African lion (*Panthera leo*) behavior, monitoring, and survival in human-dominated landscapes

By

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“When spider webs unite, they can tie up a lion.” -Ethiopian Proverb

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ACRONYMS AND ABBREVIATIONS

ACC	African Conservation Centre
AIC	Akaike's Information Criterion
ANP	Amboseli National Park
EGR	Eselenkei Group Ranch, Amboseli ecosystem, Kenya
GPS	Global Positioning System
KWS	Kenya Wildlife Service
IFM	Incidence Function Model
IUCN	International Union for Conservation of Nature and Natural Resources
LG	Lion Guardians
MCP	Minimum Convex Polygon
MGR	Mbirikani Group Ranch, Amboseli ecosystem, Kenya
MPT	Maasailand Preservation Trust
NP	National Park
OGR	Olgulului Group Ranch, Amboseli ecosystem, Kenya
PA	Protected Area
PCF	Predator Compensation Fund
TAWIRI	Tanzania Wildlife Research Institute
VHF	Very High Frequency

GLOSSARY OF MAA AND SWAHILI TERMS

Boma	Thorn bush corrals used to keep livestock overnight
Manyatta	The combination of *bomas* and the surrounding dwellings of the livestock owners and their extended families

INTRODUCTION TO THE DISSERTATION

Across the globe, most carnivore populations have been in decline due to human activities. Sometimes declines are due to direct persecution and in other cases, declines are linked to the secondary effects of human-induced deteriorations of prey populations and habitat. In almost all cases, the trend is that carnivores having been losing ground to humans for centuries (Woodroffe 2000, Treves and Karanth 2003). The human population continues to expand exponentially, particularly in developing countries where biodiversity is at its highest. While boasting some of the world's highest human growth rates, the African continent also supports some of the globe's most impressive mammalian biodiversity (Western 2003), particularly of the order Carnivora (Balmford et al. 2001). Of the Carnivoran families, perhaps none rank higher than the family Felidae in terms of human-wildlife conflict (Frank and Woodroffe 2001, Macdonald and Loveridge 2010). While they are at the forefront of conflict with people, large felids are also gauges of conservation impact and the 'miner's canaries of terrestrial biodiversity' (Macdonald et al. 2010).

With the rapid spread of humans across Africa, many carnivore species are coming into direct conflict with people over increasingly limited resources e.g., prey, habitat, etc. African lions (*Panthera leo*), the largest of the African felids, play a central role in maintaining the ecological structure of terrestrial communities across the broad range of habitats where they are found (Mills et al. 1995, Sinclair 2003). Lions are currently classified as Vulnerable on the Red List of Threatened Species of the World Conservation Unions (IUCN) and in continual decline due to human influence. In the last century, African lions have been extirpated from 80 to 85% of their range (Chardonnet 2002, Bauer et al. 2008, Riggio 2011), and estimates of the number of surviving lions on the continent vary between 29,000 (IUCN 2006) to 32,000 (Riggio et al. 2012), down from an estimated 500,000 in 1950 (Myers 1975). The foremost factor leading to lion-human conflict and subsequent lion decline is retaliatory killing after lion depredation on livestock, with conflict exacerbated by the depletion of natural prey, habitat disturbances and livestock management practices (Nowell and Jackson 1996, Woodroffe and Ginsberg 1998, Hilton-Taylor 2000, Ray et al. 2005a, Linnell et al. 2008).

Even though predation on livestock by large carnivores is an ancient conflict (Guggisberg 1975), we know little about the individual carnivores that routinely prey on livestock. In the early twentieth century, some considered carnivore depredation on domestic livestock to be an aberrant form of behavior, done only by old or injured individuals (Finn 1929). Today, the discussions on the characteristics of livestock-raiding carnivores i.e. ‘problem animals’, is ongoing; Linnell et al. (1999) define a ‘problem animal’ as an individual that kills more livestock per encounter than other individuals. There is increasing evidence on several species, showing that many individual carnivores, especially the large felids, regularly prey on livestock (Stander 1990, Stahl et al. 2001, Woodroffe and Frank 2005, Wang and Macdonald 2006). However, little is known about the characteristics of specific individuals that raid stock, i.e. what makes a particular individual a ‘problem animal’ (Linnell et al. 1999).

We do know that livestock depredation can occur in patterns, yet these patterns vary across the globe. Many studies have found livestock depredation to be highly seasonal; Butler (2001) found that in agro-pastoral communities of Zimbabwe, more attacks occurred on livestock in the dry season, while Saberwal et al. (1994) found Asiatic lion (*Panthera leo persica*) attacks on livestock increased during rainy season. Whether wet or dry, seasonal increases of depredation seem to be associated with regional relationships between rain-fall and wild prey availability (Kolowski and Holekamp 2006). Hussain's (2000) studies showed that snow leopards in northern Pakistan kill livestock most frequently in winter months when wild prey is scarce. In both Kenya and Tanzania, carnivore depredation on livestock is highly correlated with seasonal variation in local prey availability (Rudnai 1979, Patterson et al. 2004, Ikanda 2005, Woodroffe and Frank 2005).

In the Himalayas, changing ratios of wild and domestic ungulates resulted in high levels of livestock depredation; when livestock exceeded the number of wild ungulates within protected areas, snow leopard and wolf depredation rates rose (Mishra 1997). Low levels of wild prey have been linked to increases in depredation on livestock by wolves (*Canis lupus*) in southern Europe (Meriggi and Lovari 1996) and in North America (Mech et al. 1988) and by lions in northern Kenya (Woodroffe and Frank 2005). Conversely, on Mbirikani Ranch in Kenya, where the number of livestock is two and half times more than the recommended commercial stocking rate (Ntiati 2002), Maclennan et al. (2009) found that carnivore attacks on livestock were not correlated to the density of livestock, the ratio of wild herbivores to domestic stock, or the actual wild prey density of the study region. Similarly, wolf predation on livestock in Wisconsin, North America (Treves et al. 2004) and Eurasian lynx (*Lynx lynx*) depredation in western Europe (Stahl et al. 2001) still occurs when wild prey populations are high. The high rates of livestock depredation even in areas with adequate wild prey populations have been attributed to the existence of problem animals.

Although retaliatory killing of African lions in response to livestock depredation is a leading cause of their continent-wide decline (Bauer 2008), few studies have examined the characteristics of lions that regularly prey on livestock. In Namibia, Stander (1990) examined 22 cases of stock-raiding by lions that originated from a national park and found while some lions became habitual stock killers, others rarely, if ever, killed livestock. Stander (1990) also found the habitual problem lions were nearly always males of varying ages. Similarly, in Kenya, Woodroffe and Frank (2005) proposed that heightened stock-raiding in one area was due to inefficient husbandry measures. They further speculated that livestock raiding could be reduced by careful livestock management and selective removal of problem individuals.

Stander (1990) attributed high levels of human-lion conflict to the movement of lions out of protected areas in search of migrating prey in Namibia, while studies in other areas ascribe increased conflict to the rapidly growing rural populations living adjacent to protected areas or moving into wilderness areas (Pitkin 1995, Stander 1997, Nagendra et al. 2010). Both factors are no doubt important as there are few protected areas in Africa large enough to support viable lion populations (Brashares et al. 2001, Loveridge et al. 2001).

Over half of Africa’s surviving lions are found in East Africa, primarily in Tanzania, due to the country’s vast protected areas (Mésochina et al. 2010); 40% of its total land cover is designated as protected areas. Tanzania also has a robust trophy hunting industry that places high value on lions (Packer et al. 2009, Packer et al. 2010). In contrast, Kenya’s protected areas only cover 8% of the country’s total land mass (Mwangi 1995, Sindiga 1995, Bauer and Van Der Merwe 2004, Okello and Kiringe 2004); Kenya has only one large contiguous protected area, consisting of Tsavo East and Tsavo West National Parks, while the majority of its protected areas are small (averaging 830km^2), and lack buffer zones (Okello and Kiringe 2004). Ninety-five percent of Kenya’s rangelands are not protected (Norton-Griffiths 2000); the lack of photographic tourism and trophy hunting deprive wildlife of any significant economic value to the people inhabiting these areas. The East African lion populations are increasingly unique, as they are free-ranging, with few fences inhibiting their movements, in contrast to the robust, yet largely fenced populations of southern Africa (Van Dyk and Slotow 2003). Nowell and Jackson (1996) estimated that less than 10% of all free-ranging felids' ranges are included within the boundaries of protected areas, and over a decade later, Crooks et al. (2011) estimated that barely 5% of all carnivores' ranges are within protected areas.

While biologists have learned a great deal about the behavior, ecology and genetics of large felids, most studies have been done in protected areas with little to no human disturbance. Lions especially have been well-studied in protected areas; the longest continuous study is in northern Tanzania's Serengeti National Park and neighboring Ngorongoro Conservation Area starting in 1966 and continues today (Schaller 1972, Packer 1986, Packer et al. 1988, Hanby et al. 1995, Packer 2000). Other well-studied populations include South Africa's Kruger National Park (Smuts 1978, Mills et al. 1995, Funston et al. 2001), Zimbabwe's Hwange National Park (Loveridge et al. 2007, Davidson et al. 2011), and Botswana's Mkagadigadi Pans National Park (Hemson 2003). Very few studies in Africa have focused on carnivores in regions impacted by humans (see: spotted hyenas (*Crocuta crocuta*, Pangle and Holekamp 2010, Yirga et al. 2012) and lions (Woodroffe and Frank 2005, Frank 2011)).

Recent studies in the Americas and Europe have begun to focus more on carnivore populations in human-dominated landscapes such as pumas (*Puma concolor*) and jaguars (*Panthera onca*) (Michalski et al. 2006, Palmeira et al. 2008), wolves (Mech and Boitani 2003, Treves et al. 2004), lynx (Stahl et al. 2001), and bears (Ursus americanus, Beckmann and Berger

2003, Ursus arctos, Smith et al. 2005, Ursus maritimus, Dyck 2006, Ordiz et al. 2012). However, many of these studies concentrated on the levels and patterns of conflict between the carnivore populations and livestock-producers, with little attention paid to individual behaviors of the persecuted or impacted carnivores.

Nearly a decade ago, many authors recognized that to effectively conserve species impacted by anthropogenic threats, animal behavior would need to be incorporated into conservation biology (Caro and Durant 1995, Curio 1996, Ulfstrand 1996, Strier 1997, Caro 1998, Sutherland 1998, Caro 1999, Shumway 1999, Reed 2002, Festa-Bianchet and Apollonio 2003, Blumstein and Fernandez-Juricic 2004, Linklater 2004), yet few studies have integrated the two fields (Angeloni et al. 2008). In recent years, the continued divide between conservation biologists and animal behaviorists has constrained the use of behavioral data by conservation groups (Blumstein and Fernandez-Juricic 2004). However, an animal’s behavior is influenced by its current state and conditions, which are themselves influenced by its surrounding environment. Thus behaviors affected by anthropogenic threats are of particular interest to conservation. Additionally, behavior also influences demographic processes that determine population persistence (Angeloni et al. 2010, Tuomainen and Candolin 2011). Ethologists focusing on conservation may provide insights by elucidating the behaviors that affect vulnerability to human impacts (Blumstein and Fernandez-Juricic 2004). Conservation goals would be advanced if ethologists studied animals that occur in human-altered environments as well as species that are charismatic vertebrates, flagship species, and species of conservation concern (Caro 1998, 1999, Caro and O'Doherty 1999, Shumway 1999, Linklater 2004, Caro 2007), such as African lions.

With the exception of studies in the low human-density Laikipia region of Kenya (Woodroffe and Frank 2005, Frank 2011), African lions living in human-dominated landscapes and with constant anthropogenic threats have been virtually ignored. A few studies have explored human impacts on lion populations that originate in protected areas and move into proximity to human settlements or are affected by trophy hunting on the borders of the protected areas (Yamazaki 1996, Loveridge et al. 2007, Packer et al. 2009, Packer et al. 2010). The landscape of fear theory (Brown et al. 1999) predicts that hunted predators would respond to humans as prey respond to predators, by increased vigilance or avoidance behaviors. Valeix et al. (2012a) applied this ecological theory of animal behavior to a population of lions dwelling primarily within a protected area. Although protected areas are necessary for long-term persistence (Woodroffe and Ginsberg 1998), most of the lands required for carnivore survival are outside protected areas, in lands that are affected by human populations (Nowell and Jackson 1996, Crooks et al. 2011). By applying behavioral ecology to lion conservation, we can better understand lions' behavioral adaptations to human threats and influences so as to more effectively conserve them.

For conservation consideration, a primary consequence of the rapid growth of human populations is a general ecological deterioration of the lands that support them (Soule and Orians 2001). These human-altered landscapes often surround protected areas and, in the ecological literature, are referred to as the matrix: areas that are no longer suitable for long-term maintenance of wildlife populations (Vandermeer and Carvajal 2001). However, some consider many of these areas, although depleted, to have the potential to support wildlife, albeit at lower densities than found in protected areas (Jules and Shahani 2003, Gehrt et al. 2010). Furthermore, they may be essential to maintaining the viability and connectivity of larger protected populations. Human-altered landscapes may therefore be important components of effective conservation strategies (Soule and Orians 2001), but further understanding of their role in larger ecological process is critical to achieving conservation success.

Data on home range size, movements, and demography of large carnivores living in close proximity and in conflict with humans may help develop strategies for coexistence (Olson et al. 2002, Angeloni et al. 2008). Africa, where large carnivores still exist amongst burgeoning human populations, presents an opportunity for the study of carnivore adaptations to human-altered landscapes and possible avenues of coexistence.

In this dissertation, I present the first long-term study of a lion population living on non-protected human-dominated lands and that is often in direct conflict with humans. I explore basic behavioral and ecological characteristics of the lion population, particularly in relation to human settlements and stock-raiding behaviors, and examine the effectiveness of employing local lion killers in lion monitoring. I then examine the metapopulation of lions in Kenya and Tanzania and incorporate specific life-history traits to consider the implications for regional lion conservation.

Study System

Due to the broad expanses of semi-arid climate, livestock production is the only viable economic pursuit across much of East Africa (Galaty and Johnson 1991). For millennia, the practices of pastoralists have been compatible with diverse wildlife communities (Anderson and Grove 1989, Marshall 1990), resulting in expanses of non-protected land that supported abundant wildlife populations as well as large numbers of people. These areas have been identified as globally important to conservation, even though they are under no formal protection (Niamir-Fuller et al. 2012).

Of the pastoral tribes of East Africa, Maasai are the most prominent and powerful (Spear and Waller 1993), inhabiting the vast rangelands of southern Kenya and northern Tanzania. Maasai have long been viewed as “people of cattle” whose lives depend on sweeping stretches of pasture and perennial access to water for long-term survival. Maasai generally only kill wildlife to protect their livestock, for traditional reasons (Berger 1993, Smith 1997), in political protest for lost grazing land or as a way to oppose conservation policy (Lindsay 1987, Standring 2004). Yet a major challenge facing Maasai herdsmen today is livestock depredation by carnivores.

Poor husbandry, such as leaving livestock unattended in open pasture, or not corralling at night, poses a significant problem as it leads to increased predation by carnivores, (Conforti and Cesar Cascelli de Azevedo 2003). Properly implemented husbandry techniques have the dual effect of reducing livestock killed by carnivores and, in the long term, preventing the development of stock-raiding individuals (Linnell et al. 1999, Ogada et al. 2003, Woodroffe and Frank 2005). When stock raiding does occur, carnivores are usually killed or, in rare cases, translocated (Stander 1990, Woodroffe and Frank 2005). Based on the hypothesis that bad-behaving individuals are responsible for a disproportionate amount of livestock predation, effective conservation and problem animal control requires understanding the circumstances that lead to stock-raiding and the characteristics of individuals that become chronic problem animals in order to develop effective, targeted mitigation approaches.

The Amboseli ecosystem is recognized worldwide as a landscape where people with strong ethnic traditions, livestock and wildlife have co-existed for millennia, in spite of frequent human-wildlife conflict (Marshall 1990, BurnSilver et al. 2008). The region is in the heart of Maasailand, a 93,000 km^2 area that straddles the border between Kenya and Tanzania and has a human population that is predominately of Maasai ethnicity (Homewood et al. 2009). In the early 1990’s, in response to government restrictions and withholding of promised funds, the local Maasai communities decimated the lion population of Amboseli National Park, leaving only two lions in the entire 390 km^2 reserve (Chardonnet 2002). The Park population recovered due to immigration from surrounding communally owned lands, but since 2001, at least 207 lions are known to have been killed by people in the broader Amboseli ecosystem (Hazzah et al. *in review*). In other areas of Maasailand, lion numbers are declining at a rapid rate due to ongoing conflict with Maasai communities (Ikanda and Packer 2008).

The Amboseli-Tsavo ecosystem provides an important corridor connecting Kenya’s largest remaining lion population, associated with the Tsavo National Park complex, with the lion populations of Tanzania. The ecosystem comprises the 5,975 km^2 region between Amboseli, Tsavo West and Chyulu Hills National Parks in Kenya and Kilimanjaro National Park in northern Tanzania. The area outside the parks is divided into group ranches, land communally owned by Maasai pastoralists. The group ranch system was established in the late 1960’s to both protect pastoral rangelands from encroachment by other tribes and to constrain Maasai movements (Graham 1989, Galaty 1992, Fratkin et al. 1994). The group ranches are in arid to semi-arid zones and experience erratic unevenly distributed rainfall, ranging from 200 mm to 553mm a year (Altmann et al. 2002, Moss et al. 2004-2012). The short rains fall in November and December, the long rains from March to May (Ntiati 2002). Droughts are frequent and have been recorded in this ecosystem at least once a decade since 1930 (Campbell 1999); multi-year droughts cause drastic increases in livestock mortality and reductions in reproduction (Ellis and Swift 1988). The drought of 2008-2009, the worst in recorded history (ACC 2009, Zwaagstra et al. 2010), yielded only 190mm of rain in Amboseli in 2008, followed by only 140 mm of rain in 2009 (Altmann & Albers unpublished data; Moss et al. 2004-2012).

The ecosystem is a mosaic of habitats comprised primarily of *Acacia tortilis* woodland, mixed *Acacia mellifera* and *Commiphora rostrata* bush-lands (Kioko 2005, Worden 2007, Groom and Harris 2010). Mt Kilimanjaro, 5,898m high, and the Chyulu Hills Range, 2,300 m high, have a dominant influence on the climate and water distribution in the Amboseli ecosystem (Smith 1997, Altmann et al. 2002, Kioko 2005). A diversity of habitats are found in proximity to the higher elevations: open grass savannahs (dominant species include: *Pennisetum mezianum, Chrysopogon aucheri, Sporobolus pellucidus,* and *Digitaria milanjiana* (Groom 2007)) sloping up to the volcanic mist forests of the Chyulu Hills and Mt. Kilimanjaro, and the salt pan and lush swamps of the Amboseli basin resulting from the snow and glacial melt of Mt Kilimanjaro (Omenge and Okello 1992). Only two perennial rivers flow in the region, but the swamps of the Amboseli basin provide a permanent water source which support an abundance of large mammals and birds for which the region is famous (Berger 1993).

While the abundant wildlife provisions a lion population, this ecosystem also has one of the highest recorded rates of human-induced lion mortality in East Africa (Hazzah et al. 2009, Maclennan et al. 2009). For this reason, I chose this as an ideal area to carry out an in-depth examination of a lion population that inhabits human- and livestock- dominated landscapes and is affected by human persecution. The aims of this dissertation were four-fold: (1) to examine the basic demography and spatial characteristics of the lion population; (2) to evaluate the effectiveness of incorporating previous lion killers into the broad-scale monitoring of a low-density secretive lion population through a participatory monitoring approach; (3) to investigate the influences of human settlements on lions; and lastly (4) to examine lion populations on the broader regional scale, across Kenya and Tanzania, using a metapopulation framework and empirical knowledge of lion life-history traits.

Introduction to the Chapters

Chapter I, "Demography of a persecuted African lion population," investigates the basic demographic characteristics of a lion population on human and livestock dominated lands where unregulated, retaliatory hunting of both sexes and all ages has occurred for centuries. I also examine the individual characteristics of stock-raiding lions.

In Chapter II, "Participatory monitoring of an elusive carnivore on community lands," I test the inclusion of local communities in wildlife monitoring and conservation, i.e. participatory monitoring, as a method for collecting data on large carnivores in human dominated landscapes. Standard wildlife biology methods that are effective in protected areas with large populations of 'tame' lions may be of limited use where carnivores are persecuted, often occur at low densities, and are elusive and nocturnal.

In Chapter III, "Lion occupancy of pastoral communities in Maasailand, Kenya," I apply a novel approach of multi-strata occupancy models on two spatial scales to test theories of large carnivore and human interactions, to understand the factors that determine whether or not lions use Maasai settlements and to elucidate factors which may inform management strategies to reduce lion incursions into pastoral settlement. Since persecuted carnivores are notoriously difficult to detect reliably, particularly when in proximity to human settlement, I also examine two detection methods to compare associated detection probabilities. I consider two site covariates, distance to protected area and density of homesteads, to predict lion occupancy of Maasai settlement.

Due to anthropogenic pressures, lion populations are increasingly limited to fragmented populations, primarily associated with protected areas. In Chapter IV “A metapopulation analysis of African lion populations across Kenya and Tanzania,” I use a spatially explicit metapopulation model to investigate how sex-biased dispersal abilities of lions affect patch occupancy across Kenya and Tanzania. I also examine whether human densities surrounding the remaining lion populations affect the metapopulation as a whole.

These four chapters each contribute to a deeper understanding of the lions that prey on livestock, move amongst human homesteads and survive despite centuries of persecution. I investigate the lion’s ability to survive in a landscape of anthropogenic threats and contribute to broader conservation theories and practices for conserving this most iconic of animals.

CHAPTER I: Demography of a persecuted African lion population

INTRODUCTION

Few studies have considered the basic demographic and spatial patterns of African lions (*Panthera leo*) living in human-dominated landscapes where anthropogenic mortality is common (Gehrt et al. 2010). Worldwide, Crooks et al. (2011) found that for all carnivore species, 95% of their total range was outside protected areas, yet other authors (Woodroffe 2000, Gehrt et al. 2010) found only a small number of large carnivore species were able to survive in human-altered landscapes. If large carnivore populations are to persist, we must understand how they adapt for survival in human-altered landscapes (Linnell et al. 1999; Weber & Rabinowitz 1996). In Africa, where the diversity of carnivores is especially impressive and the landscape is rapidly and increasingly altered by humans, we know little about the ecology and behavior of large carnivores that persist outside national parks and other protected areas.

Once common across the continent, African lions have been extirpated from 80 to 85% of their range (Chardonnet 2002, Bauer et al. 2008, Riggio 2011) in the last century. Lions remain widespread in many of Africa's premier protected areas and, as the only felid species found regularly in large social groups (Kleiman and Eisenberg 1973), lions are relatively easy to study within these areas. Recent research has focused on the effects of sport hunting on lion populations originating from protected areas and migrating into the surrounding landscapes where they are hunted (Yamazaki 1996, Whitman et al. 2004, Loveridge et al. 2007, Packer et al. 2009, Funston 2011). Although sport hunting has been found to disrupt social behaviors due to removal of pride males by leading to increased rates of male infanticide and female-biased adult sex ratios and male-biased cub sex ratios (Yamazaki 1996, Becker et al. 2012); Whitman et al.

(2004) demonstrated that mortality of males over the age of six years does not result in population decline.

In this study, I examine basic demographic characteristics and spatial patterns of a lion population on human- and livestock- dominated lands without sport hunting but where retaliatory hunting by local people, of both sexes and all ages of lions, has occurred for centuries. I investigate whether lion demographics differ in this population from populations found in protected areas and those affected by sport hunting.

MATERIALS AND METHODS

Study Area

This study was conducted on 3,684 km^2 of communally-owned range of the greater Amboseli-Tsavo Ecosystem in southern Kenya, a 6,000 km^2 patchwork of non-protected grazing lands surrounding Amboseli, Tsavo West, and Chyulu Hills National Parks as well as Kilimanjaro National Park in northern Tanzania (Fig. 1.1). The unprotected area is divided into group ranches, land collectively grazed by traditional Maasai pastoralists. The landscape is dotted with clusters of Maasai *manyattas* which are the combination of thorn bush corrals or *bomas* used to keep livestock overnight, and the surrounding dwellings of the livestock owners and their extended families (Stanley 1988, Spear and Waller 1993). The clumped distribution pattern of *bomas* results in much of the land being isolated from permanent human settlement (Groom 2007). This research was conducted on Mbirikani (MGR, 1,320 km^2), Eselenkei (EGR, 769 km^2), and Olgulului (OGR, 1,595 km^2) group ranches (Fig. 1.1).

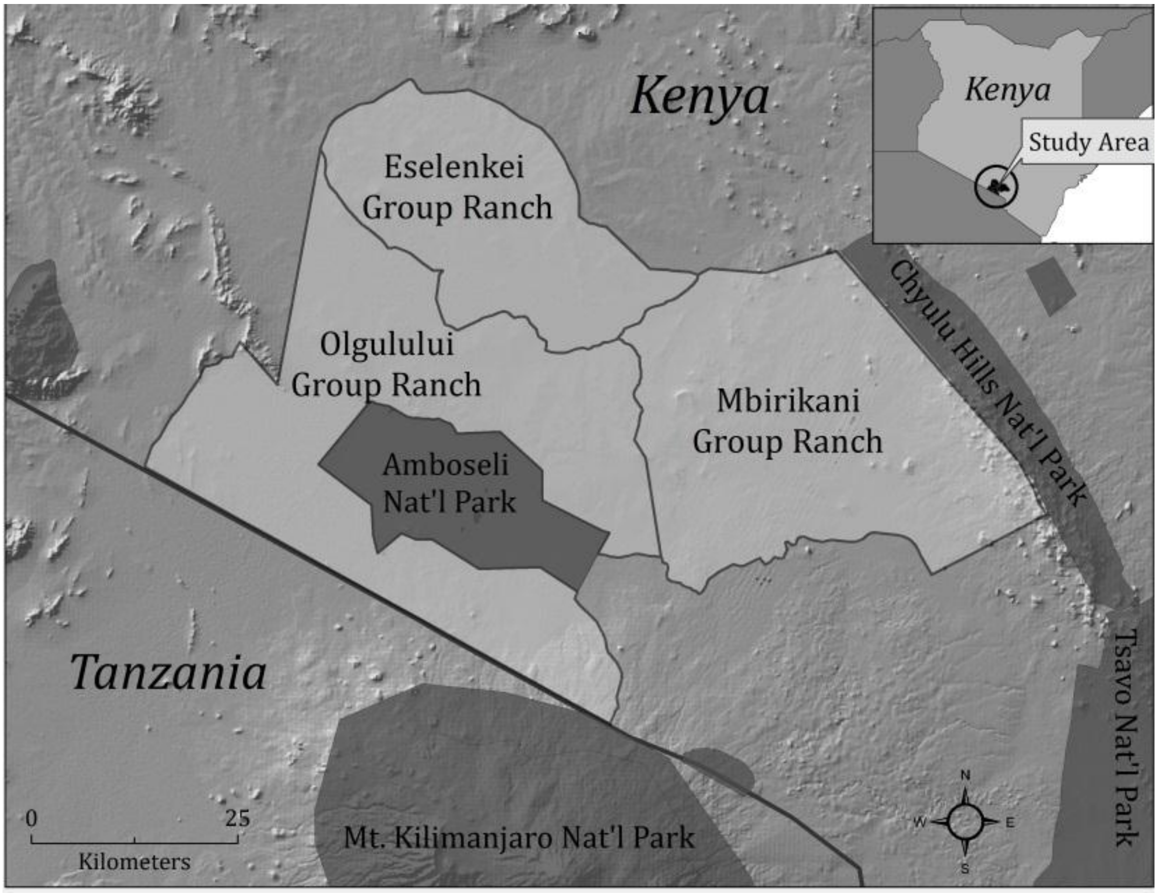

Figure 1.1: Map of study regions, three communally owned group ranches, Mbirikani, Eselenkei, Olgulului in the Amboseli ecosystem, Kenya.

The majority of the region is covered in *Acacia spp.* and *Commiphora spp.* woodlands, interspersed with expanses of open grass savannahs (dominant species include: *Pennisetum mezianum*, *Chrysopogon aucheri*, *Sporobolus pellucidus*, and *Digitaria milanjiana* (Groom 2007)). Mountainous areas border both Chyulu Hills and Tsavo West National Parks and slope up to Mount Kilimanjaro across the Tanzanian border, and there are rocky outcrops north-east of the low-lying Amboseli basin in the south of the study region. Although there are several annual rivers in the region, permanent water is scarce; a water pipeline running through the study region provides perennial water for human settlements and livestock.

The wet seasons are bimodal (March – May and October – November) with the region's annual rainfall varying greatly during the study period, between 200 mm and 558 mm (Altmann et al. 2002, Ntiati 2002, Moss et al. unpublished data). The group ranches support the full range of predator and prey species (Sinclair and Norton-Griffiths 1979, Western 1982) and function as corridors and wildlife dispersal areas connecting the national parks (Muthiani and Wandera 2000, Ntiati 2002). During the wet season, the migration of herbivores from the protected areas to the surrounding ranches nearly doubles prey biomass available to the carnivores living on the group ranches (Groom 2007). During the study period, a severe drought with two years (2008-2009) of exceptionally low rainfall (< 190 mm/year) resulted in serious population declines (> 70% loss) of wildebeest, zebra, buffalo and livestock (ACC 2009).

The group ranches of the study area support a rapidly growing human population of over 30,000 and nearly 150,000 head of livestock (Groom 2007, Kenya National Bureau of Statistics KNBS 2009, Western et al. 2009, KWS and TAWIRI 2010). Frequent conflicts between lions and people result in heavy lion mortality: between 2001 and 2011, over 250 lions died within the study region, of which at least 207 were known to be killed by people, 78% by spearing, the remainder by poisoning (Hazzah et al. *in review*). It is estimated that for every lion killed there were 10 - 50 unsuccessful hunts (L. Hazzah, *unpublished data*).

Lion monitoring began in May of 2004 with the collaring and marking of individual lions (Frank et al. 2003, Maclennan et al. 2009) and until 2007, monitoring was conducted by one biologist on Mbirikani Group Ranch (Maclennan et al. 2009). In 2007 the study expanded into a participatory monitoring program conducted by trained local Maasai warriors, Lion Guardians (LG, Chapter II; Hazzah et al. *in review*). In 2009, the LG program and lion monitoring expanded to two additional group ranches, Eselenkei and Olgulului. All spatial analyses were done using ArcMap 10.0 (ESRI 2011). Spatial layers were obtained at the district level from the Kenya Department of Resource Surveys and Remote Sensing except the protected area layer which was clipped from the World Conservation Monitoring Center's Africa protected areas database.

Detailed information on lion movements was obtained from VHF (Telonics, Arizona, U.S.A.) and GPS (VECTRONIC Aerospace GmbH, Berlin, Germany) radio-collars, as well as re-sightings of known individuals based on vibrissae patterns and other unique characteristics (Pennycuick and Rudnai 1970). The collared animals were tracked on a weekly basis. Reports and signals of lions from the Guardians were also followed up on a weekly basis to obtain sightings of collared and uncollared lions (Chapter II). However, due to the rough terrain and secretive nature of these lions, sightings were often difficult to obtain reliably. We were able to approach most lions in vehicles to within 20 - 30 m, but if approached on foot, lions fled when a person was 50 - 100 m away. Thus we usually tracked lions on foot to within 100 m but made the final approach in a vehicle.

Photographic records of identified lions were consulted to determine the identity of uncollared individuals. Each time lions were sighted, data were recorded on identity of each individual, size and age-sex structure of the group. Pride size was expressed as the number of adult and sub-adult females observed together within 200m (Bertram 1973, Whitman et al. 2004). All observed lions for each group ranch and year were compiled into annual counts of animals and used to determine population density. We defined annual estimates of lion density for the study area as the number of known lions normalized by dividing by the total area surveyed. Annual population growth was calculated as the ratio of abundances in successive years, 2004-2102 (Williams et al. 2002). Sex ratios of adults and sub-adults were determined by annual survey of all observed animals. Cub sex ratio was based on males and females in each litter. Due to the close monitoring and small population, litters were usually first seen within one to three months of birth.

To obtain estimates of age and sex-specific survival, I used a staggered entry Kaplan–Meier procedure with log-rank tests to compare survival curves of males and females in three age categories (adult, sub-adult and cub; Pollock et al. 1989). Lions were considered to be any adult at three years of age or breeding. I further separated this class into young adults (breeding or 3 years to 5 years of age), prime adults (5 to 10 years of age) and old adults (>10 years of age). Sub-adults were considered to be any lion between the age of 2 and 3 years, and cubs were all animals less than 2 years of age, separated into large (1 - 2 years old) and small cubs (< 1 year old) (Schaller 1972). Age was determined using birth month if known, or characteristics such as nose coloration, shoulder height, mane growth, cub size in relation to mother shoulder height (Whitman and Packer 2006, Ferreira 2010). I right-censored individuals still alive at the end of the study and within specified age-class. Lions were classified as either originating from Amboseli National Park or from the group ranches based on where they were born or the area of their home range. Dispersal was defined as the permanent movement of an individual out of its natal range, either alone or with age-class cohorts (Bekoff 1989, VanderWaal et al. 2009). Because lion killing is illegal, mortality of known individuals was not always confirmed, but all suspected deaths were thoroughly investigated (Hazzah 2011).

Male and female lion ranges were analyzed separately (Davidson et al. 2011). To calculate one hundred per cent minimum convex polygon (MCP) home ranges (Mohr 1947), fixes from all collars were used; locations of uncollared animals were not included. For additional analysis, I used the 90% kernel density distribution (isopleth) of locations (Silverman 1986, Worton 1989, Hemson et al. 2005, Borger et al. 2006). For kernel density analysis, I used input locations from GPS collars with scheduled hourly fixes from 6 p.m. to 8 a.m. for 14 points per day, approximately 400 points per month for each lion.

Observations of predation were opportunistically recorded by both biologists and Guardians. When a kill was found, details were recorded on species, sex, amount eaten, approximate time killed and number of lions and individuals responsible for kill, if known. Additionally, on two group ranches (Mbirikani and Olgulului), the Predator Compensation Fund (PCF) kept records of claims of livestock depredation by carnivores. PCF compensates local people for livestock killed by predators in return for agreement to refrain from lion killing; the program is described by Maclennan et al. (2009).

The program began on Mbirikani in April 2003, and expanded onto neighboring Olgulului in August 2008. The LG’s and biologists attempted to examine reported PCF claims of lion depredations on livestock. There is no formal compensation program for livestock depredation on Eselenkei yet lion depredations on livestock were commonly reported to LG and biologists by game scouts and community members.

For the purpose of this study, data collection ended in August 2012. I analyzed stock-raiding behavior by ranking the lions in six categories (Table 1.1). A second biologist, with four years of experience on the project, also independently ranked the individual lion stock-raiding behaviors to verify results.

Table 1.1: Questions used to rank lions into livestock-raiding categories based on the nine years of observations and nearly 400 verifications of livestock depredations

Questions	Lion #1	Lion #...	Lion #...	Lion #72
Taken livestock at least once, i.e. only whilst lost?	1	1	1	1
Taken livestock from *boma*?	1	1	0	1
Actively goes to bomas e.g. as a source of food?	1	0	0	0
Actively takes livestock in the bush during daytime?	1	1	0	1
Takes livestock seasonally/during particular spells?	1	1	0	1
Takes livestock on a constant basis?	1	0	0	0
Total	**6**	**4**	**1**	**4**

Categories

6 - 5 High	Chronic	Lion actively takes livestock as a source of food from *boma* or bush, usually year round
4 - 2 Med	Occasional	Lion occasionally takes livestock, sometimes specializing at *boma* or bush, often seasonally or during difficult spells
1 - 0 Low	Well-behaved	Rarely takes livestock. Generally only takes lost livestock if at all

RESULTS

Thirty-one lions were collared between May 2004 and August 2012 (11 females and eight males with VHF collars, seven females and five males with GPS collars). The GPS collars lasted an average of 376 days per collar (range 119 to 716 days). Once collars failed, they were immediately changed in an attempt to allow for continual detection of collared individuals; the average days of continuous monitoring of GPS-collared animals was 547 days (range 206 to 965 days). During the 99 month study period, a total of 117 uncollared lions were photographed, identified and monitored.

The mean density of adults and sub-adults for the nine year period was 1.2 ± SD 0.19 lions/100 km^2. Age distribution was uneven, with low numbers of sub-adults, young adults and very few older adults (<4% of population; Fig. 1.2). In 2009, adults comprised 66%, sub-adults 2% and cubs 32% of the population; in 2012 the population had a more equal composition with adults comprising 38%, sub-adults 17%, and cubs 45% (Fig. 1.2). Annual population growth rates varied considerably. I observed a net positive population growth rate between 2004 and 2011 (Fig 1.3), possibly due to the reduction in lion killing as a result of conservation interventions (Hazzah et al. *in review*).

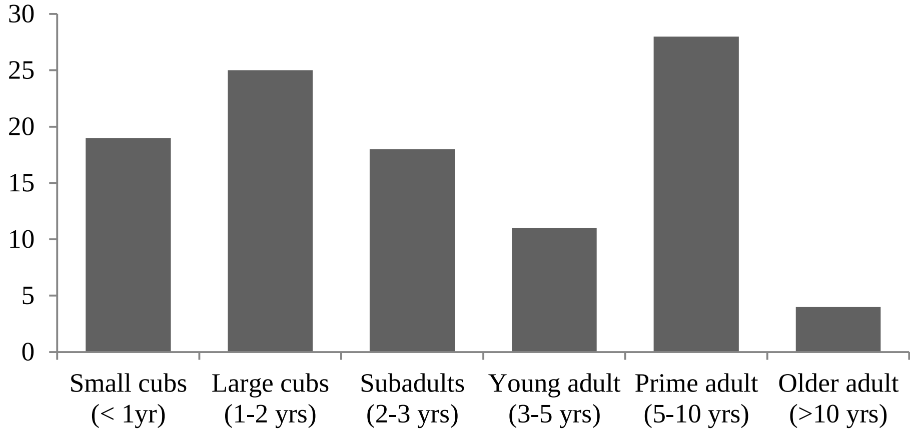

Figure 1.2: Distribution of age classes of the lion population of the group ranches of the Amboseli ecosystem, Kenya; 2011-2012

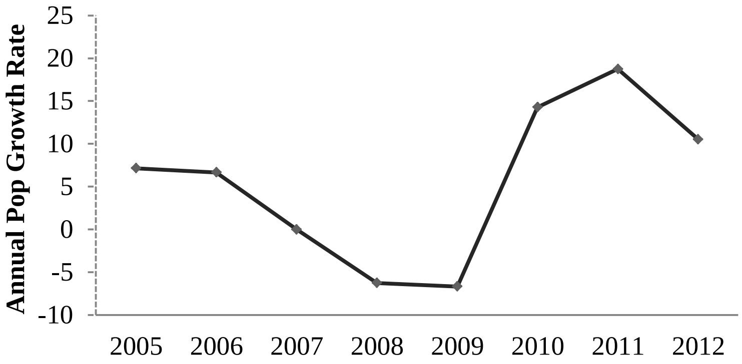

Figure 1.3: Annual growth rates of the lion population residing on Mbirikani group ranch (1,320 sq km) of the Amboseli ecosystem, Kenya, 2004-2012

Adult annual survival (Fig. 1.4) was relatively high for the monitored lions ($\bar{x}$ = 0.89 ± SE 0.02, range 0.61 to 1.00, n = 9). Few lions survived past 10 years of age (Fig. 1.2; three females, one male out of 72); log rank test found no significant difference between male and female survival curves (*p* = 0.081 at alpha value 0.05; Fig.1.4). Annual adult sex ratio ranged between 1:0.93 to 1:2.5 male to female; the nine year mean was 1:0.91.

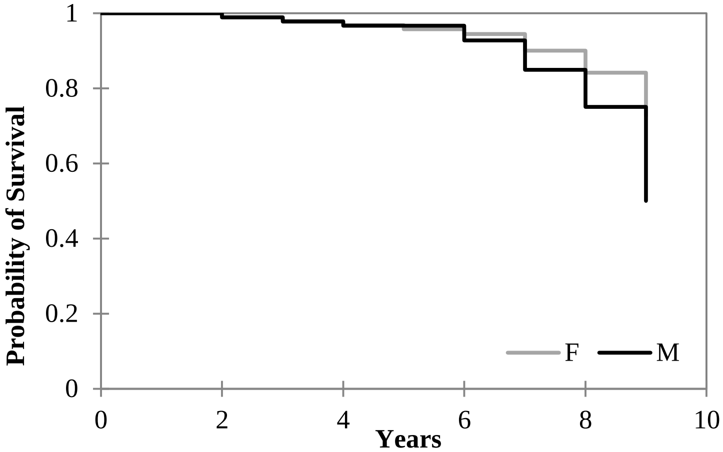

Figure 1.4: Kaplan Meier survival curve for staggered entry of adult lions in the group ranches of the Amboseli-Tsavo ecosystem

Thirty-three male and 26 female sub-adult and older independent cubs (age 1 to 2 years old but separated from mother) were monitored during the study period. Male and female sub-adult annual survival rates were equal (*p* = 0.44, $\bar{x}$ = 0.89 ± SE 0.05, range 0.79 to 1.00, n = 9 years). Ten males immigrated into the study area, while 23 males were born in the area and dispersed out (Table 1.2).

Table 1.2: Demographic data on 33 male and 26 female lions from the group ranches of the Amboseli ecosystem. Data were collected from May 2004 to August 2012

	Mean Age at Dispersal in years (SD)	**% Dispersing**	**Mean age at first mating in years (SD)**	**Mean age at first litter in years (SD)**	**Birth Interval in years (SD)**
Male	2.0 (0.7) range 0.8 to 3.4	100	3.5 (0.7) range 3 to 4.5	-	-
Female	2.3 (0.8) range 1.3 to 3.4	57.7	2.8 (0.4) range 2.5 to 4.3	3.4 (0.6) range 2.9 to 4.5	1.96 (0.7) range 0.6 to 3.3

We observed 52 litters of cubs over the entire study period. The mean number of cubs per litter was 2.56 ± SD 0.68, (range 1 - 4). One hundred and thirty-two cubs were known to have been born during the study period, of which 38 were censored at the end. Of the remaining, 34.04% died in their first year, 17.02% of the remainder died in their second year and 48.84% survived to sub-adulthood. We were able to sex 105 out of the 132 cubs. Mean litter sex ratio was 1:0.64 (n = 9 years), ranging between 1:0.3 and 1:2 male to female. We were able to confidently confirm female and cub status for 29 uncensored litters. Twelve litters were raised by solitary lioness, 92% of these were successful with at least one cub surviving to sub-adulthood, while only 9 of 17 (47.06%) from paired female litters were successful ($\chi^2 = 4.17$, $p = 0.019$).

Mean group size (number of adult and sub-adult females found together) was 1.62 ± SD 0.57 (n = 29 adult females, range = 1 - 4) and mean male coalition 1.12 ± SD 0.58 (n = 20, range 1-3). Thirty-five percent of adult males were never observed in a coalition and 65% were observed in paired coalitions. For Mbirikani, I analyzed observed group size (total, adults, sub-adults and cubs) over nine years (Fig. 1.5). Adult males were seen in the company of adult females on a mean of 21.04% of sightings (n = 20 adult males, range 0 – 69.57%) and adult females were sighted in the company of males on a mean of 7.43% of observations (n = 29 adult females, range 0 – 40.0%).

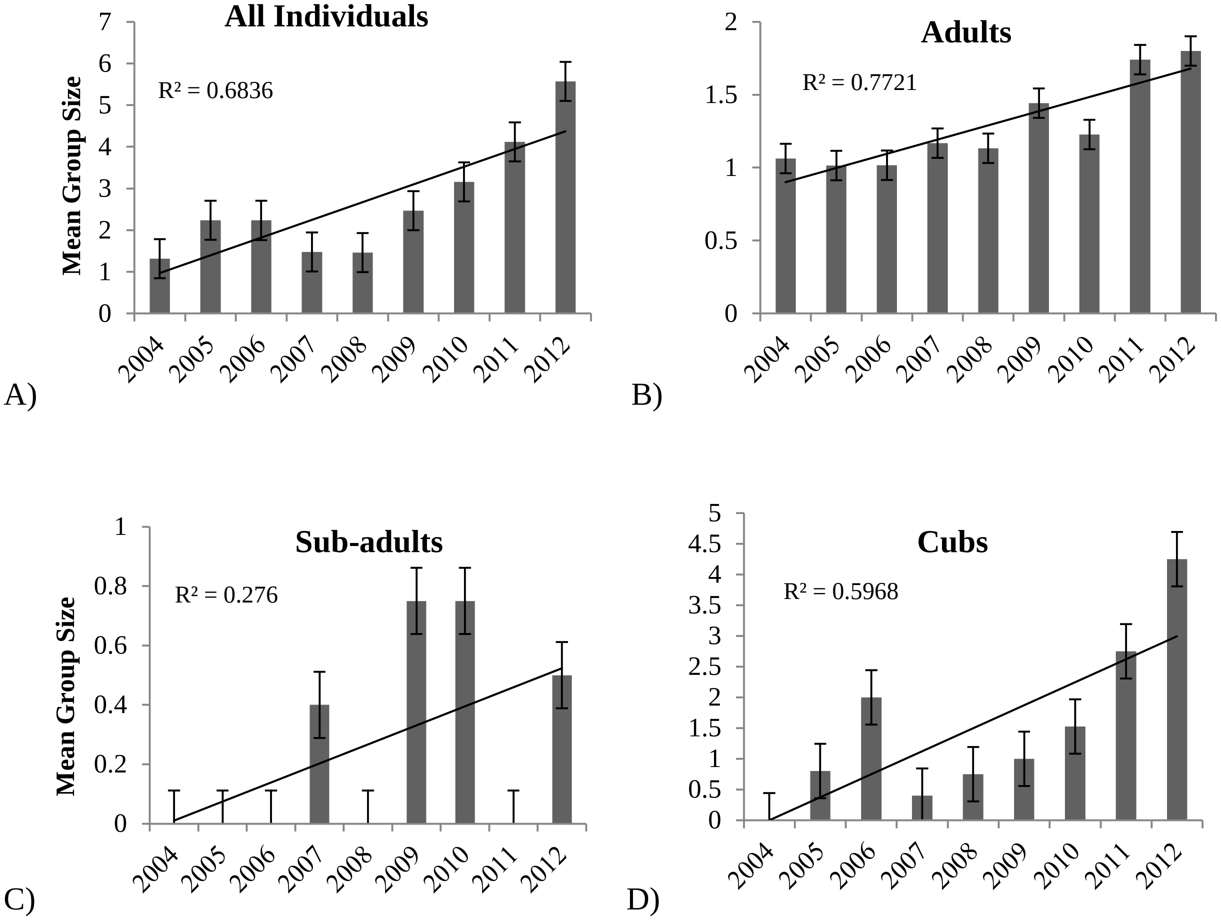

Figure 1.5: Average observed group size with trend lines and standard errors for all individuals together (adults, sub-adults, and cubs) (A) and separate (B-D), seen within 200m of each other from May 2004 through August 2012 on Mbirikani Group Ranch, Amboseli ecosystem, Kenya

Table 1.3: Home range analyses of 12 GPS collared lions, of the group ranches of the Amboseli ecosystem. Data were collected between June 2005 and August 2012. For 100% Minimum Convex Polygon analyses, all fixes (GPS and VHF) were used; for calculation of 90% Kernel Density only GPS fixes were used.

	N	**100% MCP (SD) km^2**	**90% Kernel Density (SD) km^2**
Male	5	2,848 (2,407) Range 640-6,884	774 (389) Range 257-1,346
Female	7	954 (546) Range 323-1,751	375 (237) Range 160-775

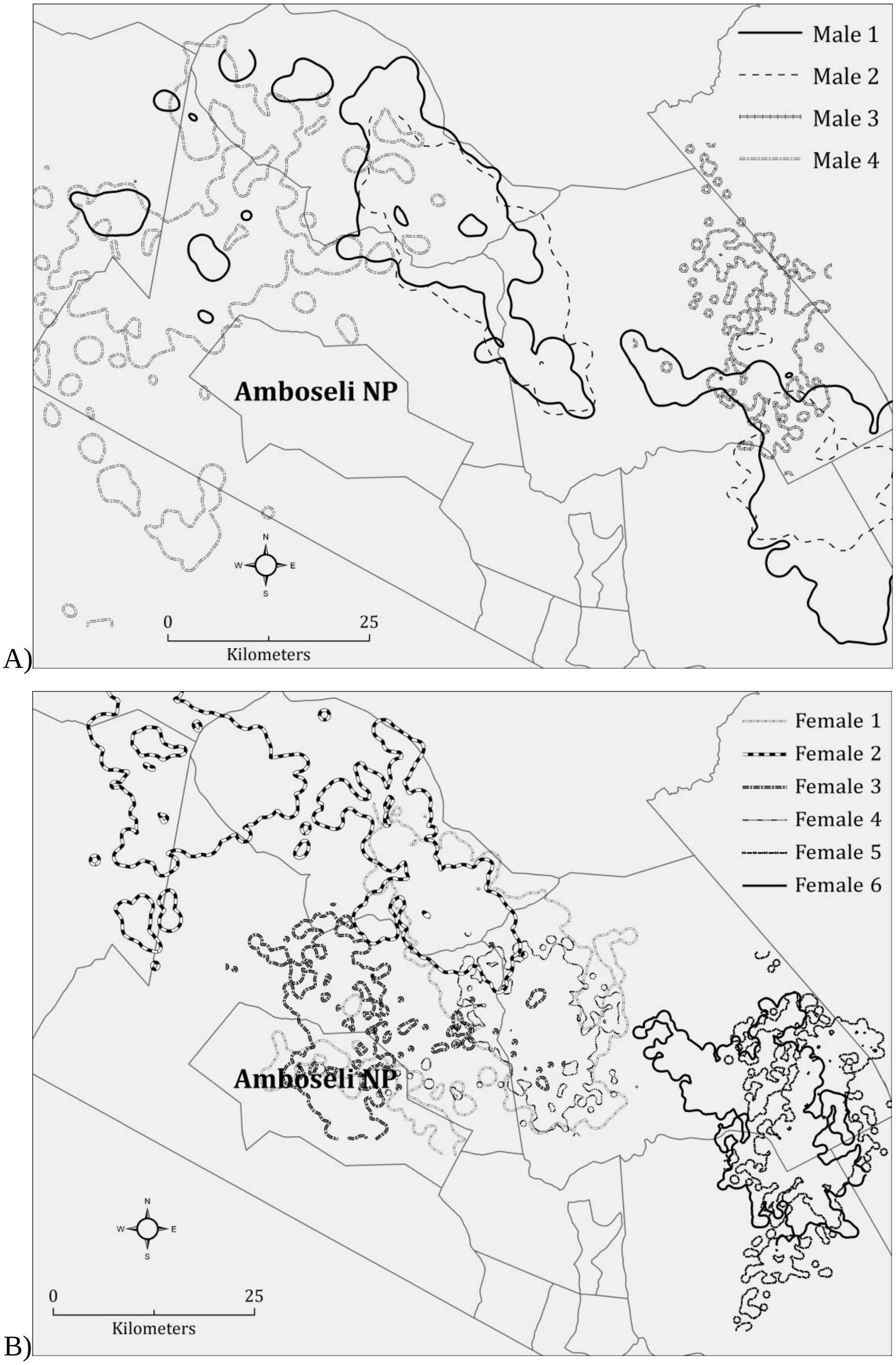

Figure 1.6: Kernel Density (90%) ranges of four GPS collared males (A) and six females (B), on group ranches of Amboseli ecosystem, 2008-2011

Lions known to originate from the group ranches rarely ventured into ANP (Fig. 1.6). Out of 66,136 GPS fixes of the 12 animals, only four animals spent time, ranging from a few hours to several weeks, in ANP. One of these animals belongs to a known Amboseli lion pride (Caceres Calleja 2009) and accounted for the majority of the points in ANP (4.8%). She spent 94.1% of the period in which she was collared in ANP. Of 267 collar days, she went on to group ranches on 31 occasions. These were short trips, usually only during the night hours; on 27 of the 31 trips, she left the Park between 9 p.m. and midnight and returned between 1 a.m. and 7 a.m. She spent a total of 378 hours on the group ranches, out of a total 6,407 collar hours. Two of the other GPS collared animals which visited ANP were a pair of her independent offspring, collared after their dispersal from the natal group. These lionesses returned to the Park on three occasions after they were first detected and collared on the group ranches. Their trips ranged from 35 hours to 11 days, for a total of 18.5 days spent in Park (1.92% of total hours monitored by GPS collar).

Of the five GPS collared males, only one male ventured into the Park, along the western border on eight occasions, but his average time spent in the Park was only 1.75 hours; he spent only 0.21% of the time he was collared (282 days, 6,780 hours) in the Park. Similar to the collared lioness that was a known Park lion, 55 out of 148 monitored lions (37.2%) were known to have originated from the Park and moved onto community lands. On two occasions, sub-adults were documented dispersing from Park prides to the group ranches. One was a temporary residency; a coalition of two young adult males remained on community lands for approximately 18 months before moving out of the study area. The second occasion, a coalition of three sub-adult females established territories and mated with group ranch males and did not return to ANP after mating.

Predation

Despite the presence of wild prey, at densities of 11.36 ± SD 1.61 wild herbivore/km^2 in dry season and 17.73 ± 2.20 wild herbivore/km^2 in wet season (Groom 2007), lion-livestock conflict was high across all study group ranches. Between 2004 and 2011, the Predator Compensation Fund handled 804 claims of alleged lion depredation on livestock on Mbirikani (data from 2004 to 2011; *unpublished*) and on Olgulului (data from 2008 to 2011; *unpublished*). During this period, every monitored adult and sub-adult lion (n = 72) was known to have killed livestock at least once and were thus known stock-raiding animals (Stander 1990, Linnell et al. 1999). There was, however, great variation between the amount and rates of depredation by individuals.

Based on nine years of observations, I divided the lions into three categories of stock raiders (Table 1.1; Stander 1990, Linnell et al. 1999). Some animals rarely took livestock and usually only killed livestock lost in the bush; I referred to these as ‘well-behaved’. The four males and three females that fell into this category were all young adults (4 - 5 years of age), and five out of seven primarily dwelled on Mbirikani group ranch. The second category were ‘occasional’ stock-raiders that took livestock sporadically, often becoming active stock-raiders during particular seasons (wet season) or times of hardship (some females increased depredations while lactating). The majority of the lions fell into this category (n = 51); with an almost even number of males and females (24:27) and a broad range of ages (1 year of age to more than 10 years of age). The last category, ‘chronic’ livestock killers, took livestock year round and very regularly from Maasai *bomas*. Eight males and six females (19% of adult and sub-adult population) were chronic problem animals; all initiated stock-raiding as independent older cubs or sub-adults ($\bar{x}$ = 1.95 years ± SD 0.79, range 0.92 to 3.0). Six of the fourteen chronic problem animals were older cubs orphaned due to their mothers being speared (n = 2), being abandoned due to drought (n = 2), or being forced to disperse when a new male took over group and repeatedly attacked the older cubs (n = 2). Once on their own, they began regularly preying on livestock from Maasai *bomas*.

Of chronic problem animals, six originated from ANP (46.2%) and seven from the group ranches (53.9%) even though the proportion of monitored lions from ANP was less than half (37.2%) of total monitored population ($\chi^2 = 0.16$, $p = 0.69$). The animals that were occasional stock-raiders showed a more equal distribution between animals from ANP and from the group ranches (56.9% originated from group ranches, n = 29, and 37.3% from ANP, n = 19; $\chi^2 = 0.70$, $p = 0.40$), but it was the last category of stock-raiders, the animals that very rarely took livestock where the difference was apparent; the majority of 'well-behaved' lions originated from the group ranches (85.7%, n = 6) while only one lion known to originate from the Park was rarely observed taking livestock (14.3%, n = 1; $\chi^2 = 1.4$, $p = 0.24$).

Lion Guardians and biologists (Chapter II) found 440 kills of 18 wild prey species and documented details of 390 lion attacks on six domesticate species. Diversity of prey species doubled from 11 documented before the drought to 23 after (Table 1.4).

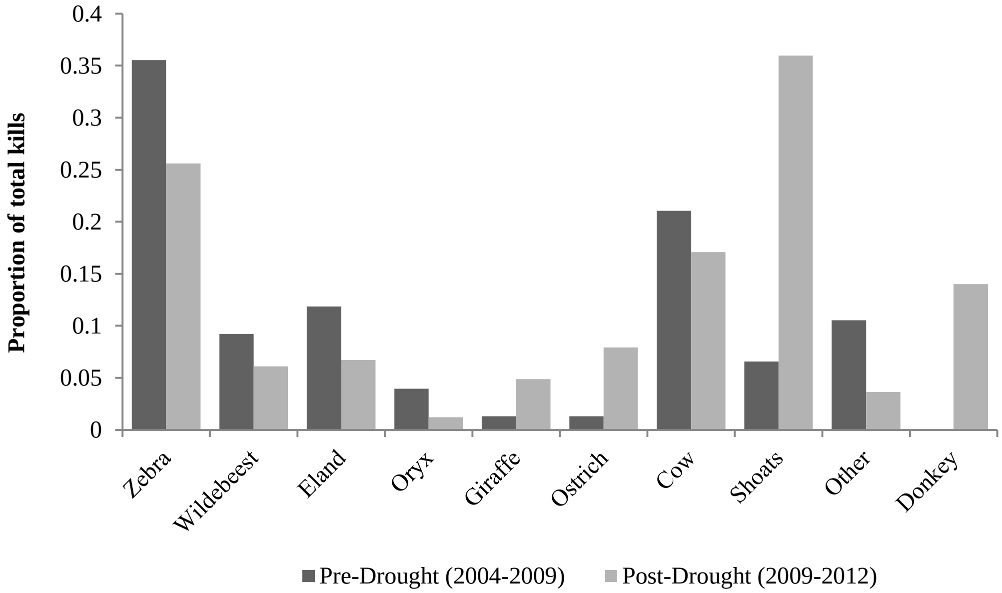

Figure 1.7: Proportional consumption of observed lion prey for two time periods; pre-drought (May 2004 to September 2009) and post-drought (October 2009 to August 2012), on the group ranches of the Amboseli ecosystem, Kenya

Table 1.4: Observed lion prey species for two time periods; pre-drought (May 2004 to September 2009) and post-drought (October 2009 to August 2012) on the group ranches of Amboseli ecosystem

Pre-drought (#/month)	**Post-drought** (#/month)	
Cow (0.24)	Aardvark (0.02)	Hartebeest (0.02)
Donkey (0.46)	Birds (0.02)	Hyena (0.02)
Eland (0.19)	Buffalo (0.02)	Impala (0.02)
Grant's Gazelle (0.02)	Camel (0.02)	Lesser Kudu (0.57)
Giraffe (0.06)	Cow (0.29)	Oryx (0.14)
Goat/Sheep (0.52)	Dog (0.02)	Ostrich (0.77)
Oryx (0.08)	Donkey (1.97)	Porcupine (0.02)
Ostrich (0.03)	Eland (1.26)	Warthog (0.02)
Thompson's Gazelle (0.03)	Grant's Gazelle (0.03)	Waterbuck (0.02)
Wildebeest (0.45)	Gerenuk (0.02)	Wildebeest (1.86)
Zebra (0.79)	Giraffe (1.51)	Zebra (3.51)
	Goat/Sheep (10.34)	

After the 2009 drought, we saw an increase in the number of ostrich and giraffe taken as prey (Fig. 1.7). A total of four giraffe, three of which were juveniles, were killed during the years of 2004 to 2008 while 53 giraffe kills, only eight juveniles, were observed 2009 to 2012. Most notable of these were the multiple observations (n = 37) of lone sub-adult males or one to two lioness taking down adult giraffe. On 25 occasions, we were able to confirm the identity of the lion(s) which killed the giraffe; five chronic livestock-killing problem animals (two young adult females and three young adult males) were involved in nine giraffe kills, nine kills made by well-behaved animals (one adult male, one young adult male, one adult female, and one young adult female), and seven kills made by occasional stock-raiders (all adult females). In one week, a young female, with her first litter of young cubs, managed to take three giraffe, two juveniles and one adult. Another young solitary male killed two adult bull giraffe also within a week's time.

Similar to giraffe kills, pre and post drought observations of ostrich kills were markedly different; two were observed during 2004 to 2008 and 27 post-drought, 2009 to 2012, with 11 ostrich kills occurring during the month of October 2010. Comparable trends were also seen for livestock depredations with a threefold increase from approximately 4.9 attacks per month within the study area pre-drought to 14.5 post drought. Three donkeys were reported killed before the drought while 69 donkeys were killed after; 34 shoats (goat and sheep) before, 362 after drought; cattle remained relatively unchanged with 16 taken before and 10 post-drought (Fig. 1.7). Livestock depredation rates by lions returned to pre-drought rates 12 months after the drought broke (Predator Compensation Fund, *unpublished data*).

During the entire study period, we observed nine occasions of surplus killing of livestock by lions, where lions killed considerably more than they could eat (Kruuk 1972); two occasions occurred pre-drought, three occurred at the height of the drought when the livestock were at their weakest and four occasions occurred a year later when livestock predation rates were beginning to return to pre-drought rates. The incidents consisted mostly of domesticate animals left in the bush at night and lions killing many (up to 21 sheep and goats during one incident) and only eating very little e.g. one goat or part of a sheep.

DISCUSSION

Although abundant in the Amboseli region into at least the 1950’s (Hemingway and Hemingway 1999), lions had declined to low levels by this century (Chardonnet 2002, Bauer and Van Der Merwe 2004). They were temporarily eliminated within ANP by retaliatory killing in the 1990’s, but recolonized the Park from the north-east (Chardonnet 2002); thus the lions of the group ranches may provide an important source population to the adjacent protected areas. They now occur at low densities (1.2 lions/100 km^2) on the communally-owned group ranches of Amboseli-Tsavo ecosystem, while in neighboring Amboseli NP, the estimated density of adult and sub-adult lions increased from 7.9/100 km^2 in the initial survey in 2005 to 9.5/100 km^2 in the most recent estimate in 2009 (van der Werf 2008, Watts and Holekamp 2008, Caceres Calleja 2009).

I observed a net positive population growth rate between 2004 and 2011, possibly due to the reduction in lion killing as a result of conservation interventions (Hazzah et al. *in review*). Age distribution of the study population was skewed with few older adults yet in recent years the population began to show a more equal composition, similar to patterns reported by Schaller (1972) in the Serengeti and Stander (1991) in Etosha NP, Namibia.

In contrast to the female bias seen in other areas, the 1 to 0.91 adult sex ratio of the lion population on these unprotected communal lands is slightly biased in favor of males. By comparison, the sex ratio within Amboseli National Park is 1:1.5-1.7 (Watts and Holekamp

2005, van der Werf 2008), 1:2 in Selous, Serengeti, Kgalagadi, and Kunene regions (Schaller 1972, Packer et al. 1988, Stander 1991, Creel and Creel 1997, ALWG 2003, 2004). Where sport hunting targets males, more extreme bias toward females occurs: 1:6.3 in Hwange NP, Zimbabwe (Loveridge et al. 2007), 1:5.7 in Savuti Game Reserve, Botswana (Cooper 1991), 1:4.3 Luangwa Valley, Zambia (Yamazaki 1996). This result is unexpected because although Maasai lion hunting is largely retaliatory, targeted at a lion that has killed livestock, Hazzah et al. (2011) found that more males than females were killed in this region between 2001 and 2011 (males = 57%, females = 43%, $z = 1.99$, $p = 0.02$, n = 183). During traditional Maasai lion hunts, killing a male lion provides the greatest prestige (Hazzah et al. 2009). Even with this additional mortality, I still observed a male-biased sex ratio at all ages, most pronounced among cubs**.**

For the protected Serengeti population, Packer and Pusey (1987) reported that males disperse from their natal prides at about 4 years of age, and that about one-third of females disperse at 2.76 ± SD 0.24 years of age (VanderWaal et al. 2009). In the persecuted low density population of the Amboseli region, all males and nearly two thirds of females dispersed at a mean ages of 2.0 and 2.3 years respectively.

Early age of dispersal and increased rate of female dispersal may be due to several factors. Low population density and small group sizes due to persecution may create opportunities for sub-adults to move into new areas without encountering territorial residents. Over one-third of males were solitary while the remaining were found in pairs; no larger coalitions were observed. Mate fidelity appeared to be low; 47 of 52 litters (90.39%) were, to our knowledge and observations, from different males. Only two separate females (five litters between them) were observed mating and bearing litters from the same male coalition. In another case, I observed a female mating with five different males and producing two litters in a 26 month period.

Mean female age at first mating, less than 34 months old, is substantially younger than other studies (42-54 months, median = 48 months (Schaller 1972, Packer et al. 1988)). This may be due to early dispersal of females, thus bringing them contact with unrelated males; in the absence of older females, puberty and estrous may begin at earlier ages (Schramm et al. 1994). Average birth interval and litter sizes are in line with other studies (Schaller 1972, Packer and Pusey 1983, Pusey and Packer 1987, Packer et al. 1988, Skinner and Smithers 1990). The broad variation in inter-litter birth intervals may be in part due to a high rate of unobserved mortality of young litters due to the secretive nature of the females and inaccessibility of particular habitats. Although infanticide was only confirmed once during the study period, it may occur more frequently due to the low mate fidelity and wide movements of males among groups of females (Pusey and Packer 1994). Contrary to findings from Serengeti (Packer et al. 1988), solitary females successfully raised litters with regularity. This could be in part due to the low numbers of hyenas and lions found on the group ranches compared to Serengeti and other protected areas.

Given the dearth of pride males, cub mortality was relatively low. Packer et al. (1983, 1988, 2000) documented cub mortality as 100% when fathers were not resident and available to protect their cubs from infanticide. Again, this low mortality could be partially due to the low numbers of hyenas and lions. Although infanticide may not be high on this population, the spearing of females with dependent cubs did lead to cub mortality; on four occasions, females were speared or poisoned and their cubs were orphaned and died.

High turnover of adult males may cause male bias in cub sex-ratio (Schaller 1972, Pusey and Packer 1987, Whitman and Packer 1997). The Trivers-Willard effect (Trivers and Willard 1973) has been well-documented in other species and may function in lions (Ferreira et al. 2012): in a polygynous mating system, females in good physical condition or high social rank may benefit from investing differentially in male offspring, which would be expected to gain more mating opportunities themselves as adults.

The low population density may be a factor in the small group sizes found in this region. Mean female group size was 1.62, compared to means of 4 – 7 (range 3-21) in the ecologically similar Serengeti (Bertram 1973, Pusey and Packer 1987, Hanby et al. 1995, Mosser and Packer 2009), and of 5.17 ± SD 2.48 individuals in adjoining ANP (Caceres Calleja 2009).

Studies of other low density lion populations also show small group size: Makgadikgadi Pans National Park, Botswana, density = 0.74/100 km², female group size = 1.2 (Hemson 2003) and the Kunene region of Namibia, density = 0.28-0.35/100 km², female group size = 1.2 (Desert Lion Conservation 2006). Small groups or singles may be an adaptation to human persecution; on seven occasions, I observed groups of up to ten individuals breaking up into singles or pairs after a Maasai hunting party either attempted or succeeded in spearing a lion. They remained separated for periods ranging from a few days to at least three years.

I found a significant increase in the total number of individuals, number of adults and cubs observed together annually. Increase in total group size in recent years presumably results from an improved production of litters and survival of cubs and sub-adults. These findings support that targeted conservation efforts, which contributed to reduction in the number of lions killed (Hazzah et al. *in review*), are increasing the survival and production of cubs and sub-adults; the lion population is beginning to exhibit social patterns more similar to those found in protected areas. Between 2004 and 2011, I never saw a female with both cubs and sub-adults, but since 2011, I have observed four females producing a second generation of cubs while their previous cubs, now sub-adults, remained with them, forming a more traditional multi-generational pride structure. Throughout the nine year study, males only associated with females when they were in estrus or had killed large prey; otherwise they moved separately. This pattern is similar to that described in the Asiatic lion (*P. leo persica*) populations in the Gir Forest (Chellam and Johnsingh 1993), but atypical for African lions.

Females utilized broad overlapping areas and male ranges usually covered several female ranges. This pattern has been described for other low density populations, which are also associated with large home range size (Van Orsdol et al. 1985, Hemson 2003). The observed lion home ranges from across Africa vary between 22 and 226 km^2 (Van Orsdol et al. 1985). Only the desert lions of Namibia have been reported to inhabit larger home ranges than the Amboseli lions (MCP male average 5,498 ± SD 3,701 and female average 2,343 ± SD 1,383; Stander 2009). The largest range found in this study was from an adult nomadic male.

Lions inside ANP have small ranges (20-97 km^2) centered primarily on permanent water and areas of high prey density (van der Werf 2008, Caceres Calleja 2009). The observed large ranges of the lions residing on the surrounding group ranches may be a result of several factors including low density itself, the lack of water, lower prey densities than found in protected areas, and reduced competition for space and mates (Yamazaki 1996, Valeix et al. 2012b).

Although other studies (van der Werf 2008, Caceres Calleja 2009) have reported that the lions in ANP rarely ventured out to the surrounding group ranches, I found that a significant portion of lions moved from ANP onto the group ranches (37% of all monitored adult and sub-adults), particularly during the wet seasons when prey species migrated out of the park (Groom 2007) or as sub-adults dispersing into areas of lower density. Furthermore, although all animals were known to take livestock, the lions originating from the group ranches were more often ‘well-behaved’. This may be due to these animals having lived with anthropogenic threats and thus being more wary of livestock and human settlements.

In a classic example of social learning (Kitchener 1999), I found that if one adult female was a stock-raider then all her associates were stock-raiders or became stock-raiders soon after companionship was formed. On four occasions (3 males and 1 female), I observed previously ‘well-behaved’ lions becoming active stock-raiders after becoming mates and companions of a chronic stock-raider. A coalition of three adult females frequently took livestock during the rainy seasons when they left the Park and their three female offspring continued as chronic stock-raiders after they dispersed to the group ranches. They took livestock year-round and as they became permanent residents on the group ranches, chronic stock-raiding has now been observed in their offspring. This third generation of females are currently still sub-adults residing with their mothers, yet they often make forays to Maasai *bomas* and raid on their own.

Both sexes are equally likely to be stock raiders in all stock-raiding categories, but Funston et al. (2011) found males to be more likely habitual stock-raiders and thus more likely to be killed in retaliation in the Kgalagadi Transfrontier Park. In the Amboseli population, stock-raiding behavior seems to be more strongly associated with age than sex as young animals orphaned, abandoned, or offspring of chronic stock-raiders, often became the primary ‘problem animals’. Furthermore, I observed that by killing lionesses in response to livestock depredation, humans could actually be creating more problem animals if the female had older cubs.

Although several studies have shown that low wild prey densities may be a strong contributor to high livestock depredation rates (Meriggi and Lovari 1996, Woodroffe and Frank 2005, Kolowski and Holekamp 2006), Maclennan et al. (2009) found that predator attacks on livestock were not correlated to the density of livestock, the ratio of wild herbivores to domestic stock, or the actual wild prey density of the study region.

Due to the low prey populations post-drought, we observed lions dying from starvation. This was the only time during the study period that lions were observed to be in poor health. In reaction, lions diversified their diet from their primary prey (zebra and wildebeest) to other species. Giraffe and ostrich which were rarely taken when food was more abundant became prominent in the post-drought diet and the total number of species taken by lions doubled. Lion dietary adaptation during times of drought has been observed by others (Hirst 1969, Packer et al. 1990, Loveridge et al. 2006). Even single females and sub-adult males took adult giraffe and ostrich on 37 occasions. As Packer et al. (1990) suggested, solitary females were able to secure enough food; other than the brief period after the drought broke, I never observed a solitary female in poor health or losing a kill to other lions or hyenas, almost certainly due to the low densities of both lions and hyenas. Conversely, the same study (Packer et al. 1990) suggested that for lions to successfully hunt large prey, they would need to do so in groups of 5 to 7. As lions in the study region were frequently found alone or only with young offspring, they were clearly able to take large prey after the drought drastically reduced availability of their normal prey (Packer 1986, Hayward and Kerley 2005).

Surplus killing is not uncommon among large carnivores, particularly the *Felidae* family (Kruuk 1972, Fox et al. 1991, Odden et al. 2002, Sangay and Vernes 2008), when a predator encounters large numbers of easily caught prey such as livestock that lack anti-predator behaviors (Linnell et al. 1999), or wild animals in unusual circumstances, such as heavy storms (Kruuk 1972). During this study, the nine incidents of surplus killing by lions involved groups of livestock left out in the bush at night. Linnell et al. (1999) cautions that surplus killing does not necessarily indicate the existence of a problem animal, but on each of these occasions, a chronic stock-raider was involved.

Lions are a robust species, with potential to breed rapidly and recover quickly from overexploitation by humans if conditions improve (Smuts 1978, Funston 2011). The behavioral flexibility documented in this persecuted population allows them to persist under heavy human pressure, and presumably to recover quickly if prey were to remain abundant and human pressures are relaxed. These intrinsic biological traits have been identified as important factors for carnivores persisting close to humans (Cardillo et al. 2004). Understanding how lions adapt to human landscapes and threats is critical to long-term conservation of the largest of Africa's remaining carnivores.

Chapter II: Participatory monitoring of an elusive carnivore on community lands

INTRODUCTION

Conflict with large carnivores is a major concern for pastoralist communities worldwide (Treves and Karanth 2003). The earth's human population has surpassed 7 billion, tripling since 1940, and is expected to reach 10.5 billion between 2040 and 2050 (Worldometers 2010, U.N. Secretariat 2011, U.S. Census Bureau 2012). Due to human population growth and expansion, available habitat, natural prey and water resources are rapidly diminishing, forcing large carnivores to turn to easily accessible livestock (Hoogestein 2000, Inskip and Zimmermann 2009).

Conserving and studying large carnivores is often difficult due to rough terrain and their nocturnal habits and wariness in response to historic or neighboring persecution (Loveridge and Canney 2009, Pangle and Holekamp 2010). Incorporating local people into the monitoring of carnivore populations could contribute to deeper understanding of threatened carnivores, paving the way to the successful conservation of rapidly declining species (Pusey and Packer 1987, Mills and Allendorf 1996, Danielsen et al. 2009).

Western scientists have been conducting ecological and conservation studies in Africa for decades, but local communities have rarely participated in the research other than as rangers or laborers (Trinkel et al. 2008). Although the traditional ecological knowledge of local people is often ignored (Huntington 2000, Trinkel et al. 2008), the need to involve them in wildlife research and conservation has been emphasized by many (Eltringham 1984, Stander 1993, Mech 1995). Furthermore, the conservation of carnivores depends largely on the desires and decisions of the local communities, as they are the ones who bear the costs of carnivores (Treves and Karanth 2003) and could potentially participate in the benefits i.e. tourism profits, employment, etc. Large carnivores are unlikely to persist in close proximity to humans unless local people are interested in and have a role in their conservation (Laarman and Durst 1987, Mech 1995, Stander et al. 1997).

In this paper, I examine how the union of modern wildlife research methods with local peoples' traditional tracking and ecological knowledge can provide reliable data on a persecuted, difficult-to-study, African lion (*Panthera leo*) population. I investigate how participation in monitoring can transform former lion killers into citizen scientists, highlighting the conservation importance and biological implications of involving local communities in carnivore conservation.

Theory and background

Monitoring of biological resources is necessary for the conservation and long-term management of harvested, threatened or rare species (Yoccoz et al. 2001, Holthausen et al. 2005). An essential first step is obtaining an understanding of the current status, fluctuations and trajectories of important populations (Morrison et al. 2008). Wildlife monitoring provides data on the success and efficacy of management and conservation actions and population status of focal species over time (Bailey 1984).

Participatory monitoring is defined as the monitoring of wild flora and/or fauna carried out on a local scale by individuals with little or no formal education; local people are directly involved in data collection (Danielsen et al. 2005). More theoretically, participatory monitoring engages 'average citizens' through direct experiences (Jakubowski 2003). Research has found that participants in experiential and participatory programs have an increased tolerance for other cultures and an increased readiness to assist others (Conrad 1982, Fazey et al. 2006).

Although many developing countries have high concentrations of threatened species and biological hot spots (Danielsen et al. 2007), there are few wide-scale monitoring schemes currently running (Danielsen et al. 2003). This is primarily due to the high cost, and the lack of skilled professionals and available resources (Danielsen et al. 2005). In developed countries, however, there are many examples of participatory monitoring programs that work with educated volunteers, often referred to as 'citizen science' (Butcher 1990, Lepczyk 2005, Galloway et al. 2006, Delaney et al. 2008, Silvertown 2009). The lack of similar programs in developing countries may be due in part to the absence of a culture of volunteerism and low level of wealth (i.e., people cannot afford to volunteer their time when they need to be earning money to feed their family) (Danielsen et al. 2009).

Studies in developing countries have found that investment in monitoring that combines conventional scientific methods with local participation is more effective in producing positive outcomes than a similar level of investment in scientific monitoring alone (Yoccoz et al. 2003, Danielsen et al. 2009). With systematic training and good sampling design, studies such as Stander et al. (1997) examining a variety of species with Ju/'Hoan San trackers in Namibia, and Anadón et al. (2009) surveying tortoises with sheepherders in Spain, have shown that participatory monitoring programs are able to yield reliable results comparable to those of professionals. Others, however, have had varying results, specifically in regards to estimations of fish abundance by local fishermen in the Philippines (Uychiaoco et al. 2005), migratory marine birds (Gilchrist et al. 2005) and pastoralists' knowledge of rangeland indicators in Botswana

(Reed et al. 2008). Few studies have evaluated the accuracy of local-based monitoring of a wide-ranging carnivore across a broad scale (Stander 1998), or increased understanding of other mega-fauna (e.g. tigers, elephants and other key species in Laos; Steinmetz 2000). Here I examine the accuracy of Maasai warriors at monitoring numbers, prey selection and movements of a low density lion population.

Maasai warriors have been tracking and killing lions for centuries (Spear and Waller 1993), and thus it was a natural transition to engage them in the study of lions. Although Maasai do not routinely hunt other wildlife (Spear and Waller 1993, Campbell et al. 2001), young men do hunt and kill lions for a variety of reasons (Ikanda and Packer 2008, Hazzah et al. 2009, Hazzah 2011). The warriors' foremost responsibility is to defend their communities from cattle rustlers and livestock predators, primarily lions (Tignor 1972), and they kill lions that take livestock or come in close proximity to homesteads. By killing lions, warriors demonstrate their strength and courage as well fulfilling their cultural roles as community protectors (Ikanda and Packer 2008, Hazzah et al. 2009, Goldman et al. 2010). In the Amboseli ecosystem, between 2001 and 2011, more than 207 lions were killed by Maasai (Hazzah et al. *in review*), reducing the lion population to low numbers and density. Approximately 24 lions were removed annually, equivalent to roughly 40% of the current lion population being killed each year.

MATERIALS AND METHODS

Study area

This study was conducted on the communally-owned Maasai group ranches of the greater Amboseli -Tsavo Ecosystem in southern Kenya, a 6,000 km² patchwork of protected and unprotected areas. The protected areas include Amboseli, Tsavo West, and Chyulu Hills National Parks as well as Kilimanjaro National Park in northern Tanzania (Fig. 2.1). The unprotected area is divided into group ranches, land communally-owned by the traditional Maasai pastoralists. This research was conducted on an area of 3,684 km^2, comprising Mbirikani (MGR, 1,320 km^2), Eselenkei (EGR, 769 km^2), and Olgulului (OGR, 1,595 km^2) group ranches.

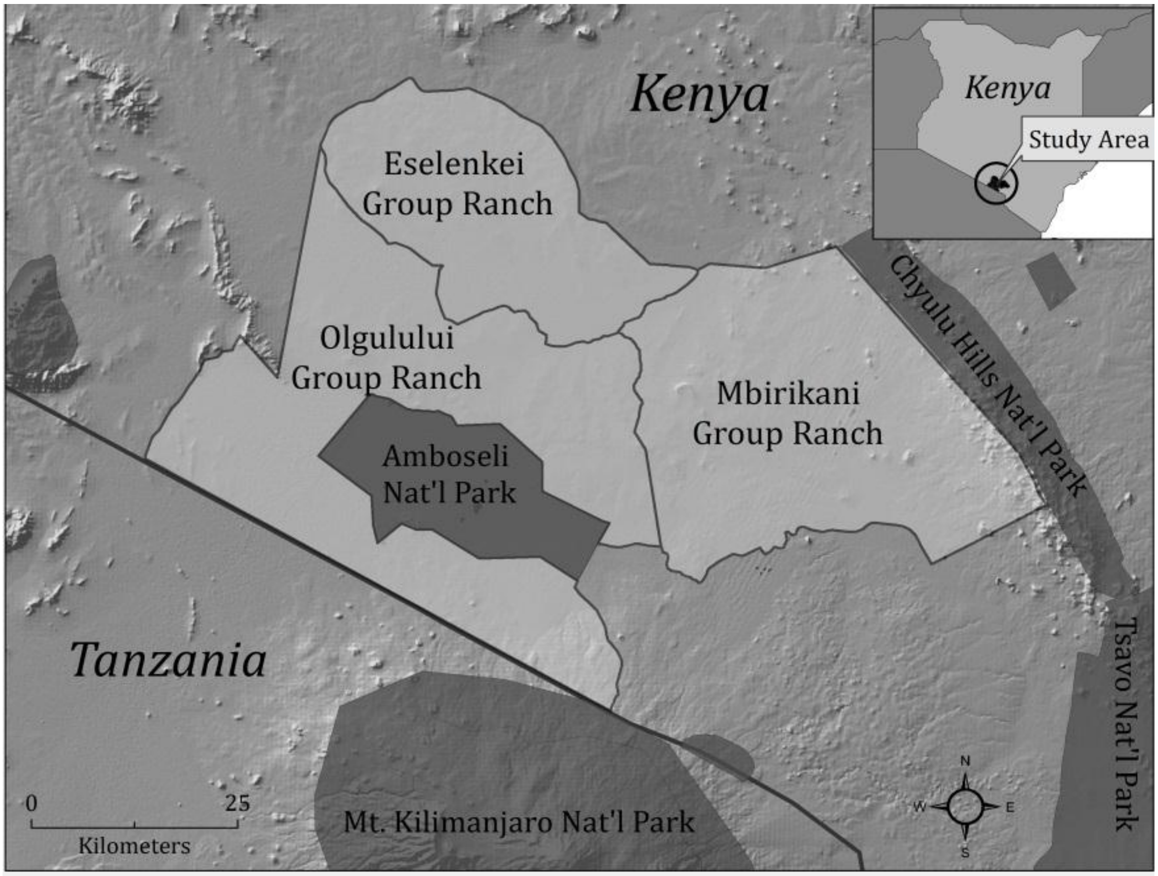

Figure 2.1: Location of study area within the Amboseli-Tsavo ecosystem, Kenya

The group ranches support the full range of predator and prey species (Sinclair and Norton-Griffiths 1979, Western 1982) as well as a rapidly growing human population of approximately 30,000 people and nearly 150,000 head of livestock (Kenya National Bureau of

Statistics KNBS 2009, KWS and TAWIRI 2010). The group ranches function as corridors and wildlife dispersal areas connecting the national parks (Muthiani and Wandera 2000, Ntiati 2002). During the wet season, the migration of herbivores from the protected areas to the surrounding ranches nearly doubles the prey biomass available to the carnivores living on the group ranches (Groom 2007).

The majority of the lions in the ecosystem resides on the group ranches year round and rarely, if ever, enter ANP (Chapter I). A small percentage of lions reside primarily inside ANP, hereafter referred to as Park lions, but routinely visit the surrounding group ranches. They tend to leave ANP for short and sporadic hunting bouts, which become more frequent during the wet seasons and are difficult to monitor (Watts and Holekamp 2005, van der Werf 2008, Caceres Calleja 2009). The result is a highly stochastic situation with great variability in the numbers of lions using the community lands immediately adjacent to the park at any point in time, particularly during wet seasons and severe droughts.

The wet seasons consist of the short rains, primarily November and early December, and the long rains from March through May (Ntiati 2002). The regions' annual rainfall varied greatly during the study period, between 140 mm and 558 mm (Altmann et al. 2002, Moss et al. unpublished). Droughts have been recorded frequently in this ecosystem (Campbell 1999); multi-year droughts cause severe ungulate mortality (Ellis and Swift 1988), as recently demonstrated by the 2008-2009 drought (ACC 2009).

From 2004 to 2007, lion monitoring was conducted by one biologist on Mbirikani Group Ranch (see Maclennan et al. 2009 for more information). In 2007 the study expanded into the Lion Guardians program, which employs traditional Maasai warriors as citizen scientists to collect data across Mbirikani and two additional group ranches, all of which are heavily impacted by humans and livestock.

Lion Guardians

The high level of lion killing spurred a local study of Maasai attitudes toward wildlife and conservation (Hazzah et al. 2009) which suggested that a participatory conservation program employing Maasai warriors might address many of the underlying anti-wildlife attitudes found in this region. The Lion Guardian program was initiated on MGR in January 2007. The majority of Guardians are former lion killers. Guardians live and work in their home communities, wear traditional clothing and carry out the expected duties of a Maasai warrior. The program was founded on Maasai cultural values and the number of LG hired is determined by the density of lions and the degree of livestock depredation in a specific area (see Hazzah et al. *in review* for further details).

The LG program has three primary aims: 1) to minimize lion killing, 2) to assist communities in proactive mitigation of conflict with predators and 3) to monitor demography and movements of the lion population. This study explores the third aim, which involves broad scale participatory monitoring and investigation into previously hard-to-study lion behaviors. At the request of the Maasai communities, the LG program expanded twice in 2009 and once more in 2010. By the end of 2011, 30 Guardians were employed across the three group ranches in the study area. At time of hiring, approximately 95% of the warriors were non-literate. One or two trained biologists, the program’s Maasai coordinators, and more experienced Guardians taught the new employees basic literacy and Kiswahili, in addition to field skills that enable them to collect and report accurate data and conflict mitigation skills that enable them to assist their communities in avoiding livestock losses to predators. Their newly acquired competence also instilled them with prestige and a sense of accomplishment (Stein 1995).

The Guardians were taught conventional scientific methodologies as well as basic wildlife natural history, methods of identifying individual lions (Pennycuick and Rudnai 1970), interpretation of spoor (animal tracks; Appendix A), identification of kills, etc. Beginning in 2007, each time a lion was radio collared or identified using unique characteristics, the Guardians gave it a descriptive Maasai name. After the initial training period, the Guardians were deployed in their home communities and lions were regularly located on foot or by vehicle.

Report Verifications

Each Guardian remained resident in his home community and patrolled a zone of roughly 100 km^2 surrounding it. When he encountered fresh (≤ 24hrs) lion tracks or a radio signal, he reported to the base camp or a biologist by mobile phone. When fresh lion tracks or a kill were reported to a Guardian by a community member, the Guardian verified the report for accuracy before reporting it.

The Guardian reported the number of lions, their age and sex as interpreted from the tracks, as well as the name of the particular lion or lions he believed to be present. Each report was recorded in full and repeated back to the Guardian to ensure accuracy and clarity. A biologist would respond to and verify a random selection of reports, without prior knowledge on the part of the Guardian.

Upon responding, biologist and accompanying trackers all compared and verified the number, age and sex of the lions which left the tracks. If tracks were unclear, a photographic guide was used to assist in accurate identification. Tracks were followed until a positive identification of any lions could be made by obtaining clear sightings and/or the VHF signal of a collared individual. Visual identification was not always possible due to the inaccessible habitats and the secretive nature of these persecuted lions.

Lion Population

Collaring and marking of trapped individuals began in early 2004, (see Frank et al. 2003, Maclennan et al. 2009 for more details on immobilization methods used). All collared animals were tracked weekly, but sightings or fixes within 100m were obtained less often. Before the LG program was initiated, collared lions were routinely tracked from an airplane or by vehicle.

Once a lion was photographed and identified as a unique individual, it was then considered a known animal. Throughout the 2007-11 study period, individual profiles of each identified lion (photographs of unique characteristics) were compiled, and upon each sighting, the profiles were consulted to determine the individual's identity. Sightings were compiled into annual counts of known animals and used to determine 'true' density, defined as the number of known lions normalized by dividing by the area surveyed (in this case, the group ranch) to give an estimate of lion density for that particular area. The counts of known animals were compiled for each group ranch (MGR, EGR, and OGR) within the study area for each year (2009, 2010 and 2011). Frequencies of discovering unknown lions were compared to distinguish changes in proportion of the population recognized before and during the program. Opportunistic prey observations were either observed and recorded by biologists (2004-2006) or reported by Guardians and randomly verified by biologists.

Spoor Surveys

Spoor surveys are an indirect method of sampling large carnivores which is cost-effective, repeatable and applicable to broad areas (Smallwood and Fitzhugh 1995, Stander 1998, Funston et al. 2010). Lion abundance is estimated by measuring ‘spoor density’, defined as the number of different lions tracked per kilometer of road or path examined (Stander 1998). Although density estimates derived from spoor surveys may often be species- and site-specific, they accurately reflect true density of lions (Funston et al. 2010). Previously, spoor surveys in Africa have been conducted from vehicles, but with my focus on participatory monitoring on unprotected, communally-owned land, I explored the use of surveys conducted on foot as a way to estimate lion abundance.

On consecutive days each week, every Guardian conducted a spoor count (Appendix A) along two predetermined transects, totaling 10 to 12 km, originating from the Guardian’s home community. Transect routes generally followed established foot trails or two-track roads with minimal livestock/vehicle traffic, and were selected to cross a variety of habitats and to be as straight as possible, with the requirement that the route not turn back on itself.

Lion Guardians’ zones and their routes were selected to give good spatial coverage and representation of the study area (Fig. 2.2), with the requirement that each Guardian be based in his home community; thus each spoor route was centered in a Maasai community. The number of routes is the basic sample size in the statistical analyses, with each route independent of the others. Routes were planned in order to achieve a high ‘penetration index’, the ratio of km^2 surface area per kilometer of route surveyed; Stander (1998) suggested a ratio of 6.5 to obtain an accurate density estimate.

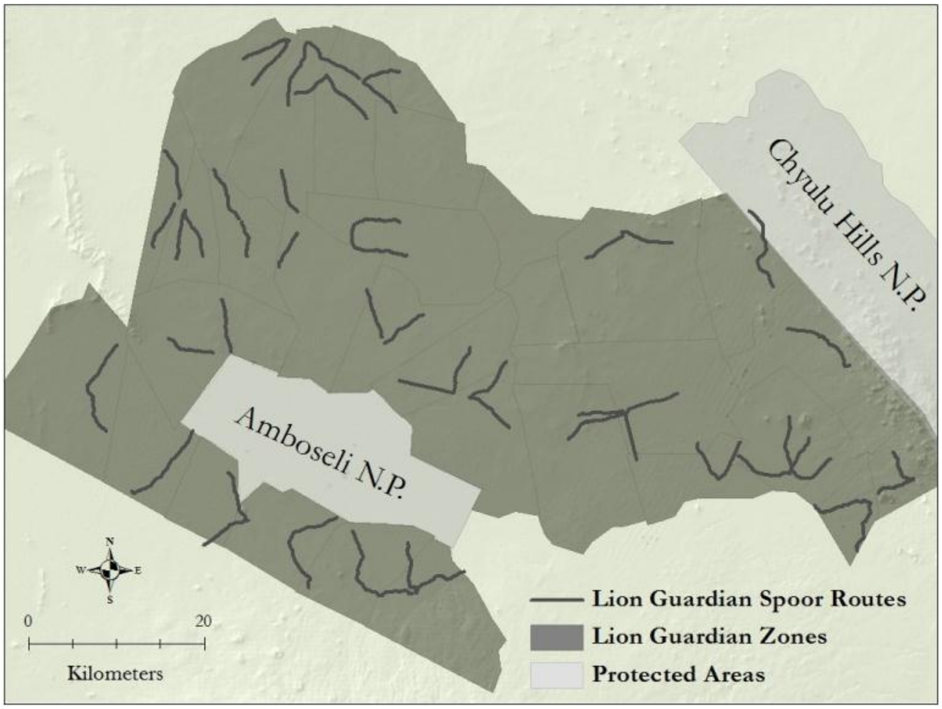

Figure 2.2: Map of LG spoor routes, LG zones, and neighboring protected areas in the Amboseli ecosystem, Kenya; August 2009 – December 2011

As spoor are most visible in early morning hours (Rezendes 1992) and because livestock movements during daylight disrupt tracks, all routes started at or before 7 a.m. and ended around 10 a.m. The spoor of five carnivore species (lion, spotted hyena, leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*)) and the primary lion prey species for this area (plains zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), Maasai giraffe (*Giraffa camelopardalis tippelskirchi*), the common eland (*Taurotragus oryx*), and the lesser kudu (*Ammelaphus imberbis*)) were counted and recorded on simple data forms. Spoor were counted if judged to be less than 24 hours old. To minimize error, the Guardian used a photographic guide to confirm species identity every time a carnivore track was encountered. All ungulate species were also included on the spoor guides for additional reference. If lion spoor were fresh, the Guardians reported them to base camp. I assumed that any bias by each Guardian would be consistently in the same direction and approximately constant from year to year.

Spoor Analysis

For this indirect method, my objectives were (1) to study the correlation of the two measured variables, spoor density and lion density, for a given area and time and (2) to be able to predict lion density given a value for spoor density. The objectives were limited to study of the relationship of lion density and spoor density in unprotected areas not under the influence of saturated lion populations. I treated lion density as the dependent variable and spoor density as the predictor variable in a linear regression model, conditioned on the observed values of spoor density (Fox 1997). I used R 2.14.2 for all statistical analysis (R Development Core 2011).

I calculated lion spoor density (e.g. the number of lion spoor found per kilometer surveyed) for each route each week for 2.5 years (August 2009 through November 2011). For analysis, I used the average for each area and each time period. Areas surveyed were MGR (1,320 km^2) and EGR (769 km^2). Due to the wide variability introduced by its small sample size and the variable short term movements of lions from the high density protected population of ANP onto the surrounding communal lands of OGR, I omitted OGR data from the spoor analysis. MGR and EGR represent two replicates of similar unprotected areas away from the direct influence of the saturated population of lions in ANP. On each replicate, the relationship between lion density and spoor density was the slope of a least squares linear line. That metric allowed us to predict that an increase of 1 mean lion spoor per 100 km surveyed reflected as a lion density increase of *x* number of lions per 100 km^2.

RESULTS

Lion Guardian Reporting Accuracy

A total of 247 reports by 30 Guardians were verified by biologists over the 30 month period May 2009 thru November 2011. The Guardians' reports of lion sign and presence had 93.1% accuracy (Fig. 2.3).

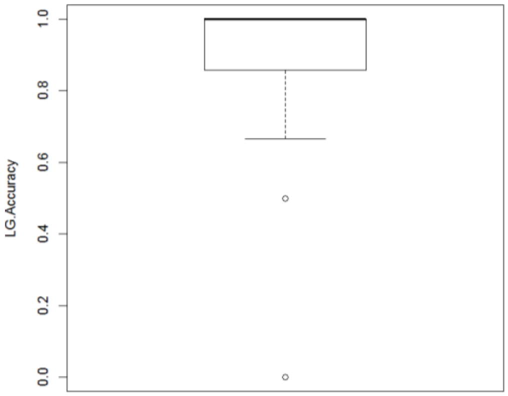

Figure 2.3: Boxplot of Lion Guardian accuracy for three group ranches (Mbirikani, Eselenkei, Olgulului), May 2009-November 2011 (n = 247 reports)

Of the reports where gender could be determined, Guardians accurately reported the gender of the lions 92.8% of the time. Of the reports where the number of lions could be confidently verified, the number of individuals was accurately reported 94.3%. Of the reports where the biologist was able to confirm a lion's identity (44.5% of the verified reports), the Guardians accurately predicted the individual lion's correct identity 90.9% of the time.

The majority of the inaccurate reports (n = 17) were due to: miscounting the number of small cubs (n = 3), mistaking a female with older cubs as a male with two females (n = 2), mistaking a female with a sub-adult male as two males (n = 2), mistaking two sub-adult males as two adult males (n = 2), miscounting the number of males due to unstable volcanic soil (n = 1), and misidentifying the species (n = 2; tracks belonged to male cheetah). The remaining inaccurate reports (n = 5) were due to Guardians relaying reports given to them by community members without first verifying the report themselves.

Improved Data Quantity and Quality

Lion research was initially conducted for three years on MGR by one biologist identifying and monitoring lions through radio telemetry before the LG program was initiated (Maclennan et al. 2009). After three years of intensive work, he had cataloged nine individual known adult and sub-adult lions. He estimated a further three to nine unknown individuals, difficult to identify with certainty, which used MGR group ranch intermittently. Thus, inclusion of these unknown individuals yielded a population estimate of 12 - 18 total individuals. Within 18 months of initiating the LG program, the number of positively identified adult and sub-adult lions had doubled (Fig. 2.4) from nine to 18 within the same area. As there was no change in prey numbers or water distribution, I attribute this not to an actual increase in the lion population, but rather to the ability to obtain firm identification of previously suspected but unverified individuals as a result of the involvement of the Guardians and local communities.

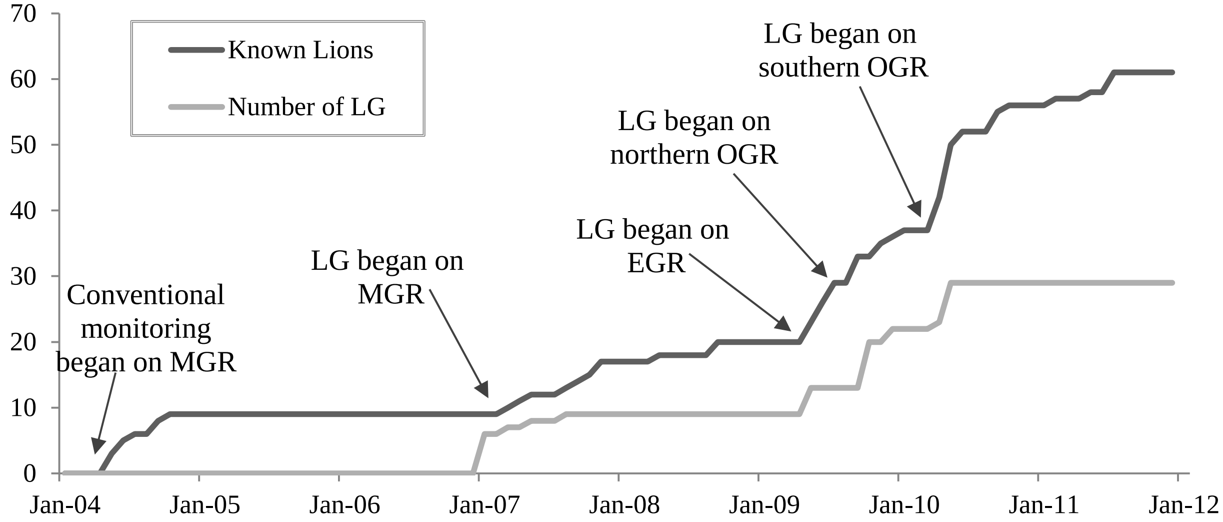

Figure 2.4: Known lions and number of LG over time for three areas, Mbirikani group ranch (MGR), Eselenkei group ranch (EGR) and Olgulului group ranch (OGR), Amboseli-Tsavo ecosystem, Kenya; May 2004-December 2011

Through biologists' response to Guardian reports, I documented that 63 adult and sub-adult (≥ 2 years) lions used the study area. The average density of lions over the 30 months of this study was 1.2 ± SD 0.16 lions/100km^2. By comparison, Amboseli National Park has a density eight-fold higher, 9.5 ± SD 2.15 lions/100 km^2 (Watts and Holekamp 2005, van der Werf 2008, Caceres Calleja 2009). In the time between the final LG expansion in the Amboseli ecosystem in mid-2010 and the end of 2011, I had identified only one 'new' adult lioness with two older cubs, transient wet-season visitors from Amboseli Park that returned to the Park after only one week on communal land. In June 2011, I detected three new sub-adult males, presumably young dispersers from outside the study area (Hanby and Bygott 1987).

Fig. 2.4 demonstrates the increase in number of lions detected and monitored after the implementation of the LG program on each Group Ranch, showing that known numbers tended to level off after an average of 5.5 months, indicating that essentially all resident lions had been identified. Additionally, the proportion of all identified, uncollared lions to the total of identified lions increased from an average of 0.07 during the pre-LG period to 0.39 after the LG program began operating (Fig. 2.5).

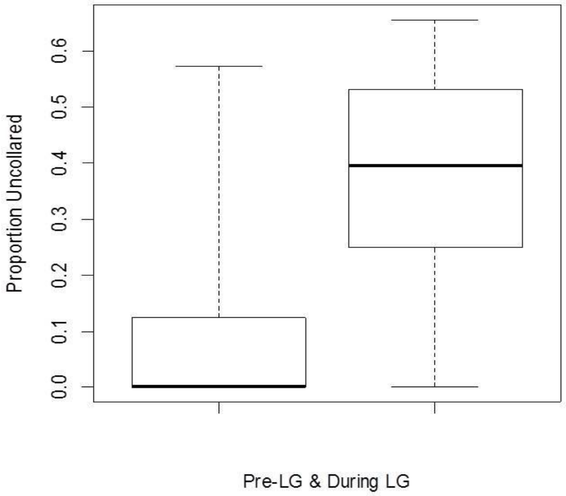

Figure 2.5: Proportions of known but uncollared lions monitored before and during LG program on Mbirikani group ranch, Kenya; May 2004 - December 2011

Furthermore, due to the increased manpower, intensity of sampling and wider distribution of Guardians across the ecosystem, more detailed data on lion movements were obtained, resulting in substantially increased mean home range size estimates. The lions' 100% Minimum Convex Polygon (MCP - Mohr 1947), based solely on sightings and VHF telemetry, before LG, averaged 243.49 km^2 ± SE 15.70 (n = 9). After the Guardians were deployed, the lions' average 100% MCP almost doubled to 477.03 km^2 ± SE 10.83 (n=33). The number of lion sightings increased as well. Before LG, lions were seen 122 times in the 32 month period from May 2004 to November 2006; once the LG program started, lions were seen 834 times in a 60 month period, a mean of 3.8 visual observations per month before LG and 13.9 with LG.

From 2004 to 2006, before the inception of the LG program, biologists found 63 lion kills of wild prey, while in 2007-2011, during LG operations, a total of 751 kills were found. On MGR the number of kills found per month with the LG program increased more than four-fold compared to the number found by a single biologist in a vehicle (Fig. 2.6).

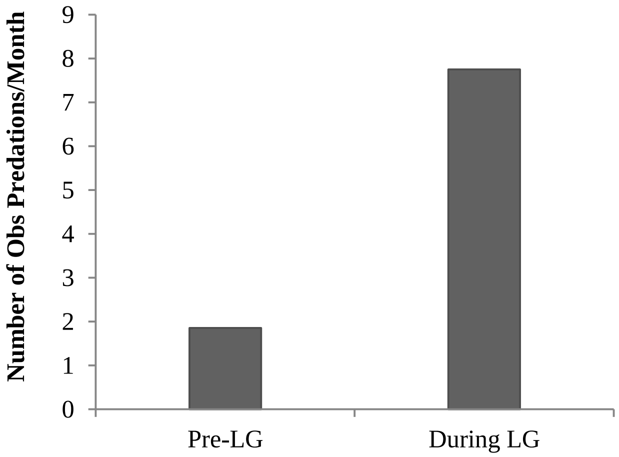

Figure 2.6: Number of observed lion predations found per month before and during LG program on Mbirikani group ranch, Kenya; May 2004 - December 2011

Spoor Counting Results

Lion Guardians conducted 2,308 spoor counts along 29 weekly routes. Transect length was limited due to the fact that it was being covered on foot, with a mean route length of 12.17 km ±1.55 km. Route penetration index equaled 9.77, providing less coverage than suggested by Stander (1998). The routes used for analysis were sampled 56 to 108 times (mean = 93.8 ± SD12.2) over a 108 week period for a total of 19,561 kilometers surveyed.

Data pooled at the group ranch level (n = 2) yielded positive correlations for the areas (Fig. 2.7: MGR r = 0.89 and EGR r = 0.75).

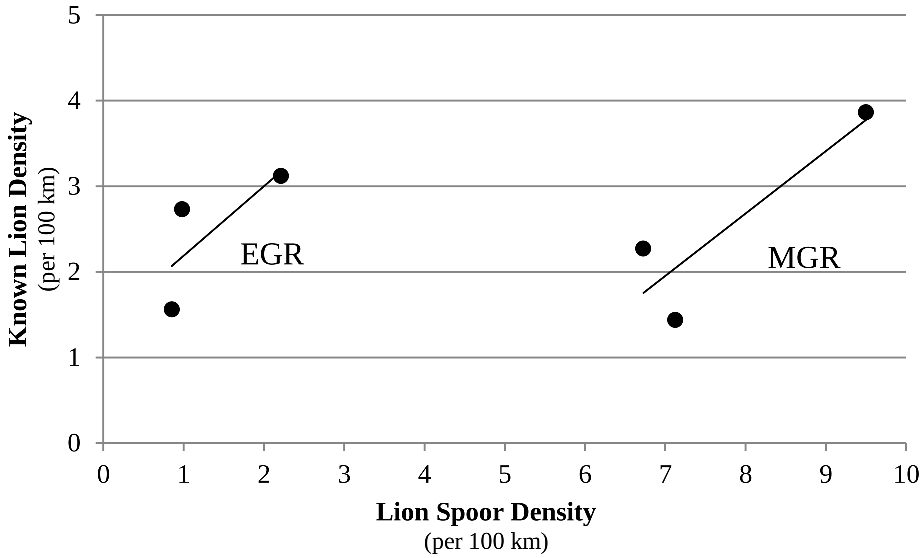

Figure 2.7: Known lion density plotted against reported lion spoor density for three years (2009, 2010, 2011) on Eselenkei group ranch (EGR) and Mbirikani group ranch (MGR), Amboseli ecosystem, Kenya

The relationship between lion density and spoor density yielded the two models in Fig. 2.7 with slope parameters of 0.73 and 0.81. Thus, an increase of 1 mean spoor per 100 km, reflects an increase in the lion density of 0.73 lions per 100 square km on MGR and 0.81 lions per 100 square km on EGR. The mean slope is large compared to the standard error of the mean (t = 16.47, df = 1, $p < 0.025$), implying that there is a positive relationship between lion density and spoor density in these unprotected community lands. Equivalently, the 95% confidence interval on the mean slope does not contain 0.0 (mean slope = 0.78 ± SD 0.60).

I subsequently averaged the coefficients in the two models (MGR $y = -3.15 + 0.73x$; EGR $y = 1.37 + 0.81x$) to obtain one model with mean slope of 0.77 to predict lion density from spoor density in this human-dominated landscape. This averaged model is

$$y = -0.89 + 0.77x$$

where x is the mean spoor density per km and y is lion density per square km. An increase of 1 mean spoor per 100 km surveyed predicts an increase of 0.77 in lion density per 100 km^2 area. Thus, if LG reported an average increase of 2.5 lion spoor found per 100 km surveyed, then we could expect an increase of approximately two lions found in the area.

DISCUSSION

Danielsen et. al. (2003) postulated that a key determinant of the sustainability of conservation in developing countries might be the ability of conservation authorities and scientists to accept that participatory monitoring could positively inform resource management. My results show that the union of modern wildlife monitoring with local peoples' traditional tracking and ecological knowledge can provide reliable data over a large geographic scale on carnivore populations that are difficult to monitor. I demonstrate that traditional Maasai warriors can accurately monitor numbers, predation ecology, and movements of elusive lions that are difficult to study with standard scientific methods. Due to wide and intensive coverage of the region by 30 Guardians on foot, sightings and radio locations were more frequent than those obtainable by a single biologist in a vehicle. I was able to expand lion monitoring to an ecosystem level because local warriors were able to access nearly all habitats.

Data quality and quantity improved substantially with the inception of the LG program, allowing a program employing only one to two trained biologists to cover an extensive area of over 3600 km^2 for a fraction of the cost of traditional monitoring by only trained biologist; it is much more cost effective to employ local people. The Guardians were able to track and, together with the biologists, individually identify an entire population of low density and nocturnal lions.

Over 90% of the Guardians' reports were accurate and many of the inaccuracies were due to difficult scenarios where misinterpretations were expected and explainable. Furthermore, the increased number of observers and consequent intensity of coverage led to a significant increase in number of prey kills detected, and hence our ability to study the predation ecology of a persecuted lion population in a human landscape (Chapter I).

The spoor routes conducted by the Guardians produced a model which can be used to accurately predict lion density from spoor density, a relatively simple and low cost technique that can be used to quickly estimate lion populations in similar unprotected areas. For additional replication of the models, it would have been ideal to bootstrap the data by, for example, randomly splitting MGR and EGR into two subsets of approximately equal size and repeating the regression of lion density on spoor density; this proved to be impossible because the calculation of true lion density cannot be automated. The replication of the relationship between spoor and lion density on two separate areas with similar ecological and social conditions and similar proximity to a protected areas provided the randomization and scale to afford a combined model which offers strong estimates of lion density from spoor counts. When applying models to a broad landscape with varying levels of protection, it is important to consider widely differing densities and movements between protected areas and the surrounding unprotected lands.

Even though the increase in local tolerance towards wildlife is difficult to measure (Bruskotter and Fulton 2012), we have observed, through the process of collecting biological data and identifying the lion population, that the Guardians displayed great interest in naming the lions, as well as in spending time watching them. The Guardians videotape and photograph the lions and show this footage to their communities, telling stories to the elders, women and children about the lions, using the lions' given Maasai names. A recent survey found that 60% of the respondents sampled throughout the ecosystem knew the given Maasai name of at least one lion in the ecosystem (L. Lenaiyasa, *unpublished*). Personalizing individual lions not only provided the Guardians and their communities with a sense of 'ownership', but may simultaneously deter those communities from killing a well-known local lion personality.

I believe this engagement has brought about a shift in the Guardians' attitudes toward lions and their desire to protect them. The transformation from lion killer to lion protector is difficult to quantify, but it is evident through their actions. For example, together with local stakeholders, LGs have prevented over 100 lion hunts by reminding their community of the value of lions. They have used very creative tactics to dissuade angry community members from killing lions (e.g., telling people that if they kill a collared lion, the collar will take a picture of them and send it straight to the wildlife authorities). Their willingness to get between the spears of their peers and a lion they have been protecting is ample evidence of an attitude-behavioral shift.

The Lion Guardian example demonstrates that participatory monitoring is an effective and reliable alternative when conventional monitoring across a broad area is not feasible. I recognize that local knowledge cannot be accepted unquestioningly (Reed et al. 2008), but my data suggests that engaging local communities in carefully designed lion monitoring provided accurate data and improved knowledge. The marriage of conventional monitoring with community participation can be a powerful approach having both conservation importance and biological implications for the wildlife dwelling in human-altered systems.

CHAPTER III: Lion occupancy of pastoral communities in Maasailand, Kenya

INTRODUCTION

African lions (*Panthera leo*) have survived in pastoral landscapes for centuries (Marshall 2000, Marshall and Hildebrand 2002, Bauer and Van Der Merwe 2004). Although some authors have suggested that large carnivores cannot endure in landscapes where poorly managed livestock production is the primary livelihood, due to retaliatory killing and subsequent extirpation of carnivores by livestock owners (Weber and Rabinowitz 1996, Linnell et al. 1999), lions have persisted near Maasai pastoralist communities of southern Kenya for decades (Western and Henry 1979, Spear and Waller 1993, Hemingway and Hemingway 1999, Chardonnet 2002). Southern Maasailand supports high densities of people (8.14 to 21.63 people/km^2), their livestock (37.6 to 60.1 head of livestock/km^2)(Kenya National Bureau of KNBS 2009, Western et al. 2009, Hazzah 2011), with moderate densities of prey species (11.36 ± SD 1.61 herbivore/km^2) (Groom 2007) and low densities of lions outside the protected areas (0.012 adult and sub-adult lions/km^2) (Chapter I).

This study was conducted outside protected areas on communally owned Maasai group ranches of the Amboseli Ecosystem in southern Kenya, a 6,000 km^2 patchwork of protected National Parks and non-protected areas including Amboseli, Tsavo West, and Chyulu Hills National Parks in Kenya, and Kilimanjaro National Park in northern Tanzania. The non-protected area is divided into group ranches, land communally owned and grazed by traditional Maasai pastoralists.

Lions have been hunted by pastoralists for centuries (Chardonnet 2002, Hazzah et al. 2009), with at least 207 lions killed within the study area between 2001 and 2011 (Maclennan et al. 2009, Hazzah et al. *in review*). The hunting and killing of carnivores leads to behavior modifications such as increased nocturnality and avoidance of human communities (Frank and Woodroffe 2001, Boydston et al. 2003, Pangle and Holekamp 2010, Carter et al. 2012, Valeix et al. 2012a). On the pastoral grazing lands of southern Kenya, lions are secretive and nocturnal (Mogensen et al. 2011) making them difficult to study, particularly in close proximity to human communities (Ruth et al. 2003, Ordiz et al. 2011).

Even though the lions of the Amboseli region are persecuted, they still routinely attack livestock in Maasai *bomas* (traditional livestock enclosures and homesteads (Stanley 1988, Spear and Waller 1993)). During the study period from Aug 2009 to Dec 2011, lions reportedly attacked livestock on 804 occasions (PCF, *unpublished data*). Approximately half of these incidents were verified and mapped; of these, 64.3% occurred at or within one kilometer from a Maasai *boma*. A cluster of *bomas* comprising a Maasai settlement is thus both a food source and a danger to lions.

Hemson and colleagues investigated lion use of the wider areas surrounding pastoralist communities (Hemson 2003, Valeix et al. 2012a). Here I explicitly examine lion occupancy of Maasai settlements on both broad and fine scales in relation to *boma* density, as a proxy for human and livestock densities, and proximity to a protected area. Due to the difficulty of detecting large persecuted carnivores, I examine and compare detection methods of lion presence in human areas. With better detection and understanding of the influences of human communities, conservationists can better design and implement lion conservation strategies in human-dominated landscapes.

MATERIALS AND METHODS

Modeling Approach

I used occupancy models (Hines and MacKenzie 2004) to examine lions' visitation to Maasai settlements. My first objective was to compare multiple detection methods of lion presence in Maasai settlements. The occupancy models for multiple detection methods permit estimation of occupancy at the larger scale, psi (Ψ) which corresponds to lions' use of the group ranches, and at a smaller scale, theta (Θ), the probability of lions being present at the local survey site, in this study, the Maasai settlements, and a detection probability estimate (p).

My second objective was to explore the influence of site covariates on lion occupancy of Maasai settlements. Based on findings of previous studies that carnivores originate from protected areas and move in to surrounding human-dominated landscapes (Woodroffe and Ginsberg 1998, Hemson 2003, Loveridge et al. 2010), I decided to use distance to neighboring National Parks as a covariate. National Parks in the region often have higher lion density (Watts and Holekamp 2005, van der Werf 2008, Caceres Calleja 2009) and lower human density than the Maasai communities of adjacent lands; both these factors could influence lion occupancy. I hypothesize that the probabilities of occupancy will be negatively associated with distance to protected areas. Secondly, I used density of *bomas* as an additional covariate that could influence lion occupancy. In line with the ecological 'landscape of fear' theory (Brown et al. 1999, Laundré et al. 2001) and previous findings (Valeix et al. 2012a) that lions avoid human communities, I expected to find large scale occupancy (Ψ) to be either constant across survey sites or negatively associated with *boma* density.

Study area

This research was conducted on three group ranches of the Amboseli ecosystem (Fig. 3.1): Olgulului (1,595 km^2), Eselenkei (769 km^2) and Mbirikani (1,320 km^2), with a human population of approximately 30,000 (Kenya National Bureau of Statistics KNBS 2009). The area comprises semi-arid savannah shrub with a bimodal rainfall pattern averaging between 200 and 500 mm annually (Altmann et al. 2002, Moss et al. 2004-2012) .

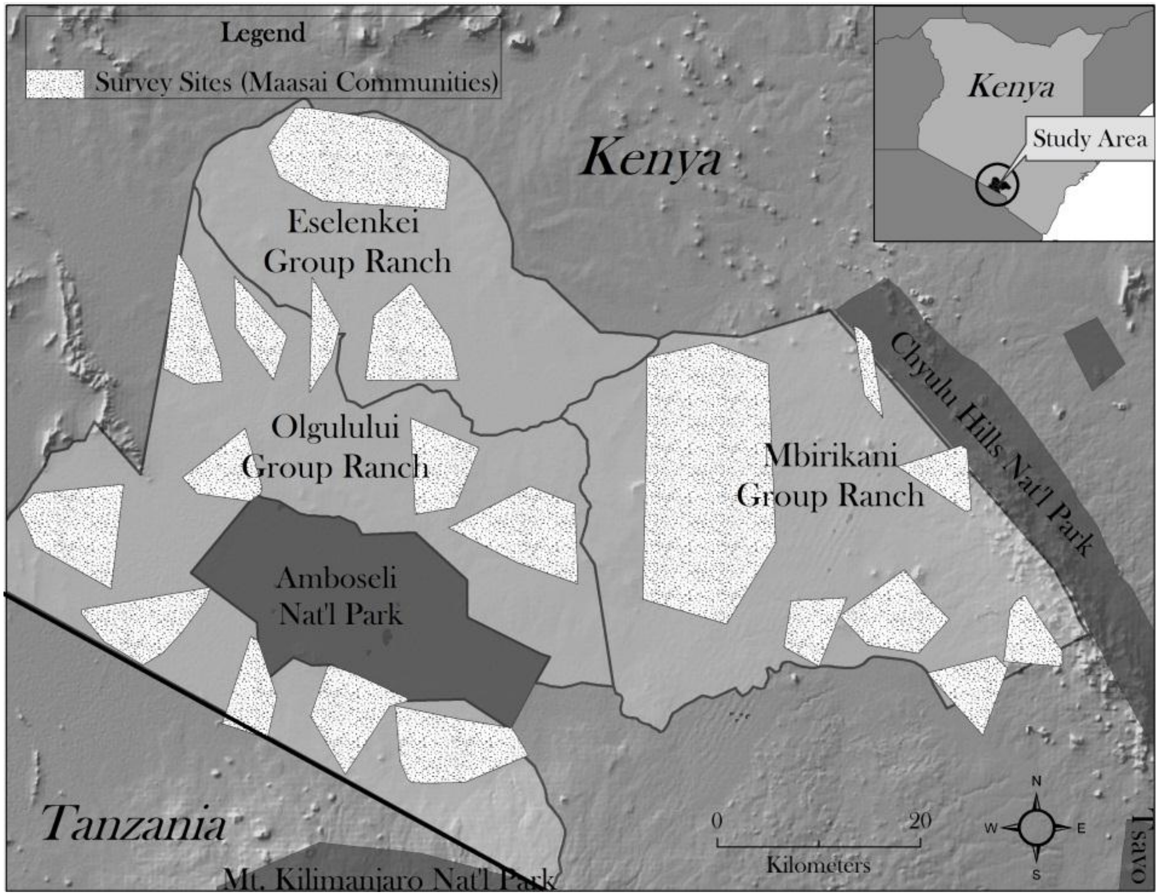

Figure 3.1: Group ranches, Maasai communities and National Parks on study areas in southern Kenya

Survey Methods

I examined lion occupancy of 20 Maasai settlements, defined as clusters of *bomas*, from August 2009 to December 2011 (Fig. 3.1). Permanent *bomas* were mapped using a handheld

Global Positioning System (eTrex, Garmin 2010) and divided into settlements by constructing polygons around clusters. There were no data available to determine the distance at which lions respond to settlements thus I used a previous study from the Amboseli region that found mammal species to react to human structures at a distance of 237 – 285 m (Okello and Kioko 2010), and assuming carnivores will react to areas with higher densities of people and livestock at farther distances, I buffered the community polygons with a distances of 237 m for the communities with the lowest densities of *bomas* (≤ 3.5 *bomas*/km^2), 261 m for the communities with a moderate level of *boma* density ($> 3.5 < 10$ *bomas*/km^2), and 285 m for the communities with the highest levels of *boma* density (≤ 10 *bomas*/km^2) using ArcMap 10 (ESRI 2011).

I first examined the efficacy of two detection methods; walked spoor routes and spatial locations of collared lions. The walked spoor routes were centered in the communities and conducted by trained Maasai warriors, Lion Guardians (Chapter II; Hazzah et al. *in review*). Each route averaged 10 to 12 km in length and was conducted each week from sunrise to 10 a.m. Lion Guardians, trained Maasai warriors, recorded tracks of five large carnivores (lion, spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*)), and five primary prey species (plains zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), Maasai giraffe (*Giraffa camelopardalis tippelskirchi*), the common eland (*Taurotragus oryx*), and the lesser kudu (*Ammelaphus imberbis*)). Each settlement area had one to three Lion Guardians, each with his predetermined spoor route, and data from four weekly routes were collapsed into one monthly detection per survey site.

The second detection method was monitoring of radio-collared lions (GPS Plus, VECTRONIC Aerospace GmbH Berlin, Germany; VHF MOD-500, Telonics Inc., Mesa, AZ, U.S.A). Collaring began in early 2004 (see Frank et al. 2003, Maclennan et al. 2009 for more details on immobilization methods used and early monitoring details). For the purpose of this study, I only considered the 13 females and 9 males collared and closely monitored during the study period, 37% of a population of 60 adult and sub-adults in the area. I determined presence/absence of marked lions by mapping all lion relocations and examining buffered settlements each month for lion presence. Similarly, I gathered presence/absence data, based on fresh sign or sightings of lions along spoor transects, for each settlement for each month.

Site Covariates

I calculated the distance to nearest protected area (*DistPA*) by measuring the shortest Euclidean distance from each community boundary to the border of the nearest protected area. I measured the second covariate, *boma* density (*BomDen*), as the number of permanent *bomas* per community divided by area of the polygon. I used z-transformations to standardize each covariate (Donovan and Hines 2007).

Statistical Methods

To explore possible changes in occupancy state between the sampling seasons, I combined the data from both detection methods into one dataset with 20 sites and 29 survey months and fit both single-season and multi-season models to the data (Nichols et al. 2008). All models were run in the program PRESENCE (version 5.1; Hines and MacKenzie 2004).

To obtain unbiased estimates of large-scale occupancy psi (Ψ) and detection probability for all methods (p), I collapsed data for both detection methods across all sampling periods and areas and ran a single-season multi-method model. By collapsing the data into one detection history, I obtained detection by at least one method or non-detection by both methods (Nichols et al. 2008). Secondly, detection probability (p) was calculated by applying the single season, multi-method model separately to each detection method.

I then considered ten *a priori* models with psi (Ψ) either held constant or separately varied by site covariates *BomDen* and *DistPA*. Theta (Θ) was held constant or varied over time, and detection probability (p) was either held constant, varied with time (p_t), detection method (p^s), or both (p_{s+t}) (Nichols et al. 2008, Chiari et al. 2012). Models were fit to a combined data set with both detection methods included for each survey period. Since there were two detection methods for each survey period and site, I set the number of occasions per season to two and used a single-species, single-season, multi-method model; maximum likelihood estimates were obtained using the program PRESENCE (Hines and MacKenzie 2004). I used Akaike's Information Criterion (AIC, Akaike 1973) to identify the most parsimonious model that best explained the variation in the data (Burnham and Anderson 2002, Cooch and White 2002).

RESULTS

The twenty settlement polygons ranged from 11 to 309 km^2 in area. On the combined dataset, I found no difference between the single season and multi-season models (p = 1, AIC = 807.49 and -2*LogLike = 803.49) and thus I accepted the null model, implying that occupancy state across the system was constant among seasons and it was appropriate to fit a single-season model to the data. The large-scale unbiased estimate of occupancy was high ($\Psi = 1.0$) meaning that probability of lions occurring in the larger study region was estimated as constant.

The model selection statistics for the *a priori* models (Table 3.1) provided strong evidence that occupancy probability was influenced by sampling method (p^s). Evaluating the Akaike's weight of evidence (*w*) (Donovan and Hines 2007), I concluded that both models that incorporated site covariates had the most support (combined weights = 0.82, AIC varied < 0.13), followed by the model with psi Ψ and theta Θ held constant while detection probability varied between detection methods p^s (Table 3.1). The top three were models with detection probability differing between detection methods p^s (combined weights = 1.0, AIC varied < 2).

I assessed model fit in PRESENCE (Hines and MacKenzie 2004) and found $\hat{c}$ to be approximately 1 for all models (Table 3.1), suggesting that the models adequately explain the variation in the observed data (MacKenzie and Bailey 2004, Donovan and Hines 2007).

Table 3.1: Results of models of lion occupancy at pastoral communities in southern Kenya, 2009-2011

Model	**Ψ**	**(SE)**	**Θ**	**(SE)**	**K**	**Sgfnt Digits**	**-2log(L)**	**AIC**	**ΔAIC_C**	**w**	**Model Likeli-hood**	**$\hat{c}$**
$\Psi(DistPA), \Theta, p^s$	0.87*	0.06	0.77	0.04	4	8.2	1314.2	1322.2	0.0	0.4	1.0	1.0
$\Psi(BomaDen), \Theta, p^s$	0.87*	0.07	0.77	0.04	4	7.7	1314.3	1322.3	0.1	0.4	0.9	1.0
Ψ, Θ, p^s	0.79	0.04	0.79	0.04	3	8.3	1317.9	1323.9	1.7	0.2	0.4	1.1
Ψ, Θ_t, p^s	1.00	0.00	0.73*	0.14	32	-2.3^	1276.9	1340.9	18.8	0.0	0.0	0.9
Ψ, Θ, p	0.79	0.05	0.79	0.05	2	7.3	1357.5	1361.5	39.3	0.0	0.0	1.1
Ψ, Θ, p_{s+t}	0.77	0.05	0.77	0.05	60	5.9	1256.1	1376.1	53.9	0.0	0.0	1.2
Ψ, Θ_t, p	1.00	0.00	0.72*	0.14	31	2.5	1315.5	1377.5	55.3	0.0	0.0	0.9
Ψ, Θ_t, p_t	1.00	0.00	0.73*	0.17	88	5.6	1210.5	1386.5	64.3	0.0	0.0	0.9
Ψ, Θ_t, p_{s+t}	1.00	0.00	0.73*	0.16	89	2.3^	1210.5	1388.5	66.3	0.0	0.0	0.9
Ψ, Θ, p_t	1.00	0.00	1.00	0.00	59	5.8^	1271.9	1389.9	67.7	0.0	0.0	0.9

* Parameter estimate reported is the mean value, ^Numerical convergence may not have not been reached. K is the number of parameters in the model, -2log(L) is twice the negative log-likelihood value. Akaike Information Criteria (AIC), Akaike weight (*w*), and the difference between small sample AIC (**AIC_C**) relative to the top model, ΔAIC_C (Burnham and Anderson 2002), are all reported as well as $\hat{c}$ as a measure of model fit

I used 3,596 walked spoor surveys with 146 missing observations and 7,395 lion relocations within the communities (15.4% of 48,142 locations) to compare detection methods. Of the relocations of radio-collared animals, 1.6% were from VHF collars and 98.4% were taken by the 9 GPS collars. Detection probability (p) for both methods in the combined model was 0.52 (SE 0.02, 95% CI 0.47 - 0.56). When modeled alone, detection probability (p) of the spoor routes was the same at 0.52 (SE 0.02, 95% CI 0.47 - 0.56) but radio collars probability of detection decreased to 0.36 (SE 0.02, 95% CI 0.32 - 0.40).

When analyzed as part of the *a priori* models (top four models, Table 3.1) both detection methods were consistently good at detecting lions in the community areas (Spoor Route $\bar{x}$ = 0.63 ± SE 0.08; Radio-marked lions $\bar{x}$ = 0.45 ± SE 0.07; Table 3.2), although walked spoor routes were routinely better. The model averaged detection probabilities were 0.63 (SE 0.08) for spoor routes and 0.45 (SE 0.07) for locations of radio collared lions.

Table 3.2: Detection probability estimates and associated standard errors from the suite of occupancy models constructed using presence/absence data collected from spoor routes and radio-marked lions in southern Kenya, 2009-2011.

Model	Spoor Routes^	(SE)	Radio-marked lions#	(SE)
$\Psi(DistPA),\ \Theta,\ p^s$	0.65	0.04	0.42	0.03
$\Psi(BomaDen),\ \Theta,\ p^s$	0.65	0.04	0.42	0.03
$\Psi,\ \Theta,\ p^s$	0.64	0.04	0.42	0.03
$\Psi,\ \Theta_t,\ p^s$	0.68	0.03	0.45	0.03
$\Psi,\ \Theta,\ p$	0.51	0.03	0.51	0.03
$\Psi,\ \Theta,\ p_{s+t}$	0.67*	0.16	0.43*	0.13
$\Psi,\ \Theta_t, p$	0.55	0.03	0.55	0.03
$\Psi,\ \Theta_t,\ p_t$	0.70*	0.15	0.47*	0.16
$\Psi,\ \Theta_t,\ p_{s+t}$	0.70*	0.15	0.47*	0.16
$\Psi,\ \Theta,\ p_t$	0.52*	0.13	0.33*	0.10

* Parameter estimate reported is the mean value

^Data collected by trained scouts walking designated transects each week and recording number of lion spoor per kilometer.

#Data for radio-collared lions were collected during weekly attempts at locating collared animals and obtaining spatial locations.

For both site covariates, as the measure (distance or density) increased, the probability of occupancy decreased (Figs. 3.2 and 3.3). Standard errors are low for both (*DistPA* mean SE 0.06, range 0.05 - 0.27 and *BomDen* mean SE 0.07, range 0.05 - 0.26) and the confidence intervals did not include zero.

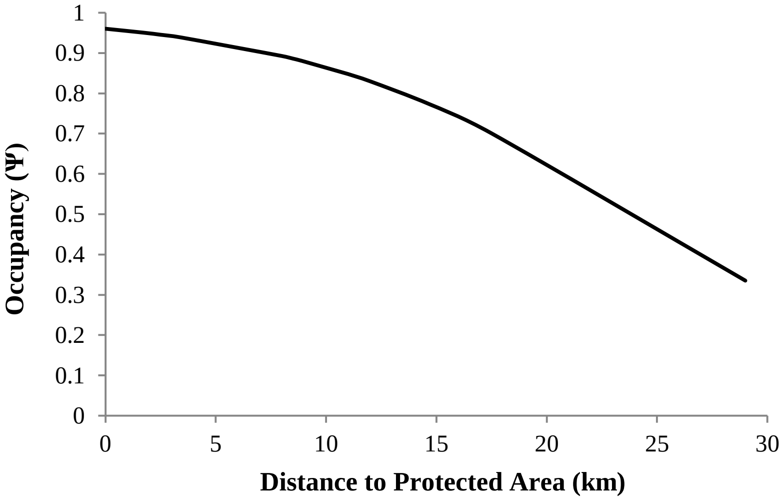

Figure 3.2: Occupancy estimates for survey sites plotted against site covariate 'Distance to Protected Area' (Euclidian distance reported in kilometers)

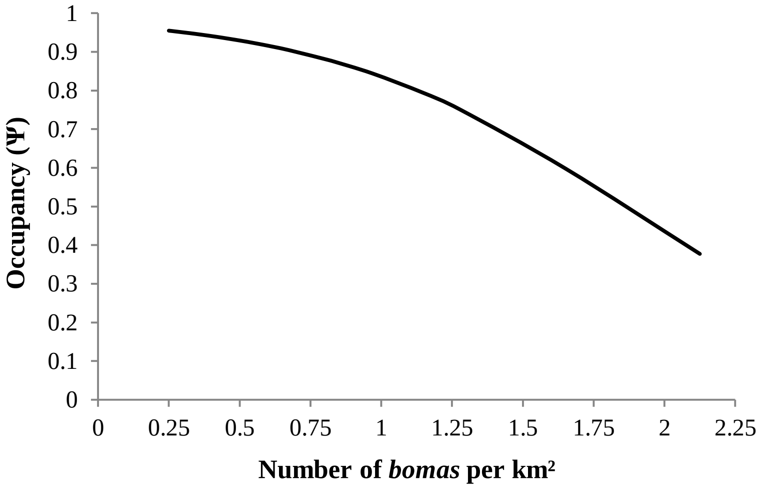

Figure 3.3: Occupancy estimates for survey sites plotted against site covariate 'Numbers of *bomas* per km^2 of survey site'

DISCUSSION

I provided estimates of occupancy of lions at two spatial scales; across pastoralist rangelands (Ψ) and at the more localized *boma* cluster or settlements (Θ). Even though lions occurred at low densities across the group ranches, I found they regularly inhabit the broader study area (the group ranches), as well as the finer scale (the Maasai settlements). My estimates of probabilities of lions within Maasai settlements are high and only slightly less than the group ranches; the densely inhabited settlements are seemingly important to lions in this region and are not avoided. I believe these methods and estimates of occupancy could serve as initial values for further studies examining carnivore occupancy in similar human-dominated landscapes.

The occupancy approach is well suited for monitoring populations of rare and elusive species (MacKenzie et al. 2005, Joseph et al. 2006). In comparison of the two detection methods, spoor routes proved to be slightly more reliable than radio collaring as a tool for detecting and estimating lion presence in community areas, possibly due to the higher sample size and the ability to detect the entire population. In addition to the low cost, reliability and conservation benefits of employing local community members to conduct spoor surveys (Chapter II; Stander et al. 1997, Danielsen et al. 2009), walked spoor routes were a reliable detection method for the presence/absence data necessary to conduct occupancy analyses of focal species.

The multi-strata models also allowed me to estimate occupancy probabilities at two spatial scales. I applied the approach where I knew lions occurred at low densities across a broad area but were thought to generally avoid the sampled areas, i.e. the Maasai settlements (Nichols et al. 2008). In this study, I applied the occupancy approach to test theories of large carnivore and human interactions as well as to elucidate factors which may inform management strategies to reduce lion occupancy of pastoral communities.

Lions occurred more regularly in settlements that are closer to national parks, probably due to movements out of high density into lower density areas. Lions that reside on the non-protected areas may also move towards the protected areas to access higher densities of prey (Worden 2007). However, the high estimation of site occupancy (95% of sites ≥ 0.70) could be due to close proximity of the survey sites to a protected area, as 13 out of 20 were within 10km of a protected area. There was a negative correlation between the distance of a community to a protected area and the occupancy estimate of each site ($r = -0.94$, $n = 20$, $p = < 0.001$).

Although lions were less likely to occupy settlements with higher densities of humans and livestock, estimates of occupancy of even densely populated settlements were still high (> 1 *boma*/km^2, $\Psi = 0.79 - 0.37$). Although lions near Hwange NP and Makgadikgadi Pan NP were found to strongly avoid human communities (Loveridge et al. 2010, Valeix et al. 2012a), lions in the Amboseli region routinely come into close proximity of humans, possibly because they frequently take livestock from in or near *bomas* in spite of the risk of retaliatory killing by humans. *Bomas* are thus a potential, albeit risky, food source due to the high numbers of corralled livestock. Furthermore, most of these lions reside predominantly on the ranches rather than within the national parks, and are thus somewhat habituated to human presence and disturbance. More study is necessary to analyze lion behaviors (e.g., speed of travel, etc.) while in close proximity to humans, however, my results show that large felids, such as lions, while avoiding the highest densities of people and livestock, regularly frequent human communities, even when highly persecuted.

CHAPTER IV: A metapopulation analysis of African lion populations across Kenya and Tanzania

INTRODUCTION

African lions once roamed the greater part of the African continent. As habitat generalists, they occupied a wide range of biomes from tropical rainforests to the interior of the Sahara desert (Nowell and Jackson 1996). Over the past century, it is estimated that lions' range has been reduced by over 80% (Riggio 2011). Across the majority of their present-day range, lion populations are now primarily associated with protected areas and managed hunting areas (Bauer et al. 2008).

Several strongholds of free-roaming lions remain in the east African countries of Tanzania and Kenya. Although both countries have strong tourism economies and Tanzania a strong trophy hunting sector (Packer et al. 2009, Lindsey et al. 2012), all based largely on lions (Jules and Shahani 2003, Van Dyck and Baguette 2005), lions are under threat in both countries. They are declining due to indiscriminate killing by humans (Ikanda and Packer 2008, Hazzah et al. 2009) as well as from depletion of their prey base (Bauer 2008, Ogutu et al. 2011) and overexploitation due to poor management of trophy hunting (Packer et al. 2009, Packer et al. 2010). Habitat conversion outside of protected areas has led to lion populations becoming increasingly divided into smaller distinct units that are currently under threat from further isolation (Bauer and Van Der Merwe 2004).

Although lions are able to subsist in a wide variety of habitats, they are most successful in areas with low to medium human densities (Chardonnet 2002, Frank 2011, Riggio 2011). Due to anthropogenic pressures, the once-continuous network of lion populations across East Africa now exhibits a metapopulation structure (McCollough 1996): distinct populations within a wider landscape with limited migration between them (Hanski and Simberloff 1997). Conservation planning for lions across eastern Africa requires an understanding of the broader network of lion populations.

Metapopulation analysis is an effective tool to better understand broad area population dynamics and the effects of species-specific life-history traits on population connectivity (Driscoll 2007), considered critical to modern wildlife conservation and management (McCollough 1996). Numerous wildlife populations are becoming increasingly isolated with regional extinction imminent for many species (Wiens 1996). A metapopulation, an assemblage of populations linked through migration, functions at a larger scale than individual populations and can provide further insight into the dynamics of each component population in reference to the system as a whole (Hanski and Gilpin 1997, Stacey et al. 1997).

Migrating individuals can re-colonize suitable patches after a local extinction has occurred, as well as enable a “rescue effect” in which immigrating individuals protect a dwindling local population from extinction (Brown and Kodric-Brown 1977, Hanski 1999). Successful recolonization is dependent on the dispersing individuals surviving ‘the matrix’, an area between populations which is generally not suitable for long-term survival and reproduction (Ricketts 2001, Vandermeer and Carvajal 2001, Jules and Shahani 2003). Traversing the matrix poses the largest threat for dispersing migrants (Hanski and Zhang 1993, Vandermeer and Carvajal 2001), especially for large carnivores that are inherently in conflict with humans (Treves and Naughton-Treves 1999, Treves and Karanth 2003).

Understanding the broader population dynamics of large carnivores can be particularly challenging given their longevity, large ranges, and the lack of empirical data on dispersal abilities, particularly when in the matrix (Vandermeer and Carvajal 2001, Hellgren et al. 2005).

Reliable knowledge of the species' dispersal ability enables conservationists to maintain viable populations within proximity to other populations, thus ensuring sustainable exchange of individuals (Verner 1992). Although dispersal is one of the most important of ecological processes, it remains one of the least understood (Bowler and Benton 2005). Particularly with current rates of fragmentation and isolation, it is increasingly important to understand species' dispersal characteristics and their role in maintaining the larger metapopulation (Wiens 1996).

As with other polygynous mammalian species (Greenwood 1980), male lions nearly always disperse from their natal area, often traveling two to three times farther than females (Schaller 1972, Pusey and Packer 1987, Funston 2011). Females generally stay with their natal pride or establish neighboring home ranges ('stepping stone' dispersal - Kimura 1953, Schaller 1972). Based on these generally accepted dispersal characteristics, I combine empirical data on the life-history traits and current geographic status of lion populations in a fragmented landscape with a spatially realistic modeling approach (Hanski 1994b, Gilpin 1996, Hanski 1999) to examine the lion metapopulation of Kenya and Tanzania.

The incidence function model (IFM; Hanski 1994b, Hanski et al. 1994), one of the most commonly used metapopulation models, was created to use empirical data to examine the effects of patch area and isolation on patch occupancy. IFM can be built with snapshot presence/absence data of a species at a particular site, the simplest form of data that can be collected during field studies. Good models are insightful to conservation management as they can help managers evaluate the current state and consider a system's future (Gilpin 1996); the simple and applicable IFM has high conservation value for evaluation of populations on a broad-scale (Hanski 1994b).

The IFM assumes that suitable habitat occurs in discrete patches surrounded by unsuitable matrix, and that occupancy of each patch is determined by local colonization and extinction events (Moilanen and Hanski 1998, Hanski 1999). Extinction is negatively associated with patch area and colonization is negatively associated with patch isolation, so patch occupancy should increase with area and decrease with isolation (Hanski 1994a). Extinction and colonization are also assumed to depend on factors such as patch area (a proxy for local population size), spatial arrangement of patches, patch edge characteristics, dispersal ability of the species, and regional environmental stochasticity. In IFM models, the incidence is given as a function of connectivity and patch size (Hanski 1994b); in this study, factors were calculated from empirical data on lion populations.

Using IFM, I explore the occupancy probability of particular lion populations (i.e. patches) in a spatially realistic lion metapopulation, where both distance between patches and area of patches vary (Hanski 1994b). I use the IFM to consider the effect of sex-specific dispersal characteristics on metapopulation connectivity, the impact of human densities, and the threat of isolation on the remaining lion populations (Moilanen and Hanski 1998) across Kenya and Tanzania.

MATERIALS AND METHODS

Modeling Approach

To fit the incidence function model, I used a special case of generalized linear models with binomial error and logistic link function on the response of incidence (i.e. rate of occurrence) data for each habitat patch (Oksanen 2004). The necessary data inputs were incidence data (J_i; 1 for presence, 0 for absence), area of each patch (A_i), and xy coordinates of the center of each patch. I then calculated d_{ij} (all pairwise distances between patches), α (a dispersal parameter and, in this study, estimated from actual dispersal data, equal to 1/maximum dispersal) and lastly S_i (a connectivity value). I used the negative exponential functional form of S_i because it is the more conservative option and given the intense research on lion populations by a wide variety of stakeholders across Kenya and Tanzania, I believe the occurrence of false negatives (Type II error) to be negligible (Hanski and Simberloff 1997, Mackenzie et al. 2002, Moilanen and Nieminen 2002).

Data for the Model

I used the most recent and authoritative sources to identify and map all lion populations from both countries, Mésochina et al. (2010) for Tanzania and the Conservation and Management Strategy for lions for Kenya (Kenya Wildlife Service 2008). In the Mésochina et al. report (2010), lion populations were identified by reported frequency of observation; weekly and monthly sightings were considered permanent populations. Areas for which there was no information available were omitted. In the Kenya report, all populations labeled as ‘known permanent’ were mapped. Henceforth, I use the term ‘patch’ as synonymous with a distinct lion population. In total, there were 25 patches with areas ranging from 86 to 127,515 km^2 (Fig. 4.1).

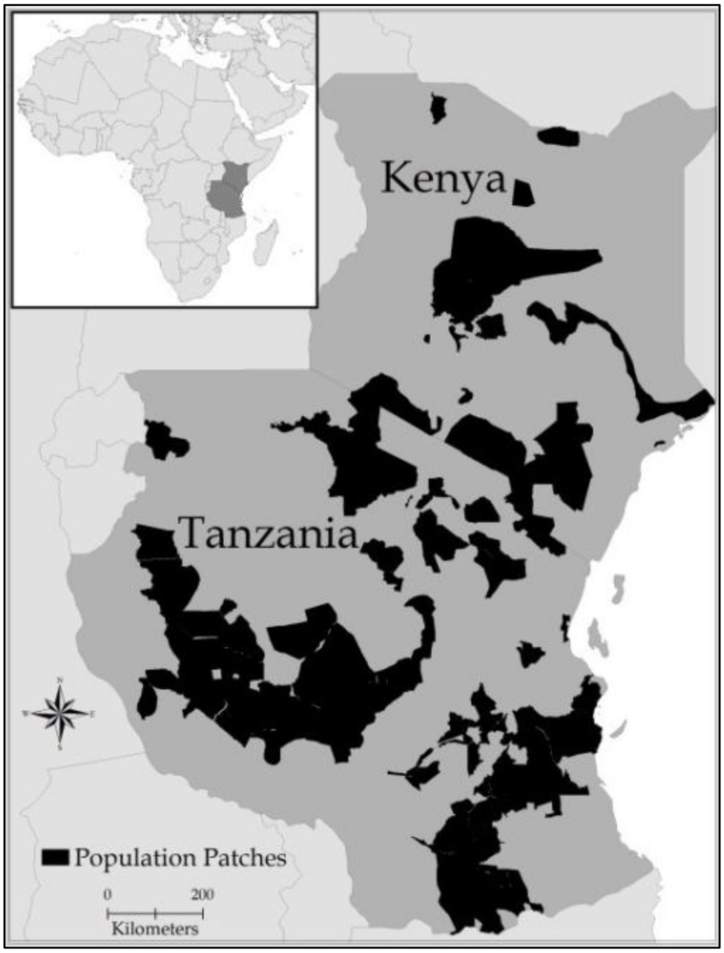

Figure 4.1: Map of study area, black areas indicate patches of permanent lion populations (n = 25) across Kenya and Tanzania

Once all patches were identified, maps were sent to regional experts (conservationists, biologists, etc.) who were familiar with current lion population status in their areas. Experts only identified areas that contained, to the best of their knowledge, a breeding lion population; they did not include areas where only male lions or dispersers were seen infrequently. This method gave a presence-absence scenario for patch occupancy.

Patches were mapped and measured (km^2) using ArcMap 10.1 (ESRI 2011), and the centroid of each patch was used to calculate the pairwise Euclidean distances between patches. I subtracted the radii of the pair of patches for each pairwise distance, so the distances could be interpreted as the shortest straight-line distance between the edges of the paired patches.

I gathered actual dispersal distances from the literature and unpublished reports (Pusey and Packer 1987, ALWG 2003, 2004, Desert Lion 2007, Funston 2011) and from data of the Living with Lions project in the Amboseli ecosystem (Chapter I). I used the maximum reported dispersal distance of 343 km and 128 km for males and females as the dispersal parameter (α).

Human density was calculated for each patch from the 2009 census of Kenya (Kenya Bureau of Statistics 2009) at the sub-location level and the 2002 census for Tanzania (National Bureau of Statistics Tanzania 2002) at the ward level. I averaged the human density for each patch area.

Statistical Methods

I followed the methods outlined in Hanski (1994b) and Oksanen (2004); I performed the IFM in program R version 2.14.0 (R Development 2011). I included the rescue effect in the model and added the mean human density for each of the patches as a covariate in the model. Therefore, my full model added one new term to Eq (9) in Oksanen (2004):

$$\log\left(\frac{J_i}{1-J_i}\right) = -\log(ey) + 2\log(S_i) + x\log(A_i) + \log(H_i)$$

$$logit(J_i) = \beta_0 + 2\log S + \beta_1 * \log A + \beta_2 * \log H$$

where J_i is the incidence in patch i, S_i is a measure of connectivity, A_i is each patch's area, and H_i is the mean human density of each patch. When fitting the full model, the intercept,

$\widehat{\beta 0}$ was log(ey), $\widehat{\beta 1}$ was an estimate of the stochasticity parameter $\hat{x}$, $\widehat{\beta 2}$ was the parameter estimate for human density entering the model as a linear factor.

Furthermore, additional model parameters were A_0, the minimum suitable area, also referred to as critical patch area, and $\hat{x}$, a stochasticity parameter; when $\hat{x}$ is large (> 1), there is a range of patch sizes beyond which extinction becomes very unlikely, whereas if $\hat{x}$ is small (< 1), there is no such critical patch size and even large populations in large patches have a substantial risk of extinction. Lastly, parameters e, the intrinsic extinction rate, and y', colonizing ability, were included.

I used $\hat{x}$ and A_0, to find $\hat{e}$:

$$\hat{e} = A_0^x$$

Then I was able to use $\hat{\beta}_0$ and $\hat{e}$ to solve for y'.

I used Akaike's information criterion (AIC) to choose between the nested models (Burnham and Anderson 2002). The reduced model included human density additive to patch area and a null model did not include human density. The connectivity term, 2ln(S_i), was used as an offset in all models (Oksanen 2004).

RESULTS

There were 25 total patches with an average area of 13,898 ± (SD) 28,639 km^2. The observed fraction of occupied patches was 0.60. Mean human density value per patch was 162 ± (SD) 475 per km^2. The average distance among all 25 patches was 546 km, varying from 63 to 1,461 kilometers (Fig. 4.2).

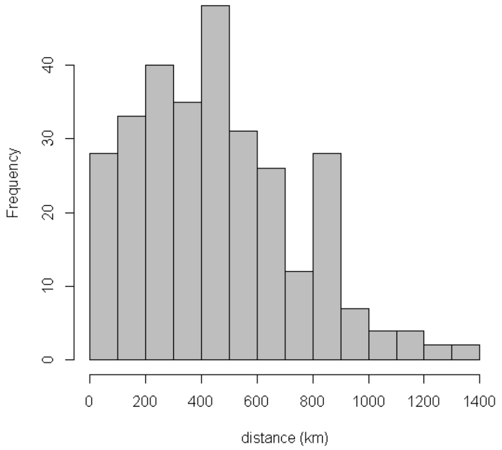

Figure 4.2: Distances between Kenya and Tanzania lion population patches in kilometers, 2008-2011

Table 4.1: Model outputs of IFM for four models using different alpha values (male and female dispersal distances) plus two models with human density as a covariate

	AIC	**$\hat{x}$ (SE)**	**e**	**y'**	**$\bar{S}$ ± SD**
Male Null	39.08	0.44 (0.25)	7.04	3002.46	33.06 ± 10.52
Male Human Density	41.03	-0.06 (0.24)	7.05	2381.55	33.06 ± 10.52
Female Null	45.61	0.81 (0.28)	38.40	470.13	8.53 ± 5.03
Female Human Density	47.43	-0.11 (0.25)	38.96	303.44	8.53 ± 5.03

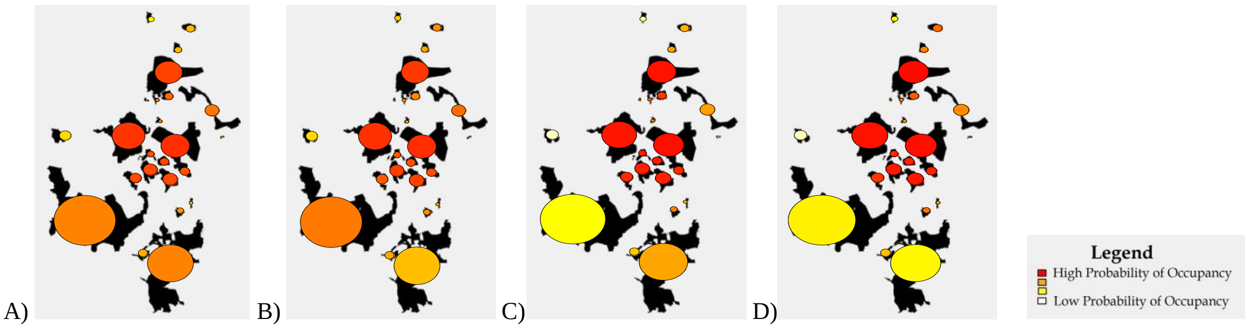

Figure 4.3: Probability of occurrence based on the IFM for both male and female dispersal given null and human density A) male dispersal null model B) male dispersal human density model C) female dispersal null model D) female dispersal human density model. In plotting the results, we used color to show the predicted incidence: the redder, the higher the incidence

The male null model was the best model (Table 4.1). Furthermore, I found significant differences between the S_i (i.e. the connectivity or isolation) values between the male and female models (t = 21.16, $p < 0.001$, df = 24). Due to the increased ability of males to move through the matrix (male $a = 0.0029$ versus female $a = 0.0078$), the male model had much higher values of S_i (Table 4.1). Particularly for the largest patches (area > 40,000 km^2), the difference between the isolation values was apparent (male $\bar{x} = 14.78 \pm$ SD 1.32, female $\bar{x} = 1.02 \pm$ SD 0.56, n = 2).

I used the estimated model parameters (Table 4.1) to determine probability of occupancy of the individual patches (Fig. 4.3). With regards to area size and effect on patch occupancy, the more moderate-sized patches (2,000 < area < 40,000 km^2) all had a relatively high probability of occupancy ($\bar{x}$ 0.72 ± SD 0.21, n = 15), while the smaller patches (area ≤ 2,000 km^2) had much lower occupancy probabilities ($\bar{x} = 0.41 \pm$ SD 0.17, n = 8). Surprisingly, the largest patches (area ≥ 40,000 km^2) also had much lower occupancy probabilities ($\bar{x}$ 0.45 ± SD 0.15, n = 2).

Adding the human density parameter did not seem to have an influence on either male or female model; the influence of human density in the reduced models was not significant (p = 0.81 and 0.67). However, the human density parameter did negatively affect the colonization parameters (C) of the models for both sexes (male models $t = -2.82$, $p = 0.007$; female models $t = -2.91$, $p = 0.005$, two-tailed tests at alpha level 0.05). Furthermore, the patches with the highest associated human density (>2,000 people/km^2, n = 2), had a decreased probability of occupancy in the models with human density added (mean $\Psi = 0.60$ to 0.54 in male model and 0.57 to 0.47 in female model); this difference is reflected in the different color for that patch in the occurrence maps (Fig. 4.3).

DISCUSSION

The present-day fragmentation of the East African lion population into patches associated primarily with protected areas fits the metapopulation framework. Population patches are well delimited and cover only a fraction of the total area, allowing us to apply a metapopulation approach to the network of remaining lion populations across Kenya and Tanzania. In particular, I considered the impact of sex-specific dispersal characteristics on regional lion populations. For this study, with only one snapshot of population occupancy, I was able to see the strong differences between male and female dispersal abilities on connectivity, isolation and probabilities of occurrence.

Male lions' ability to 'rescue' declining populations (Björklund 2003) over 300 km away was strong, particularly since dispersal ability is pliant (Van Dyck and Baguette 2005). If occupied patches, i.e. lion populations, are maintained and migration is allowed, then the males' strong rescue ability (Reed and Levine 2005) allowed for higher probabilities of patch occupancy and stronger values of connectivity. Yet even the average distance between current populations was over 500 km, well beyond the dispersal abilities of male lions. Thus survival while in the matrix and a constant flow of male dispersers from stable populations are important. If male lions are not able to disperse from stable populations, as may be the case where adult male survival is low i.e. sport hunting areas (Yamazaki 1996, Loveridge et al. 2007, Packer et al. 2009, Becker et al. 2012), this could result in a lower rescue effect for the broader metapopulation, causing in an increased risk of extinction for local populations (Brown and Kodric-Brown 1977).

To avoid local extinction from occurring, it is only necessary for one or two dispersers in each generation to survive the matrix and recolonize extinct patches (Mills and Allendorf 1996, Stacey et al. 1997, Vandermeer and Carvajal 2001, Jules and Shahani 2003), allowing populations to persist in stochastic environments (Fahrig and Merriam 1985, Hanski and Gilpin 1991, Beier and Barrett 1993). The models showed males to have poor colonizing ability in comparison to females (y'), thus once patch extinction has occurred, recolonization would be dependent upon female lions being able to reach the empty patch. Female lion dispersal ability was limited; when populations go extinct, recolonization will not occur if distances between patches exceed female dispersal ability or if females are not able to survive the matrix. This has profound implications for the overall metapopulation; the female models showed an extinction rate five-fold higher than the male models. Moreover, the dispersal value used for both male and female models was the maximum dispersal value reported, well above the averages described in the literature. Thus, this analysis is a ‘best case scenario’. If more typical dispersal distances were used, the connectivity between populations would be significantly lower.

Dispersal occurs in and is dependent on the matrix (Ricketts 2001), in this case largely non-protected, human-dominated landscapes. Little is known about lion dispersal and survival in human-dominated areas (Frank 1998, Maclennan et al. 2009) although as top predators, lions are especially vulnerable and even minor human-induced changes (either negative or positive) can have large impacts (Woodroffe and Ginsberg 1998, Ray et al. 2005a, Ray et al. 2005b). Wildlife or stakeholder carrying capacity (i.e. the amount of wildife local residents are willing to 'live with' - Decker and Purdy 1988, Carpenter et al. 2000) is an approach that aims to increase tolerance of local communities, increasing the number or density of lions that communities are able to tolerate or accept. Increasing tolerance of local human communities to allow movement of even a few individuals through non-protected or partially protected areas could play a vital role in maintaining the existence of carnivores, both in order to maintain populations and to allow greater exchange between populations (Linnell et al. 2001). Tolerance of carnivores by the human communities living in non-protected areas would allow greater connection of populations and although protected areas are necessary for long-term persistence (Woodroffe and Ginsberg 1998), they are not enough as most of the lands required for carnivore survival are outside protected areas, in lands that are affected by human populations (Nowell and Jackson 1996, Crooks et al. 2011).

Even though human density was not a significant factor for either model, I suspect that further study (i.e. surveys over longer time periods) would reveal longer-term impacts of human density on extinction and/or colonization rates. However, I believe tolerance and management policies may be more important factors than human population densities (Linnell et al. 2001, Treves and Karanth 2003, Allendorf and Allendorf 2012).

Fragmentation and isolation are among the key limitations of metapopulation maintenance (Wiens 1996, Hanski 1997, Prugh et al. 2008). I found that even the largest patches were negatively affected by isolation, suggesting that a centrally located network of moderate-sized populations has greater probabilities of occupancy than either the few large isolated populations or the smaller well-connected patches as shown by the lower probabilities of occurrence for the two largest, yet isolated patches of southern Tanzania. Further, I found the stochasticity parameter ($\hat{x}$) to be less than one for all models, implying that in this metapopulation, there is no patch immune from going extinct (Hanski 1992).

With only data on areas, locations and patch occupancies, I was able to analyze the effects of patch area, isolation and dispersal abilities on lion populations on a metapopulation scale. Since concern over lion extirpation throughout Africa is real and immediate, if lions are to persist throughout Africa, conservationists must incorporate available tools, including metapopulation approach and life-history traits, to understand the broader networks of populations and the movement between them. This knowledge will provide scientists with the leverage needed to make responsible and effective policy decisions about large-scale lion populations across Africa.

DISSERTATION CONCLUSION

The purpose of this dissertation was to investigate aspects of ecology, behavior, and conservation of lions outside protected areas in the context of human settlements, human persecution and livestock depredation. The group ranches of the Amboseli ecosystem were an ideal setting for this research as they combine a traditional pastoral community with high levels of lion predation on livestock and human retaliation against lions.

I investigated lion behavior and conservation at several spatial scales. In some cases, my work focused on the individual traits of a problem animal and in others I worked at the broader metapopulation level. To summarize the key findings of my studies: in Chapter I, I found that lions were able to adapt behaviorally and ecologically to human persecution. Persecution led to lower population density than found in protected areas, and basic aspects of behavioral ecology were affected: social groups were smaller and lacked the traditionally-observed pride structure, females reproduced earlier and were more likely to disperse, and mate fidelity was low, with males less likely to hold groups of females than observed in protected populations. I also elucidated the characteristics of ‘problem’ lions. By understanding the development of stock-raiding behaviors, conservationists and managers can implement effective mitigation measures of problem animal control, such as aiming lethal control only at known chronic stock-raiders and also recognizing that orphaned older cubs are likely to turn to stock-raiding.

In Chapter II, I studied the accuracy of non-literate Maasai warriors, trained in field biology techniques, including radio telemetry, spoor transects, and human-lion conflict mitigation, in monitoring a lion population. One biologist and 30 trained warriors were able to identify and monitor lions within a 3,684 km² unprotected area. The results of this chapter showed that incorporating local communities in lion monitoring can be an effective tool for both collecting data on elusive carnivores across a broad geographic scale, as well as improving predator conservation in rural communities. The study demonstrated that the simple method of walked spoor counts conducted by local community members can be an accurate technique for monitoring wildlife in rural landscapes and involving rural non-literate communities in wildlife studies. Deploying simple monitoring methods in a participatory framework can contribute greatly to wildlife monitoring and conservation.

In Chapter III, I tested a novel approach to detect lion presence near human habitations and found that although heavily persecuted by people, lions still regularly come in close proximity to Maasai settlements. Settlements nearer to protected areas are more likely to be visited by lions than those farther away. These findings suggest that informed conservation methods should focus on the settlements most likely to be visited by carnivores, so that conflict can be pro-actively mitigated. Furthermore, the results show that walked spoor transects can be an effective method to measure lion presence in Maasai settlements.

In Chapter IV, I present a metapopulation analysis that showed how the limited dispersal ability of female lions has implications for the conservation of the broader lion metapopulation of Kenya and Tanzania. In addition, contrary to many conservation approaches, no population, regardless of size, is unaffected by isolation from other patches, emphasizing the long-term importance of retaining viable populations in the non-protected areas between protected areas. The group ranches of the Amboseli ecosystem are a good example, providing connectivity between the Tsavo National Park complex, Amboseli National Park, and the lion populations of the Maasai Steppe in northern Tanzania.

The non-protected regions of the world are essential to carnivore conservation; if large carnivores can survive, as either populations at low densities or as dispersers moving between larger populations, there is hope for the future of wildlife conservation. Overall my work indicates that lions can and do persist in non-protected, human- and livestock -dominated areas in spite of decades of persecution. Relatively few studies have collected quantitative ecological data on an elusive, large carnivore population outside protected areas. While no single study can expect to provide definitive answers to a problem as broad and ancient as human-carnivore conflicts and coexistence, I hope my results will be useful locally, regionally and internationally and will contribute to the emergent conversation on wildlife adaptation to human-altered landscapes.

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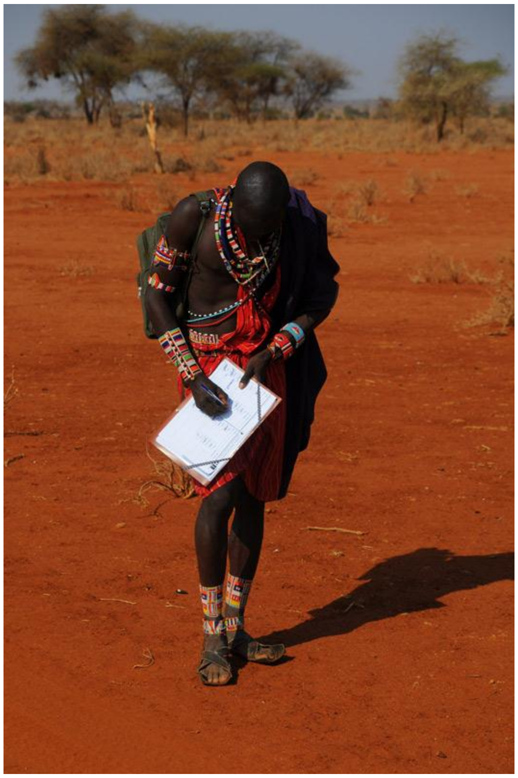
APPENDICES

Appendix 1

Photographs of spoor and spoor counting technique:

Photograph by S. Dolrenry

Photograph by P. Briggs



Photograph by P. Briggs