodroffe & Frank, 2005, Tumenta et al., 2012). Furthermore, livestock husbandry practices (Stahl et al., 2001; Madhusudan, 2003; Ogada et al., 2003; Polisar et al., 2003; Rabinowitz, 2005) and the characteristics of villages attacked and livestock enclosures used (Van Bommel et al., 2007; Ogada et al., 2003) have been found to influence livestock depredation.

In our study, the period before the drought and the post-recovery year 2012 can be characterized by a lower incidence of predation. All predator species except for lions, had the highest livestock predation rates during the drought and low predation rates before the drought period and during post recovery. Although multiple studies on Kenyan rangelands concluded that lions are the most serious livestock predator, and that predation by hyenas is relatively infrequent (Ogada et al., 2003; Patterson et al., 2004, Sogbohossou et al., 2011), we found relatively lower predation rates by lions compared to hyenas. In addition, jackal and cheetah were responsible for more attacks than lions. Lion had highest predation rates during the year immediately after the drought (2010) but also had low predation rates in the year before the drought period (2008) and during post recovery (2012). Livestock depredation by these large predators could be attributed to a depletion of natural prey and loss of habitat due to the severe drought. In the northern region of Ethiopia, where the natural prey base was depleted, spotted hyenas were highly dependent on anthropogenic food sources (Kolowski & Holekamp, 2006; Abay et al., 2011; Yirga et al., 2012). The relative availability of stock animals may also have influenced the involvement of predators. Patterson et al. (2004) reported low hyena depredation on ranches on which the majority of stock animals were cattle. The low frequency of hyena and leopard depredation in some areas may thus result from the rarity of their preferred livestock prey size (sheep and goats).

We found significant differences between dry and wet seasons in predation incidence per species of large carnivores. Livestock predation was high during wet season for lion and leopard, whereas the opposite was true for hyena, cheetah and jackal. Rudnai (1979) was unable to associate rainfall with predation frequency, while others found higher predation rates during the dry season (Butler, 2000; Ikanda, 2005).

5.5.2 Influence of drought on specific livestock predation in relation to wild prey abundance and rainfall

Our data support the important relationship between livestock predation, rainfall and prey abundance. Patterson et al. (2004) and Woodroffe & Frank (2005) suggested that the seasonal local availability of natural prey is the main factors influencing livestock predation. Whether the wet or dry season brings increased depredation is then likely to be dictated by the regional relationship between rainfall and natural prey. Whereas the dry season in some regions is associated with increased natural prey and reduced livestock depredation, the inverse has been shown in areas where prey numbers peak in the wet season (Ikanda, 2005; Kolowski & Holekamp, 2006; Ottichilo et al., 2000). Our result shows similar trends, directly relating prey abundance with rainfall, while lack of wild prey also influences livestock predation rates. Our study also shows that most livestock attacks by carnivores, particularly hyena's, occurred during the severe drought year of 2009. This happened for all livestock types (goats/sheep, cattle and donkeys) with lower predation in the years before and after the drought.

We found that when annual herbivore numbers showed a significant decline during the drought year (2009) and directly after the drought (2010), large carnivore livestock predation increased simultaneously. Wild herbivore decline due to the impact of the drought was evident for all herbivores. There was a slight recovery during the 2011 and 2012 post-drought periods, when livestock predation declined substantially.

Our findings contradict those of Woodroffe & Frank, (2005) and Patterson et al. (2004), who conducted research in Laikipia and Tsavo National Park and found fewer livestock losses to predators during a severe multi-year drought and more predation during the rainy season. Conversely, we found higher livestock loss due to large carnivores (except for lion) during dry season and our results also show an overall negative relationship between mean annual rainfall and mean annual predation rates both before and after the drought except for hyena. However, there was a positive relationship between mean annual rainfall and mean annual lion predation rates. In the Makgadikgadi and Ngorongoro Conservation Area, clear seasonal trends in livestock predation were recorded (Kolowski & Holekamp, 2006). These were related to wild prey availability and stock raiding, which decreased when migratory wild prey were present in large numbers, despite local increases in lion populations. As migrant zebra and wildebeest moved to other areas, local livestock predation increased despite a local decline in lion density (Hemson et al., 2009; Ikanda, 2005). In this case some lions remained resident in areas in which they could kill wild prey when it was abundant and livestock when migrants were scarce. The predominance of jackal, spotted hyena and leopard as livestock-killing predators has been reported in many areas (Yirga et al., 2012; Hawkes, 1991; De Iongh et al., 2009; Abay et al., 2011; Sogbohossou et al., 2011).

5.5.3 Community attitudes and views

Livestock continue to be a major source of livelihoods for the Maasai community around Amboseli NP. Our results show that a majority of the respondents depend on livestock (cattle, goats, sheep and donkeys). A few respondents depend on trade, whereas a limited number of respondents depend on agriculture. The major issue identified by all respondents was the problem of livestock predation by large carnivores. Hyenas were identified as the most problematic animals, followed by lions and cheetahs in that order, while an insignificant number of respondents perceived jackal to be a problem animal. This is contrary to the findings of Tumenta et al. (2012) who suggested that in north Cameroon, lions were the most important predator from an economical point of view, mainly killing cattle. We found that lions killed 232 heads of cattle during the study period, compared to 480 killed by hyenas.

Our results on predation trends show that jackal kills more livestock than lions in absolute numbers because of the large number of goats and sheep they killed. Livestock predation remains a significant problem around the park. Other researchers also found predation by lions and other predators (hyenas and jackals) to be a serious issue around Waza National Park in Cameroon (Bauer & Kari, 2001; Bauer, 2003; Van Bommel et al., 2007). The respondents further explained that destruction of property during the night is common, and that they worry about restrictions in movement of school-going children in the morning and evening restriction for those attending social gatherings.

Respondents indicated that there was a seasonal variation in livestock predation, indicating more predation during the wet season than in the dry season. Our findings were similar to the predation patterns described by Bauer (2003), during the dry season around Waza NP. In Amboseli NP, prey normally congregate at the swamps during the dry season, resulting in temporary residence of lions around these swamps. This result in lower livestock predation rates by lions during the dry season. However, during the wet season, when wild prey migrates outside Amboseli NP, the frequency of livestock predation by lions increases. This is however, the opposite of the predation pattern of spotted hyenas, which shows a relatively constant livestock predation rate in both wet and dry season. This could be due to intrusions into the park by pastoralists, resulting in an almost permanent presence of livestock within the park during the dry season (De Iongh et al., 2008).

Our results show that major community benefits of living next to Amboseli NP are the attraction of tourists, and provision of bursaries for school children, employment and social projects such as health care and water provision. It has been suggested that "the success of any community-based wildlife conservation will depend on ensuring that individuals derive benefits from conservation and sustainable management of the resource" (Gillingham & Lee, 1999; Brüner et al., 2001). Tourism is often seen as effective mitigation for human–wildlife conflict by conservation authorities and organisations; however its scope as such has been questioned (Gillingham & Lee, 1999). Indeed, our respondents also reported problem animals, restricted movements, arrest/harassment by ranger, loss of grazing land to be disadvantages of living adjacent to the park. It does seem possible that there is weak link between benefit accrued from the park through tourism that could act as a catalyst for pro-wildlife attitudes around Amboseli NP. Tourism in the area does not seem to be having a wider effect on community attitudes towards all large carnivores. There is a need to clarify to the community these important linkages, however, it may be that they are already aware and are not satisfied.

Increasing the resilience of carnivore populations by increasing the area in which people can co-exist with large carnivores is a logical strategy for large carnivore conservation (Linnell et al., 2001; Sillero-Zubiri & Laurenson, 2001). By doing so, protected carnivore populations separated by land utilised for livestock or agriculture may re-establish connectivity and gene flow. Of considerable concern is that in many cases at present, lion populations outside protected areas are absent or threatened (Woodroffe & Ginsberg, 1998; Woodroffe., 2000).

Management of the predation sites (disposal of kills), and prompt response to community distress and predator kills are very important measures in resolving conflicts and reducing the frequency of predator attacks. Our results show that nearly all (94.6%) of the respondents consume livestock meat killed by predators. This probably had a significant impact on the number of immediate repeated attacks by lions, depending on whether the predator in question had fed on the kill or not.

The greatest impediment to pastoralism was identified as recurrent drought, predation by large carnivores, livestock diseases, and diminishing pasture. The drought-coping mechanisms identified were migration to other areas, sale of livestock and diversification of livelihoods. The drought of 2009 was identified as the worst in terms of livestock loss and poverty in history.

We conclude that large carnivores create problems because of their feeding habits, wide-range requirements and the need for substantial prey populations, which inevitably brings them into conflict with people. Large protected areas or well-managed landscapes with corridors and conservation-friendly local communities can provide relative long-term security to predator populations.

To manage wildlife outside protected areas effectively, or even to secure protected areas themselves, the benefits from wildlife must outweigh the costs to neighbouring local communities. The compensation schemes introduced earlier have a relatively positive impact on community attitudes and reduced retaliatory lion killing in Amboseli. The government of Kenya recently initiated a change in policy and introduced further compensation for damages caused by wildlife, including human death and injuries. It is expected that this change will have a significant positive impact on the attitude of the communities and promote more tolerance for lions and other carnivores.

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Questionnaires

To whom it may concern

I am a student at Leiden University, Institute of Environmental Sciences, The Netherlands, pursuing a Doctor of Philosophy degree (PhD) in conservation biology.

As part of the course requirements, I am undertaking a research project on the interaction between lions, livestock and people around Amboseli National Park. As such, I am administering a questionnaire on local community involvement with wildlife, particularly large carnivores such as lions, and their views towards conservation and management.

Please assist by taking time to fill out the attached questionnaire as sincerely as possible.

The results of the questionnaire shall not be used for any other purpose except the one for which the data has been collected.

Thank you in advance.

Date ________________________

1 Gender
2 Village name
3 Cultural boma
4 District
5 Age
6 What is the size of your household?
7 Could you rank Forest found in your area in order of importance to you?
8 Could you rank Wildlife found in your area in order of importance to you?
9 Could you rank Water found in your area in order of importance to you?
10 Could you rank Pasture found in your area in order of importance to you?
11 How do you rank the status of the natural resources in your area in the last 10 years?
12 How often do you see lions in your area during wet season?
13 How often do you see lions in your area during dry season?

14 How often do you see Hyena in your area during wet season?
15 How often do you see Hyena in your area during dry season?
16 How often do you see Leopard in your area during wet season?
17 How often do you see Leopard in your area during dry season?
18 How often do you see Cheetah in your area during wet season?
19 How often do you see Cheetah in your area during dry season?
20 How often do you see Wild dog in your area during wet season?
21 How often do you see Wild dog in your area during dry season?
22 How often do you see Jackal in your area during wet season?
23 Does your village have any problem concerning wild carnivores?
24 If yes: what are the major problems?
25 When did you experience last incident?
26 Which carnivore species often cause problems?
27 Where were livestock preyed on?
28 When is the problem more prevalent?
29 What would you do once you encounter livestock killed by predators?
30 Do people eat livestock meat kiled by predators?
31 Under what circumstance do you experience predator immediate repeat attack?
32 What preventive measures do you personally use to mitigate cattle and donkey attacks in your boma?
33 What preventive measures do you personally use to mitigate calves attacks in your boma?
34 What preventive measures do you personally use to mitigate shoats attacks in your boma?
35 What preventive measures do you personally use to mitigate cattle and donkey attacks on grazing grounds?
36 What preventive measures do you personally use to mitigate calves attacks on grazing grounds ?
37 What preventive measures do you personally use to mitigate shoats attacks on grazing grounds ?
38 What preventive measures do you personally use to mitigate shoats attacks on grazing grounds ?
39 What preventive measures do you personally use to mitigate shoats attacks in your boma?
40 What preventive measures do you personally use to mitigate calves attacks on grazing grounds ?

41 What preventive measures do you personally use to mitigate calves attacks in your boma?

42 What would you do once you encounter livestock killed by predators?

43 When is the problem more prevalent?

44 Which carnivore species often cause problems?

45 To whom do you report the problem of predation?

46 Where were livestock preyed on?

47 If yes: what are the major problems?

48 Are you aware of Olgulului predator compensation scheme?

49 Have you benefited from the predator compensation scheme?

50 What were the benefits?

51 Are you happy with the predator compensation scheme?

52 Is there anything you are not happy about predator compensation scheme?

53 What are they?

54 How would you like the compensation scheme be improved?

55 If you are asked to contribute towards compensation scheme would you?

56 If yes, in what ways?

57 What do you consider as the major obstacles for pastoralism in the future?

58 Do you see any solution for these problem?

59 If yes, what are the solutions?

60 Who should solve these problems?

61 What are your plans for the future in relation to livestock?

62 In other parts of Kenya pastoralism has changed significantly. sedentarization, decrease of herds, etc. 63. What is your opinion about these changes?

64 What do you do in case of serious drought?

65 How did drought of 2009 affect you?

66 How did you cope?

67 Would you do the same in case serious drought occurs again?

68 If no give reasons

6

Synthesis, Conclusions, and Recommendations

6.1 Lion population response to environmental stochasticity and implications for conservation: A synthesis

The description and prediction of stochastic events and their impact on population dynamics in time and space is fundamental to ecology and conservation biology. Ecologists are increasingly aware of the importance of climatic variability in natural systems. Some authors have predicted that, with climate change, the frequency and severity of stochastic climate events will increase (Jededia et al., 2013). The dynamics of every population has both deterministic (predictable) and stochastic (unpredictable) components that operate simultaneously (MacArthur, 1972). Russell (1993) defined stochasticity as temporal fluctuations in terms of mortality and reproduction rate of all individuals in a population. A major challenge for ecologists is to predict the possible consequences of climate change in terms of an increase in stochastic events and based on this, to propose adaptation and mitigation measures (Wim et al., 2010). Climate change affects both the mean and the variability in climatic factors and the effect of changes in variability is poorly understood. Unpredictable catastrophes that suddenly reduce a population substantially, such as might occur in droughts, fire, floods, landslides, volcanic eruptions, or epidemics, are now classified as forms of stochasticity (Russell, 1993; Johst & Wissel, 1997).

Evolution is an expected response to environmental change, similarly, climate change and other environmental shifts are widely acknowledged to be important drivers of ecological change (Parmesan & Johe, 2003). Organisms are subject to selection imposed by the range of environmental variation experienced by their ancestors. Variability is a critical environmental factor and may therefore have consequences for vital population dynamics (Parmesan & Johe, 2006). Rainfall variability therefore is considered important as it influences the dynamics of African ungulates, and change in rainfall variability equally alters carnivore abundance. Several studies have shown adverse impact of drought on predator biomass (Ottichilo et al., 2000; Georgiadis et al., 2007). Other factors regulating predator biomass are prey abundance, retaliatory killing and disease.

Fluctuations in population size often appear to be stochastic, or random in time as demonstrated by mortality, reproduction and dispersal (Parmesan, 2006). Stochastic environmental fluctuations can have important implications for the conservation of small single populations and for metapopulations.

Stochasticity also can interact with human exploitation of the environment or other factors such as disease and can cause the collapse of ecosystem, or it can cause extinction of a population harvested under a strategy, which deterministically would produce a sustained yield. The impact of environmental stochasticity may lead to extinction irrespective the size of the population. It therefore constitutes an important risk for population decline, in all populations regardless of their abundance at a given location. Because organisms are subject to selection imposed by the range of environmental variations, therefore changes in the variability of a critical environmental factor may have consequences for vital survival rates and population dynamics.

Under stable climatic conditions, carnivore population dynamics depend more on prey –predator relationships and availability of prey and water than on climatic factors (Carbone & Gittleman, 2002). Consequently one could assume that the diversity of carnivores would be less dependent on climatic-environmental conditions than that of herbivore abundance.

6.2 Lion population trends and response to environmental stochasticity

In my study in the Amboseli ecosystem, human-induced mortality and climatic variability had significant effects on lion pride organization and social structure. The drought affected the availability of prey, and as a result lion livestock predation increased, along with lion retaliatory killing. Loveridge et al. (2006) and Yamazaki (1996) found that social behaviour of prides was disrupted by the removal of pride males by sport hunters leaving gaps within the territorial structure. In my study, the significant change in age structure after the drought year in 2009 was an indication of a growing lion population, with more juveniles than adults expected to fill this territorial vacuum. The changes in social structure I detected in my study, with a smaller group size after the drought and an increase in the Male: Female ratio, are an indication of a disturbed social structure. Previous studies have found that lion group size is correlated with prey size and prey availability and lion density is influenced by multiple factors, related positively to herbivore biomass, as well as annual, mean rainfall and with interactive effects between rainfall and soil nutrients (Schaller, 1972; Van Orsdol et al., 1985; Hanby et al., 1995, Ogutu et al., 2008).

In my study, the Vulnerability Index (VI) for lions as a function of Drought Severity Index (DSI) and Prey Availability Index (PAI) was highest in 2010, the year directly after the drought and showed a gradual increase during 2011 and 2012. My study also shows that the year directly after the drought (2010) was crucial for lion survival and determined the outcome in terms of mortality and lion population structure. My interpretation is that, although drought also affected livestock, people moved away with their livestock and returned after the rains, heightening predation and retaliatory killing. The drought Vulnerability Index can be used to plan mitigation measures and identify drought coping or adaptation mechanisms for lions in other areas.

6.3 Lion home range, movement patterns and connectivity provides opportunity for mitigation and adaptation

My study shows in many occasions, that both the collared male and female lions moved far from Amboseli NP into the surrounding communal group ranches. Furthermore, one of the males collared in this study spent a great amount of time in the neighbouring country of Tanzania, located south of the park. Evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. My study indicated that the lion populations in Amboseli NP are not isolated, as wildlife corridors exist between the park and the group ranches and some of the lions even established new territories in Tanzania. This ability to disperse and survive in the surrounding landscapes and possibly connect with other lion populations serves an important function in the gene flow within the metapopulation. To restore the populations of prey species and thereby reduce the vulnerability of the lions in the face of climatic fluctuations, there is need for concerted efforts to implement measures such as the establishment of community conservancies and corridors to other protected areas within the region.

This example shows how a complex interaction may occur in ecological responses to extreme climates and climate change. MacDonald (1983) suggested that resources and especially food dispersion are the main factors determining the home range size of large carnivores. During the wet season, when food is abundant due to the large herds of herbivores dispersing outside the park, the lions increased their home range. Due to the expansion and contraction of home ranges in response to prey availability, the total prey biomass within the home range may remain relatively constant. According to the finding of Bauer & de Iongh (2005), home range size is mainly determined by how food is distributed in space, while group size is determined by prey size and quality of food patches.

Ecologists have viewed species' niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers) (Turner et al., 2005; McCarty, 2001). Patterns of change in the home range size (the size of the minimum area that can sustain the individual's energetic requirements) over time can provide important insights into the ecological and evolutionary responses of mammalian communities to new environmental conditions (Van der Putten et al., 2010). Understanding the ability of species to shift their ranging pattern is of considerable importance, given current rapid climate change. Furthermore, a greater understanding of the spatial population dynamics underlying range shifting is required to complement the advances made in climate niche ecology. There is no doubt that climate plays a major role in limiting terrestrial species' ranges (Turner et al., 2005; Wilson et al., 2005; Parmesan, 2006, Pearson & Dawson, 2003). There is a strong trade-off between climate tolerance and resource/habitat preferences on one hand and a relaxation of selection for climate tolerance (Turner et al., 2005; McCarty, 2001). Climate variability (change) can alter the setting of range limits, leading to range expansion or contraction (Owen-Smith & Ogutu, 2013, Ogutu & Owen-Smith, 2003). Many such range shifts have been reported over the past decades and this process is presumed to continue (Turner et al., 2005; Parmesan & Yohe, 2003; Easterling et al., 2000). Stochastic weather patterns can force wide-ranging species such as lions beyond current reserve boundaries, into areas where there will be greater conflicts with humans (Tuqa et al., 2014). Climate events affected the habitat quality, food supply and access to resources (Wilson et al., 2005, Ogutu & Owen-Smith, 2003, Owen-Smitt & Ogutu, 2013), which in turn, as our results show, influenced the lions' home-range and movement patterns.

The role of the Maasai community in conservancies such as Kitirua trust, Eselengei and Kitenden corridor are thereby crucial. An understanding of an animal's ranging patterns provides an important insight on how it uses its resources. Under conditions of fragmented habitats, severe climate conditions such as severe drought can create new challenges for lion conservation due to effects on prey availability and subsequent influences on their ranging patterns.

6.4 Lion prey availability and diet shift – a realized niche in constrained predator-prey relationships

My research findings supports widely held perspectives that lions are opportunistic feeders, generally thought to prey on medium-to–large-sized ungulates. My study showed that lions are able to persist on a varied diet in a stochastic environment with extreme drought, by partially shifting or expanding their feeding niche and including smaller animals such as impala, warthog, or porcupine, and larger animals such as giraffe and buffalo as well as cattle. This partial shift and diversification of prey shows ecological resilience and the adaptability to a changing stochastic environment by lions. Much of ecology is built on the assumption that species differ in their niches and their responses to temporal fluctuations in the environment (Adler et al., 2006; Kneitel et al., 2004). Periodically, there are natural fluctuations in all seasonal parameters such as temperature, precipitation or the amount of vegetation cover (Wichmanna et al., 2005). We can assume that although the population dynamics of a species is well adapted to seasonal variations such as dry and wet, it might not be adapted to non-seasonal variation such as a stochastic drought phenomenon. Habitat use and prey selection by individual animals results from patterns ultimately driven by habitat-dependent fitness (Hirzel & Le Lay, 2008), that is, the fundamental niche is subjected to natural selection (Austin et al., 2013). For a niche to evolve, the new conditions must not lie too far outside the ancestral niche of any organism. In this case, natural selection tends to act upon principally as a conservative force (Holt & Gaines, 1992). In the case of gradually, directionally changing environmental conditions, a species is subjected either to track its environment across space or to go extinct (Lande & Shannon,1996).

6.5 Livestock predation trends, community knowledge and attitude

My study results showed that prey abundance and seasonality in rainfall influences livestock predation rates. Further, my study also showed that most livestock predation attacks by large carnivores occurred during the wet season, with the exception of the drought year 2009. This applied to all livestock types: goats/sheep, cattle and donkeys, for which there were low predation rates in the years before and after the drought.

I found that, when herbivore numbers showed a significant decline during the drought year and during the years after the drought, carnivore livestock predation increased simultaneously. Wild herbivore decline was evident across the three categories; larger herbivores (buffalo, giraffe and eland) medium sized herbivores (wildebeest, zebra and waterbuck) smaller herbivores (Thomson's gazelle, Grant's gazelle, warthog and impala). Other studies, such as Patterson et al. (2004) and Woodroffe & Frank (2005) suggested that this trend may be ultimately driven by seasonal variation in the local availability of natural prey. Whether the wet or dry season causes increased depredation is then likely to be dictated by regional relationships between rainfall and natural prey. Various studies have demonstrated that livestock depredation is more common in areas with low prey abundance (Sillero-Zubiri & Laurenson, 2001; Polisana et al., 2003; Treves et al., 2003; Rabinowitz, 2005; Bagchi & Mishra, 2006; De Iongh & Bauer, 2008). Local environmental conditions such as rainfall (Patterson et al., 2004; Woodroffe & Frank, 2005), livestock husbandry practices (Madhusudan, 2003; Ogada et al., 2003; Polisara et al., 2003; Rabinowitz, 2005) and characteristics of attacked villages and livestock enclosures (Linell et al., 2001; Ogada et al., 2003) have been found to influence livestock depredation. Whereas the dry season in some regions is associated with increased natural prey and reduced livestock depredations, the inverse has been shown in areas where prey numbers peak in the wet season (Ikanda, 2005). In the northern region of Ethiopia, where the natural prey base were highly depleted spotted hyena depend entirely on anthropogenic food (Yirga et al., 2012; Kolowski & Holekamp, 2006).

Although multiple studies on Kenyan rangelands concluded that lions are the most serious livestock predator and that hyena predation is relatively infrequent (Frank, 2000; Ogada et al., 2003; Patterson et al., 2004), my study showed that lion predation rate were relatively low as compared to hyena.

To manage wildlife outside protected areas effectively, or even to secure protected areas themselves, the benefits of wildlife must outweigh the costs to neighbouring local communities. The compensation schemes introduced earlier have relatively positive impacts on community attitudes and have reduced lion killing in Amboseli. With the Kenya government policy change and introduction of wildlife compensation for life and property damage in 2014, we expect a significant positive impact on community tolerance for lions and all other carnivores.

Livestock continue to be a major source of livelihoods for the Maasai community around Amboseli NP. My result shows that a majority of the respondents depend on livestock. The major problems identified by all respondents was the problem of livestock predation by large carnivores. Hyena was identified to be the most problematic animal, followed by lion and cheetah in that order, while insignificant numbers perceived jackal to be a problem animal. Our result on predation trends show that jackal kills more livestock than lion in terms of numbers of young goats and sheep. Respondents recognized that there was a seasonal variation in livestock predation, indicating more predation during the wet season as opposed to dry season.

My results show that major community benefits of living next to Amboseli NP are the attraction of tourists, bursaries for schools children, and source of employment and “Social Projects” such as livestock/grazing and water provision. On the other hand respondents also reported problem animals, restricted movements, ranger arrest/harassment, loss of grazing land to be problems emanating from the park.

Management of the predation site (disposal of kills), a prompt response to community distress and predator kills are very important measures in resolving the conflict and reducing the frequency of predator attacks. Our results show that nearly all 94.6% respondents consume livestock meat killed by predators. This had significant impact on the immediate repeat attack of livestock, with varying time periods depending on whether the predator in question had fed on the kill or not.

The greatest impediment to pastoralism was identified as recurrent drought, predation of livestock diseases and diminishing pasture. The drought coping mechanisms identified were migration to other areas, sale of livestock and diversification of livelihoods. The drought of 2009 was identified as worse in terms of livestock loss and poverty in the history.

I conclude that large carnivores create problems because of their feeding habits and wide-ranging requirements and the need for substantial prey populations, which inevitably brings them into conflict with people. Large protected areas or well-managed landscapes with corridors and conservation-friendly local communities can provide relatively long-term security for viable predator populations. To manage wildlife outside protected areas effectively, or even to secure protected areas themselves the benefits from wildlife must outweigh the costs to neighbouring local communities.

6.6 Conclusions

In my study, I discuss the response of lion populations to effects of climate variability (severe drought) and their strategy to persist and interact with people/livestock. I assessed several aspects of lion populations: lion population density and social structure, ranging patterns and movements, the diet and relationships with prey and livestock predation trends.

1 Severe drought had an effect on Amboseli lion social structure, with smaller group size and a decreased male to female sex ratio after the drought, a result of low food availability because of the drought. This increased the lion Vulnerability Index in 2010 as a result of increased human-induced mortality; furthermore, livestock predation by lions increased, as did retaliatory killing of lions.
2 Climate events such as drought affected the habitat quality, food supply and food access, which in turn influenced the lions' home-range and movement patterns. Conditions of fragmented habitats can create new challenges for lion conservation due to effects on prey availability and subsequent influences on their ranging, far and wide beyond small protected area such as Amboseli. The long-term lion study through GPS/GSM collars has revealed useful information on corridors used by carnivores and herbivores within the Amboseli ecosystem and connectivity with other conservation areas.
3 My findings confirmed that lions are opportunistic feeders that are generally thought to prey on medium-to-large-sized ungulates, but are able to adapt to stochastic events such as drought. When preferred prey were not available, they partially shifted and fed more on smaller animals

such as impala, warthog, porcupine and expanded to larger prey such as giraffe in 2010 and 2011.

4 Prey abundance and seasonality in rainfall influenced livestock predation rates. The negative attitude of pastoralist community correlates with the intensity of livestock predation by large carnivores in Amboseli ecosystem. Annual herbivore numbers showed a significant decline during the drought year and during the years after the drought while livestock predation by carnivores increased.

5 Lion populations showed a high resilience in coping with drought stochasticity to survival by increased reproduction of cubs after the drought

6.7 Recommendations for conservation and management

The continued existence of large populations' of lions and other large carnivore species in the Amboseli rangelands indicates the presence of a healthy and functional ecosystem. The majority of wildlife in this ecosystem lives outside the protected areas most of the year and is under intense pressure from human activities. These include the interaction with incompatible land use such as agriculture and high-density settlements. The increasing livestock numbers in the area forms another challenge, through competition for forage and water resources with wildlife especially during the dry season. Furthermore, poaching poses a threat to animals outside the boundaries of protected areas as they become easy targets. Wildlife species are generally adapted to their environments and slight changes in habitat or climate are often reflected in population changes.

- A climate-change strategy needs therefore to be developed: a science-based analysis of ecological factors that affect species' adaptation and determines subsequent mitigation measures. The potential impacts of climate change in terms of stochastic events such as recurrent droughts should be assessed on a species by species basis for both carnivore and herbivore dynamics. This will enable the tracking of daily movements and seasonal migrations, and changes in vegetation conditions. Drought, being a driver of climate change, has the potential to alter migratory routes and timing, which may in turn lead to increased human-wildlife conflicts.

- Community participation in conservation and decision making is very important to ensure the survival of large carnivores and other wildlife within the group ranches. Trans-boundary ecosystems should be supported by the respective governments to establish buffer zones surrounding Amboseli NP and assuring connectivity to critical wildlife areas such as the Kitenden Corridor, linking Kilimanjaro national park with ANP. The Amboseli population may act as an important gene pool which might be prone to extinction, if passage through the corridor is blocked.

- Enforcement policies and legislation such as the Land use policy, the Draft land act, the Draft land registration bill, the Draft wildlife policy, the Wildlife conservation and management ACT 2013 are important. Other economic instruments, which ensure payment for ecosystem services, should be implemented as well, to secure the corridors and migratory routes of wildlife through easements, leases and direct purchases. The development of programmes that involve communities in wildlife conservation is an important tool for wildlife management.

- The promotion of community wildlife conservancies, game scouts, associations and other eco-tourism ventures will provide direct benefits. In order to meet both the conservation goals and livelihood needs of the communities, proliferation of awareness in conservation and public education is critical in promoting lion and other carnivore coexistence with people and to promote tolerance.

- Human-wildlife conflicts have increased in Amboseli NP as the park continues to be engulfed by unsustainable land use, including agriculture and infrastructure developments. During the dry periods, wildlife strives to survive in unfamiliar territories and becomes overwhelmed by intense competition for meager resources such as water, forage and space, and exposure to poaching and diseases. More research needs to be conducted in this field to find ways in which people can coexist with large carnivores.

- Further research is needed to confirm the low heterozygosity and genetic variability identified by Bertola (2015) of the Amboseli lion population. This management option requires extensive financial resources and expertise. For this to be feasible, the government should solicit financial support from international conservation donors.

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Summary

Understanding 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

Keywords:
Severe drought, climate variability, lion population, home range, movement patterns, diet, livestock predation, Amboseli National Park, Kenya

Wild carnivores are an important component of many ecological systems and play a significant role in maintaining ecosystem health. Being at the top of the food chain, carnivores have important ecological impacts, including the regulation of mesopredators, maintenance of healthy prey populations, alterations in the spatial distribution of prey and associated changes in vegetation structure. Important cascading trophic effects, caused by population changes of their prey or of sympatric mesopredators, may result when some of these large carnivores are removed from ecosystems. The removal of top predators from ecosystems often causes dramatic changes in biodiversity and community structure, and can have severe consequences for the functioning of ecosystems and ecosystem services.

Historically, the conservation of biodiversity throughout the world has been facilitated by the designation of protected areas (PAs). These are areas set aside principally for the protection and conservation of biological diversity, and of their natural and associated cultural resources. 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 National Park (ANP) in Southern Kenya, with a surface area of only 370 square km. Large carnivores such as lions usually have large home ranges and therefore only large PAs can provide adequate protection.

Climate change and associated climate variability is one of the greatest conservation challenges of the 21st century. Climate variability is expected to exacerbate climate-mediated biodiversity loss through fragmentation of wildlife habitats and the spread of alien invasive species. The impact of climate variability is generally compounded by environmental degradation.

Moreover, anthropogenic activities are exerting additional pressure on biodiversity. Dwindling natural resources result in deterioration of rangelands and diminishing grazing areas for wildlife. The displacement of animals and increasing migrations due to pastoralist activities may further enhance the impact of increased drought prevalence and scarcity of water resources, which could lead to more human-wildlife conflicts.

In African savanna environments, vegetation growth and hence food production for herbivores depends strongly on rainfall during the wet season. Determining biological and environmental factors that limit the distribution and abundance of organisms is central to our understanding of the dynamics of animal populations. It is crucial for predicting how species may respond to large-scale environmental change, such as drought (short term) and climate change (long term). Wildlife populations may increase or decrease dynamically, depending on rainfall. Plenty of rainfall may lead to an increase in animal populations, as improved range conditions result from the growth of forage and from the abundant water necessary to maintain basic metabolism. Large mammal communities are ultimately limited by their food supply through mortality and reproductive stress.

It is known that droughts may have disruptive effects on the vegetation, which in turn affects animal populations through enhanced mortality, first of the weaker animals and later of the ones that are more fit. Such changes may lead to age-restricted mortality, reduced fecundity and reproduction, the restriction of animal movements and ultimately a strong reduction in population size and density. This was confirmed through my PhD research; I found that drought had a severe impact on herbivore populations and on the social structure of the lion population in ANP.

My research covered three years before/during (2007-2009) and three years after the drought (2010-2012). The main aim of my research was to understand the effects of lion-prey interactions during and after a severe drought and the impact of this drought on lion density and social structure, ranging patterns, diet and prey relations, as well as their interaction with local communities.

My PhD research revealed that human interventions enhance the impact of climate variability and extreme drought. The years after the extreme drought were characterized by increased retaliatory killing of lions by Maasai herdsmen in the surrounding cattle areas.

Large carnivores are particularly vulnerable to habitat loss because they have large home ranges and require extensive, intact habitats to survive. Disturbance due to human activities, such as encroachment of cultivation and settlements, causes a decline in areas of natural habitat and reduces space for grazing by wild herbivores. My PhD research confirmed that habitat loss and habitat fragmentation are among the most important factors influencing the threat of species extinction.

Like elsewhere in Kenya, increasing human encroachment into predator ranges is displacing prey species, resulting in increased livestock-predator interactions and subsequent predation incidents. Livestock predation is the main reason why locals kill predators in the Amboseli Ecosystem (AE).

Diseases such as canine distemper virus and feline immunodeficiency virus are also known to severely impact large carnivore populations, including lions, elsewhere in sub-Saharan Africa. In my research area however, no cases of disease in the lion population have been reported in the recent past.

The lion population in the AE has strongly declined since the last century, with only small populations remaining in the Amboseli National Park (ANP) and in the Mbirikani-Chyulu area. 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 was re-established. Considering the rate of killing which occurred during 2000-2007, this reservoir population headed towards depletion again, almost leaving ANP without any lions, and no source of replacement.

In an attempt to improve the status of ANP's lion population, retaliatory killing was strongly reduced after the start of a compensation scheme supported by the Maasai Conservation Trust in 2007. However, in spite of the reduced overall mortality due to retaliatory killing, I found that in the years after the drought, mortality due to increased human-lion conflicts increased considerably. My research also showed a negative Vulnerability Index (VI) after the severe drought in 2009, indicating higher vulnerability of the lion population during that time. The positive VI in 2011 marked the first signs of recovery. We recorded 28 lions killed around the park during the post-drought period of 2010-2012, compared to 14 before/during the drought (2007-2009); among the first were five pride males. After the drought (2010-2012), the lion population showed a significant change in structure, with a decrease in male-female sex ratio (due to a decline of males), a significant increase in adult group size and a significant decline in juvenile to adult ratio (due to an increase of juveniles). All these changes corresponded to increased lion vulnerability in 2010. We noticed that during this period, male lions were targeted more than females by Maasai warriors (Moran), potentially due to cultural practices (use of manes and claws). The increase in juveniles may have been the result of less competition between pride males and consequently less infanticide. The reduced group size was probably a response to lower prey densities and a drought-resilience mechanism. We found strong positive correlations between the home range size and distance moved in 24 hours before and during the drought, indicating that lions moved more in a smaller home range, while after the drought there was a significant negative correlation, indicating that the lions moved less in a larger home range. This could be explained by the lower densities of prey animals after the drought. A weak positive correlation was evident between lion home range size and rainfall (2010-2012). The male and female home ranges varied over the study period, with male home ranges being significantly larger. The core home range areas (10% Kernel and MCP) and movement patterns overlapped with permanent swamps and areas of high prey density inside the protected area. During the years before/during the drought (2007-2009), the lions' preferred prey species were wildebeest and zebra. The drought resulted in mass mortality among wildebeest and zebra, forcing the lions to shift towards smaller prey species (Thomson's gazelle, ostrich, and warthog) and larger prey species (giraffe and buffalo), in addition to livestock in the year directly after the drought (2010). Diet composition recovered to some extent in 2011 and 2012, when the lions shifted back to their preferred medium-sized prey such as zebra and wildebeest. There were significant differences in livestock predation patterns before/during and after the severe drought (2008-2009): before/during the drought, 1982 head of livestock were killed compared to 2544 after the drought. In total, 3497 of the kills were sheep and goats, 742 cattle and 295 donkeys. Results further show a negative relationship between rainfall intensity and the number of livestock predation incidences for both the periods before and after the drought, with more livestock killed during periods with higher rainfall. We also found that herbivore abundance within the park had a significant effect on livestock predation intensity. Livestock predation increased exponentially after the drought, when wild herbivore numbers were low.

My research demonstrated that the structure of the lion population in ANP changed (male-female ratio; juvenile-adult ratio and group size) in response to the severe drought of 2009. The lions' diet composition changed mark-

edly in the year directly after the drought, when fewer medium sized zebra and wildebeest were taken, but more larger and smaller prey species.

The lion-prey system showed a remarkable resilience, with signs of restoration within two years after the drought (2011), indicated by an increased reproduction rate of the lion population and a return to the pre-drought diet composition. The increase in reproduction is remarkable, considering the high mortality, particularly of male lions, through retaliatory killing by Maasai warriors in the years directly after the drought (2010-2011). A possible explanation of this may be a substantial reduction in pride takeovers and subsequent infanticides by adult male lions.

My research showed that with the existing animal corridors intact, allowing gene flow between distinct prides, the lion-prey system was able to cope with sudden extreme droughts. I suggest that these corridors are essential for the long term survival of the lion population in the Amboseli ecosystem.

Samenvatting

Belangrijke effecten op de voedselketen, veroorzaakt door veranderingen in prooipopulaties of populaties van meso-predatoren, kunnen optreden als grote carnivoren uitsterven.

Het uitroeien van grote carnivoren heeft daarom vaak ernstige gevolgen voor het functioneren van ecosystemen en van ecosysteemdiensten.

Historisch spelen beschermde gebieden een belangrijke rol bij de bescherming van biodiversiteit. Dergelijke beschermde gebieden worden vaak specifiek gereserveerd voor strikte bescherming van biodiversiteit en hiermee geassocieerd cultureel erfgoed. Deze beschermde gebieden alleen zijn echter niet voldoende om het behoud van biodiversiteit en specifieke soorten zoals grote carnivoren op de lange termijn te garanderen, omdat veel van deze gebieden te klein zijn om levensvatbare populaties te handhaven. The Amboseli National Park (ANP) is een voorbeeld van een klein park, met een oppervlakte van slechts 370 vierkante km. Grote carnivoren hebben over het algemeen grote territoria en dit kleine park biedt daarom te weinig bescherming.

Klimaatverandering in combinatie met klimaatvariatie zal in de toekomst een van de grootste uitdagingen worden voor natuurbescherming in de 21e eeuw. Antropogene interventies zullen daarbij de aanwezige druk op de kwetsbare biodiversiteit verder vergroten. Klimaatvariatie zal naar verwachting resulteren in het verlies van inheemse soorten en de verspreiding van invasieve soorten. Klimaatvariatie gaat bovendien vaak gepaard met een algemene degradatie van het milieu. Natuurlijke hulpbronnen worden dan ook steeds schaarser als gevolg van verlies van biodiversiteit, degradatie van weidegronden en een afname in de beschikbare vegetatie als voedselbron voor wilde herbivoren.

Met het wegtrekken of helemaal verdwijnen van soorten als gevolg van een toename van begrazing door vee kan het effect van klimaatvariatie en extreme droogtes worden versterkt, met als uiteindelijk gevolg een toename van conflicten tussen mens en dier.

In de Afrikaanse savanne is de groei van vegetatie, en daarmee de productie van voedsel voor herbivoren, sterk afhankelijk van de mate van regenval tijdens de regentijd. Daarnaast zijn er diverse andere milieufactoren die een belangrijke invloed kunnen hebben op de verspreiding en abundantie van diersoorten. Het is dan ook van cruciaal belang om deze factoren te identificeren, en met name als we willen voorspellen hoe soorten reageren op grootschalige milieuveranderingen, zoals extreme droogte (korte termijn) en klimaatverandering (lange termijn). Populaties van wilde soorten kunnen sterk toenemen of afnemen op basis van fluctuaties in regenval. Een hoge frequentie van regenval kan leiden tot een sterke toename van populaties, omdat het voedselaanbod dan toeneemt door vegetatiegroei en een verhoogde beschikbaarheid van water, noodzakelijk voor het handhaven van het basaal metabolisme van soorten. Populaties van grote zoogdieren worden daarbij uiteindelijk in hun groei beperkt door het voedselaanbod dat een directe invloed heeft op de balans tussen sterfte en geboorten.

In mijn PhD onderzoek heb ik een aanzienlijk effect aangetoond van droogte op de aantallen herbivoren en op de sociale structuur van de leeuwenpopulatie. Ook werd duidelijk dat de negatieve effecten op de vegetatie een directe invloed hadden op verhoogde sterfte onder herbivoren. In dit proces worden eerst de zwakkere dieren geraakt en in een later stadium van droogte de sterkere dieren. Een dergelijk proces leidt tot leeftijdsafhankelijke sterfte, dalende vruchtbaarheid en reproductie, een reductie in de migratie van herbivoren en tenslotte een sterke afname van abundantie en dichtheid.

Mijn onderzoek dekte drie jaar voor en tijdens een grote droogte (2007-2009) en drie jaar erna (2010-2012). Het belangrijkste doel van mijn onderzoek was het analyseren van de respons van leeuw-prooi-interacties gedurende en na een ernstige droogte en de impact van deze droogte op de dichtheden van leeuwenpopulaties, sociale structuur, grootte van leefgebieden, dieetsamenstelling en interacties met prooidieren en lokale Maasai-gemeenschappen.

In mijn onderzoek vond ik een verhoogde sterfte onder leeuwen als gevolg van wraakacties door Maasai in de omliggende veegebieden, hetgeen aangaf dat er een direct additioneel effect was van menselijk landgebruik. Er zijn in zijn algemeenheid veel factoren die het landgebruik kunnen beïnvloeden. Grote carnivoren zijn per definitie kwetsbaar voor het verlies van habitat, omdat ze grote leefgebieden hebben en ook grote natuurlijke gebieden nodig hebben om te kunnen overleven. Verstoring door menselijke activiteiten, zoals de zich uitbreidende landbouwgebieden en dorpen, tast het natuurlijke habitat aan, waarmee ook graasgronden verloren gaan voor wilde herbivoren.

Mijn PhD onderzoek bevestigde dat het verlies van habitat en habitatfragmentatie tot de factoren behoren die het verdwijnen van soorten kunnen bewerkstelligen.

Zoals in veel gebieden in Kenia het geval is, worden wilde herbivoren verdreven door menselijke activiteiten, waardoor het aantal conflicten tussen veehouders en carnivoren en het aantal aanvallen op vee toeneemt. Aanvallen op vee vormen de belangrijkste aanleiding tot het doden van carnivoren bij de lokale bewoners in het Amboseli ecosysteem (AE).

Ziekten als hondsdolheid en feline immunodeficiery virus (FIV), die een belangrijke oorzaak van sterfte onder leeuwen zijn geweest in het recente verleden, leken gedurende mijn onderzoek van ondergeschikt belang.

De leeuwenpopulatie in AE is sterk afgenomen sinds de vorige eeuw. Tegenwoordig zijn er alleen nog enkele kleine populaties aanwezig in ANP en in het Mbirikani-Chylu gebied. Begin jaren negentig werd de populatie leeuwen in ANP vrijwel geheel uitgeroeid door vergiftiging en de jacht met speren door Maasai krijgers, waarna de populatie zich weer gedeeltelijk herstelde door migratie van een aantal leeuwen naar het park uit de omliggende gebieden. De populatie was echter nog steeds klein en het reservoir dat de omliggende gebieden bood was minimaal, waardoor de extreem hoge sterfte onder leeuwen gedurende 2000-2007 had kunnen leiden tot een nieuwe uitstervingsgolf van leeuwen in ANP.

Na de aanvankelijke hoge sterfte van leeuwen in de periode vóór 2007, bleek de introductie van een compensatieplan in 2007 te resulteren in een sterke afname van het aantal gedode leeuwen.

Ondanks de sterke afname in sterfte onder leeuwen, vond ik dat na een afname in sterfte gedurende 2007-2009, in de jaren na de extreme droogte de sterfte sterk toenam als gevolg van een toename van het aantal conflicten. De verlaging van de “Vulnerability index” (VI) voor 2010 die ik vond, duidde op een verhoogde kwetsbaarheid direct na de droogte. In 2011 was er echter al sprake van een licht herstel, met een verlaagde kwetsbaarheid.

Er werden 28 leeuwen gedood rond het park in de periode na de extreme droogte (2010-2012), terwijl in de jaren voor/tijdens de droogte 14 leeuwen werden gedood (2007-2009), waaronder in het eerste geval 5 dominante mannelijke leeuwen. Na de droogte vertoonde de leeuwenpopulatie een belangrijke verandering in structuur, met een afname in de ratio man-vrouw (als gevolg van een afname van het aantal mannelijke leeuwen), een afname in de groepsgrootte en een afname van de ratio jonge leeuwen-volwassen leeuwen (als gevolg van een toename in het aantal jonge dieren). Deze veranderingen traden tegelijkertijd op met een toename van de kwetsbaarheid (VI) van de leeuwenpopulatie in 2010. Gedurende deze periode werden er meer mannelijke leeuwen gedood dan leeuwinnen door Maasai krijgers (Moran), waarschijnlijk mede voor het traditionele gebruik van manen en klauwen. De toename in het aantal jonge dieren was mogelijk een gevolg van minder competitie tussen mannelijke leeuwen en minder infanticide als gevolg hiervan. De kleinere groepsgrootte is waarschijnlijk een reactie op lagere prooidichtheden en geeft de veerkracht van de leeuwenpopulatie weer.

Er waren sterke correlaties tussen de grootte van de leefgebieden en de afstanden afgelegd in 24 uur voor en na de droogte, waarbij bleek dat leeuwen grotere afstanden afleggen in een kleiner leefgebied voor en tijdens de droogte, terwijl na de droogte de afgelegde afstanden kleiner werden in grotere leefgebieden. Dit kan worden uitgelegd door de lagere dichtheden van prooidieren na de droogte. Er bestond een zwakke positieve correlatie tussen de grootte van het leefgebied van leeuwen en regenval. De oppervlakte van de leefgebieden van zowel mannelijke leeuwen als leeuwinnen varieerde in de tijd, waarbij de leefgebieden van de mannelijke leeuwen significant groter waren dan die van de leeuwinnen. De kerngebieden (10% Kernel en MCP) en de verplaatsingen per 24 uur overlapten voor permanente moerassen en gebieden met een hoge prooi dichtheid binnen het park.

Gedurende de jaren voor/tijdens de droogte (2007-2009) waren de geprefereerde prooidieren zebra en wildebeest. De droogte resulteerde in massale sterfte onder zebra en wildebeest, waardoor de leeuwen gedwongen werden in het jaar direct na de droogte (2010), naast vee ook kleinere prooidieren (Thomson gazelle, struisvogel en wrattenzwijn) en grotere prooidieren (giraffe en Afrikaanse buffel) te kiezen.

De samenstelling van het dieet van de leeuwen vertoonde een licht herstel in 2011 en 2012, toen leeuwen weer vaker op zebra's en wildebeesten jaagden.

Er was een significant verschil in aanvallen op vee door carnivoren voor/tijdens en na de droogte; voor/tijdens de droogte werden 1982 stuks vee gedood door carnivoren, na de droogte 2544 stuks vee. In zijn totaliteit waren 3497 van de gedode dieren schapen en geiten, 742 runderen en 295 ezels.

De resultaten lieten verder een negatieve relatie zien tussen regenval en de frequentie van aanvallen op vee zowel voor/tijdens als na de droogte, waarbij meer vee werd gedood gedurende de regentijd. Ook was er een duidelijk verband tussen de abundantie van prooidieren in het park en de predatie van vee. De predatie op vee nam exponentieel toe na de droogte, toen de aantallen prooidieren laag waren.

Mijn onderzoek toont aan dat de leeuwenpopulatie in Amboseli Nationaal Park een verandering in structuur en dieet vertoonde in reactie op een extreme droogte, maar dat het herstel al in het tweede jaar na de droogte zichtbaar was, met als indicatie een verhoogde reproductie en een licht herstel van het oorspronkelijke dieet. Het leeuw-prooisysteem vertoont daarmee een opvallende veerkracht. De toename in reproductie is opmerkelijk, als we de hoge sterfte van leeuwen na de droogte als gevolg van de jacht door Maasai krijgers (2010-2011) in ogenschouw nemen.

Een mogelijke verklaring hiervoor is dat er door de excessieve sterfte van volwassen mannelijke leeuwen minder wisselingen van troep plaatsvonden en dus minder infanticides. Mijn onderzoek toont daarbij aan dat, indien de bestaande corridors intact blijven die uitwisseling van genen mogelijk maken, het leeuw-prooisysteem in staat is te herstellen van ernstige droogte. Mijn suggestie is dat deze corridors essentieel zijn voor de toekomst van het Amboseli ecosysteem.

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Curriculum vitae

Tuqa Jirmo Huqa was born on 28 March, 1973 in Northern Kenya, Marsabit County and Moyale District Obbu division. He attended Sololo primary school 1980-1987 and Marsabit boys' secondary school between 1988 and 1991.

He was employed as a ranger with Kenya Wildlife Service immediately after secondary education in 1992. He was among the pioneer team that provided wildlife security as Kenya's law enforcement and anti-poaching squad; employed and relied upon by Dr Richard Leakey when elephant poaching was at its peak.

Between 1994 and 1997, he was selected to participate in an on-job training program under a scholarship of WWF at the College of African Wildlife management, Mweka, Tanzania and graduated with first class honors in wildlife management.

He won a scholarship from UNESCO world heritage fund in 2001 and obtained an advanced diploma in Wildlife Management at the College of African wildlife management in Mweka.

Between 2003 and 2006, he attended Moi University and graduated with a Bachelor of Science degree in wildlife management, sponsored by African Wildlife foundation (AWF).

In 2006 he attended a short course on strategy for Nature Conservation in Brazil.

From 2010 to 2012, he achieved a Master of Science degree in Biological Conservation at the University of Nairobi, covering spatial and temporal variation on livestock predation by large carnivores around Amboseli National park.

In 2010, he started a PhD at Leiden University – Institute of Environmental Sciences (CML) – The Netherlands on lion population response to climate variability in the Amboseli ecosystem.

He attended several paramilitary courses on wildlife law enforcement at the KWS field training school Manayani.

He served as senior warden in several national parks and managed areas outside parks and Kenya water catchment such as Mau forest.

Currently he is senior warden for conservation education at the Kenya Wildlife Service.

He is a member of several professional societies, including the African Lion Working Group (ALWG) and World Congress on Protected Areas.