Demography, population dynamics, and the human-lion conflicts: lions in the Ngorongoro Crater and the Maasai steppe, Tanzania

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Chapter 1

General Introduction

Status of large carnivore populations worldwide

The world is currently experiencing high rates of species extinction. The current rate of species extinction is estimated to be 100 times higher than natural background rates (Gittleman and Funk, 2001; Baillie, Hilton-Taylor and Stuart, 2004). Species of large carnivores have faced dramatic contraction in their ranges and their populations have declined worldwide due to human population increases and fragmentation of habitat (Fuller, 1995; Gittleman and Funk, 2001). Some species of large carnivores (such as grizzly bear (*Ursus arctos horribilis*), black bear (*Ursus americanus*), gray wolves (*Canis lupus*), mountain lions (*Puma concolor*), and Florida panthers (*P.c. cory*) were in the verge of extirpation before concerted government conservation efforts were launched (Dunlap, 1988; Hummel and Pettigrew, 1991; Clark, Curlee and Reading, 1996; Laliberte and Ripple, 2004). In India, an estimated population of 40, 000 tigers (*Panthera tigris tigris*) 100 years ago has declined to less than 3600 (Check, 2006). The Asiatic lions (*Panthera leo persica*) once distributed across Northern Greece and Bengal is now restricted to a 1,400 sq km reserve in the Gir forest in India with only about 250 individuals remaining (Saberrwal et al., 1994). The wolf population in Europe declined dramatically following the industrial revolution, now there are signs of recovery due concerted conservation effort (Merrigi and Lovari, 1996). The African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*) and the African lion (*Panthera leo*) populations have all declined dramatically over the last three decades in most of their historical ranges. These species are now restricted in small and isolated reserves (Woodrooffe and Ginsberg, 1997; Ogada et al., 2003; Woodroffe, 2001; Patterson et al., 2004). In central and southern America, jaguar (*Panthera onca*) and puma (mountain lion) (*Puma concolor*) population decline have been documented since the 1960s (Polisar et al., 2003). The jaguar has completely disappeared in the southwestern USA, while the gray wolf has been eliminated in 97% of its range in the USA (Weber and Rabinowitz, 1996).

Therefore, it is not surprising that most species of large carnivores are classified as threatened or endangered in the International Union for the Conservation of Nature and Natural Resources (IUCN) red list (Baillie, Hilton-Taylor and Stuart, 2004).

The major threats facing large carnivore populations include habitat degradation, (Fuller, 1995; Nowell and Jackson, 1996; McKinney, 2001), over exploitation through hunting and use of body parts for medicine (Weber and Rabinowitz, 1996) and diseases can cause dramatic decline in populations and prevent population recovery (Woodroffe and Ginsberg, 1997; Packer et al., 1999; Kissui and Packer, 2004). Certain biological traits might predispose species to vulnerability of disappearance: Purvis et al., (2000) present an analysis of several predictions regarding traits that correlate vulnerability of extinction. They show that species with small geographical range, low density, species at higher trophic level of food chain and low reproductive rates tend to show higher vulnerability of extinction. Unfortunately, most of these attributes occur in most of the large carnivore species, suggesting that long-term conservation of these species presents an enormous challenge to conservation biologists and wildlife managers. Cardillo et al., (2004) and Purvis et al., (2000) have further shown that risks of disappearance of carnivorous species increased dramatically by the interaction between biological traits and exposure to anthropogenic influences. Perhaps the most serious anthropogenic threat to large carnivores is human-carnivore conflicts mostly involving livestock predation and occasionally attacks on humans (Packer et al., 2005).

Management of carnivore populations

Wildlife management is the management of wildlife populations to attain a particular goal, which is often to increase the population, decrease the population, sustain harvested yield or maintain the population at a particular desired level. It can be manipulative by direct or indirect alteration of some aspects in the ecosystem such as food supply or control of disease epidemic to influence numbers in the population. It can also be protective in which external influences to the population are minimized (Sinclair, Fryxel and Caughley, 2006). This definition is centered on the population itself, which is the core of management. However, a broader definition of wildlife management need be more holistic to include the human dimension in the management of wildlife populations.

In recent years, it has become increasingly clear that management of wildlife populations can not succeed without the involvement of the people living in constant interaction with the wildlife, especially in human-dominated landscapes (Newmark and Hough, 2000). This framework plays a pivotal role in the current effort by governments and conservation entities in promoting and improving the strategies for carnivore conservation (Primm, 1996; Weber and Rabinowitz, 1996; Maddox, 2003; Mishra et al., 2003). The extirpation of carnivores in many parts of the world due to direct persecution by humans led to the establishment of laws to protect and regulate the exploitation of carnivorous animals (Fuller, 1995; Baillie, Hilton-Taylor and Stuart, 2004).

Securing wildlife habitat is an important first step to the protection of carnivores; this is especially important because of the widespread destruction of wildlife habitat, blockage of wildlife migratory corridors and reduction of natural prey which constitutes carnivore conservation threats (Woodroffe, 2000). However, habitat protection by itself is not adequate to stem the decline in carnivore populations, application of behavioral and ecological research on carnivore species, social and geo-political considerations need to be taken into account. Various forms of carnivore population management strategies are practiced today as a result of advances in ecological research and management techniques. Some notable examples include reintroduction of carnivore species in areas where extirpation had occurred e.g. wolves reintroduction to Yellowstone National Park (Weber and Rabinowitz, 1996) and lynx reintroduction in Colorado (Scott, Murray and Griffith, 1999) in the USA. Lion translocation experiments have been conducted in several South African reserves such as Hluhluwe Umfolozi Park and Makalali Reserve as efforts to invigorate the gene pool of small and isolated populations. However, the success of any reintroduction/translocation depends on many factors, such as detailed understanding of behavior and ecology of the targeted species, and translocation of wildlife remains controversial among some wildlife managers and conservationists.

More support from governments and NGOs to put in place initiatives for carnivore conservation has led to the listing of some carnivore species as vulnerable, threatened or endangered on the IUCN red list with major implications on the levels and options of consumptive utilization (Baillie, Hilton-Taylor and Stuart, 2004). In 2004 concerns over the current status of the African lion led to a proposal to the Convention on

International Trade in Endangered Species of Wild Fauna and Flora (CITES) to upgrade its current listing on appendix II to appendix I, which would have effectively ended its current consumptive utilization including trophy hunting in range states. Weber and Rabinowitz, (1996) present some examples of the deliberate initiatives taken by various individuals, organizations and governments to reverse the declining populations of some of the world's large carnivores.

Scientific research on behavioral ecology and population dynamics of individual carnivore species have led to the development of a host of tools and concepts for conserving carnivore populations (see Shivik, 2006). Theoretical and empirical modeling approaches play a big role in determining management options and implications of different carnivore population dynamics and management approaches (Treves and Karanth, 2003).

Population regulation

In ecology, population regulation is fundamental to understand various processes in a population including intraspecific competition, predation dynamics and evolutionary processes (Murdoch 1994; Sinclair, 2003). The past century saw many debates regarding the mechanisms and the empirical basis of population regulation (Kingsland, 1995). In recent years, however, there is more consensus among ecologists regarding the concept of population regulation (Sinclair, 2003). Turchin, (2003) provides a detailed review of the literature on population regulation and offer a unified explanation behind the notion of population regulation.

Population regulation is closely linked to the concept of density-dependence. Density dependence is a functional relationship between per capita rate of population change and population density (Murdoch, 1994; Sinclair, 2003). One aspect of interest that has occupied ecologists for decades has been the detection of whether regulation in a population occurs or not (Murdoch, 1994), and the ecological mechanisms behind it (Turchin, 2003; Sinclair, 2003). For regulation to occur, some form of negative feedback between per-capita growth and population density is necessary (Turchin, 2003). The ultimate goal is to determine mechanisms that explain regulation. Although extensive research is now available on population regulation especially for ungulate species (e.g.

Sinclair, Dublin and Borner, 1985; Keith, 1983) and small mammalian populations (e.g. Turchin, 2003), little is known about regulation of large mammalian carnivore populations such as the African lion.

The African lion

Ecology and behavior

Among felids, the African lion is the only social member in which related females band together in groups called prides. A pride comprises an average of 2-9 related females (range 1-18), their dependent cubs, sub-adults and a resident coalition of 2-6 males (Schaller, 1972; Bygott, Bertram and Hanby 1979; Packer, Scheel and Pusey, 1990; Packer and Pusey, 1993). Female lions reproduce all-year round, litters are commonly born synchronously within a pride (Bertram, 1975). Cubs born less than one year apart constitute a cohort (Packer and Pusey, 1993). Gestation averages 110 days with a mean inter-birth interval of 20 months (Schaller, 1972). Litter size in lions range from 1-6, but in the wild over 98% of litters contain between one to four cubs, with 70% containing two to three cubs (Packer and Pusey, 1987). Cub mortality is highest in the first year; it drops dramatically from year 3 and stays at lower levels until the 11th year when it picks up again (Packer, Tatar and Collins, 1998).

Prides are territorial; they defend exclusive territories against other prides and often occupy the same range over several generations (Schaller, 1972; Packer and Pusey, 1993). Individuals in the same pride usually interact amicably except for occasional squabbling when feeding at a carcass. Lions can identify others by roaring, thus it is possible to identify intruders to a territory (McComb, Packer and Pusey, 1994). In Serengeti, the pride size appears to be density dependent and new pride formation is by emigrating females (Betram, 1973; Hanby and Bygott, 1987).

Individual lions in a pride sometimes hunt cooperatively, and cooperative hunting was originally proposed as an evolutionary force for social living in lions (Schaller, 1972). Macdonald, (1983), suggested resource dispersion to have been the evolutionary catalyst for group living, and might have produced constraints leading to the evolution of sociality in mammalian species. However, Packer, Scheel and Pusey, (1990), showed that foraging requirement was not sufficient to explain the observed grouping pattern seen in lions. Instead, they suggested that lions grouped to protect their young against infanticide. The need to maintain territory and females' reproductive success patterns all strongly influenced lion grouping. The most recent analysis of group living and territoriality in lions by Mosser, (2008), suggest that habitat heterogeneity could have enhanced the evolution of territoriality in lions because, as despots, large prides out-compete small ones over high quality resource patches.

A cohort of young males born in a pride forms a coalition. They leave their natal pride to enter a nomadic phase of life as a group before sexual maturity. A new male coalition gain residence into a new pride by evicting the existing coalition (Bygott, Bertram and Hanby, 1979), and evicts or kills any cub less than 2 years old (Packer and Pusey, 1984). While male coalitions may comprise of siblings or closely related males, unrelated male companions (Bygott, Bertram and Hanby, 1979; Packer and Pusey, 1982) may also form coalitions. The dispersing male coalitions can move over considerable distances from their natal prides like in the Serengeti plain (Hanby and Bygott, 1987; Pusey and Packer, 1987), but might also settle closer to their natal pride like in Kruger NP (Funston et al., 2003). Males engage in territorial patrols and defense of their cubs. Therefore, male presence is crucial for cub survival and successful recruitment of offspring. A coalition should retain residence for at least two years to successfully raise their young; frequent replacement of resident males severely depress cub recruitment, and could have cascading effects leading to the overall population decline (Whitman et al., 2004; Loveridge et al., 2007). Larger male coalitions have high per-capita reproductive success (Bygott, Bertram and Hanby 1979).

The diet of the African lion constitutes a broad range of prey species that vary between habitats depending on the most common and locally available prey species. Medium (100-300kg) to large (average 400+kg) prey is the most preferred range of species (Hayward and Kerley, 2005). Lions can take prey as small as warthog (Scheel and Packer, 1995) and in the Ngorongoro Crater I have observed lions prey upon an ostrich. The preferred prey in the Serengeti NP, Ngorongoro Crater and Kruger NP are the medium size wildebeest and zebra, and the large buffalo (Schaller, 1972; Mills and Shenk, 1992; Scheel 1993; Funston, Mills and Biggs, 2001; Kissui and Packer, 2004). In a review paper, Sunquist and Sunquist, (1997), have shown that abundance of prey species, size of the prey, temporal and spatial distribution of prey and defense and anti-predatory tactics of the prey may affect prey preferences for lions. In addition, environmental factors such as vegetation height, time of the day, terrain, may all affect the hunting success and therefore prey preference of a predator (Mills, Biggs and Whyte, 1995; Funston, Mills and Biggs, 2001; Hopcraft, Sinclair and Packer, 2005). Predator related behavioral traits such as grouping pattern and hunting strategy may also influence prey preference and hunting success (Packer, Scheel and Pusey, 1990).

Human-lion conflicts

The International Union for Conservation of Nature (IUCN) lists persecution of carnivores by humans through intentional killing with weapons or poison as a top threat to long-term survival of many wild carnivore populations. Human-carnivore conflicts are prevalent in areas where people live adjacent to protected areas. Most wide-ranging carnivores utilize areas adjacent protected areas as part of their home ranges, thus come into frequent contact with people (Meriggi and Lovari, 1996; Sillero-Zubiri and Laurenson, 2001; Macdonald and Sillero-Zubiri, 2002; Woodroffe and Frank, 2005, Kolowski and Holekamp, 2006). The drivers of human-lion conflicts include rapidly growing human population with the associated land-use changes and habitat fragmentation. People move to areas closer to wildlife thus encroaching on wildlife habitat. The decline in wild prey may cause carnivores to shift to predate livestock (Mishra et al., 2003). Some ecosystem level processes such as seasonal migration of ungulates may influence livestock predation patterns like in the Northern Tanzania's Maasai steppe ecosystem (*ibid*) where livestock predation by lions and hyenas is higher in the wet season when these predators follow the migratory herbivores into dispersal areas in communal lands. Environmental factors can influence livestock predation; Patterson et al., (2004) reported a correlation between monthly rainfall and attacks on livestock by lions in the Kenyan reserve, Tsavo NP. Variations in habitat and the local abundance and distribution of natural prey could influence livestock predation pattern (Polisar et al., 2003; Patterson et al., 2004; Woodroffe and Frank, 2005).

A wide range of management tools are being developed and applied to mitigate the impact of humans on carnivore populations. In areas where traditional livestock husbandry is still practiced like in the Maasai landscapes of Eastern Africa, studies have shown that some alterations in husbandry can improve livestock security and reduce livestock losses (e.g. Ogada et al., 2003; Kolowski and Holecamp., 2006, Woodroffe et al., 2007). Livestock predation is a behavioral trait manifested by certain individuals in a population becoming habitual livestock killers (Stahl et al., 2002; Mitchell, Jaeger and Barret, 2004), and lethal control has been advocated where it is possible to identify specific individuals as habitual livestock killers (Woodroffe and Frank, 2005). Shivik, (2006), provides a detailed description of contemporary tools and concepts for managing predators.

Study sites

This study was conducted in two sites; the Ngorongoro Crater (Fig. 1.1) and the Maasai steppe (also known as Tarangire-Manyara ecosystem) (Fig. 1.2). The lion populations in these sites have contrasting ecological environment. Here I will provide a general background about each study site and introduce the key questions explored. Additional details on the study sites are provided in chapters where respective questions are treated.

The Ngorongoro Crater

The Ngorongoro Crater Area (NCA) (Fig. 1.1) is an 8,292 km^2 multiple land-use area in which human development activities as well as wildlife conservation and tourism are carried out concurrently. Within the NCA is the largest caldera in the world believed to have formed due to volcanic activities to the west of the Gregory Rift Valley. This caldera has generally been called the Crater and hence the name Ngorongoro Crater. The Crater floor is about 250km^2 and about 400-610m deep. The NCA is inhabited by teeming numbers of herbivore and carnivore populations. Significant changes in the wildlife populations have occurred in the Ngorongoro Crater over the last 2-3 decades: the abundance of several major herbivore species have changed, for example, Cape buffalo increased dramatically from an average of about 1280 animals (in 1978, 1980 and 1981) to an average of 3980 animals from late 1998 to early 2000, an increase of over 200%. Wildebeest decreased from an average of about 13920 animals (1978-80) to an average of about 11230 animals (1998-2000), while zebra remained nearly constant at an average of about 4080 animals (1977, 1978 and 1980) versus 4180 animals (1998-2000) (Runyoro et al., 1995; Estes, 2002; Estes, Atwood and Estes, 2006).

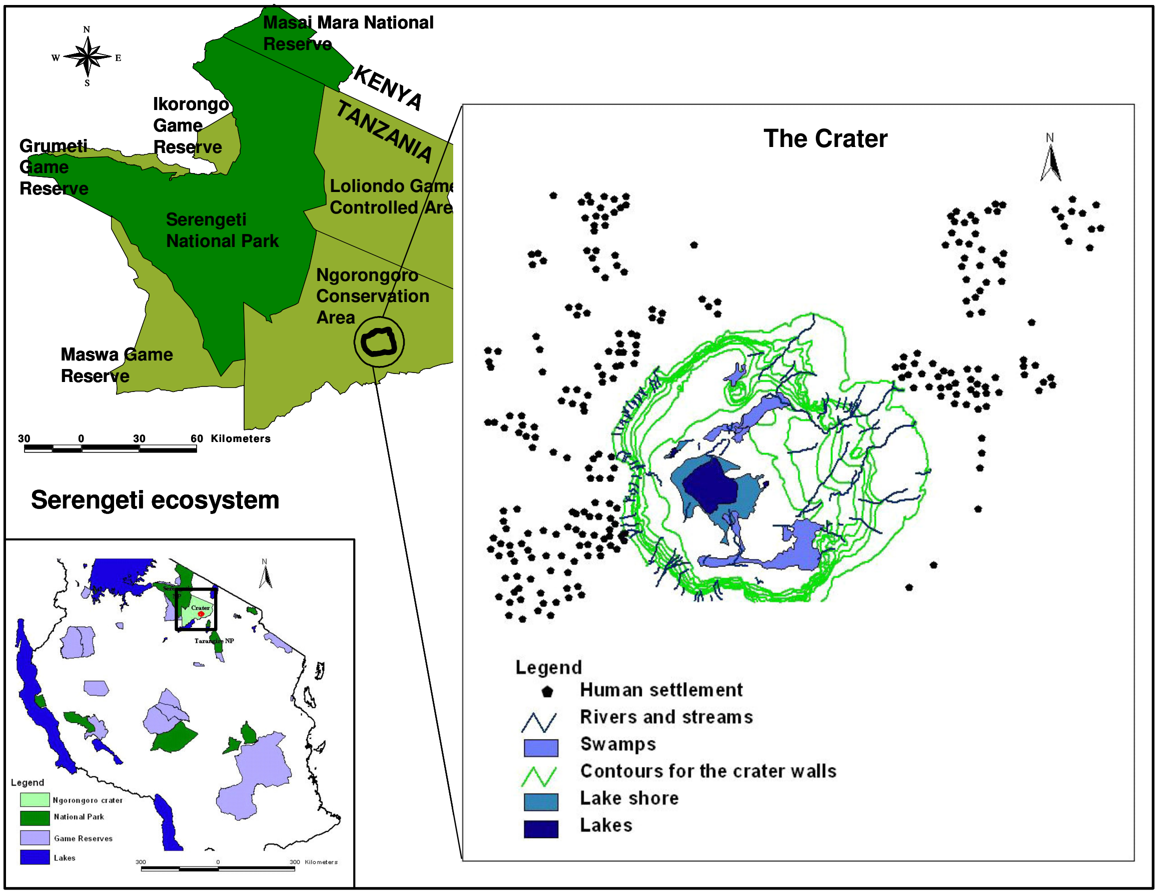


Figure 1.1. Map of the Serengeti ecosystem with the Ngorongoro Conservation Area (NCA), and location of the Crater. The distribution pattern of human settlement adjacent the Crater was adapted from Tanzania Wildlife Research Institute (TAWIRI) survey conducted in 1998.

In the mid 1980s, the lion population in the Crater started declining from more than 120 individuals, the number reached in the early 1980s to fewer than 40 in 2002 after several years of stead growth (Fig. 1.2). The Crater lions have been monitored continuously since the 1960s. For a long period no lion has been recorded to have successfully immigrated into the Crater and establish breeding status. So, breeding has been between genetically related individuals over several generations. This has raised concerns over the genetic integrity of the Crater lions and the effects associated with inbreeding depression. Packer et al., (1991) assessed the genetic status of the Crater lions and found lower heterozygosity and higher levels of sperm abnormality compared to the adjacent Serengeti and Manyara lion populations. Sea lions have been found to be more susceptible to diseases due to inbreeding depression (Acevedo-Whitehouse et al., 2003), but more research is needed to understand the role of inbreeding in demography and persistence of wild populations (Keller and Waller, 2002).

The observed persistent declining trend of the Crater lion population prompted the need to understand factors limiting population growth. There were two research questions of interest: first, what are the limiting factors for the Ngorongoro Crater lion population growth? What mechanisms are responsible for holding the population at a persistently low level? Could it be disease or food related limitation? Using long-term data I tackle this question in chapter 2 and provide insight into the factors responsible for the observed population trends. The second question is how the landscape, lion population demography and anthropogenic factors affect the persistence of individual lion prides in the Crater? Could it be cub productivity, adult female mortality, landscape related factors or anthropogenic factors? These questions are explored using long-term lion demography data in conjunction with the landscape and human influences in chapter 3.

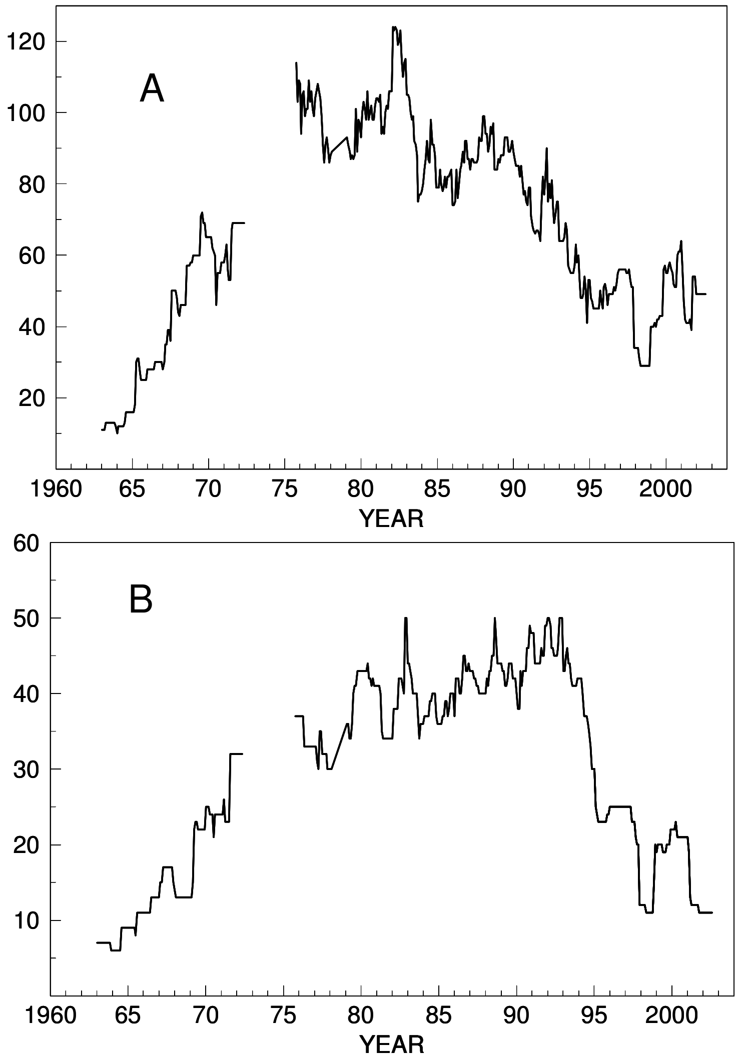


Figure 1.2. Monthly population size of the Ngorongoro Crater lions from 1963-2002. A: total population (adult male, adult female and cubs); B: number of adults (males + females). No observations were made during (1973-1974).

The Maasai Steppe

The second study area, the Maasai steppe, includes the lion population in Tarangire National Park and the areas surrounding the Park (Fig. 1.3). The Tarangire lions remain safely within the confines of the National Park during the dry season, but they spend up to six months in dispersal areas in village land during the wet season (Fig. 1.4). This suggests that Tarangire lions are highly dependent on communal lands during half of the year. Tarangire NP (2,600 km^2) borders Simanjiro Game Controlled Area (GCA) to the east. To the north-east, the Park borders Lolkisale GCA. To the north, Mswakini juu and Mswakini chini villages are immediately adjacent to the Park border. To the south, the Park borders Mkungunero (GCA), while Lake Burunge GCA is to the west (Fig. 1.3). Tarangire NP is 1100-1500m above sea level, located approximately $3^{0}\,50^{'}$ S and $36^{0}\,00^{'}$ E. The Maasai steppe experiences two major seasons, the wet season (November-May) and the dry season (June-October) with an average annual rainfall of about 600mm. Characterised by an arid woodland savannah climate, the Maasai steppe has undulating landscape dominated by *Acacia spp* and baobab trees especially in Tarangire NP. Other vegetation type associations include riverine grassland, combretum-Dalbergia woodland, and *Euphorbia spp*.

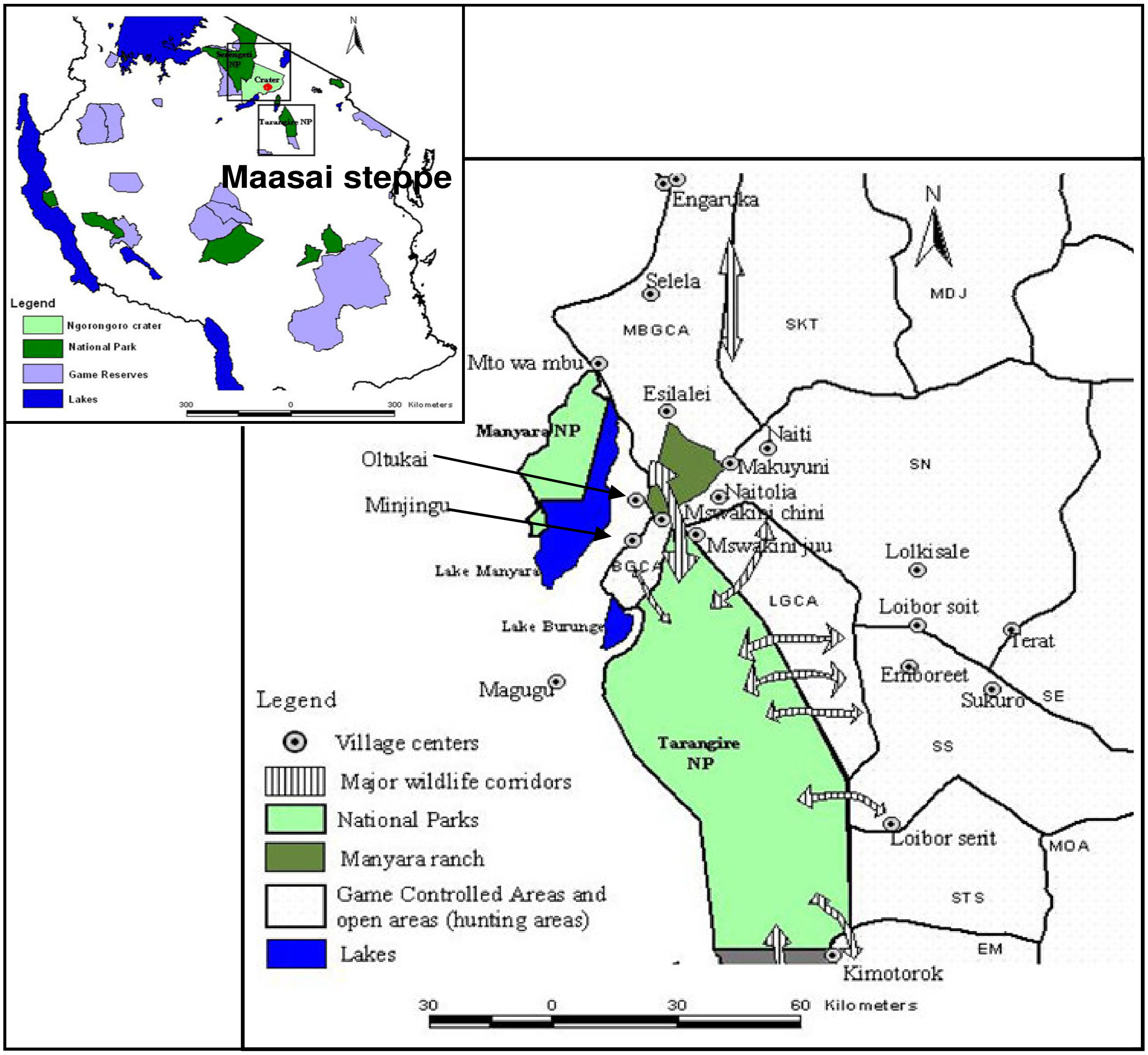
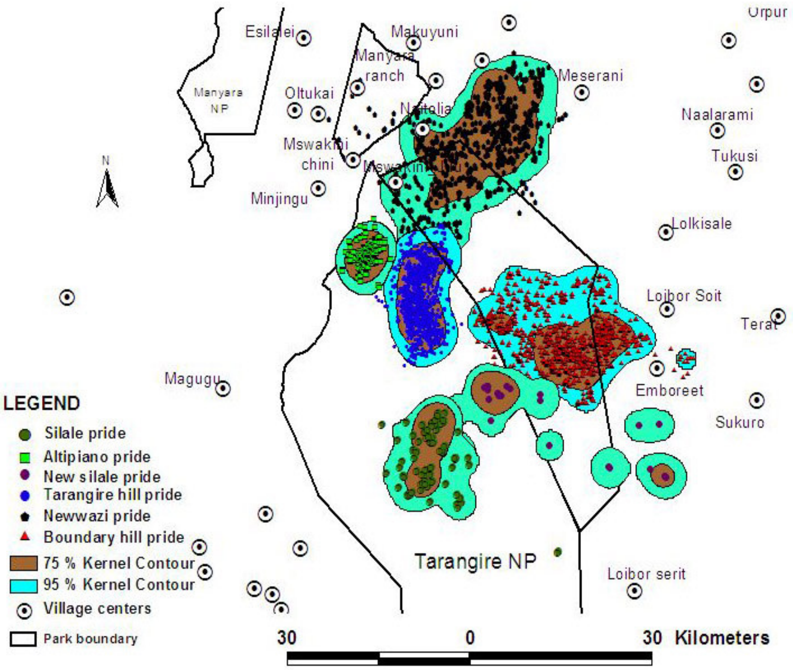


Figure 1.3. Map of the Maasai steppe showing Tarangire NP, Manyara NP and the surrounding village and hunting areas. Names of hunting areas shown: EM = East Mkungunero, STS = Simanjiro, MOA=Masai open area, SS= Simanjiro South, SE = Simanjiro East, SN = Simanjiro north, LGCA = Lolkisale Game Controlled Area, BGCA = Burunge game controlled area, MBGCA = Mto wa mbu game controlled area, SKT = Kitumbeine, MDJ = Monduli juu. Major wildlife corridors are mapped according to studies by Kahurananga and Silkiluwasha, (1997) and TMCP, (2000).

Home ranges (kernel contours) and locations of some Tarangire lions during the wet season



Home ranges (kernel contours) and locations of some Tarangire lions during the dry season

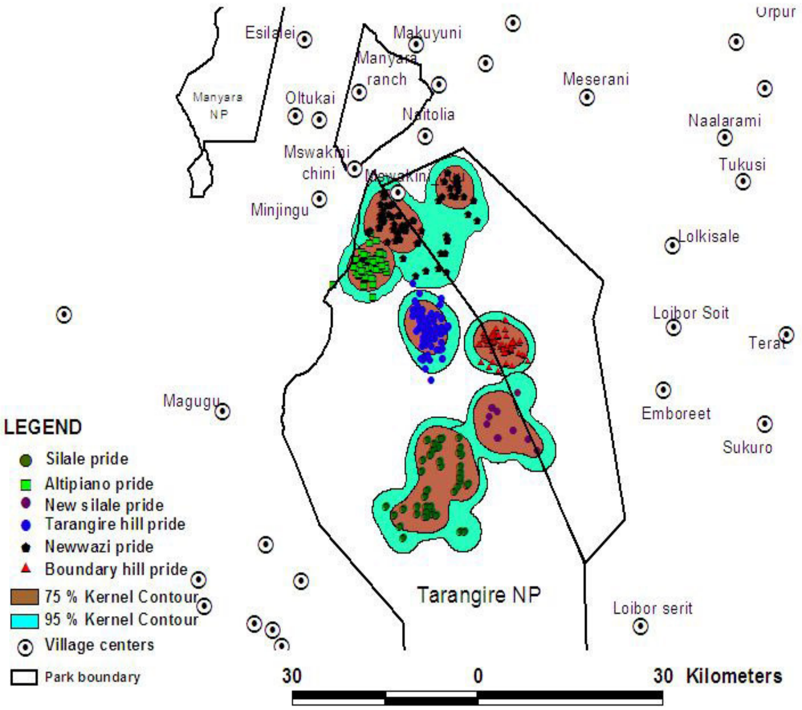


Figure 1.4. Seasonal movement of lions between Tarangire NP and the adjacent communal village lands. The home ranges represent 75% and 95% kernels estimation. Each dotted color represents different pride. Data collected 2003-2007.

Tarangire lion population ecology and demography

Monitoring of the Tarangire lion population has been underway since 1998. Observations were made opportunistically until 2003 when radio telemetry became the primary technique for collecting ecological and demographic data. The use of radio telemetry has made it possible to collect detailed information on seasonal movement pattern (Fig. 1.4) and information on mortality, recruitment and reproduction. The monthly total number of lions present in the study area over 2003-2007 is presented in Figure 1.5. In 2005, the population showed a brief recovery from the 2004 drop, but the numbers have declined persistently since 2005 with the largest drop in 2006. The 2005/2006 drought that occurred in the general Maasai steppe region might have exacerbated the huge decline in lion numbers in 2006. The first half of 2007 showed some signs of recovery, but it remains to be seen if the upward trend will be sustained to reach the 2003 levels.

When lions leave the Park at the onset of the wet season and spend up to six months in the villages they are subject to retaliatory killing by livestock keepers due to livestock predation. Lions are also subject to killings due to trophy hunting while out side the Park during half of the year. It is possible that the levels of retaliatory lion killing might have increased in recent years thus more lions are simply falling victim to retaliatory killings when they venture outside the Park. On the other hand, the level of off-take from trophy hunting might have also increased in recent years. Thus, the combined effect of retaliatory killing and trophy hunting might be depressing the lion population growth in Tarangire NP. This is a typical case of the edge effect on a population of a large carnivore. At least 133 lions have been killed in retaliation to livestock predation from 2004 to July 2007 in villages around Tarangire (see chapter 4), but the levels of recent trophy off-take in hunting blocks adjacent Tarangire NP are unknown.

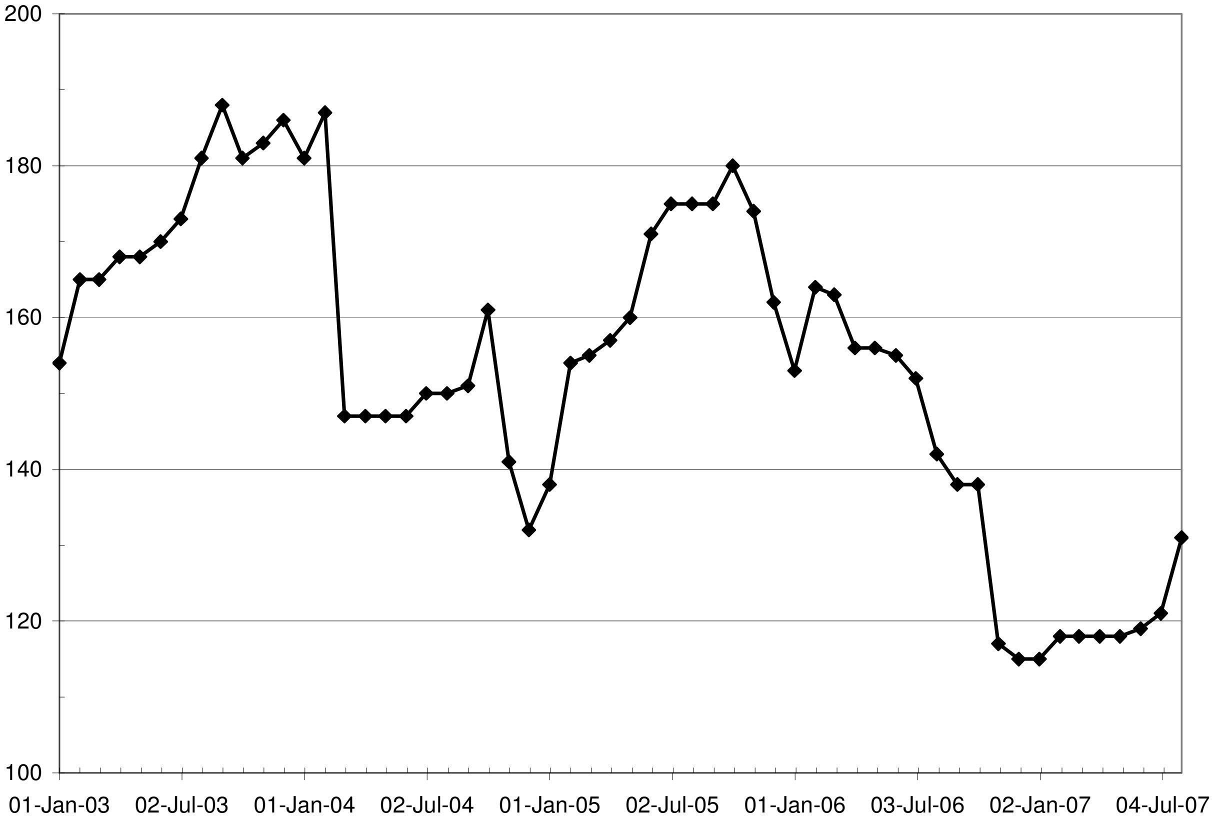


Figure 1.5. The monthly numbers of lions in Tarangire NP's core lion study area over the 2003-Jul 2007

The age-sex structure of the Tarangire lion population (Fig. 1.6) shows a fairly equal sex ratio for juveniles and sub-adults, but many more adult females than adult males, suggesting either higher male dispersal rates from the study area or much higher male mortality rate. Adult sex ratios in the Serengeti and Ngorongoro are roughly 3-4 females per male whereas the ratio in Tarangire is closer to 10 females per male. The very low number of adult males may reflect high off-takes from hunting that encircle the National Park or greater numbers of males being killed in retaliation for cattle killing (human-lion conflicts).

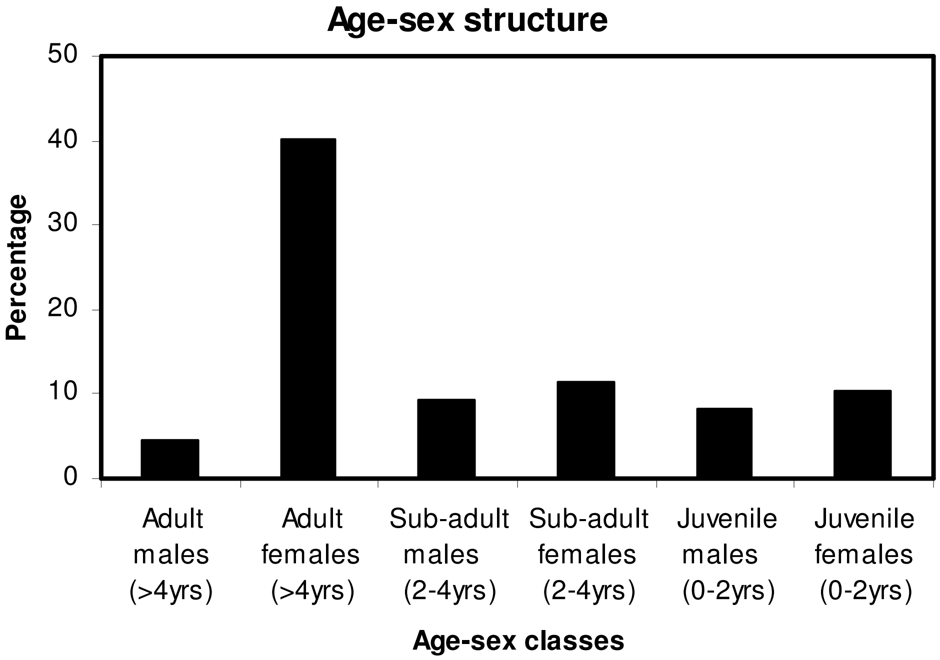


Figure 1.6. Age-sex composition of the Tarangire lion population for data collected during 2003-2006

The primary inhabitants in the Maasai steppe are pastoralists. Because of the extensive seasonal movement by lions (Fig 1.4) between the park and dispersal areas adjacent the park, there is increased potential for livestock predation. The Maasai pastoralists suffer livestock losses and they retaliate by killing predators indiscriminately. In chapter 4, I investigated the pattern of livestock predation by lions and compared it to spotted hyenas (*Crocuta crocuta*) and leopards (*Panthera pardus*) which also engage in livestock predation. I compared how retaliatory killing due to livestock predation affected these three species of predators.

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Chapter 2

Top-down population regulation of a top predator: lions in the Ngorongoro Crater

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Summary

Efforts to determine whether populations are regulated by bottom-up or top-down processes have been hampered by difficulties in accurately estimating the population's carrying capacity and in directly measuring food intake rate, impacts of interspecific competition and exposure to natural enemies. We report on 40-yrs data on the lion population in Ngorongoro Crater, Tanzania, which showed strong evidence of density dependent regulation at 100-120 individuals but has remained below 60 for the past decade despite consistently high prey abundance. The lions enjoy higher per capita food intake rate and higher cub recruitment at low population density, and inter-specific competition has not increased in recent years. These animals have suffered from a number of severe disease outbreaks over the past 40 years, but whereas the population recovered exponentially from a severe epizootic in 1963, three outbreaks between 1994 and 2001 have occurred in such rapid succession that the population has been unable to return to the carrying capacity. The Crater population may have become unusually vulnerable to infectious disease in recent years due to close proximity to a growing human population and a history of close inbreeding. The Crater lions may therefore provide important insights into the future of many endangered populations.

Introduction

Populations can either be regulated by "bottom-up" processes (e.g. food limitation) that are inherently density dependent or by "top-down" processes (e.g. "natural enemies" such as predators or parasites) that operate independently of population density. In food-limited populations, reproductive output declines through reduced pregnancy rate, delayed maturity and/or lower survival as the population approaches the "carrying capacity," and density-dependent effects directly contribute to population regulation through competition for food (e.g. Sinclair, *et al.*, 1985; Mduma, *et al.*, 1999). While the incidence of infectious disease generally increases with population size (Anderson & May 1991), incidence of multi-host pathogens can be essentially independent of population density in a given host species (Cleaveland, *et al.*, 2001). Infectious disease can make a significant impact on population size (Holmes 1982; Scott & Dobson1989) and may persistently hold populations below carrying capacity (Sinclair1979; Torchin, *et al.,* 2003; Mitchell & Power 2003).

Carnivore populations appear to be sensitive to all of these factors. Food shortages are known to play an important role in infant mortality through abandonment (Packer & Pusey 1984), and starvation (e.g. Packer & Pusey 1995); social behavior can also have a considerable impact through infanticide (Packer 2001) and territoriality. Disease outbreaks can reduce population sizes by over 35% (Fosbrooke 1963; Roelke-Parker, *et al.*, 1996; Sillero-Zubiri, *et al.*, 1996; Peterson, *et al.*, 1998), and competition with other carnivores can be severe both through feeding competition (Cooper1991; Mills & Biggs 1993) and predation (Kruuk 1972; Laurenson 1995, Crabtree & Sheldon 1999; Durant 2000). In small isolated populations, inbreeding may play an additional role by reducing reproductive rates (Peterson, *et al.*, 1998) or rendering individuals more susceptible to disease (Acevedo-Whitehouse, *et al.*, 2003; Reid, *et al.* 2003).

Although numerous inferences have been made about population regulation in carnivores, most studies have been too narrowly focused to provide comprehensive data on demography, ecology and genetics. The field has consequently been mired in controversy, e.g. the demise of the Serengeti wild dogs (Burrows, *et al.,* 1994 vs. Creel 2001) and the genetic vulnerability of cheetah (Caro & Laurenson 1994 vs. O'Brien 1994). In this paper, we provide the first direct measurements of food availability, interspecific competition, infectious disease and infanticide in a well-defined population. The lions of the Ngorongoro Crater, Tanzania have been monitored since the early 1960s, and there is virtually no immigration into the Crater population. These animals have a known history of close inbreeding (Packer, *et al.,* 1991), and lions are an excellent species for assessing the mechanistic role of food limitation (Krebs 1995), since recent food intake can be measured both from the size of their prey and the profile of their bellies (Bertram 1975; West & Packer 2002). Prey availability is also easily measured since the Crater herbivores have been censused regularly for the past 40 yrs (Runyoro, *et al*., 1995). We utilize all available data between 1963 and 2002 to assess long-term changes in prey abundance and the impact of disease outbreaks on the lion population, but our detailed data on diet and food intake were collected during two intensive study periods: 1982-1983, when the Crater population reached its all-time high and averaged 105 individuals (Cairns 1990), and 1999-2000, when the population averaged only 50 individuals and a severe drought provided a temporary boost in food availability (Kissui 2001).

Materials and Methods

The Ngorongoro Crater is a 250 km^2 caldera located at the western edge of the Gregory Rift with walls 400-610 m high (Fig. 2.1). The Crater floor enjoys a year-round supply of water from seasonal rainfall and permanent streams originating from the Northern Highland catchment forest, supporting large numbers of resident ungulates through persistent grass growth at the edges of marshes and swamps (Estes 2002). Individual lions are identified from whisker-spot patterns (Pennycuick & Rudnai 1970) and natural markings (Packer, *et al*., 1991). Dates of birth are inferred from characteristic behavior of females around parturition (Packer, *et al*., 2001). During the two intensive study periods, every individual in the population was located 2-3 times every 10 days, and prey selection/preferences were estimated from census data collected in 1978-1980 and 1998-2001. Major herbivore species have been censused by ground counts conducted in the wet and dry season most years since 1964 (Runyoro, *et al.,* 1995; Estes 2002).

Diet and food intake were recorded from 0630-1830 hrs with a 2-3 hr gap in the afternoon. Carcass data included species, age-sex class (based on body size, size/shape of horns, and coat color) (Sinclair 1977). “Observed food intake rate” is the total biomass of carcasses obtained during each study period divided by the total number of "female sightings." "Female sightings" are tabulated as follows: a lone female observed on three days contributes three female sightings, whereas a group of five females observed on two days contributes 10 female sightings.

As an upper limit of carcass biomass, we assume that the lions always consumed the entire carcass; as a lower limit, we assume they only consumed the amount still available when first observed. Estimates are adjusted according to live weight, total carcass weight, proportion of lean meat and proportion of inedible matter (Sachs 1967; Packer, *et al.*, 1990). At the onset of each observation, the carcass was categorized as 1: intact, 2: viscera partially absent but muscle tissue intact, 3: viscera absent but muscle intact, 4: three-fourths of muscle remaining, 5: half remaining, 6: quarter remaining. We also estimated recent food intake from the standing profile of each lion (Bertram 1975), which provides a more complete measure of food intake, including night-time feeding when lions are most active, and indicates whether a lion has fed even when no carcass had been observed. The belly scale ranges from 1, indicating maximal distension, to 5 at increments of one quarter (0.25). Bone-marrow condition reflects fat content and, hence, health at death (Sinclair & Arcese 1995). Samples were obtained from long bones, and five categories were scored according to texture and color: solid white fatty, white opaque gelatinous, translucent gelatinous, red gelatinous and absent. For multiple carcasses, weight and health of the median carcass was used.

We estimated the selection ratio ($\hat{w}_i$) for a prey species *i* as (o_i / π_i), where o_i is the proportion eaten and π_i is the proportion in the prey population (Höner, *et al.,* 2002, Manley, *et al.*, 1993). The standardized selection ratio (B_i) is calculated as $\hat{w}_i / (\sum_{i=1}^{I} \hat{w}_j)$ and estimates the probability of a particular prey species *i* being selected if all prey types were equally available; standard errors and χ^2 statistics were determined following Manly, *et al.* (1993). Statistical analyses used SAS for Windows V8 Release 8.2; p-values are two tailed.

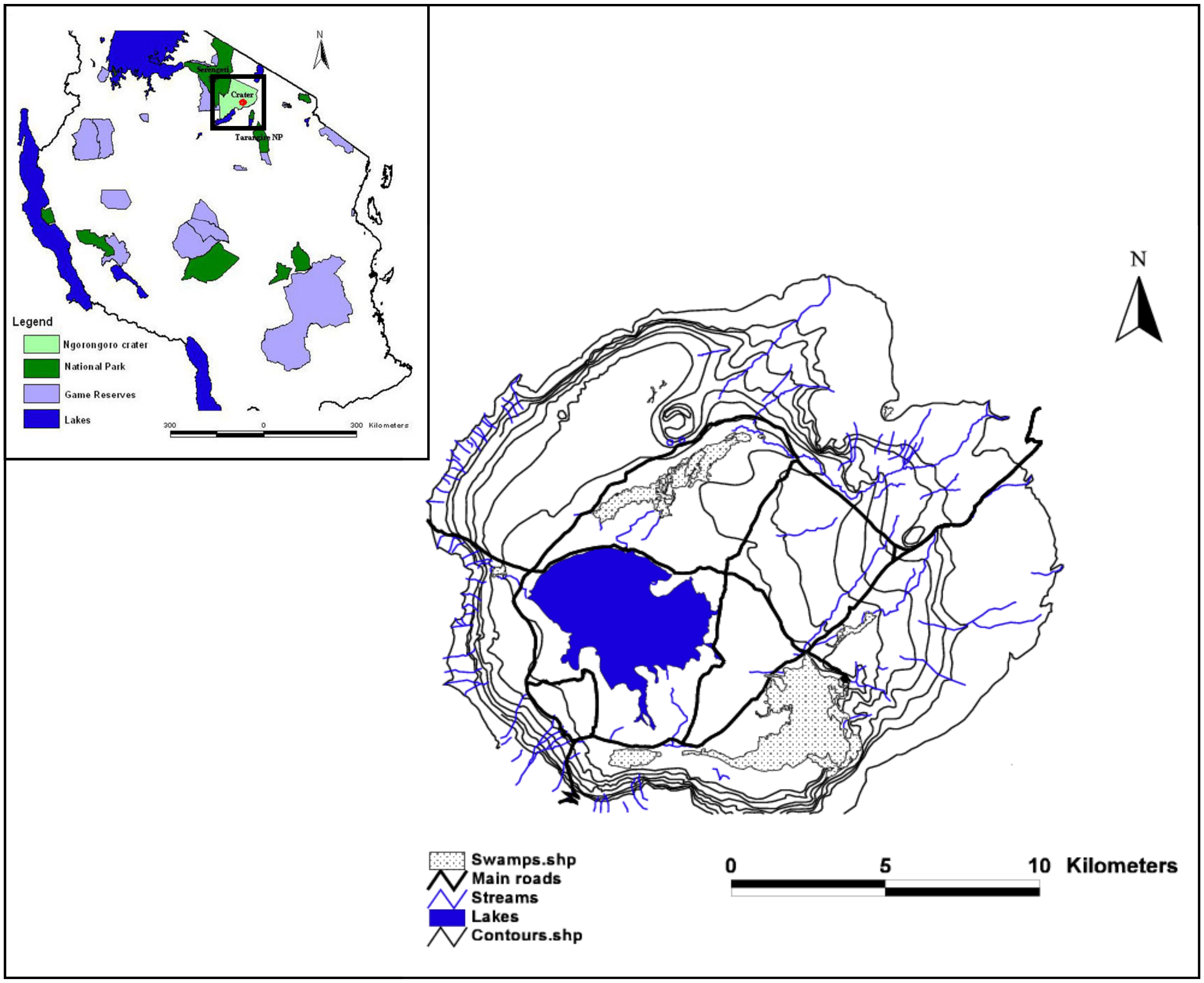

Figure 2.1. Map of the Ngorongoro Crater floor

Results

In 1962, the Crater lion population crashed from 75-100 to 12, coincident with an outbreak of blood-sucking stable flies (*Stomoxys calcitrans*) (Fosbrooke 1963; Packer, *et al.*, 1991). Subsequently, the population climbed rapidly to reach 100+ by 1975 (Fig. 2.2a), then averaged around 100 until 1983 when it went into a persistent decline, and it has generally remained below 60 animals since 1993, reaching a low of 29 in 1998. At a coarse level, these changes are not correlated with an overall change in prey availability on the Crater floor, either in terms of the number of medium-size herbivores (wildebeest plus zebra) or of Cape buffalo (Fig. 2.3). We combine zebra with wildebeest because lions catch both species with similar success, but buffalo are more formidable (see below).

The abundance of buffalo and wildebeest changed between the intensive study periods: buffalo increased over 200% from 1,280 in the high-lion-population-density years (1978, 1980-81) to 3,982 in the low-lion-population pre-drought years (1998-2000), whereas wildebeest decreased by about 20% from 13,924 animals (1978-80) to 11,234 (1998-2000). Zebra remained nearly constant at about 4,081 (1977-78, 1980) vs. 4,184 (1998-2000). During the drought of 2000, the Crater buffalo fell by 45% to 2,206 by early 2001 (Estes 2002), but wildebeest (10,956) and zebra (3,852) were largely unaffected. Table 2.1 presents selection indices and prey preferences for the lions during "high lion density" (1982/3), "low lion density – pre-drought" (1999-March 2000), and "low lion density – drought" (May.-Nov. 2000). The standardized selection ratios (B_i) indicate that at high population density, the lions selected buffalo more often than wildebeest and zebra, and both buffalo and zebra were taken more often than expected from their abundance. During both low lion-density study periods, lions selected buffalo more than zebra and wildebeest, and buffalo were taken more often than expected from abundance, but the selectivity for buffalo was far higher during the drought. We categorized prey into large (>300 kg live weight: adult buffalo, eland, rhino and hippo), medium (100-300 kg: adult wildebeest, zebra and hartebeest, yearling buffalo, and hippo and rhino calves) and small (<100 kg: adult gazelle, reedbuck, warthog and ostrich, and wildebeest, zebra, and buffalo calves) and found that the lions' diet contained a similar proportion of medium-size prey during the high and low population (pre-drought) periods, whereas the proportion of large prey increased during the 2000 drought (χ^2 = 27.28, d.f. = 4, $p < 0.01$, n = 418). Thus, the Crater lions showed an increasing preference for buffalo through the course of the three study periods, while buffalo increased in abundance until the end of the drought.

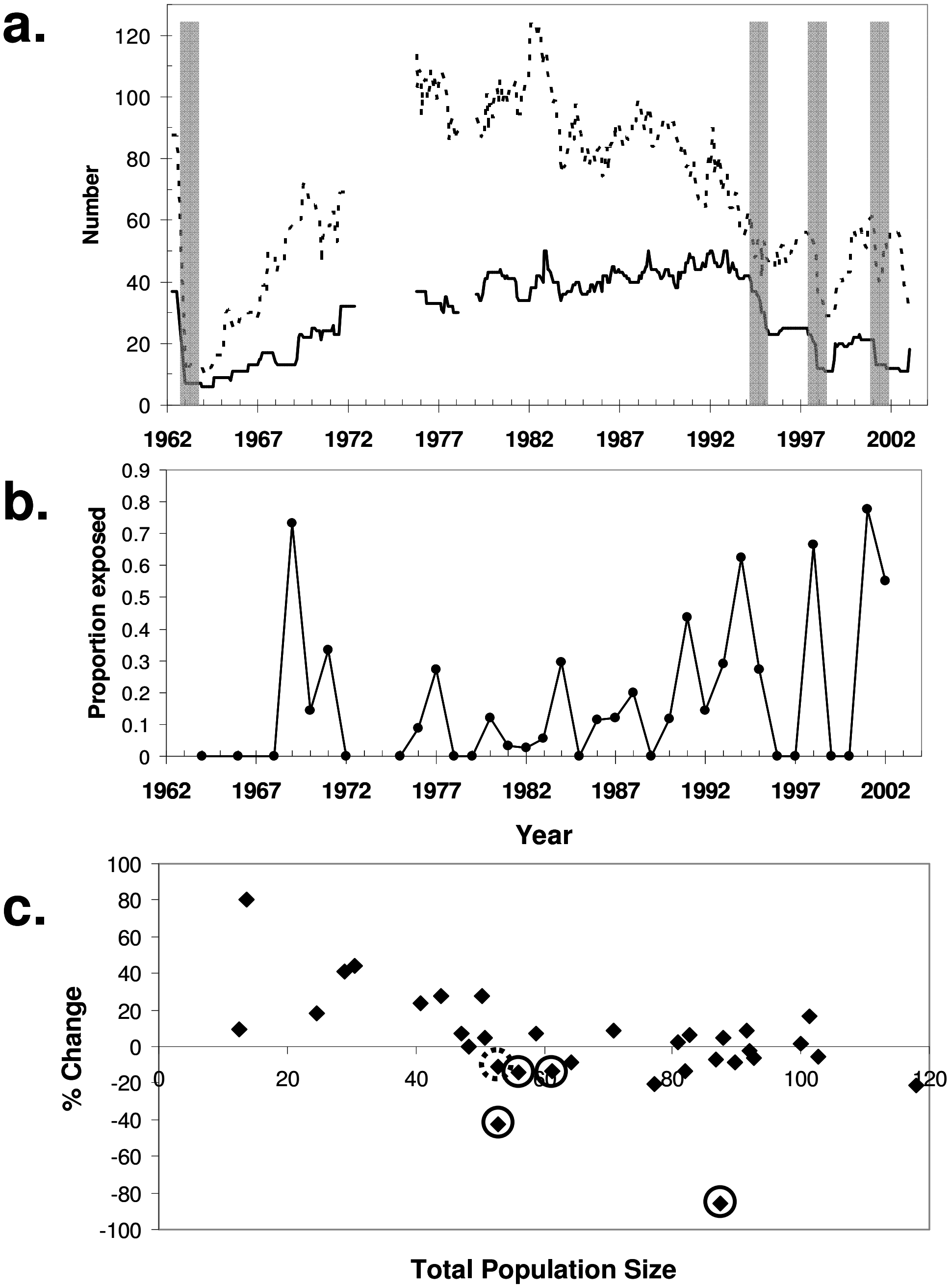

Figure 2.2. Demographic trends. (a) Total population size (dotted line) and the number of adults aged 4 years or older (solid line) for each month in the period 1963–2003; vertical bars indicate timing of die-offs. (b) Proportion of cubs less than 1 year old exposed to male takeovers each year. (c) Annual rate of population change as a function of population size. Data from disease outbreak years (1962, 1994, 1998 and 2001) are circled; the dotted circle is the second year of the 1994 die-off. Since buffalo are far larger than wildebeest or zebra, the lions had access to greater prey biomass in the two low lion-density periods than at high population density.

Table 2.1. Estimated selection indices and prey preferences for the Ngorongoro Crater lions during the three intensive study periods. Scavenged carcasses were excluded from this analysis.

Prey species	Prey population (n)	Population Proportion (π_i)	Carcasses (u_i)	Carcass Proportion (o_i)	Selection Ratio ($\hat{w}$)	Standardized Ratio (B_i)	SE ($\hat{w}$)	χ^2	p-value	Preference
	1982-83 (High lion density)									
Zebra	4258	0.159	34	0.234	1.471	0.287	0.191	6.10	0.01	+
W/beest	18450	0.691	85	0.586	0.849	0.166	0.056	7.41	0.01	-
Buffalo	1498	0.056	18	0.124	2.214	0.432	0.341	12.69	0.00	+
Gazelle	2507	0.094	8	0.055	0.588	0.115	0.258	2.55	0.11	0
Total	26713	1	145	1	5.1214	1				
	Mar. 99-Apr. 2000 (Low density pre-drought)									
Zebra	4604	0.189	17	0.145	0.769	0.203	0.192	1.45	0.23	0
W/beest	12175	0.499	57	0.487	0.975	0.257	0.093	0.07	0.79	0
Buffalo	4593	0.188	39	0.333	1.769	0.467	0.192	16.07	0.00	+
Gazelle	3004	0.123	4	0.034	0.277	0.073	0.247	8.59	0.00	-
Total	24375	1	117	1	3.791	1				
	May-Nov. 2000 (Low density drought)									
Zebra	5465	0.247	24	0.180	0.731	0.089	0.151	3.16	0.08	0
W/beest	12338	0.557	34	0.256	0.459	0.056	0.077	49.10	0.00	-
Buffalo	1778	0.080	74	0.556	6.926	0.847	0.293	408.01	0.00	+
Gazelle	2553	0.115	1	0.008	0.065	0.008	0.240	15.15	0.00	-
Total	22134	1	133		8.1811	1				

(Thomson's gazelle and Grant's gazelle are combined as 'gazelle'; w/beest = wildebeest).

The Crater lions enjoyed higher food intake rates at low population density than at high density (Fig. 2.4). Per capita, females gained access to considerably more meat in the later study periods (Fig. 2.4a), due both to a greater frequency of carcasses (0.10/female/day in 1999/2000 vs. 0.07/female/day in 1982/1983) and to a greater proportion of large prey (especially buffalo) in the diet. Meat availability skyrocketed during the drought of 2000 (Fig. 2.4a) when the frequency of carcasses was 0.16/female/day. Consistent with the overall trend, each age-sex class enjoyed substantially higher belly sizes (and hence food consumption) at low population density (Fig. 2.4b). However, belly sizes were no higher during the drought than in the preceding months, despite a much higher availability of meat, suggesting that the lions were already obtaining as much meat as they required during the low density pre-drought period and that they did not completely consume the drought-stricken buffalo carcasses.

We have little evidence that lions suffered from increased competition with hyenas in recent years. Spotted hyenas are most successful in stealing carcasses from lions when they greatly out-number them, and hyenas are far less successful at supplanting male lions than females. However, the relative abundance of hyenas was no higher in the 1990s than in earlier years nor has there been a significant change in the adult sex ratio of the lion population. Despite the relatively small size of the lion population in recent years, the hyena/lion population ratio was only 4.2:1 in the late 1990s (Höner. *et al*., 2002) compared to an estimated 14:1 in the late 1960s (Kruuk 1972) when the lion population was nevertheless able to grow rapidly (Fig. 2.2a).

Höner, *et al*., (2002) report 22 cases in which hyenas obtained carcasses from lions during 1996-1999. However, during our low density study periods in 1999-2000, we observed lions feed from more than 260 carcasses, but hyenas never succeeded in supplanting the lions. We only observed the hyenas waiting until the lions had finished the meat and scavenging the bones and skin after the lions had moved off. Nevertheless, hyenas are sufficiently nocturnal that our sampling techniques might not reveal the true extent of competition between the two species. We therefore checked for feeding competition with hyenas by measuring the amount of meat already eaten and the amount still remaining when lions were first observed at a carcass.

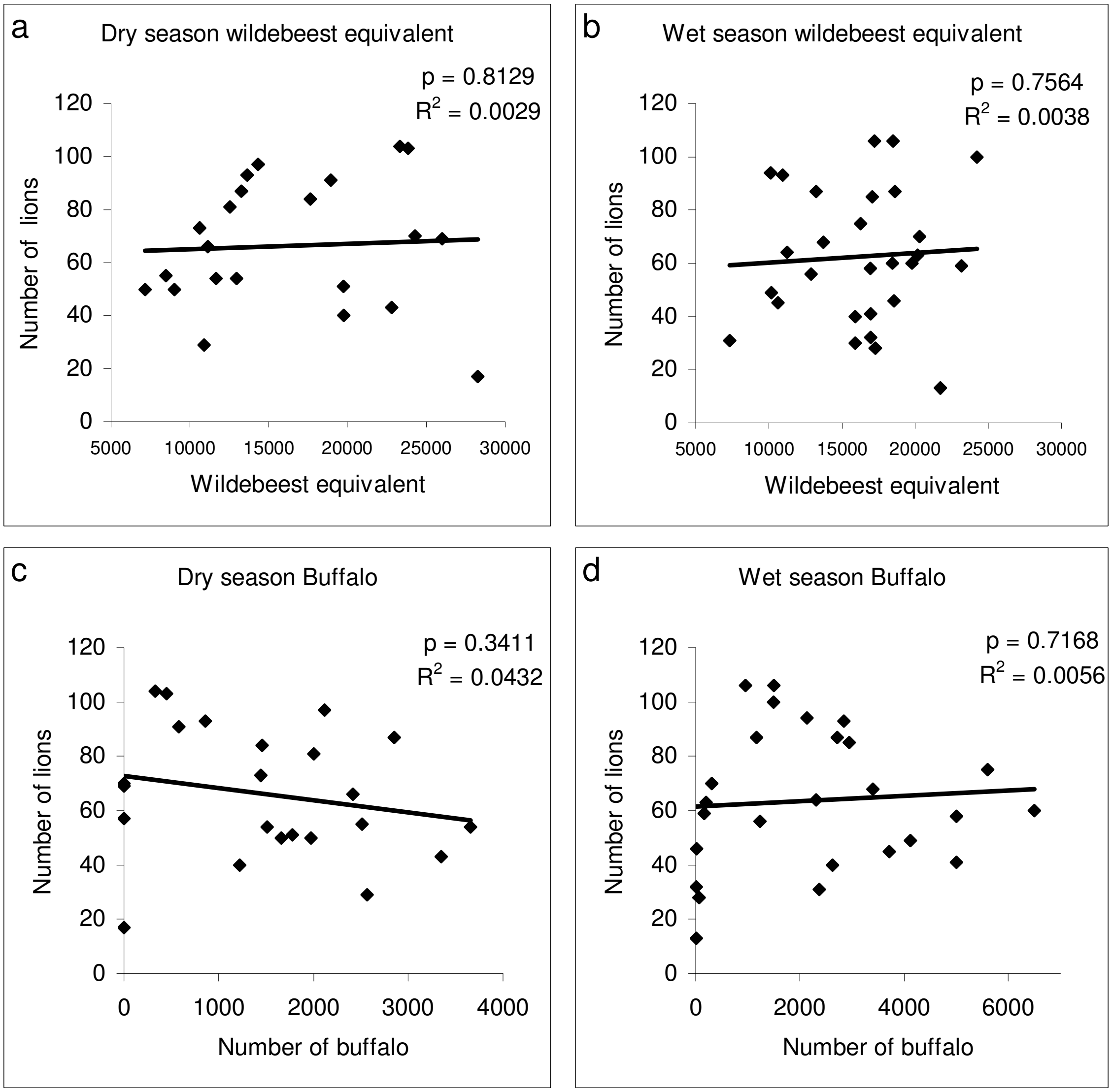

Figure 2.3. Relationships between herbivore numbers and lion population sizes, 1964–2001. (a) Number of zebra and wildebeest, combined into a single measure with 1 zebra= 1.35 wildebeest, each dry season. (b) Wildebeest equivalents each wet season. (c) Number of buffalo each dry season. (d) Buffalo each wet season.

If lions suffered greater scavenging from hyenas in recent years, the lions should have eaten less meat from each carcass. The amount of meat already eaten when the lions were first encountered at a kill did not differ among the three periods (ANOVA, F=1.92, P=0.15, n=253), but there was a significant difference in the amount of meat still remaining (ANOVA, F=15.24, p<0.01, n=253) with the highest amount remaining during the 2000 drought period (Table 2.2a).

Table 2.2a: Amount of meat already eaten, amount remaining and the mean number of females observed at each carcass during each study period. Values are mean ± SE.

Period	Mean kg meat already eaten	Mean kg meat still remaining	Mean no. of females (≥2 yrs old) observed
1982-83 (n=75)	95.64 ±11.89 *	53.63 ±11.72*	6.23±0.43
Mar 99-Apr 00 (Pre-drought) (n=72)	72.85±8.64*	70.02±11.12*	2.65±0.17*
May-Nov.00 (Drought)(n=106)	104.78±12.46*	138.93±12.37	2.69±0.13*

* Means not significantly different

Table 2.2b: GLM model for female belly sizes during high population density and the two low population density periods.

Parameter	Sum of squares	F	P
Number of ≥2 yr old females feeding at carcass	0.00	2.02	0.89
Amount eaten by observer's arrival at carcass	3.72	18.49	<0.01
Study period	2.42	6.01	<0.01
Total females at carcass x time period	0.33	0.83	0.44
Amount eaten by observer's arrival x time period	2.00	4.97	0.01

If the Crater lions suffered from greater levels of hyena scavenging in recent years, the lions should have consumed less meat at each kill – and had concomitantly smaller belly sizes for a given carcass size. We therefore used a Generalized Linear Model (GLM) to compare the belly sizes of female lions (≥2 yrs old) observed at each carcass, adjusting for the amount of meat already eaten and the number of female lions present at the carcass (Table 2.2b). The relationship between belly size and the amount of meat already eaten showed a significant interaction with study period: belly size depended on the amount of meat already eaten both during high population density (t = -4, p<0. 01, $R^2 = 0.20$) and pre-drought low population density (t = - 4.23, p<0. 01, $R^2 = 0.20$), but not during the 2000 drought (t = -0.52, p = 0.60, $R^2 = 0.00$), suggesting that lions ate a comparable proportion of meat per carcass in the first two study periods, but maintained a more constant belly size when food was superabundant during the 2000 drought.

Finally, even though lions and hyenas both specialize on the same prey species and might therefore be expected to suffer from exploitation competition, lions were significantly more likely to kill adults whereas hyenas took more juveniles (P<0.01 for buffalo and P<0.02 for wildebeest). Thus the two species show a degree of niche separation by specializing on different age-sex classes.

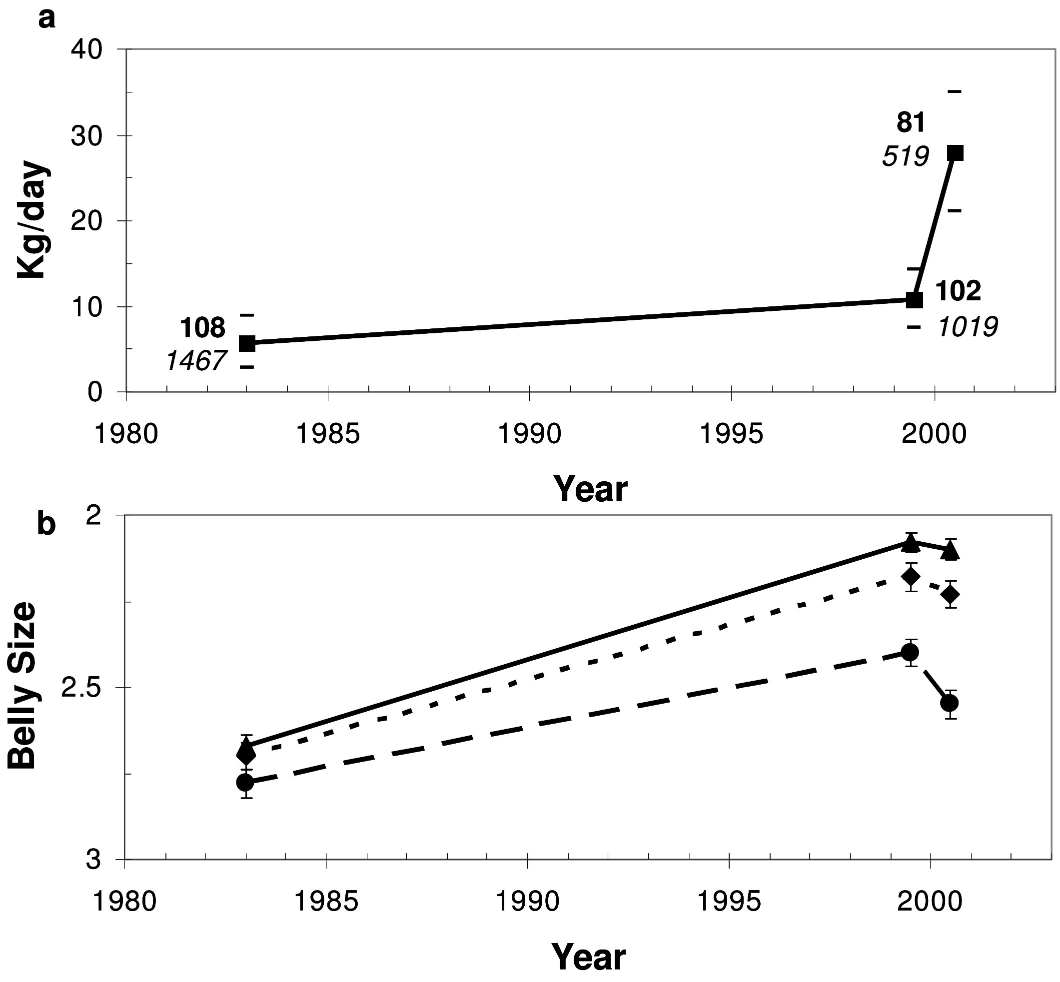

Figure 2.4. Measures of food intake. (a) Food acquisition calculated as described in methods. Upper dashes indicate maximum food available; lower dashes represent the minimum; squares are the midpoints between the two limits. Bold numbers indicate the numbers of carcasses; italics indicate the number of female sightings. (b) Mean ± S.E. for belly-size measurements during 1982–1983 and 1999–2000. Smaller numbers indicate more distended bellies and, hence, higher food intake. Cubs are designated by triangles and solid line, females by circles and dashed line, and males by diamonds and dotted line. Lions had significantly higher belly sizes in 1999–2000 than in 1982–1983 ($p<0.01$ for all tests).

Data from the Serengeti suggest that foraging group size has a significant impact on food intake (Packer, *et al.*, 1990), and, in 1999-2000, the Crater lions showed a significant interaction between prey size and prey health for small (≤3) vs. large (≥4) feeding groups. Feeding group is the number of females (≥2 yrs) present at the kill, and prey size is the average live weight of prey. Compared to smaller groups, large groups were better able to include large healthy prey in their diet (t-test, $t_{0.05}$, d.f. = 67, $P<0.01$). Thus small groups may be restricted to large prey in poor health, and any difference in foraging success between high and low population densities might only result from differences in foraging group size. However, the number of females/carcass was greater at high population density than at low densities (Table 2.2a). Thus the lions gained less food at high density despite foraging in larger groups perhaps due to greater within-group feeding competition.

The long-term data suggest that the lions have been struck by four deadly disease outbreaks over the past 40 yrs. During the *Stomoxys* plague of 1962 more than 80% of the estimated population disappeared (Fosbrooke 1963). In 2001, six Crater lions were found dead between 7 Jan. and 18 Feb., and 34% of the total population (n=61) had died/disappeared by 5 April. Veterinary investigation determined that the die-off resulted from a combination of tick-borne disease and CDV (T. Mlengeya, R. Koch, L. Munson & C. Packer, unpublished). The population suffered similar declines in 1994 and 1997 (Fig. 2.2a), and Fig. 2.5 shows that the age-specific annual mortality for all three time periods was the same as for the 1994 CDV outbreak in the Serengeti (Roelke-Parker, *et al.*, 1996). Unfortunately, no veterinary investigations were permitted in the Crater between 1991 and 2001, so we lack diagnostic data from 1994 and 1997.

Incoming males typically kill small cubs, and the proportion of cubs exposed to male takeovers varied each year (Fig. 2.2b). Due to the small size of the Crater floor, there have been several periods when one or two large coalitions controlled the entire population, resulting in periods of extreme instability when they were finally replaced. Consequently, the overall population showed short-term drops during these peak replacement years. For example, the strong upward trend in the population in the 1960s was temporarily reversed in 1968 when a large proportion of cubs were exposed to takeovers. Similarly, several takeovers occurred shortly after the population reached its all-time high in 1983, and the overall population dropped by 1984 though the adult population remained unchanged (Fig. 2.2a). The proportion of cubs exposed to takeovers has increased in recent years as a result of the high adult mortality in 1994, 1997 and 2001. Several resident male coalitions were ousted shortly after being reduced by disease, thus social factors amplified the effects of epidemics by increasing the incidence of infanticide.

The lion population showed clear signs of density-dependent reproductive performance (Fig. 2.2c). Except for disease-outbreak years, population growth was always positive when the population was <60 individuals, but negative 9 out of 16 yrs when the population exceeded 60. The population showed no sign of lowered reproductive performance over the past 10 yrs, increasing at the same density-dependent rate (in the absence of disease) as during the post-*Stomoxys* recovery period in the 1960s.

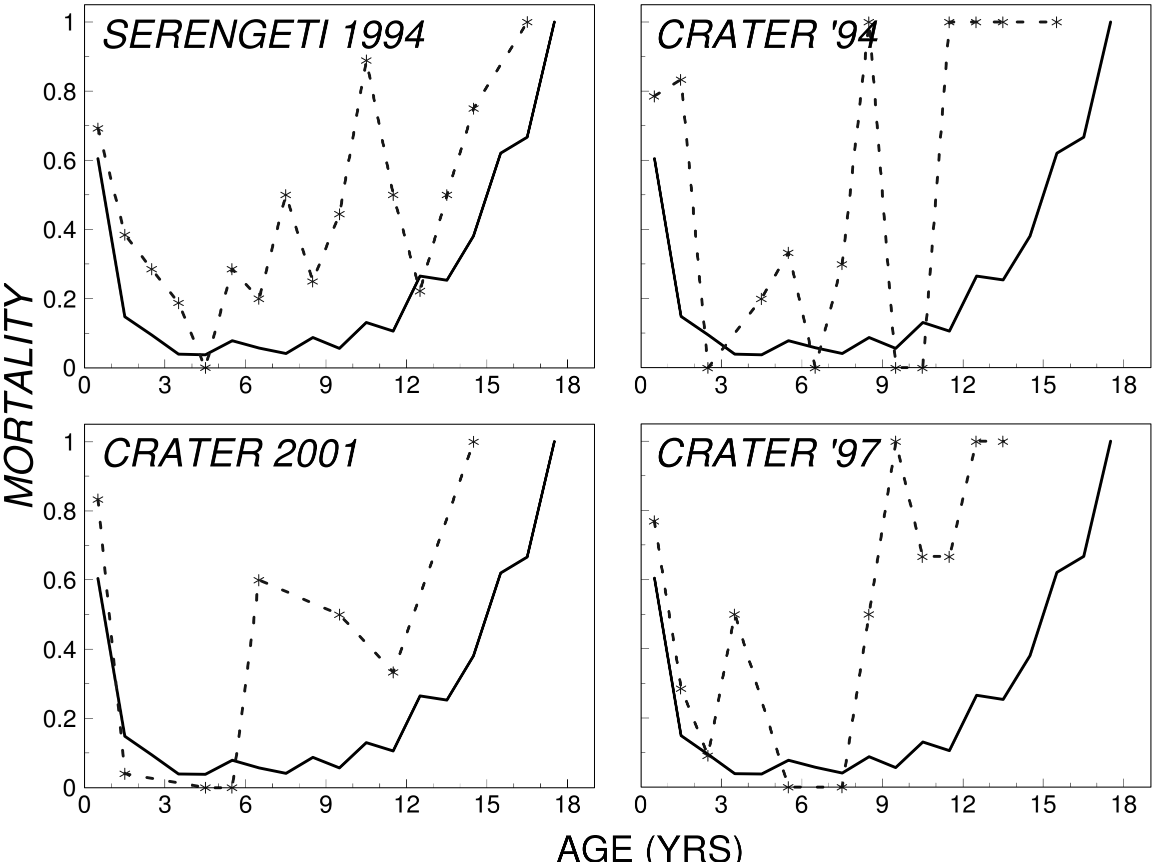

Figure 2.5. Age-specific annual mortality during known and presumed disease outbreaks. Dotted lines indicate annual mortality during the 1994 CDV outbreak in the Serengeti, the 2001 CDV outbreak in Ngorongoro and the undiagnosed outbreaks in 1994 and 1997. The solid line in each graph shows the background age-specific mortality of the Serengeti and Ngorongoro lions for the period 1966–1995.

Discussion

The comprehensive long-term data on the Crater lions provide a unique opportunity to evaluate the importance of food limitation on population regulation. The maximum of 124 individuals in 1983 almost certainly reflects the upper limit of the carrying capacity. If the lion population subsequently declined due to a drop in carrying capacity, the lions should have shown similar rates of food intake and demographic performance in the low population density years of 1999/2000 as in the high density years of 1982/1983. However, the lions enjoyed higher food intake and improved reproductive performance at lower population densities. In fact, the lions may have already fed at their maximum requirement in 1999, since their belly sizes were just as large as when meat was super-abundant in the drought of 2000 (Fig. 2.4b).

Kruuk (1972) found that the Crater lions stole more food from spotted hyenas than *vice versa* in the 1960s, and Hanby, *et al*., (1995) found that the Crater lions obtained 21% of their prey biomass from hyenas while losing no *edible* biomass to hyenas in 1976-77. Höner, *et al.,* (2002) suggested that the situation had changed by the late 1990s, but our data do not support their proposition. While large groups of hyenas may occasionally take kills from the Crater lions, we only observed hyenas feeding on scraps after the lions had left voluntarily. In fact, Höner, et al's data confirm that lions usually surrender a carcass only after they have eaten their fill. In the hyena "takeovers" that Höner, et al. observed in detail, the lions had already eaten a minimum of 13 kg per capita in 11 of 16 cases. Since lions eat 8 kg per day when prey is super-abundant (Packer, *et al.,* 1990), hyenas only prevented lions from exceeding their daily requirement 5 times during Höner, et al.'s entire study. More importantly, if lions lost significant food to hyenas, lion belly sizes should have declined in recent years, but belly sizes were significantly higher in 1999/2000 than in 1982/83, and the relationship between belly size and the amount of carcass eaten was the same in 1982/83 and the pre-drought 1999/2000 period. Further, hyenas were far more numerous than lions in the 1960s (Kruuk 1972), yet the lion population increased eight-fold from 1963 to 1975. Finally, there is scant evidence of "exploitation competition" between lions and hyenas: lions preferentially feed on buffalo *vs*. wildebeest for hyenas, and lions mostly capture adult buffalo and wildebeest whereas hyenas specialize on juveniles of these two species.

Disease therefore appears to be the only factor that has held the Crater lion population below its carrying capacity for the past 10 yrs. The importance of disease is emphasized by the severe drought of 2000 which enabled the lions to gain access to extraordinary quantities of meat, but the population nevertheless suffered a dramatic decline at the beginning of 2001 due to the CDV outbreak. The adult population declined strikingly during three distinct periods: 1994, 1997 and 2001. The 1994 die-off coincided with the severe CDV outbreak in the Serengeti (Roelke-Parker, *et al.*, 1996). The 1997 die-off coincided with the El Niño floods in East Africa; the Crater floor was impassable for about 3 mos, thus we lack direct observations of morbidity or mortality. During each interim period, reproductive rates were sufficiently high that the population would have recovered at a similar rate as in 1963-1975 except for the sharp decline at the next die-off.

What could have caused disease to become more prevalent and/or harmful compared to the 1970s and 1980s? We suggest two possibilities: First, the human population in the Ngorongoro Conservation Area has grown considerably over the past 20 years, especially in the highlands immediately surrounding the caldera. Larger human populations result in higher numbers of domestic dogs, the presumed reservoir of CDV in Northern Tanzania (Cleaveland, *et al.*, 2001), and larger populations can more readily sustain the infection. Second, the weather in East Africa was more variable in the 1990s than in the 1970s and 80s, and all four lion die-offs coincided with drought or flood. The 1962 *Stomoxys* plague coincided with heavy floods that immediately followed a severe drought in 1961. The 1994 die-off followed a severe drought in 1993, the 1997 die-off coincided with the El Niño floods, and the 2001 CDV epidemic followed the drought of 2000. Drought may bring different host species into contact at waterholes, and flood may create conditions favorable for pathogens. Regardless of the precise cause, these frequent outbreaks provide important insights into the likely future of many other small, genetically vulnerable carnivore populations. While the Crater lions have largely been isolated by natural geographical barriers, most other carnivore populations have only recently become fragmented due to habitat loss. Our data clearly show that endangered populations can remain at serious risk even with a large, stable food supply and no real threats from competing species.

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Chapter 3

Persistence and local extinction of lion prides in the Ngorongoro Crater

Submitted as:
Kissui, B.M., Mosser, A., Packer, C. Persistence and local extinction of lion prides in the Ngorongoro Crater, Tanzania. *Population Ecology*.

Abstract

Resource dispersion theory predicts that in group-living species, the spatial distribution of key resources may influence group size and home range size, and could lead to inter-group competition over scarce resources with larger groups out-competing smaller groups. African lions (*Panthera leo*) live in groups (prides) that exhibit predominantly group territorial behavior, where larger prides are more successful in defending their home ranges and out-compete small prides over high quality resources. The persistence of a pride is expected to depend on its ability to compete against neighboring prides as well as its average rates of reproduction and adult survival. Using long-term data (1975-2005) for the Ngorongoro Crater lion population we examined how the persistence of lion prides of different size was influenced by demography, landscape variables and, anthropogenic factors. Pride persistence to 10 years depended on adult female density (pride size), cub productivity (ultimate source of new females), and proximity to rivers. In addition to these factors, short term pride persistence (5 years) was influenced by frequency of male takeovers, disease epidemics and the amount of vegetative cover. Prides closest to rivers had higher adult female density while male takeovers were less common for such prides. Adult female mortality increased with disease epidemics, but females with territories closest to rivers experienced the lowest mortality. Cub productivity was highest in pride territories closest to rivers and areas with higher vegetative cover. The intensity of use of the Crater by Maasai pastoralists did not appear to influence pride persistence in the short as well as the longer term. The growth and population size of the Crater lions is closely linked to demographic performance of

individual prides, while territorial behavior plays a key role in mediating the interactive effects of landscape and demography.

Introduction

Population persistence is closely linked to landscape features and habitat quality through food supply (Miyashika et al., 2007), hunting success (Funston et al., 2001; Hopcraft, Sinclair and Packer, 2005), breeding success and individual survival (Stralberg and Williams 2002; Peak, Thompson III and Shaffer, 2004), carrying capacity (Hayward, O' Brien and Kerley, 2007), parasitism and predation risks (Budnik, Thompson and Ryan, 2002). Resource dispersion theory predicts that in group-living species, the spatial distribution of key resources may influence group size and home range size, and could lead to inter-group competition over scarce resources (Bradbury and Vehrencamp, 1976; Macdonald, 1983), with larger groups out-competing smaller groups. Territorial species are predicted to follow an ideal despotic distribution in which some individuals or groups may select high quality areas in a landscape and exclude competing groups (Fretwell and Calver, 1968; Zimmerman, LaHaye and Gutiérrez, 2003).

African lions (*Panthera leo*) live in groups called prides and exhibit predominantly group territorial behavior (Schaller, 1972; McComb, Packer and Pusey, 1994). A pride territory is inherited by successive generations of the pride females, and 30% of female cohorts form new prides by dispersing from existing prides and settling nearby (Pusey and Packer, 1987). Thus, pride home ranges persist for generations. Male lions are usually transient members of prides; they are replaced by new males who become resident for 2-4 years before being replaced by yet another coalition. Solitary females are unable to maintain exclusive home ranges and experience low reproductive success (Pusey and Packer, 1987; Packer and Pusey, 1995) whereas large prides are more successful at defending their home ranges and out-compete small prides over high quality resources (Mosser, 2008). High quality landscape-patches for lions provide high hunting success, shelter for hiding cubs, water and minimum disturbances from humans (Spong, 2002; Hopcraft, Sinclair and Packer, 2005; Packer et al., 2005; Mosser, 2008).

Ultimately, female survival and reproductive success depends on her pride: female lions are remarkably egalitarian, with no significant within-group variation in individual reproductive success (Packer, Pusey and Eberly, 2001). Given the importance of group size in maintaining successful reproduction (Pusey and Packer, 1987; Packer and Pusey, 1995; Packer, Pusey and Eberly, 2001), and the greater reproductive success of daughters who are recruited into their natal pride (compared to dispersing daughters, Pusey and Packer, 1987) pride persistence can be viewed as the single most important variable determining lifetime and intergenerational reproductive success.

In this paper, we use long-term data for the Ngorongoro Crater lion population to identify the variables that influenced the persistence of lion prides from 1975 to 2005. A pride's persistence is expected to depend on its ability to compete against neighboring prides as well as its average rates of reproduction and adult survival. We used an information-theoretic approach (Burnham and Anderson, 2002) with Akaike's Information Criterion (AIC) to select the best approximating model and considered two sets of variables to be most important in determining pride persistence: first, demographic factors associated with pride size, composition and female age, the pride and population level densities of adult females, the frequency of male takeovers and the number of males in the pride (incoming males kill un-weaned cubs and evict sub-adults, and females sometimes die in defense of their dependent offspring; larger male coalitions are better able to defend their prides (Bygott, Bertram and Hanby, 1979; Packer et al., 1988), and exposure to outbreaks of infectious disease (the Crater lions have been exposed to numerous severe disease outbreaks in the past 15 yrs, Kissui and Packer, 2004). Second, we explored variations in landscape variables, including distance to rivers, roads and swamps, amount of vegetative cover, and exposure to localized anthropogenic factors (level of use by Maasai pastoralists who sometimes kill lions for ritual purposes or in retaliation for cattle killing, Ikanda, 2006).

Methods

Study area

This study was carried out in the Ngorongoro Crater, a 250 km^2 caldera at the western edge of the Gregory Rift, with walls 400-610m high located in Northern Tanzania (Fig. 3.1). The dominant resident ungulate populations include wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), buffalo (*Syncerus caffer*) and Grant's gazelles (*Gazella granti*). There is also a small number of warthogs (*Phachochoerus africanus*), hartebeests (*Alcelaphus buselaphus*), elands (*Tragelaphus oryx*), waterbucks (*Kobus ellipsiprymnus*), reedbucks (*Redunca redunca*), and bushbucks (*Tragelaphus scriptus*) (Kissui and Packer, 2004; Estes, Atwood and Estes, 2006). Most of these ungulates spend all year-round in the crater, although ~ 20% of wildebeest and zebra migrate to the Serengeti plains seasonally (Estes and Small, 1981; Estes, Atwood and Estes, 2006). The most common prey for lions in the Crater are wildebeest and zebra; buffalo are an important component of the diet for lions in large groups, while Gazelles and other ungulates constitute a small proportion of the overall food intake (Kissui and Packer, 2004). Additional predator populations in the Crater include spotted hyena (*Crocuta crocuta*), golden jackal (*Canis aureus*) and black-backed jackal (*Canis mesomelas*). Cheetah (*Acinonyx jubatus*) and leopards (*Panthera pardus*) are rarely seen in the Crater.

Despite its relatively small size, the Crater floor exhibits a range of landscape characteristics (Fig 3.1). The Crater landscape is dominated by open grassland, but there are two *Acacia xanthophloea* forest patches and occasional patches of bush land dominated by *Euphobia bussei* species (Estes, Atwood and Estes, 2006). The Crater supports large numbers of resident ungulates owing to the permanent streams and rivers that originate from the northern highland catchment forests and permanent springs that form persistent green belts of grass growth at the edges of marshes and swamps (Estes and Small, 1981; Estes, Atwood and Estes, 2006).

With its high concentrations of wildlife, the crater forms one of the most attractive tourist destinations in Tanzania. Historically, the Maasai pastoralists were resident in the Crater floor until 1974 when the wildlife authority relocated them outside the Crater, but they were subsequently permitted daytime access into the Crater for livestock grazing and watering, and access to salt licks (Fyumagwa et al., 2007). This has led to some sections of the Crater to experience prolonged presence of humans. For example, the western section of the Crater is adjacent to Maasai pastoralists' cattle trails and tends to experience large crowds of people for most of the daytime. We classify such locations as "high use" areas compared to the eastern section where pastoralists rarely visit. The presence of livestock herders might not necessarily negatively impact the wildlife, especially ungulates, but Ngorongoro Maasai are known to kill lions with spears whenever an opportunity arises (Ikanda and Packer in press), and our long-term observations indicate that lions actively avoid encounters with Maasai. Figure 3.2 illustrates the level of human use in the Crater floor based on the amount of time livestock herders are present in each area. We categorized the level of utilization as 1= lower intensity use, 2= medium intensity use and 3= high intensity use areas.

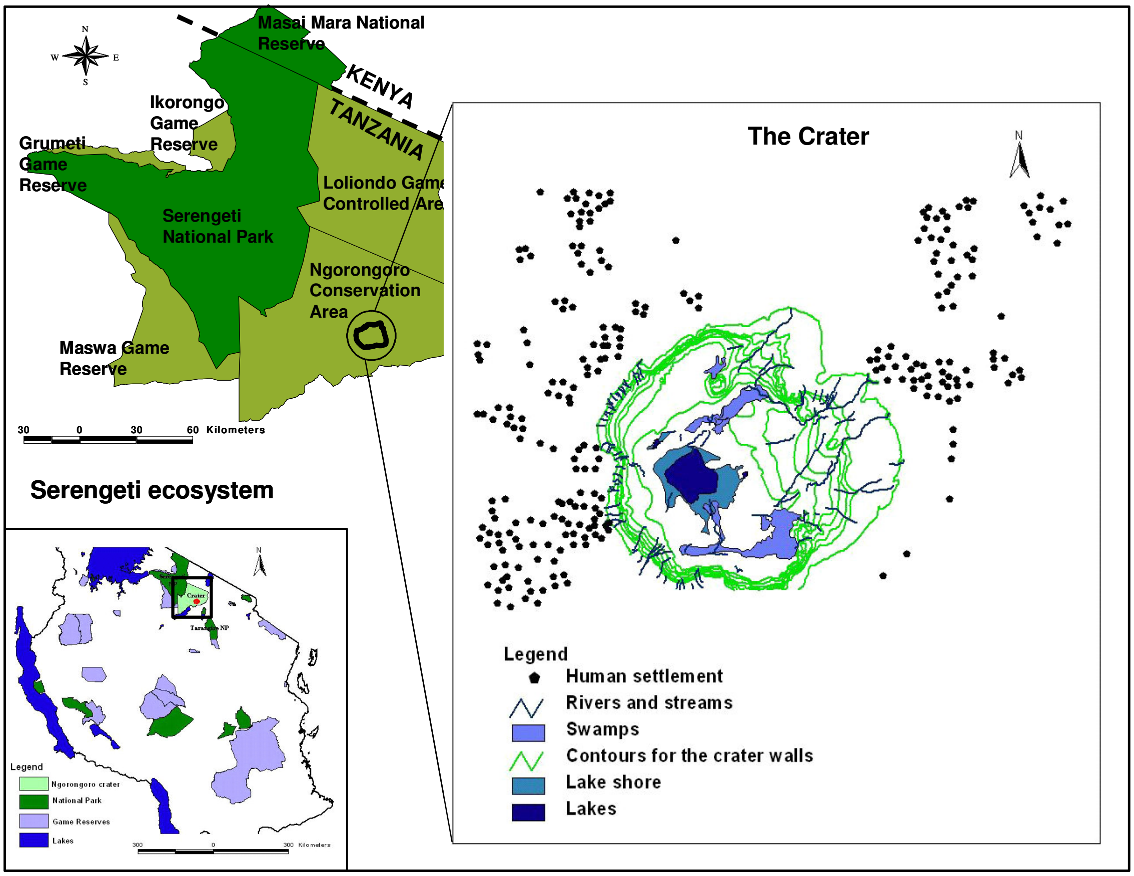

Figure 3.1. Hydrological/topographical map of the floor of Ngorongoro Crater and the distribution of human settlement adjacent to the Crater.

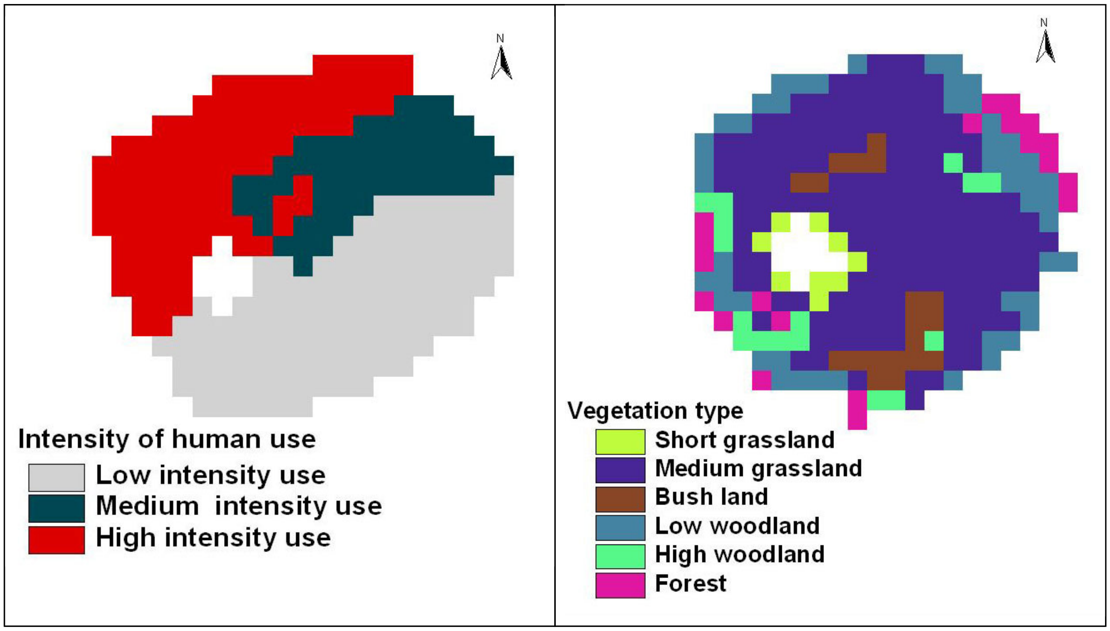

Figure 3.2. 1000m grid map of the intensity of human use across the Crater floor based on the amount of daytime that people and livestock are present in each area (left), and a grid map of the vegetation types in the Crater floor (right).

Study population

The Crater lion population has been monitored continuously since the early 1960s; lions are identified individually and records are maintained on reproductive history, maternity and ranging patterns of each individual. A lion pride typically comprises 2-9 related females (range 1-18), their dependent cubs, sub-adults and a resident coalition of 2-6 males (Schaller, 1972; Bygott, Bertram and Hanby, 1979; Packer, Scheel and Pusey, 1990; Packer and Pusey, 1993). Lions are observed on a regular basis by searching the entire study area and recording date and time of observation, pride composition and identification of individual lions, location of pride recorded using GPS (prior to the invention of GPS, pride locations were recorded on a UTM coordinate grid map that were later converted into the coordinate system used in this analysis). In addition, records are kept on births, deaths and immigration/emigration history of individual lions between prides.

Demography and pride level variables

We measured 16 demographic and pride level variables (Table 3.1). Each variable was calculated in a 2-year time step (which equals the average inter-birth interval for mothers of surviving cubs). Most cub mortality occurs prior to the first birthday (Schaller, 1972), so recruitment of yearlings is the best measure of cub productivity (Packer et al., 1988). Here, "cub productivity" is defined as the number of cubs surviving to one year of age per km^2 of pride area in a two-year time step. Female mortality is defined as the number of adult females 3+ years that died/disappeared in the two year-time step. Male takeovers were determined as the frequency of takeovers for each pride over a 2-year period; while the number of adult males was calculated as the number of males in resident coalition(s) during a 2-year period (see Table 3.1 for detailed description of all variables).

Landscape variables

We calculated landscape variables using GIS layers in Arc View 3.2, ESRI. Each layer for roads, rivers and swamps was converted into a 1000m grid, and we calculated the distance from the centroid of each grid cell to the nearest feature. For vegetation cover, a GIS layer was created by digitizing a vegetation map for the crater published by Estes, Atwood and Estes, (2006). Different vegetation types were assigned into five categories in order of increasing vegetative height and cover: 0 = short grassland, 1 = medium grassland, 2 = bush land, 3=low woodland, 4=high woodland and 5=forest. Each 1000m grid cell was assigned a corresponding categorical value of vegetation type (Fig. 3.2). We did not have sufficient long-term prey distribution data to include in this analysis; we instead rely on surrogate measures of prey availability (see below).

Anthropogenic variables

We created a GIS layer representing the level of human use in the Crater by digitizing a base map of the Crater and assigning three categorical levels of human use: 1= areas of low intensity use (none to rare daily presence of livestock and pastoralists), 2=areas of medium intensity use (occasional daily presence of livestock and pastoralists) and 3=areas of high intensity use (frequent to constant daily presence of livestock and pastoralists) (Fig. 3.2). We defined intensity of use by considering the amount of time and number of people and livestock observed in each part of the Crater daily. Like the other landscape variables, the anthropogenic variable was projected into UTM coordinate (Zone 36 S, Datum Clark 1880) at 1000 m grid resolution.

Table 3.1. Demography and pride level variables for each pride calculated over 2-year intervals from 1975 to 2005. The 2-year period starting, for example, on Nov. 1st, 1974 ended on Oct. 31st, 1976 and was labeled as 1975 in the analysis.

Sn.	Name/ abbreviation	Variable description
1	nf3	Number of adult females age 3+ years old
2	nf3km	Average density of females age 3+ years old (numf/pride territory area)
3	nf3ls	Adult females (3+ years old) mortality
4	p3fls	Proportion of adult female (3+ years old) mortality
5	fdis	Number of females age 1-2 year old with last seen date-(dispersed females)
6	numf	Average number of adult (3+ year old) females, averaged over 24 months
7	numm	Average number of resident males, averaged over 24 months
8	cubs1	Number of cubs surviving to yr 1
9	numt	Total number of lions in a pride including females, cubs and males
10	ntkm	Total number of lions in pride including females, cubs and males per pride territory area
11	fage	Average age of adult females 3+ years old
12	to	Number of takeovers per 24 months
13	K75	Pride territory size in sq km with 75% kernel
14	cubkm	number of cubs surviving to yr 1 per pride territory area
15	nf3lskm	Adult female mortality per pride territory area
16	adkm	Adult female 3+ years old per pride territory area

Lion pride home ranges

We constructed pride home ranges for each 2-year period for sightings from 15 prides. Home ranges were determined from utilization contours using a 75 % fixed kernel in Arcview GIS 3.2, with an animal movement extension. We used a smoothing parameter (h) of 2700 meters, representing the mean daily distance traveled by adult female lions in the Crater. The 75% kernel was considered an optimum compromise between large and small kernels: large kernels such as 95% typically tend to overestimate the home range, while kernels as small as 50% underestimate the home range estimate

(Worton, 1989; Mosser, 2008). The home ranges were constructed with female sightings where at least one female 2+ years old was observed. The analysis included prides that had at least 3 observations in each year to minimize bias against prides with infrequent observations. About 17 % of the years included in mapping pride home ranges had less than 20 observations; the lowest number of observations was 8, and the highest was 501 observations. However, lions have high territory fidelity; Mosser, (2008) tested the effect of small sample size on lion pride home range estimates and found no systematic error in the estimates (Mosser, 2008). Home ranges were converted to 1000 m grids, and the average territory size was 30 sq km (range 14-69 sq km).

GIS overlay analysis

Using pride home ranges as base layers, we overlaid landscape and human use layers in Arcview GIS to produce a grid with values from each input layer. The outputs produced for each 2-year period for each pride were used in the subsequent data analyses.

Data analyses

For continuous landscape variables such as distance to rivers and swamps, we averaged grid outputs from the GIS overlay analysis to obtain a mean value for each pride territory for each 2-year period. For variables such as level of human use and vegetation type for which grids had categorical values (i.e. 1, 2, 3), the most dominant category was assigned for the entire pride territory. Landscape variables for each pride territory were merged with the corresponding demographic variables to produce the final output dataset containing observations for each pride territory over each 2-year period from 1975 to 2005. Disease epidemics were designated binomially by scoring 1 for years in which a disease outbreak occurred and 0 otherwise.

We determined the dichotomous response variable, pride persistence, by scoring 1 for each year a pride was present after its appearance in the population and 0 otherwise.

The demographic and landscape variables were used as predictors. Prior to statistical analyses we used Pearson's correlations coefficients to check for redundancy in the predictor variables. We selected only one variable to use in statistical analysis when two or more predictor variables significantly correlated with each other ($rs > 0.5$, with $p < 0.05$ as threshold). Table 3.2 presents a list of predictor variables selected for construction of *a priori* models used in the subsequent analysis of pride persistence.

Using past knowledge of our study system, we constructed biologically meaningful *a priori* candidate models concerning the effects of demography, landscape variables and anthropogenic variables on pride persistence for 5 and 10 years (Tables 3.3a, b). We performed model selection with Kullback-Leibler (K-L) information-theoretic approach using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002; Anderson and Burnham, 2002). We determined the maximized Log-likelihood for each candidate model and calculated the values for AICc, ΔAICc = (AICi – min AIC): min AIC is the minimum AIC value of all models, and ωi = Akaike weight (the weight of evidence that model *i* is the best approximating model given the data and the set of candidate models considered) using equations by Burnham and Anderson, (2002).

We analyzed pride persistence to 5 and 10 years using (GENMOD and the SAS system, 9.1) with binomial distribution and logit link function (Logistic regression). To check the effect of landscape, demography and human use on cub productivity, adult female mortality and male takeovers, we used generalized linear model (GENMOD) with Poisson distribution and a log-link function. We used the log of pride territory area as an *offset* in GENMOD to model cub productivity as a rate i.e. {(number of surviving cubs)/ (home range area)}, (Flynn, 2007). In GENMOD we used pride as a random effect with years as repeated measure. We used Pearson's Chi-square to check the goodness of fit of the models.

Table 3.2. Logistic regression analysis for repeated measures data with one predictor at a time showing relationships of demography, landscape and human use with pride persistence to 5 and 10 years. These variables were used to construct *a priori* candidate models for pride persistence over the 1975-2005.

Response variable	Predictor	Estimate	SE	Effect
Pride persistence to 5 years	Adkm	11.2915	5.1536	+
	To	-1.1119	0.4091	-
	Numm	0.1473	0.0905	+
	Fage	0.0318	0.1942	+
	Epidemic	-0.7505	0.6245	-
	Riverdis	-0.002	0.001	-
	Humuse	-0.1448	0.2788	-
	Vegtype	1.5799	0.9634	+
	Roaddis	0.0003	0.0011	+
	Swampdis	0.0003	0.0004	+
	Cubkm	7.3018	3.1338	+
	f3lskm	-1.0168	3.9091	-
Pride persistence to 10 years	Adkm	5.2155	1.8509	+
	To	-0.7524	0.4261	-
	Numm	0.0297	0.0931	+
	Fage	0.0504	0.1382	+
	Epidemic	-1.1087	0.8691	-
	Rivers	-0.0015	0.0008	-
	Humuse	-0.0184	0.2573	-
	Vegtype	0.2526	0.4771	+
	Roaddis	0.0009	0.001	+
	Swampdis	0.0003	0.0004	+
	Cubkm	6.0328	2.6171	+
	f3lskm	1.4337	3.6459	+

(Abbreviations: Epidemic = disease epidemic; Riverdis = distance to rivers; Humuse = human use; Vegtype = vegetative cover; swamps = distance to swamps) (See Table 3.1 for description of the demographic variables)

Results

We considered new prides to have appeared when at least two females 2+ years old split from an existing pride and established an independent pride territory. A pride was deemed "extinct" when the number of females fell below 2 (since solitaries never succeeded in raising surviving offspring). Over the period 1975-2005, 22 prides were observed in the Crater, but 7 prides were dropped from the analysis because they were not observed sufficiently often to estimate utilization Kernels for home ranges. We therefore examined 15 prides to determine which demographic, landscape variables and human use factors were important for prides to persist 5 and 10 years into the future. At the time of this analysis, 12 (80%) of the 15 prides had gone extinct; average persistence was 18 years ± 12 years (range 2-39 years).

Analysis with one predictor at a time showed a positive relationship between pride persistence and adult female density, number of adult males, average age of females, distance to roads and swamps, cub productivity and the amount of vegetative cover (Table 3.2), but a negative relationship with male takeovers, disease epidemics, and distance to rivers, the intensity of human use and adult female mortality (Table 3.2).

Pride persistence

Fifteen candidate models were constructed from the predictor variables in Table 3.2 to determine the effect of landscape, demography and human use on pride persistence. Following Burnham and Anderson, (2002), the model with the lowest AIC and highest Akaike weight (ω_i) values is the best approximating model in the set of candidate models. Models with ΔAICc < 2 are said to have strong support and represent a confidence set of the best model, ΔAICc values 2-4 have weak support, ΔAICc values 4-7 little support and values > 7 have no support and are unlikely models given the dataset used. Table 3.3 presents results of Akaike's Information Criteria analysis for best model selection for pride persistence.

Logistic regression analysis indicated that the model containing adult female density and cub productivity was the best for predicting persistence to both 5 and 10 years (Table 3.3a, b). However, ΔAICc values for persistence to year 5 revealed that models 2-6 all had values < 2, thus constituted the confidence set of best model, while ω_i showed that the best model was only 1.3, 1.5, 1.75, 2.1 and 2.6 times as likely to be the best approximating model than models 2, 3, 4, 5 and 6 respectively. The confidence set of the best model indicated that the amount of vegetative cover, male takeovers and distance to rivers are important additional predictors of pride persistence to year 5.

Table 3.3. *A priori* Logistic regression models for repeated measures data explaining the influence of demography, landscape and human use factors on pride persistence to 5 years (Table A) and 10 years (Table B). AIC values were corrected for small sample size (n = 91 for year 5 persistence), (n=80 for year 10 persistence). A lower ΔAICc and higher ωi indicate more support for the model.

A: Persistence to year 5

Model#	Candidate models	K	LogLikehood	AICc	ΔAICc	ωi
1	adkm, cubkm	3	-35.37	76.88	0.00	0.21
2	adkm, cubkm, riverdis	4	-34.59	77.40	0.53	0.16
3	vegtype, to, adkm	4	-34.73	77.69	0.81	0.14
4	adkm, riverdis, to, cubkm	5	-33.85	78.06	1.18	0.12
5	Riverdis, adkm, cubkm, vegtype	5	-34.03	78.40	1.52	0.10
6	adkm, riverdis, cubkm, epidemic	5	-34.23	78.81	1.93	0.08
7	adkm, humuse	3	-36.54	79.22	2.34	0.07
8	adkm, riverdis	3	-36.79	79.72	2.84	0.05
9	adkm	2	-38.05	80.16	3.28	0.04
10	adkm, epidemic, humuse	4	-36.05	80.33	3.45	0.04
11	riverdis, cubkm	3	-41.45	89.04	12.16	0.00
12	cubkm	2	-42.59	89.25	12.37	0.00
13	to	2	-45.44	94.96	18.08	0.00
14	vegtype, riverdis, epidemic	4	-45.08	98.40	21.52	0.00
15	f3lskm	2	-49.12	102.32	25.44	0.00

B: Persistence to year 10

Model#	Candidate models	K	LogLikehood	AICc	ΔAICc	ωi
1	adkm, cubkm	3	-44.62	95.40	0.00	0.34
2	adkm, cubkm, riverdis	4	-43.98	96.22	0.83	0.23
3	adkm, riverdis, cubkm, epidemic	5	-43.64	97.69	2.29	0.11
4	adkm, riverdis, to, cubkm	5	-43.76	97.93	2.53	0.10
5	Riverdis, adkm, cubkm, vegtype	5	-43.88	98.16	2.76	0.09
6	cubkm	2	-47.19	98.45	3.05	0.07
7	riverdis, cubkm	3	-46.67	99.49	4.09	0.04
8	adkm, riverdis	3	-48.18	102.53	7.13	0.01
9	adkm	2	-49.73	103.53	8.13	0.01
10	adkm, humuse	3	-49.04	104.23	8.83	0.00
11	vegtype, to, adkm	4	-48.52	105.32	9.92	0.00
12	adkm, epidemic, humuse	4	-48.58	105.43	10.03	0.00
13	to	2	-53.59	111.25	15.85	0.00
14	vegtype, riverdis, epidemic	4	-52.29	112.85	17.45	0.00
15	f3lskm	2	-55.27	114.62	19.22	0.00

K = Number of estimable parameters (each covariate + intercept) in approximating model; Loglikelihood= Value of the maximized log-likelihood of the model; AICc = Akaike 's Information Criteria adjusted for small sample size; ΔAICc = (AICi – min AIC), min AIC is the minimum AIC value of all models; ωi = Akaike weight, is the weight of evidence that model *i* is the best approximating model given the data and set of candidate models considered (also represent the probability that model *i* is the best among candidate models considered).

Abbreviations: adkm = adult female density; epidemic = disease epidemic; riverdis = distance to rivers; to = male takeovers; fage = average age of adult females; humuse = human use; vegtype = vegetative cover; swamps = distance to swamps

For persistence to year 10, the model containing adult female density and cub productivity again had the strongest support (Table 3.3b), but only one other model, adding river distance to female density and cub productivity fell within the confidence set of the best model. Table 3.4a &b show the parameter estimates for the best model.

Table 3.4a. Parameter estimates for the best model for pride persistence to year 5

			95% CI	
Parameter	Estimate	SE	Upper	Lower
Adult female density	9.0274	2.9511	14.8114	3.2434
Cub productivity	5.8850	2.9435	11.6542	0.1158

Table 3.4b. Parameter estimates for the best model for pride persistence to year 10

			95% CI	
Parameter	Estimate	SE	Upper	Lower
Adult female density	3.7726	1.7806	7.2625	0.2826
Cub productivity	5.2865	1.9154	9.0405	1.5324

Effects on cub productivity, adult female mortality and male takeovers

We checked whether landscape, demography and intensity of human use had effects on the three important demographic predictor variables that influenced pride persistence (cub productivity, adult female mortality and male takeovers) by constructing a *priori* models using variables in Table 3.5. Analysis with single predictor at a time showed a positive relationship between adult female mortality and adult female density, number of male takeovers, number of adult males, average age of females, disease epidemic, and distance to rivers, level of human use, distance to roads and distance to swamps, but, a negative relationship with the amount of vegetative cover (Table 3.5). Cub productivity (i.e. number of cubs surviving to first birth day per km^2 of pride territory) was positively related to the density of adult females, number of adult males, level of human use and the amount of vegetative cover but negatively correlated with male takeovers, adult female mortality, disease epidemic, distance to rivers and roads, and distance to swamps (Table 3.5). All predictor variables followed the expected directional relationship with adult female mortality and cub productivity, except that cub productivity was slightly (though not significantly) higher in areas of high human use (Table 3.5).

Table 3.5. Poisson repeated measures model analysis for relationships between each demographic and landscape predictor with adult female mortality, cub productivity and frequency of male takeover using log of pride area as an *offset* in GENMOD. These variables were used to construct *a priori* candidate models for adult female mortality, cub productivity and frequency of male takeovers, 1975-2005. The sample size (n = 95) for each predictor.

Response variable	Predictor variable	Estimate	SE	Effect
Adult female mortality	Adult female density	2.4243	0.4770	+
	Male takeovers	0.1184	0.1802	+
	Number of adult males	0.0032	0.0503	+
	Average adult female age	0.0770	0.0615	+
	Disease epidemic	0.5231	0.2591	+
	Distance to rivers	0.0004	0.0004	+
	Human use	0.2032	0.1274	+
	Vegetative cover	-0.1931	0.2500	-
	Distance to roads	0.0002	0.0004	+
	Distance to swamps	0.0001	0.0002	+
Cub productivity	Adult female density	1.9606	0.5755	+
	Male takeovers	-0.6312	0.2408	-
	Number of adult males	0.1421	0.0607	+
	Adult female mortality	-4.8594	1.9596	-
	Disease epidemic	-0.3358	0.4185	-
	Distance to rivers	-0.0008	0.0004	-
	Human use	0.1208	0.1515	+
	Vegetative cover	0.3433	0.1722	+
	Distance to roads	-0.0004	0.0007	-
	Distance to swamps	0.0000	0.0002	-
Male takeovers	Adult female density	-1.2508	1.0930	-
	Distance to rivers	0.0016	0.0005	+
	Vegetative cover	-0.7079	0.4818	-
	Human use	0.0804	0.1423	+
	Distance to roads	0.0009	0.0005	+
	Distance to swamps	-0.0001	0.0002	-

Adult female mortality

Fifteen *a priori* candidate models were constructed to represent hypotheses explaining adult female mortality in Crater lion prides (Table 3.6).

Table 3.6. *A priori* candidate models explaining the influence of demography, landscape and human use factors on adult female mortality, 1975-2005. Models were analyzed using a Poisson generalized linear model for repeated data, corrected for small sample size (n = 95), and ranked according to ΔAICc.

Model #	Candidate model	K	LogLikehood	AICc	ΔAICc	ωi
1	adkm, epidemic	3	-58.78	123.69	0.00	0.39
2	adkm, riverdis, epidemic	4	-58.29	124.80	1.12	0.23
3	adkm, to, fage, epidemic	5	-57.59	125.52	1.84	0.16
4	adkm, humuse, epidemic	4	-58.77	125.76	2.08	0.14
5	adkm, epidemic, to, fage, riverdis	6	-57.46	127.40	3.71	0.06
6	adkm, to, numm, fage, epidemic, roaddis	7	-57.44	129.52	5.84	0.02
7	adkm	2	-65.14	134.35	10.67	0.00
8	to, humuse, epidemic	4	-73.23	154.68	31.00	0.00
9	humuse, riverdis, epidemic	4	-73.41	155.04	31.36	0.00
10	epidemic	2	-76.02	156.10	32.41	0.00
11	riverdis, epidemic	3	-75.33	156.80	33.11	0.00
12	to, epidemic	3	-75.73	157.58	33.90	0.00
13	to, humuse	3	-76.69	159.51	35.82	0.00
14	vegtype	2	-78.82	161.71	38.02	0.00
15	Swamps	2	-79.26	162.58	38.90	0.00

All terms and abbreviations as in Table 3.3.

Results suggest most support for the model containing adult female density and disease epidemic to explain adult female mortality with ωi = 0.39, while model 2 (ωi = 0.23) and model 3 (ωi = 0.16) containing distance to rivers, male takeovers and adult female age fall within the confidence set of the best model. The best model is only 1.7 and 2.4 times more likely to be the best than model 2 and 3 respectively. Parameter estimates for the best model are presented in Table 3.7.

Table 3.7. Parameter estimates and 95% confidence intervals (CI) for parameters in the best model for adult female mortality, 1975-2005.

			95% CI	
Parameter	Estimate	SE	Upper	Lower
Adult female density	2.7795	0.5000	3.7595	1.7994
Disease epidemic	0.7611	0.2433	1.2380	0.2842

Cub productivity

We used AIC to select the best approximating model among 23 *a priori* candidate models constructed to test the effect of demography, landscape and human use on cub productivity. The best fitting model had five variables; adult female density, male takeovers, number of adult males, distance to rivers and amount of vegetative cover (Table 3.8). The second model had ΔAICc > 7 suggesting no support for any alternative model in the candidate list.

Table 3.8. A *priori* candidate models explaining the influence of demography, landscape and anthropogenic factors on cub productivity during in Crater prides, 1975-2005. Models were analyzed using Poisson generalized linear model for repeated data. Models are ranked based on (ΔAICc). AIC values were corrected for small sample size (n = 95). A lower ΔAICc and high ωi indicate more support for the model.

Model#	Model Set	K	LogLikelihood	AICc	ΔAICc	ωi
1	adkm, to, numm, riverdis, vegtype	6	162.66	-312.84	0.00	0.99
2	adkm, to, numm, fage	5	157.25	-304.16	8.68	0.01
3	adkm, numm, to	4	153.68	-299.14	13.70	0.00
4	adkm, numm, riverdis, vegtype	5	154.48	-298.62	14.22	0.00
5	adkm, riverdis, numm	4	151.49	-294.76	18.08	0.00
6	numm, riverdis, f3lskm, vegtype	5	147.00	-283.67	29.17	0.00
7	numm, riverdis, f3lskm	4	145.29	-282.37	30.47	0.00
8	f3lskm, to, epidemic, riverdis	5	144.17	-278.01	34.83	0.00
9	to, epidemic, vegtype, adkm	5	143.26	-276.18	36.66	0.00
10	adkm, numm	3	138.31	-270.48	42.36	0.00
11	f3lskm, riverdis, to	4	138.14	-268.06	44.78	0.00
12	vegtype, riverdis, humuse, swamp, roaddis, epidemic, adkm	8	142.37	-267.91	44.93	0.00
13	riverdis, epidemic, humuse, adkm	5	137.00	-263.66	49.17	0.00
14	f3lskm, epidemic, to	4	135.24	-262.25	50.59	0.00
15	adkm, riverdis	3	133.92	-261.70	51.14	0.00
16	swamps, epidemic, vegtype, adkm	4	131.63	-255.03	57.80	0.00
17	vegtype, adkm	3	130.46	-254.79	58.05	0.00
18	f3lskm, riverdis	3	125.91	-245.69	67.14	0.00
19	adkm	2	123.32	-242.58	70.26	0.00
20	adkm, epidemic	3	124.02	-241.92	70.92	0.00
21	to	2	122.18	-240.29	72.55	0.00
22	adkm, humuse, epidemic	4	124.12	-240.02	72.82	0.00
23	f3lskm	2	116.11	-228.15	84.69	0.00

All terms and abbreviations as in Table 3.3.

The parameter estimates for variables in the best model are presented in Table 3.9 and indicate adult female density and the number of adult males (male coalition size) to have the strongest effect on cub productivity.

Table 3.9. Parameter estimates and the 95% confidence intervals (CI) for the best model explaining cub productivity, 1975-2005.

			95% CI	
Parameter	Estimate	SE	Upper	Lower
Adult female density	2.0320	0.6224	3.2519	0.8122
Number of adult males	0.1285	0.0428	0.2124	0.0446
Male takeovers	-0.4561	0.2459	0.0258	-0.9380
Amount of vegetative cover	0.2098	0.1931	0.5883	-0.1687
Distance to rivers	-0.0006	0.0005	0.0003	-0.0016

Frequency of male takeovers

Of the 10 a *priori* models (Table 3.10) concerning the frequency of male takeovers, distance to rivers had the strongest support. Models adding density of adult females (model 2) and vegetative cover (model 3) both are within the confidence set of the best model ($\Delta AICc < 2$). Examining the ω_i, the best model was 1.9 and 2.2 times as likely to be the best compared to models 2 and 3 respectively (Table 3.11). Distance to rivers is thus a better predictor for the frequency of male takeovers than either adult female density or vegetative cover.

Table 3.10. A *priori* candidate models explaining the influence of demography, landscape and human use on the frequency of male takeovers in Crater prides, 1975-2005. Models were analyzed using Poisson generalized linear model for repeated data. Models are ranked based on (ΔAICc). AIC values were corrected for small sample size (n = 95). A lower ΔAICc and high ωi indicate more support for the model.

Model #	Model Set	K	LogLikelihood	AICc	ΔAICc	ωi
1	riverdis	2	-71.00	146.06	0.00	0.42
2	riverdis, adkm	3	-70.60	147.34	1.28	0.22
3	vegtype, riverdis	3	-70.74	147.61	1.55	0.19
4	riverdis, adkm, vegtype	4	-70.32	148.87	2.82	0.10
5	vegtype	2	-74.02	152.11	6.06	0.02
6	adkm, vegtype	3	-73.30	152.74	6.69	0.01
7	roaddis	2	-74.38	152.82	6.76	0.01
8	adkm	2	-74.76	153.58	7.52	0.01
9	humuse	2	-75.35	154.77	8.72	0.01
10	swampdis	2	-75.41	154.89	8.83	0.01

Table 3.11. Parameter estimates and the 95% confidence intervals (CI) for the best model (distance to rivers) explaining the frequency of male takeovers, 1975-2005.

			95% CI	
Parameter	Estimate	SE	Upper	Lower
Distance to rivers	0.0016	0.0005	0.0026	0.0005

Discussion

Analysis over a 10-year time scale suggests that only female density, cub productivity and proximity to rivers determine long-term pride persistence. “Adult female density” is a measure of pride size, and larger prides would certainly be expected to persist longer, because of the competitive advantage by large groups over small groups. Territorial behavior plays a crucial role by enabling large prides to occupy high quality areas in terms of food supply and shelter. Cub productivity is the ultimate source of recruitment of all future females within a pride, and rivers have a positive effect on cub productivity and are associated with lower female mortality. In contrast, a pride’s short-term (5years) persistence depends on a broader suite of demographic and landscape variables than just female density, cub productivity and proximity to rivers.

We found male takeovers to be less common for prides located closest to rivers (Table 3.5). Apparently, such prides appear to have higher adult female densities. Prides that experience fewer male takeovers are not only subject to lower female mortality but also have fewer daughters expelled by incoming males.

According to our best-fitting model, adult female density and disease epidemics increased adult female mortality. Our measure of "female density" depended on the number of females at risk of death in each time step, and the number of female deaths per pride will inevitably be higher in larger prides; we therefore view the female density variable as a statistical "control" for mortality. Age-specific mortality typically follows a U-shaped curve, with high mortality prior to the first birthday and accelerating mortality from 11 years onward (Packer, Tatar and Collins, 1998). However, during documented disease outbreaks, lions in the middle age classes experience unusually high mortality (Packer at el., 1999; Kissui and Packer, 2004), and two disease epidemics in the Crater were inferred by abnormally high adult mortality over a short period of time (Kissui and Packer, 2004).

The most important aspect of our mortality analysis, therefore, is the finding that females with territories closest to rivers experienced the lowest mortality, and prides in these areas show higher persistence than prides further from rivers. In Serengeti National Park, proximity to river confluences increased the lions' hunting and reproductive success (Hocraft, Sinclair and Packer, 2005; Mosser, 2008), and there was close association between prey availability and riverine habitats in the Selous Game Reserve (Spong, 2002). Our results suggest that rivers directly confer advantages to adult survival, though it is not possible to determine whether this is due to better access to food or to more effective shelter. Females are known to die in defense of their cubs against incoming males (Pusey and Packer, 1987), and our analysis suggests that male takeovers increase female mortality (Table 3.5).

We found support for the hypotheses concerning the effect of adult female density, male takeovers, number of adult males, distance to rivers and vegetative cover on cub productivity. The positive relationship between adult female density and cub productivity is not surprising. Female lions are egalitarian, living in groups that breed synchronously (Packer, Pusey and Eberly, 2001), and by banding together females increase their own reproductive success, and the more females in a pride, the greater the number of cubs born. In addition, large groups gain advantage in that they can occupy high quality areas of the landscape that confer improved fitness. Similarly, large male coalitions are more successful at defending their territory and protecting their offspring (Bygott, Bertram and Hanby, 1979). Male takeovers had a negative relationship to cub productivity because takeovers are generally associated with infanticide in lions. The effects of infanticide have been repeatedly documented (e.g. Schaller, 1972; Betram, 1973; Bygott, Bertram and Hanby, 1979; Packer and Pusey, 1984).

We found cub productivity to be highest in pride territories closest to rivers. In addition to attracting prey and providing good ambush sites, rivers provide shelter and safe sites for hiding cubs, thus reducing cub mortality. Similarly, greater vegetative cover increases prey accessibility (Funston et al., 2003; Hopcraft, Sinclair and Packer, 2005), provides better shelter for cubs (Mosser, 2008), and promotes population growth (Packer et al., 2005).

In conclusion, our results demonstrate the importance of using pride persistence to gain insight into the complex population dynamics of a species with group territoriality. The growth and size of a lion population is closely correlated to the number of prides (Packer et al., 2005), and fine-scale landscape heterogeneities are intimately linked to demographic performance of individual prides, while territorial behavior plays a key role in mediating the interactive effects of landscape and demography.

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Chapter 4

Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe

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Abstract

Livestock predation is one of the most serious threats facing large carnivores today. Conservation interventions would therefore benefit from understanding the factors that increase the vulnerability of each carnivore species to retaliatory killing. The African lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*) are all killed in retaliation for livestock predation, but each species suffers differently from these impacts due to differences in predatory behavior and cultural attitudes of livestock keepers. Using detailed data on livestock predation in the Maasai steppe landscape in Northern Tanzania, I investigated how prey preference, location and timing of livestock attacks contributed to the vulnerability of lions, leopards and spotted hyenas to retaliatory killing. Reflecting their overall preference for large herbivores, lions mostly preyed upon adult cattle and donkeys. In contrast, hyenas and leopards primarily killed small stock (goat, sheep and calves) and dogs. Hyenas and leopards mostly attacked livestock at night, whereas lions often attacked grazing livestock during the daytime. These behaviors made lions the most vulnerable to direct retaliatory killing, although some villages specifically targeted hyenas with poison, and the cultural traditions of livestock keepers might also exacerbate the retaliatory killing of lions.

Key words: Cultural attitudes; Livestock predation; Retaliatory killing; Carnivores; Vulnerability; livestock keepers; Maasai steppe; Prey preference

Introduction

Many ecological, biological and anthropogenic factors operate independently or interactively to cause the global decline of carnivore species (Purvis et al., 2000; Cardillo et al., 2004; Cardillo et al., 2005; Shivik, 2006). In mammals, species with slow life histories (smaller litters, slow growth rates, late sexual maturity), complex social structure, large home ranges, large body size and lower population densities are more vulnerable to population declines (McKinney, 1997; Purvis et al., 2000; Cardillo et al., 2004; Fisher, 2003). However, the most urgent threats to large mammalian carnivores result from human population growth and the associated impacts from habitat degradation, extirpation and disease (Fuller, 1995; Nowell and Jackson, 1996; Weber and Rabinowitz, 1996; Forester and Machlis, 1996; Kissui and Packer, 2004). Habitat loss and human population growth caused range contraction and the decline in grizzly bears (*Ursus arctos horribilis*), gray wolves (*Canis lupus*), and mountain lions (*Puma concolor*) in Northern America (Clark, Corlee and Reading, 1996; Laliberte and Ripple, 2004). In Africa, habitat fragmentation and persecution by humans is linked to the disappearance of wild dogs (*Lycaon pictus*) and to the decline in cheetah (*Acinonyx jubatus*) and lions (*Panthera leo*) in most of their historical ranges such that current populations are largely restricted to isolated reserves (Ogada et al., 2003; Woodroffe, 2001; Patterson et al., 2004; Packer et al., 2005).

Conflicts caused by livestock predation lead to retaliatory killing of large carnivores. This is perhaps the most serious threat facing large carnivores amidst the ever-expanding human population. Most protected areas are too small to encompass wide-ranging carnivores. Such species must utilize adjacent dispersal areas for supplementary food (Woodroffe and Frank, 2005). Conflict-related mortality can be so high that reserve border areas could represent population sinks through an “edge effect” (Woodroffe and Ginsberg, 1998; Macdonald and Sillero-Zubiri, 2002; Kolowski and Holekamp, 2006).

Livestock predation by carnivores cause huge economic losses among livestock keepers, for example, Paterson et al., (2004) estimated livestock predation to represent 2.6 % of the herd’s economic value in a Kenyan ranch which incurred a loss of ~ $ 8749 per annum. Similarly, Mishra, (1997) reported an economic loss of $15,418 due to predation among the Indian-trans Himalayan communities equivalent to $128 loss per family per year, and Butler, (2000) recorded economic loss averaging $13 or 12% of each household's net annual income in Zimbabwe. Due to such losses and sometimes due to perceived danger by carnivores, livestock keepers have had a long history of intolerance against large carnivores (Sillero-Zubiri and Laurenson, 2001). For example, the governments in Massachusetts Bay and Virginia paid bounties for wolf scalps in the 1630s, and many wolves were killed such that by 1850s, wolves were rare in the eastern USA (Dunlap, 1988). Red foxes in the United Kingdom are deliberately killed by farmers due to perceived threat to livestock (Baker and Macdonald, 2000). However, conservation efforts can be improved by raising the tolerance of livestock keepers for wild carnivores using education and economic incentives such as realized income from ecotourism (e.g., cheetah on sheep ranches in Namibia) (Marker, Mills and MacDonald, 2003).

The level of livestock predation varies between and within regions (Graham, Beckerman and Thirgood, 2005; Kolowski and Holekamp 2006) because of differences in the abundance and distribution of natural prey (Polisar et al., 2003; Patterson et al., 2004; Woodroffe and Frank, 2005). For example, most lion predation on livestock in Botswana's Makgadikgadi Pans and Tanzania's Ngorongoro Conservation Area occurred in the season when wild ungulates were scarce (Hemson, 2003; Ikanda, 2006). But, sometimes livestock predation may be higher in seasons when natural prey is abundant (*Ibid*), suggesting that additional factors might influence livestock predation. Local variation in habitat and vegetative cover influenced lynx predation on sheep in Europe (Stahl et al., 2002), and vegetative cover alters hunting success of lions on wild prey (Hopcraft, Sinclair and Packer, 2005).

In regions with widespread livestock predation, pastoralists retaliate by indiscriminately killing predators (Woodroffe, 2001; Treves and Karanth, 2003; Polisar et al., 2003; Kolowski and Holekamp, 2006). While several studies have documented retaliatory killing of African carnivores (e.g. Ogada et al., 2003; Patterson et al., 2004; Kolowski and Holekamp, 2006), no previous study has empirically compared the relative vulnerability of sympatric carnivore species to retaliatory killing. I therefore investigated and compared how prey preference, location and timing of livestock attacks contributed to the vulnerability of lions (*Panthera leo*), leopards (*Panthera pardus*) and the spotted hyenas (*Crocuta crocuta*) to retaliatory killing in the Maasai steppe, Northern Tanzania.

Lions are social carnivores living in territorial groups, they hunt cooperatively but individual lions can capture prey twice their size. Lions can survive and prey on a broad range of species that vary between habitats (Hayward and Kerley, 2005). The most common prey species for lions are wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*), but also prey upon species as large as buffalo (*Syncerus caffer*) (Schaller, 1972; Scheel, 1993; Mills and Shenk, 1992; Funston, Mills and Biggs, 2001; Kissui and Packer, 2004) and as small as warthog (Scheel and Packer, 1991). Although lions are most active at night, they frequently hunt during the day (Schaller, 1972).

The spotted hyena is also a social carnivore living in territorial groups called clans (Kruuk, 1972). The main prey for hyenas includes wildebeest, zebra, and Thomson gazelle (*Gazella thomsonii*) (Kruuk, 1972; Höner et al., 2002). Spotted hyenas are flexible in their behavior; they breed all-year round and are active both during the day as well as at night (Kruuk, 1972; Frank, 1986). They are highly adapted to human settlement and do not appear to be afraid of humans especially at night (Kolowski and Holekamp, 2006; personal observation). Boydston et al., (2003) studied space use by spotted hyenas in Kenya and concluded that hyena behavior changed in response to changes in human activities and suggested such behavioral plasticity conferred advantages in human-dominated environments.

Leopards are widely distributed; occupy a broad variety of habitat from forest to desert (Mizutani and Jewell, 1998), and they seem to do better in human-dominated areas than lions and hyenas (Nowell and Jackson, 1996). Leopards exhibit remarkable behavioral plasticity in terms of habitat selection, activity patterns and prey selection; they can adapt to a range of environmental and anthropogenic factors such as changes in prey base and land use (Woodroffe 2000; Marker and Dickman, 2005).

The three carnivore species (lion, leopard and hyena) are sympatric in the Maasai steppe landscape and they all engage in livestock predation. I hypothesized that the species that killed the most livestock (and especially the most valuable livestock) would suffer the most retaliatory killing and that vulnerability to retaliation would depend on the location and time of day of livestock predation. Traditionally the Maasai tribe engages in ritual lion (but not hyena and leopard) hunts called *Ala-mayo* to express bravery and rite of passage to adulthood (Ikanda and Packer in press). *Ala-mayo* features organized hunting parties mostly by young morani warriors. However, *Ala-mayo* is outlawed by the Tanzanian wildlife authorities and although it is still practiced, it is less common in the Maasai steppe. The analysis presented here do not include *Ala-mayo* killings, instead the focus is on retaliatory killings associated with livestock predation. In the course of the study, every effort was made to verify livestock predation events and the associated incidences of retaliatory killing of predators. Understanding the context in which different species of predators are differentially vulnerable to causes of mortality such as retaliation due to livestock predation will provide important insights into potential mitigation efforts of human-carnivore conflicts in the Maasai steppe and elsewhere in Africa.

Study area

The study was conducted in the Maasai steppe in Northern Tanzania (Fig. 4.1), one of East Africa's most important wildlife areas with large numbers of migratory ungulates, elephants (*Loxodonta Africana*), lions, leopards, cheetahs (*Acinonyx jubatus*), hyenas and wild dogs (*Lycaon pictus*). Tarangire (2,800 km^2) and Manyara (330 km^2) National Parks are the core protected areas within the Maasai steppe, which covers a total area of >25,000 km^2 (Borner, 1985; Prins, 1987) (Fig. 4.1). Wildlife moves seasonally between the National Parks and the adjacent dispersal areas (Fig. 4.1): during the dry season (June-Nov.), the migratory species remain inside the National Parks but move into dispersal areas in village lands for most of the wet season (Nov.-May) (Lamprey, 1964; Kahurananga and Silkiluwasha, 1997; Kahurananga, 1981; TMCP, 2000).

The Maasai steppe contains the fourth-largest lion population in Tanzania, but the two core protected areas only cover ~10% of the entire ecosystem. Hyenas and leopards are very common throughout the Maasai steppe, although there are no reasonable estimates of their population sizes. The study area spans Monduli and Simanjiro districts in Arusha and Manyara regions respectively. The Maasai are the predominant ethnic group in Monduli and Simanjiro districts. They keep indigenous zebu cattle (*Bos indicus*), small stock (sheep and goats), and donkeys, and most households have domestic dogs (Sachedina, 2006). Other ethnic groups are Waarusha and Barbaig. While Barbaig have been in the Maasai steppe for many decades, most Waarusha have immigrated into the area from nearby towns, and they mostly engage in small-scale agriculture and livestock keeping.

A Maasai boma typically consist of several mud huts (homesteads) surrounding a central cattle enclosure (Plate 4.1), and each homestead may have a separate enclosure for their family's goats, sheep, and calves. These shelters generally consist of wooden walls plastered with mud and cow dung. Other ethnic groups configure their households around a single homestead with a smaller cattle enclosure and/or a shelter for smaller stock. In either case, livestock enclosures are typically made from thorn bushes and occasionally from wooden poles. The boma walls are an average of 1.5 m high and 1-1.5 m thick. Pastoralists typically take their livestock out for grazing in the morning (8-10hrs), constantly watching them throughout the day. At night, livestock are kept in the bomas.

An estimated 350,000 pastoralists inhabit the Maasai steppe, with about one million indigenous zebu cattle ((Nelson, 2005; Sachedina, 2006). The human population growth is 4% for Arusha and 3.8% for Manyara regions for the inter-census period between 1988 and 2002 (Tanzania Population and Housing Census, 2002).

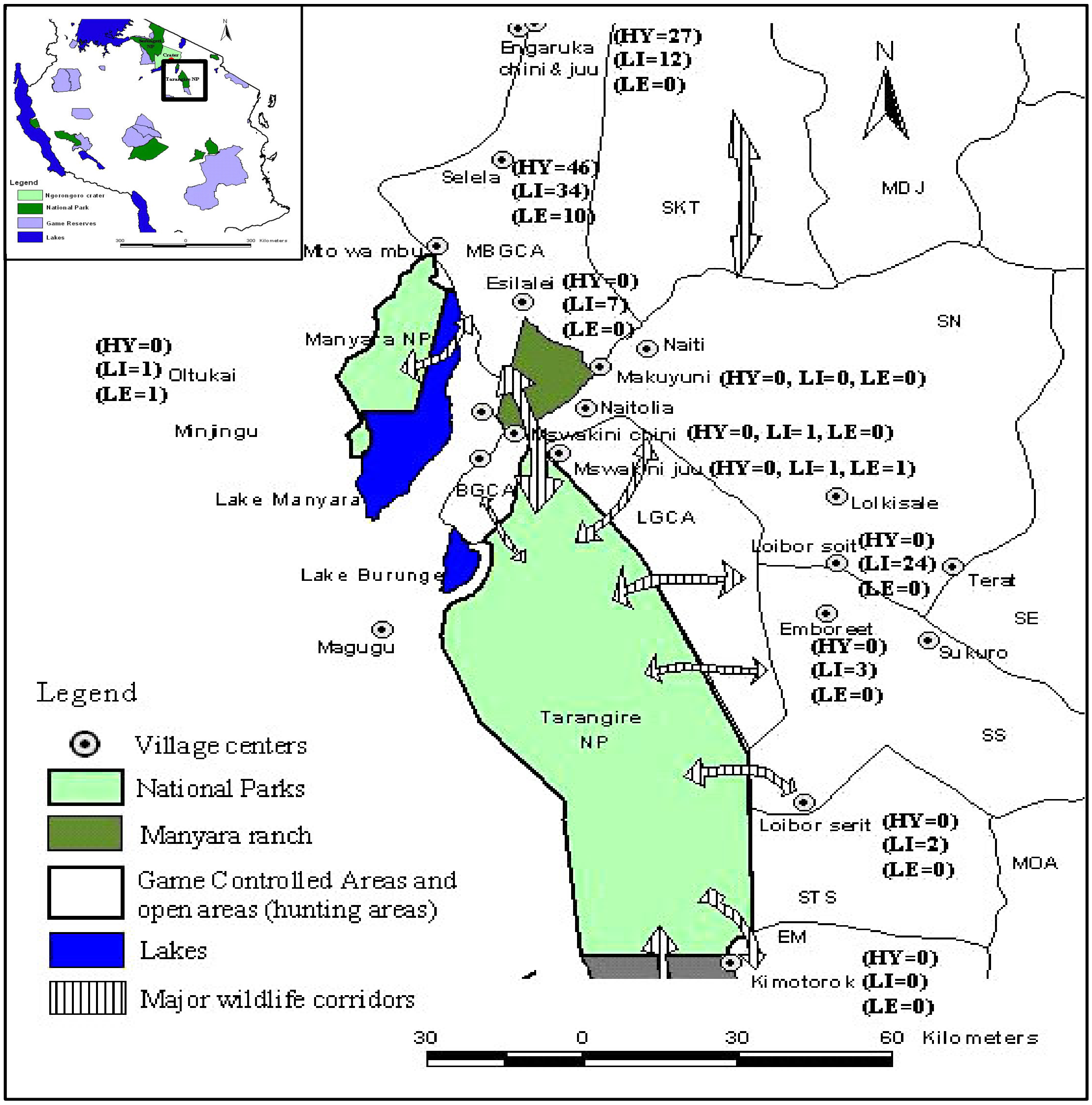

Figure 4.1. Map of the Maasai steppe showing Tarangire NP, Manyara NP and the surrounding village and hunting areas. Names of hunting areas shown: EM = East Mkungunero, STS = Simanjiro, MOA=Maasai open area, SS= Simanjiro south, SE = Simanjiro east, SN = Simanjiro north, LGCA = Lolkisale game controlled area, BGCA = Burunge game controlled area, MBGCA = Mto wa mbu game controlled area, SKT = Kitumbeine, MDJ = Monduli juu. Major wildlife corridors are mapped according to studies by Kahurananga and Silkiluwasha (1997); TMCP (2000). The number of predators killed due to retaliation in surveyed villages is shown in parentheses (HY=hyenas; LI= lions; LE=leopard). Insert is a map of Tanzania.

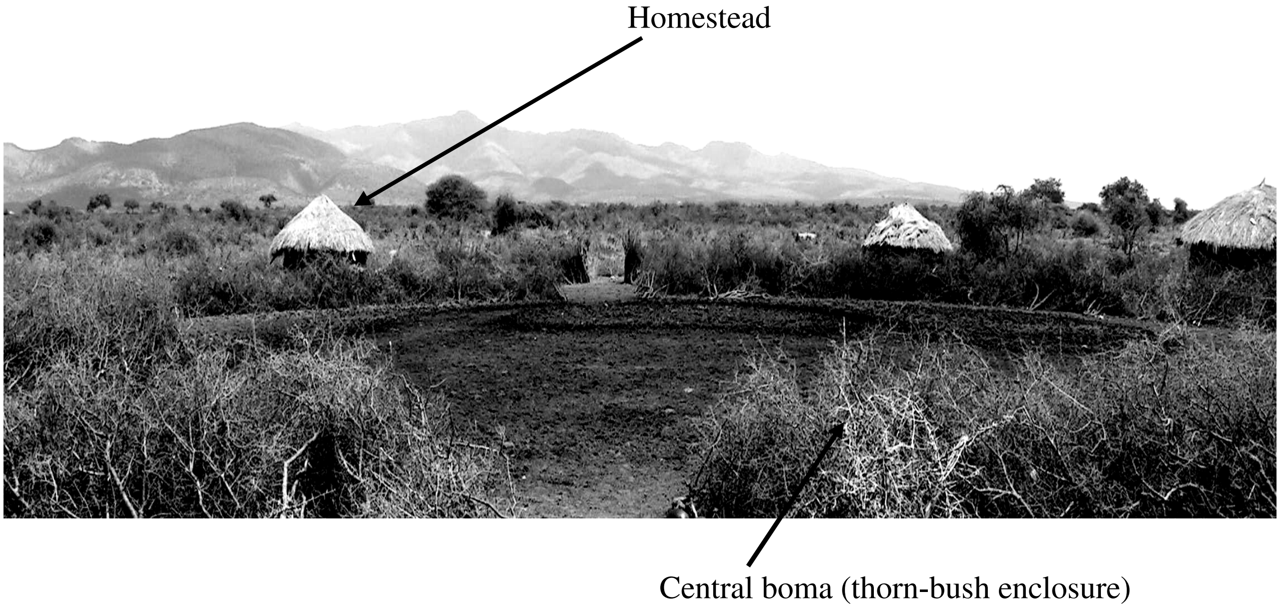

Plate 4.1: Design of a typical Maasai boma with several homesteads around a central thorn bush cattle corral where livestock from all homesteads are kept. Small stocks (goat, sheep, calves) are kept in separate small enclosures for each homestead. Each homestead owns a portion of the existing livestock herd (Picture taken Jan. 2007).

Figure 4.1 shows three types of protected areas in the Maasai steppe: National Parks are core protected areas exclusive of any form of consumptive wildlife utilization. National Parks have the highest level of wildlife protection and are patrolled by staff from the Tanzanian National Parks (TANAPA). Game Controlled Areas and Open Areas extend to village lands. Game Controlled Areas are semi-protected by the wildlife laws, but authorities allow consumptive utilization through licensed trophy hunting and livestock grazing. Open Areas are not protected by law, except for the requirement that all trophy hunting be licensed by the Tanzanian wildlife division. Lions, hyenas and leopards are all trophy-hunting species (Rodgers, Melamali and Nelson, 2003; Msoffe, 2003).

Methods

I recruited and trained 15 people, consisting of 1-2 persons resident in each of the 12 study villages across the Maasai steppe (Fig. 4.1) to maintain a detailed record of incidents (events) of livestock predation by lions, hyenas and leopards from Jan. 2004 to July 2005. To test the ability of incident recorders to discriminate between carnivore species, I presented them with a series of photographs of the targeted carnivore species. Lions, leopards and hyenas are the most common large carnivores in the Maasai steppe that engage in livestock predation (cheetah and wild dogs are very rare and only occasionally prey upon livestock). The three major species are well known by local language as *Orng'atuny* for lion, *Lugwaruu-kerii* for leopard and *Orngo'jine* for hyena. All assistants could accurately distinguish cheetah from leopard through morphology and behavior, and correctly described cheetah as primarily occupying open/sparsely-wooded grassland and mostly attacking livestock during the day, while leopards reside in thicker wooded areas and attack livestock at night in bomas. A livestock attack event was defined as an incident in which a predator attacked and killed or injured one or more livestock. Therefore, several livestock could be attacked in a single event. Livestock predation refers to an attack event that injured or killed any type of livestock.

Livestock attacks were verified in two ways (Table 4.1). About 20% of events were verified by visiting the attack site (mostly at the bomas), while about 70% were confirmed in interviews with livestock herders/owners <24 hrs of the attack. The remaining 10% were recorded during interviews with a third person, therefore representing a less certain source of information. However, there is no compensation for predation-related livestock losses in Tanzania, so there is no incentive for intentional misrepresentation. Thus, the true extent of livestock predation is probably under-reported.

Table 4.1. Percentage of livestock attack events by lions, hyenas and leopards classified according to verification method in 12 villages during 2004-July 2005 (see text for details).

		Verification method					
		Site visit		Herder/owner interview		Third party	
Village name	No. of events	n	%	n	%	n	%
Emboreet	72	13	18.06	52	72.22	7	9.72
Engaruka chini	41	9	21.95	30	73.17	2	4.88
Engaruka juu	13	3	23.08	8	61.54	2	15.38
Esilalei	29	6	20.69	20	68.97	3	10.34
Kimotorok	5	1	20.00	4	80.00	0	0.00
Loboir siret	5	2	40.00	1	20.00	2	40.00
Loibor soit	56	12	21.43	39	69.64	5	8.93
Makuyuni	14	2	14.29	10	71.43	2	14.29
Mswakini chini	8	3	37.50	5	62.50	0	0.00
Mswakini juu	11	3	27.27	7	63.64	1	9.09
Oltukai	47	9	19.15	33	70.21	5	10.64
Selela	95	18	18.95	67	70.53	10	10.53
Totals	396	81	20.45	276	69.70	39	9.85

I revisited each village at fortnightly intervals to collate attack-event information and to interview affected livestock owners for detailed information and verification. Information recorded for each event included the type and number of livestock attacked, the location and context of the attack, whether the attack resulted in fatality or injury, the name of the livestock owner, the person responsible for the livestock at the time of the attack, the species, age and sex of the predator, and the response to the attack by the livestock owners/herdsmen and the general community. Retaliatory killings were carried out cooperatively with large groups of as many as 100 people (Plate 2.2).

Plate 4.2. Retaliatory lion hunting party following an attack on two cattle by lions in the Maasai steppe in Jan. 2007.

I lived in the Maasai steppe and interacted closely with local communities for more than 1.5 yrs, which provided an opportunity to observe and learn the more subtle aspects of human-carnivore interactions and to obtain additional information on the nature of the problem.

Potential sources of bias

Although most studies of human-wildlife conflict have used similar techniques (e.g. Kolowski and Holecamp, 2006; Van Bommel et al., 2007; Woodroffe et al., 2007), these surveys suffer from three potential sources of bias. First, the Tanzanian government does not compensate for losses to predation, so pastoralists lack incentive to report livestock losses, leading to a likely underestimate of the true extent of predation. Secondly, Maasai warriors engage in ritual lion killing, *Ala-mayo,* so it is possible that some of the lion killings might have been motivated by culture rather than retaliation. However, the ease and consistency with which livestock predation could be verified makes it very unlikely that reports of lion attacks were exaggerated. Ikanda, (2006) was able to distinguish retaliation from *Ala-mayo* in the nearby Ngorongoro Conservation

Area (which serves as a well-known destination for young Maasai warriors seeking an opportunity to kill a lion). In contrast, the Maasai in the Maasai steppe relied on livestock attacks as an opportunity for *Ala-mayo* rather than fabricated lion attacks to justify *Ala-mayo*. Third, survey respondents generally bias their memory towards recent events, so all analyses were specifically restricted to the most recent events. Note, though that the attack events verification and follow-up interviews further improved the quality and reliability of the data collected for this study.

Statistical analyses: I used the χ^2 test to test the observed frequency of predation on different types of livestock and contexts of livestock attacks events by the three carnivores. Feeding preferences were calculated according to the number of attack events on each type of livestock (since multiple prey may be captured in a single event), but I made no attempt to control for variations in prey abundance.

I used the Wilcoxon (Rank sums) test to compare predation for each species of carnivore in the wet *vs.* dry season; Spearman correlations were used to examine the relationship across villages between the numbers of attacks on livestock *vs.* the number of predators killed. For all statistics, an “attack event” referred to an occasion when a predator killed or injured one or more livestock. All statistical tests were performed using SAS 9.1.

Results

Impact of predation

Figure 4.2 shows the estimated loss of cattle, goats and sheep to predation compared to other causes of livestock loss in 38 well-studied bomas. Each boma contained an average of 198.27 ± 293.25 SD cattle (range 15-1500) and 240.38 ± 240.61 SD goats plus sheep (range 35-1000). Compared to predation, the impact of disease was >10 times greater for cattle and >5 times higher for goats and sheep.

Figure 4.2. Major causes of cattle, goats and sheep losses in the Maasai steppe during 2004-July 2005

Livestock predation tactics by lions, hyenas, and leopards

A total of 396 attack events were reported on cattle, goats/sheep, donkeys and dogs during the 19 mo study period: 58.33% (n=231) were by hyenas, 25.00% (n=99) by lions and 16.67% (n=66) by leopards. Table 4.2 presents the number of attack events by lions, hyenas and leopards on each species and age-classification of livestock. Lion attacked an average of 1.7 cattle per event (range 1-6), 1.8 calves per event (range 1-3), 4.5 goats and sheep (range 1-16), 1.3 donkeys (range 1-3) and 1 dog. Hyenas attacked an average of 1.2 cattle (range 1-2) per attack event, 1.3 calves (range 1-2), 4.1 goats and sheep (range 1-50), and 1.2 donkeys (range 1-4). Leopards attacked an average of 1.7 calves (range 1-3) and 2.3 goat and sheep (range 1-10) per event.

Table 4.2. Number of attack events on different type of livestock by lions, hyenas and leopards over a period 2004-July 2005

	Cattle	Goat & sheep	Donkey	Calf	Dogs	Kids	Total
Lion	58	20	16	4	1	0	99
Hyena	9	186	18	12	4	2	231
Leopard	0	59	0	3	3	1	66
Total	67	265	34	19	8	3	396

The three carnivore species showed a significant difference ($\chi^2 = 190$, DF = 6, $P < .0001$, n = 385) in the number of attack events on each type of livestock (excluding dogs and kids in the chi-square analysis because of small sample size). Lions mostly preyed on cattle, whereas hyenas and leopards mostly took goats and sheep. Of the 67 attack events on cattle, 87% were by lions, 13% by hyenas and none by leopard. Hyenas were responsible for 70% of the 265 attack events on goat and sheep; 22% were by leopard and only 8% by lions. Hyenas also attacked the majority of calves, and hyenas and lions took similar numbers of donkeys. Leopards and hyenas were the primary predators on domestic dogs.

Wildlife prey moved to dispersal areas outside the National Parks during the wet season, and lions attacked livestock significantly more often during the wet season than in the dry season (Wilcoxon (Rank Sums) test , z = 2.3395, p = 0.0193, n=12 villages) (Fig. 4.3), as did hyenas, although this difference was not statistically significant (z = 1.5725, p = 0.1158). Leopards attacked livestock at a similar rate in both seasons (z = 1.2004, p = 0.2275).

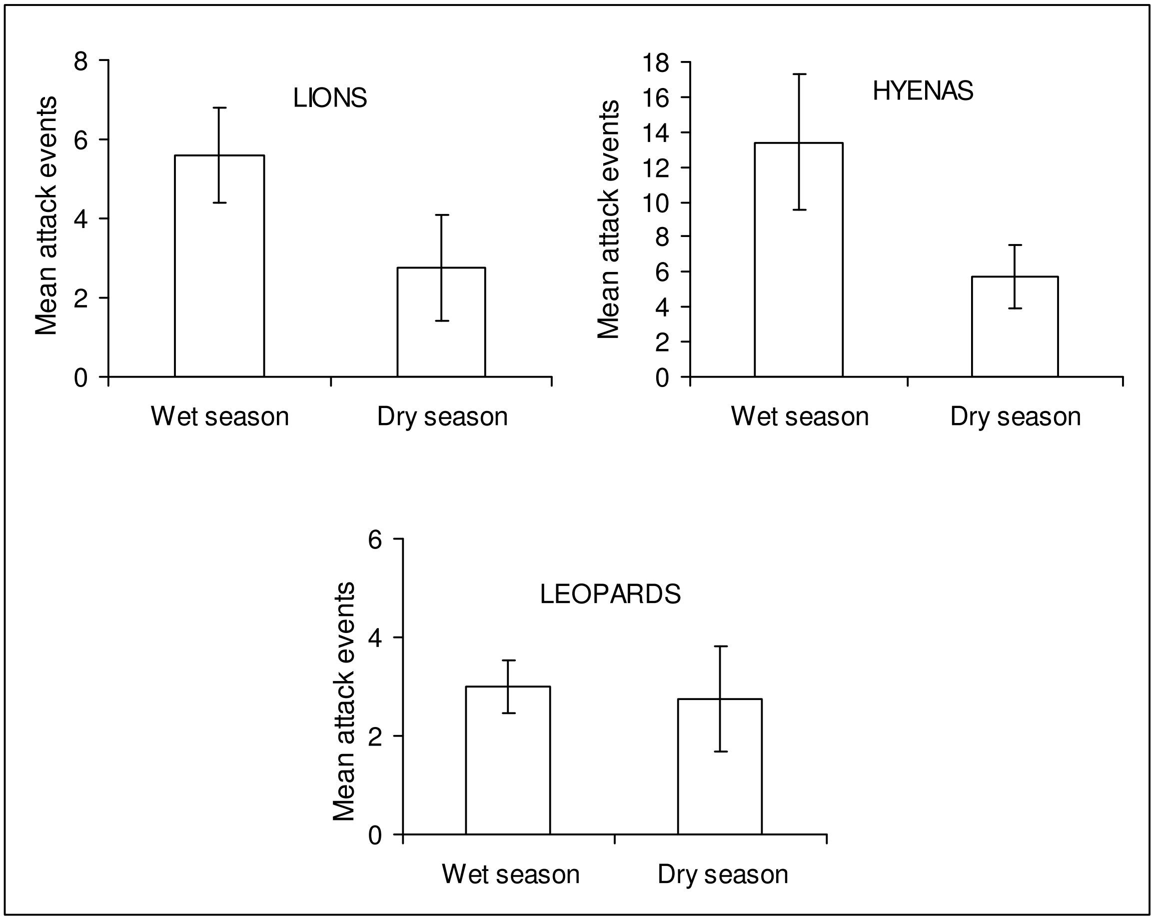

Figure 4.3. Seasonality of attack events on livestock by lions, hyenas and leopards in 12 villages. Values indicate village averages each season ±SE.

Context of livestock attack events

Livestock predation occurred in three distinct contexts: 1) while kept in bomas (enclosures) at night, 2) in the grazing field during the day, and 3) when separated from the herdsmen ("lost"). Comparing attacks in bomas *vs.* grazing sites (the third category, "lost" was excluded from chi-square because of small sample size) lions were more likely to attack grazing livestock during the day while most hyenas and leopards mostly attacked livestock at night ($\chi^2 = 48$, DF = 2, $P < .0001$, n = 374) (Fig 4.4).

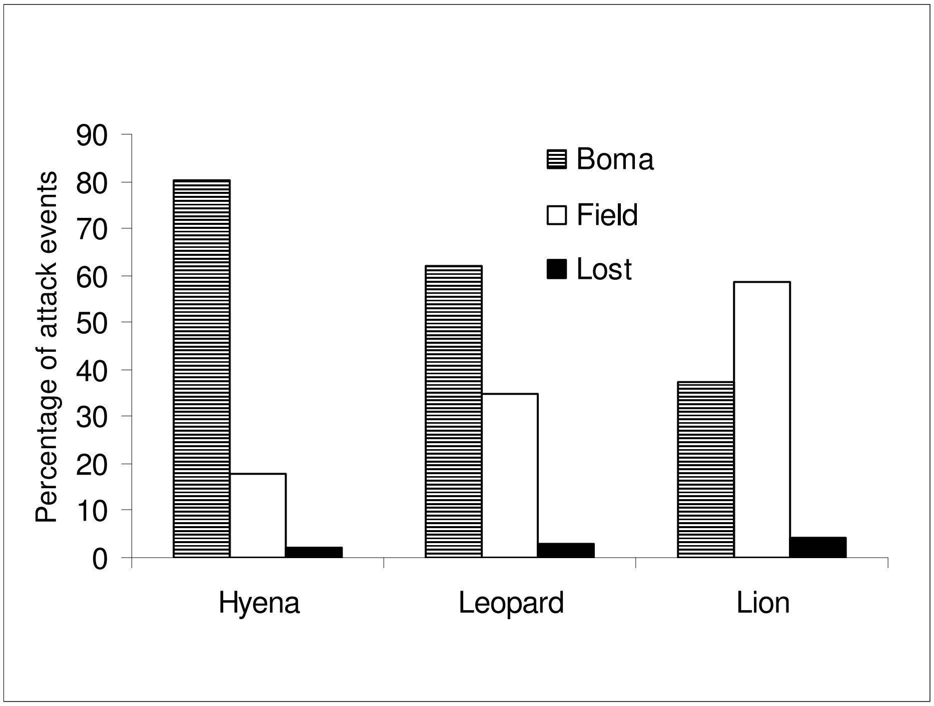

Figure 4.4. Principal contexts of livestock predation by lions (N = 99), hyenas (N = 231) and leopards (N = 66).

Livestock predation and retaliatory killing of predators

During the 19-mo study period, 85 lions were killed in the 12 villages (mean 7.08 ±10.81 SD, range 0-34 per village). Across villages, the number of lions killed was positively correlated with the number of cattle attack events by lions (Spearman correlation, $r_s = 0.6385$, $p = 0.0254$, n = 12). Similarly, the number of lions killed was positively correlated with lion attack events on goats/sheep, although this relationship was not quite significant ($r_s = 0.5351$, $p = 0.0730$, n = 12) (Fig. 4.5). The sample size for hyenas and leopards were too small to test statistically: all 71 incidences of hyena killing were recorded in the three villages (Engaruka juu, Engaruka chini and Selela) that reported using poison to remove hyenas; no other village was successful in killing hyenas (Fig. 4.5). Only two villages successfully killed leopards: one leopard was killed in Oltukai village and another 10 in Selela village (Fig. 4.5).

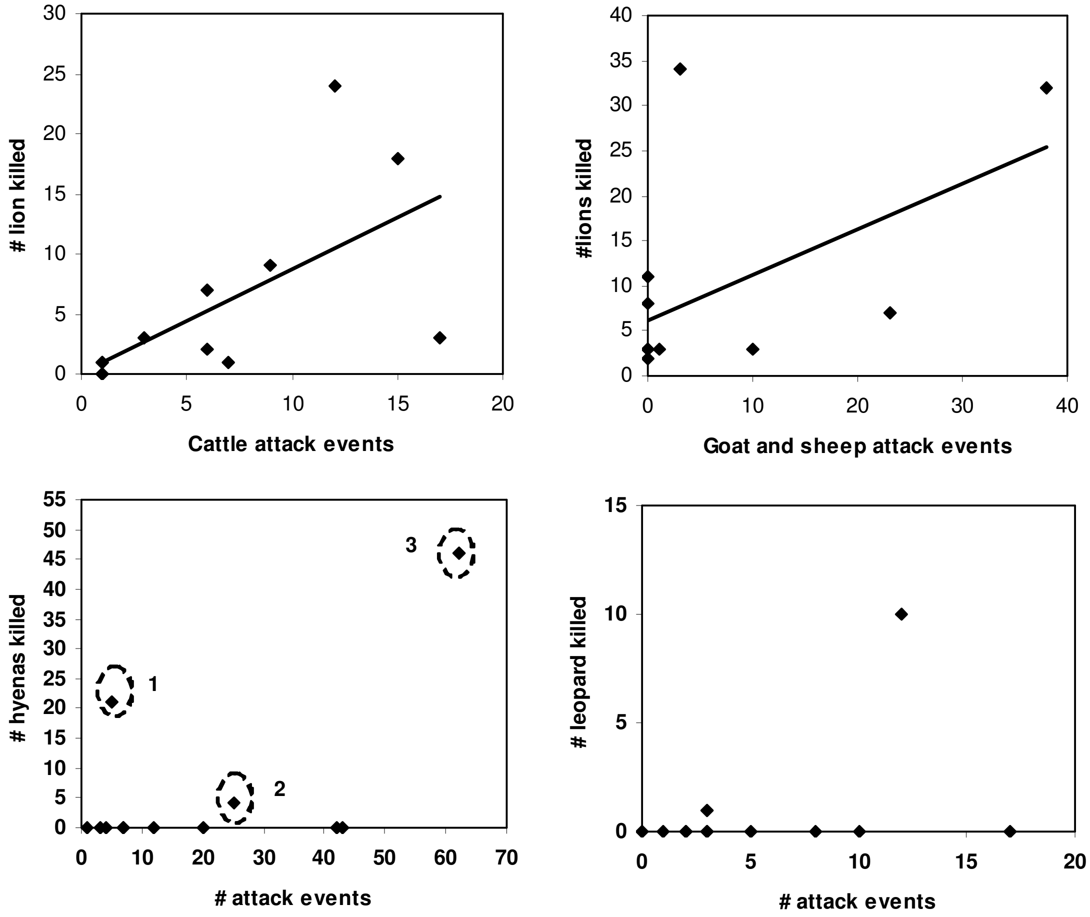

Figure 4.5. Relationship between the number of lions, hyenas and leopards killed by pastoralists in each village and the associated number of livestock attack events by each predator. Dotted circles indicate three villages (1= Engaruka chini, 2= Engaruka juu, and 3= Silale) which reported using poison against hyenas. The relationship for lion killed vs. cattle attacks and lion killed vs. goats/sheep attacks are shown with regression lines.

Discussion and conclusion

Impact of predation

In the Maasai steppe, disease claimed far more livestock than predation, yet the impact of predation was clearly high enough to provoke pastoralists into retaliating against lions, hyenas and leopards. In their review of livestock predation worldwide, Graham, Beckerman and Thirgood, (2005) reported losses ranging from 0.02-2.6% per year. While the annual loss to predation of 1% for cattle in the Maasai Steppe is comparable to other studies, the 4% loss for goats and sheep is relatively high. Kolowski and Holecamp, (2006) reported an annual loss of 0.6% for cattle and 0.2 % for goats and sheep in the Maasai Mara, Kenya. Patterson et al., (2004) reported annual losses of 2.4% for all livestock in ranches in southeastern Kenya, and Butler, (2000) reported 5% losses in Zimbabwe's Gokwe community lands.

Livestock predation tactics

Lions, hyenas and leopards showed divergent predatory behavior towards livestock with regard to type of prey they attacked, time of day, season and site of livestock attacks. Lions generally captured cattle and donkeys, reflecting their preference for large prey in wildlife areas (Schaller, 1972; Kingdon, 1997; Kissui and Packer, 2004). In contrast, hyenas and leopards both attacked small stock (goats, sheep and calves) and dogs. Similar contrasts between the three carnivore species were recorded by Patterson et al., (2004) and, Kolowski and Holekamp, (2006). Hyenas and leopards were mostly nocturnal in attacking livestock (as also noted by Kolowski and Holecamp, 2006), whereas lions frequently attacked grazing livestock during the daytime. Lions might engage in more frequent daytime livestock predation because they are least intimidated by *layon* (boys up to 15 yrs old), who serve as the primary livestock herders 80% of the time.

Lions and hyenas attacked more livestock during the wet season, while leopard attacks did not differ between seasons. The wet-season migration of abundant wild prey onto village land would be expected to decrease livestock depredation if lions, hyenas and leopards resided in these areas all year round. There are no reliable estimates of resident predator populations in the communal land, but recent studies have suggested an overall decline in abundance and diversity of wildlife species in the Maasai steppe (e.g. Rogers, Melamali and Nelson, 2003; Nelson, 2005) due to unsustainable harvests and deteriorating habitat. Lions are known to follow concentrations of migratory prey (Schaller, 1972), while hyenas commute over long distances during foraging trips (Kruuk, 1972). The results from this study therefore suggest that lions and hyenas follow the migratory prey from the National Parks into the communal lands, leading to increased opportunities for livestock predation in the wet season. The lack of seasonal variation in leopard predation suggests that leopards reside in the communal lands throughout the year and that their propensity for attacking livestock remains unchanged with the presence of migratory prey. However, additional research would clearly be needed to determine whether any of these three carnivores shows a consistent preference for wildlife prey vs. livestock.

During nighttime attacks, lions and hyenas typically break through boma walls, while leopards can leap over short walls. Lions either force their way inside or stampede the livestock, causing breakage of the boma walls. In this study, a large number of dogs were victims to predation; though Woodroffe et al., (2007) found that dogs improved livestock security both in the day-time grazing fields and in the bomas at night. However, Ogada et al., (2003) found that the presence of dogs was only associated with reduced lion predation on cattle but not on goats and sheep nor by leopards and hyenas. In other parts of Maasailand, dogs did not reduce nocturnal livestock predation by hyenas and lions, nor did predation rates depend on boma height, transparency, or thickness of thorn brush walls (Kolowski and Holecamp, 2006; Ikanda, 2006).

Predator vulnerability to retaliatory killing

Hyenas were the most frequent predators on livestock followed by lions and leopards. If livestock keepers retaliated by killing predators according to the overall frequency of attack events, hyenas should be the most vulnerable to direct retaliatory killing. Instead, lions were exceptionally vulnerable to direct retaliatory killing compared to hyenas and leopards except when poison was applied to target hyenas. Several factors could contribute to this vulnerability: first, differences between predators in their livestock predatory behaviors. Lions are more likely to defend a livestock carcass against humans, exposing themselves to frequent confrontations – which they inevitably lose. In contrast, hyenas are shy of people and run long distances immediately after a livestock attack event, moving well beyond the reach of humans; leopards are secretive, successfully hiding themselves after a livestock attack. Second, lions kill more cattle than hyenas and leopard; cattle have more value to Maasai pastoralists than the small stock typically attacked by hyenas and leopards, thus engendering more resentment against lions. The value of cattle referred here is not merely in monetary terms but also cultural. Cattle are the center of identity and the primary symbol of wealth and respect in the Maasai culture (Galaty, 1982). The loss of cattle arouses a much stronger emotional response than the loss of small stock. Third, the culture of Maasai livestock keepers could contribute to the lion killing. Killing a lion with a spear is indicative of bravery (*Ala-mayo*) and has traditionally been used as rite of passage to adulthood (Maddox, 2003, Ikanda and Packer in press), greatly increasing the incentive to participate in a retaliatory lion hunt. Such cultural sentiment is not associated with hyenas or leopards. However, the illegality of *Ala-mayo* makes it less likely for Maasai to organize unprovoked lion hunting parties, whereas Tanzanian wildlife law allows the destruction of problem animals. Thus, livestock attacks by lions trigger a swift response by the Maasai, and most lion hunting parties in the Maasai steppe are driven by livestock attack events by lions. Retaliatory lion hunts were conducted cooperatively and involved as many people as could possibly respond (except women and young children), including people outside of the affected family and totaling as many as 100 individuals (Plate 4.2). These hunts can last several days, and the Maasai will kill any lion that they encounter, including individuals that had not killed any cattle. Pastoralists do not actively hunt hyenas and leopards in the same way, instead only killing these species opportunistically, although poison seems to be the most effective strategy for targeting hyenas. Retaliatory responses against predators have been reported in some areas (e.g. Ogada et al., (2003) in Kenyan Maasai land), but not in others: Zimmermann, Walpole and Leader-Williams, (2005) found that the propensity of Brazilian ranchers to kill jaguars was not related to the number of livestock lost.

Although many behavioral and cultural factors appear to make lions particularly vulnerable to retaliatory killing by pastoralists, the use of poison to target hyenas reported in three villages may place hyenas at growing risk in “hotspots” of human-hyena conflict. Leopards were only rarely victim to poisoning, perhaps because they are less likely to scavenge than hyenas. Hyenas are difficult to kill with spears, but poison can cause wholesale killing (Kolowski and Holekamp, 2006), although the use of poison was so far confined to only three villages in a small section of the Maasai steppe. In contrast, retaliatory killing of lions was spread across the entire landscape, placing lions at greater risk on a regional scale.

Conclusion

This study provides insights into the dynamics of livestock predation among three large African carnivores and factors related to retaliatory killings. The following are possible approaches for effective long-term conservation of large carnivores in the Maasai steppe:

1. Because livestock predation is an important motivation for killing predators, human-carnivore conflicts could be reduced by improving livestock husbandry. For example, well over half of all livestock attacks occurred at night while livestock were kept in bomas. All three predators were able to surmount these simple thorn brush/wooden barriers. Chain-link fencing can be purchased locally for the price of a few livestock, and has the potential to be a cost-effective material for reducing the impact of large carnivores on livestock keepers.
2. Because lions are subject to retaliatory killing when they venture into communal lands, information on their spatial-temporal movements would identify important wildlife refuge areas. Incorporating such information into village land-use plans would help pastoralists to avoid conflict-prone areas.
3. Community outreach programs by the Tanzanian wildlife authorities (TANAPA and Wildlife Division (WD)) hold great potential to promote carnivore conservation by incorporating research findings and directly involving communities in conflict mitigation programs, primarily through improved livestock husbandry.

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