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

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

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Abstract

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

2.1 Introduction

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

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

Schaller (1972) defined a lion pride as "any resident lionesses with their cubs and attending males who share a pride area and interact peacefully". The lionesses of a pride are related and most young females become a part of their mother's pride (Heinsohn et al., 1996), thus female membership in a pride is relatively stable. When foraging in separate groups rather than as a whole lion pride may increase hunting success and limits competition while feeding (Scheel & Packer, 1991, Valeix et al., 2001). Prides can be considered fission-fusion units that consist of 2-18 females (Packer et al., 1988; Packer et al., 1990). Group size is defined as the number of adult lions observed together on an encounter, excluding cubs <2 years old (Grinnell et al., 1995; Scheel & Packer, 1991, Smuts, 1978). In contrast to females, males

never stay with the same pride throughout their lives. Males associate with a pride to protect their offspring, typically staying in charge of a pride for about 2-2.5 years (Grinnell et al., 1995), the time a generation of cubs needs to reach sub-adulthood. During male takeovers, the new males may kill or evict all cubs and juveniles in a pride to increase their own reproductive output (Van Orsdol et al., 1985; Hanby & Bygott, 1987). Males are generally expelled from their natal pride around the age of 3-3.5 years and tend to become nomadic (Grinnell et al., 1995).

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

2.2 Material and methods

2.2.1 Study area

The Amboseli ecosystem is situated across the border of Kenya and Tanzania near the foothills of Mt. Kilimanjaro. On the Kenyan side, the ecosystem covers an area of approximately 5,700 km², stretching between Mt. Kilimanjaro, Chyulu Hills, Tsavo West National Park and the Kenya/Tanzanian border (Figure 2.1). The area is generally arid to semi-arid, with an average rainfall of 340 mm per annum (Altmann & Roy, 2002, Moss et al., 2011). The area has bi-annual rainfall, short rains from November until December with longer rains in March-April (Moss et al., 2011). Within the ecosystem, there is little variation in agro-ecological zones and the area is more suitable for pastoralism than cultivation, with a high potential for conservation of wildlife and tourism enterprises (Moss et al., 2011). Administratively, the Amboseli ecosystem consists of Amboseli National Park (ANP) (392 km²) and six surrounding Maasai group ranches namely: Kimana/Tikondo, Olgulului (North, East, South, and West), Selengei, Mbirikani, Kuku, and Rombo, which cover a total area of (5,063 km²) in Kajiado County (Figure 2.1). Amboseli NP is a dry season grazing area for wildlife, which disperses widely to the adjacent group ranches during the wet seasons (November-December and March-April), when water and forage are plentiful. Although Amboseli NP is one of the leading tourist destinations in the country, with an average of 150,000 visitors per annum (Makonjo et al., 2009), its future is threatened by the loss of wildlife dispersal areas and corridors that are critical to ungulate populations (Toxopeus, 1999). Development activities around the park's edge have caused fragmentation of wildlife habitats, diminishing the dispersal areas and limiting the free movement of animals (Toxopeus, 1999).

2.2.2 Assessment of drought severity and prey abundance

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

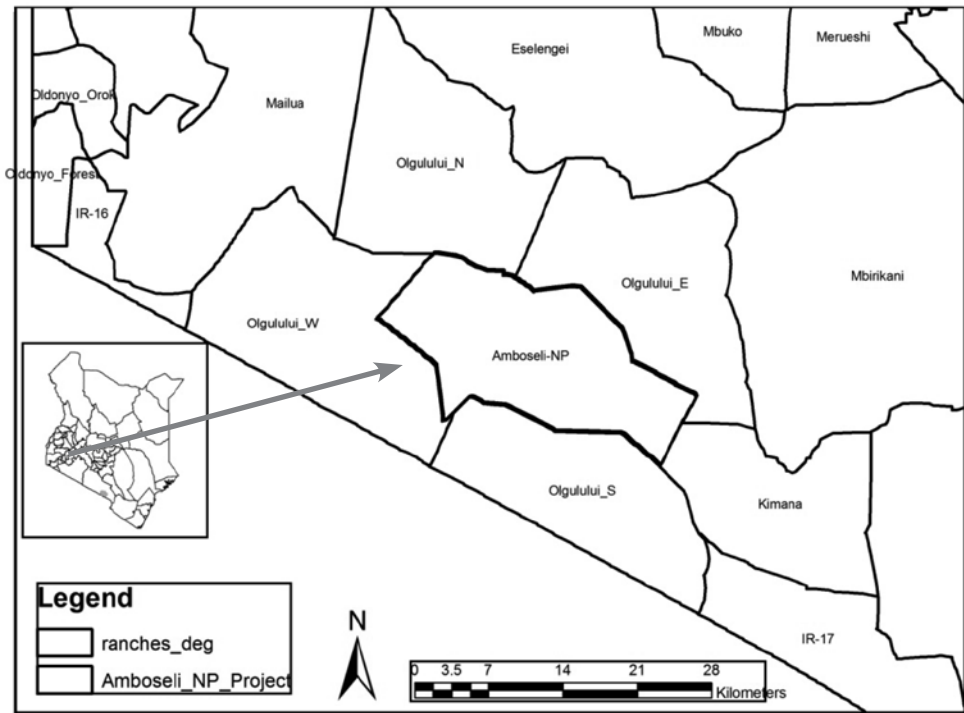


Figure 2.1

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

a park track (500 m on each side) were semi-randomly selected to cover a number of habitats (Figure 2.2). These habitats included short and tall grasslands, alkaline plains, *Acacia* woodlands, Phoenix mixed woodlands and freshwater Papyrus swamps (Moss, 2011). The transects covered a total of 10 km², which were representative for the rest of the park (396 km²).

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

These transect counts were, conducted weekly every month, when possible, at the same time, alternating between 08:00-10:00 and 16:00-18:00 hours, both during the wet and dry season. These times were chosen so that animals seeking shade during the warmer periods of the day were not overlooked. All herbivores larger than ~5 kg were recorded. Additional data included numbers of neonates within the group, habitat type, and weather

and grass conditions. Complementary data from counts conducted by the KWS and previous studies were added to assess the size of the wild prey population and how this changed over previous years. Transect counts were used to classify prey species in weight/size groups to estimate the available biomass of prey species in the national park (Hayward et al., 2007).

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

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

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

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

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

2.2.3 Field observations and sampling technique for lion population structure

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

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

Ten lions (three males and seven females) were collared in four different prides with GPS – GSM – VHF collars (Hawk) of African Wildlife Tracking (S.A), and their movements monitored online and in the field from 2007 to 2012. In addition, during 2007-2012. We spent at least two weeks per month on transect observations of lions and their prey. For this we established five transects of each 1 km long (Figure 2.2). Sightings were also made via opportunistic encounters, through information received from tourists and tour guides. Photographs were taken for each animal and a database was established; individual identification (Pennycuik & Rudnai, 1970) was more

appropriate than vocalization call-ups station, because of low response rates (Ogutu & Dublin, 1998). When no new individuals were observed, with reference to the Amboseli Lion Photo Data Base, we assumed that we had an accurate annual lion population estimate. Lion densities were calculated by dividing the annual lion population estimates by the surface area of Amboseli NP per 100 km². Lions were aged following (Whitman & Packer, 2006), with juveniles defined as <2 years, and sub-adults and adults >2years. We classified lions of adult size lacking juvenile spots as sub-adults and adults, while lions smaller than adult size having juvenile spots were considered juvenile (Schaller, 1972). The lion prides were named after the collared or dominant (alpha) female lion, resulting in Pride I (Amy-Jane), Pride II (Tato), Pride III (Belta) and Pride IV (Nane/nomad); Groups were determined as any aggregation of lions at a particular time (Schaller, 1972). Lion killing incidents before and after the drought were obtained from the KWS occurrence book (2007-2012) at park headquarters, this is where patrol units recorded any incident on a daily basis.

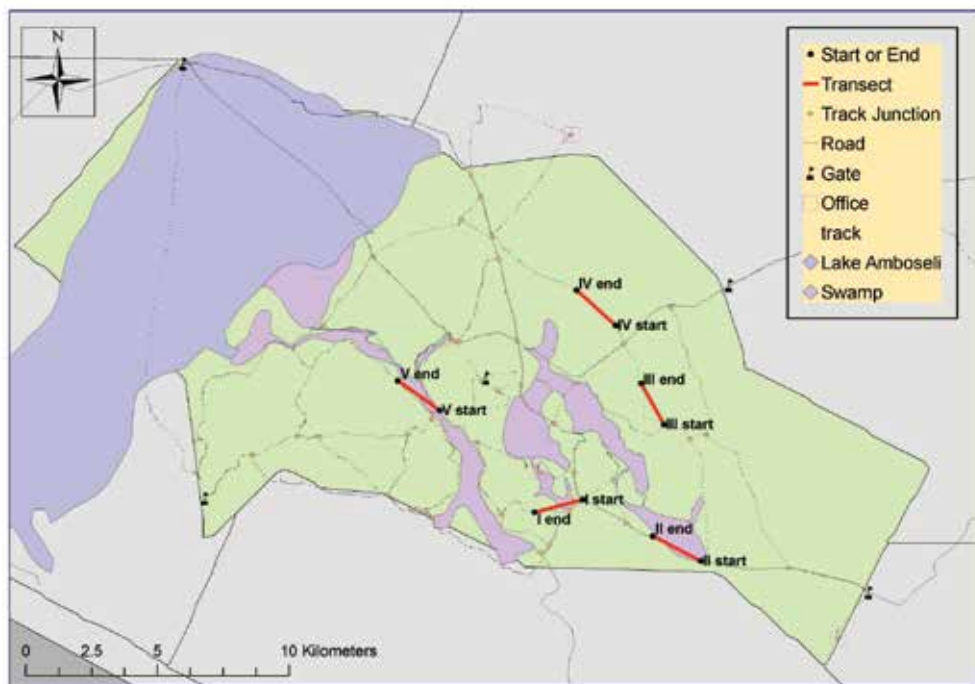


Figure 2.2
Transect count location in Amboseli National Park

2.2.4 Data analysis and statistics

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

2.3 Results

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

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

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

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

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

ificant difference in mortality in the years after the start of the consolation scheme before the drought (2007 and 2008) and after the drought (2011, 2012), (t-test, $p = 0.845$).

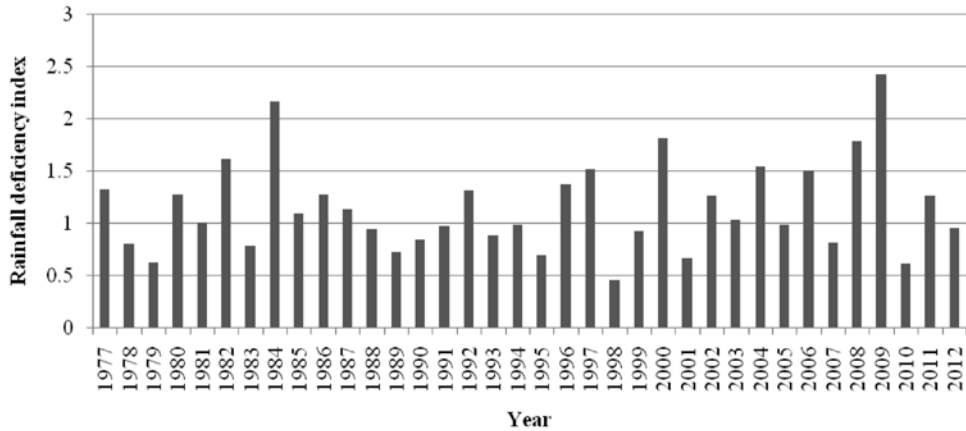


Figure 2.3
Amboseli area Drought Severity Index (1977-2012).

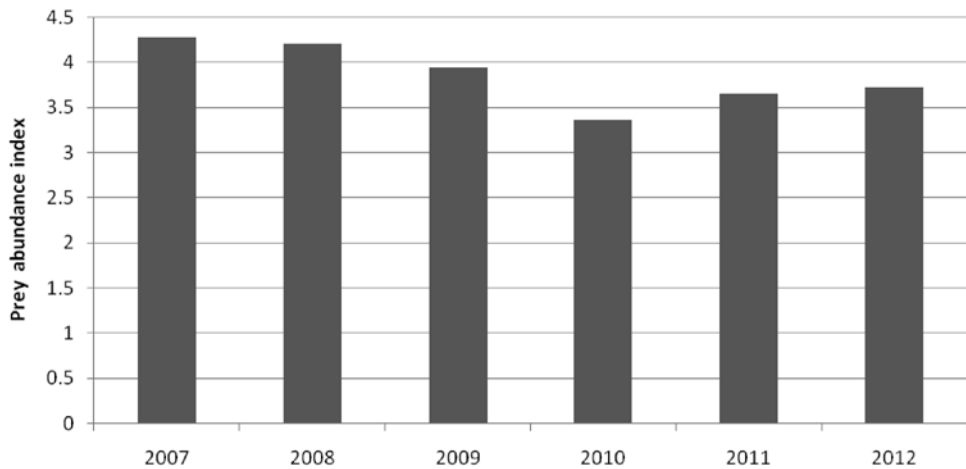


Figure 2.4
Change in annual wild prey abundance (index) for three species (Index based on log of Zebra, Wildebeest and Buffalo) 2007-2012. (Source: KWS; Amboseli NP).

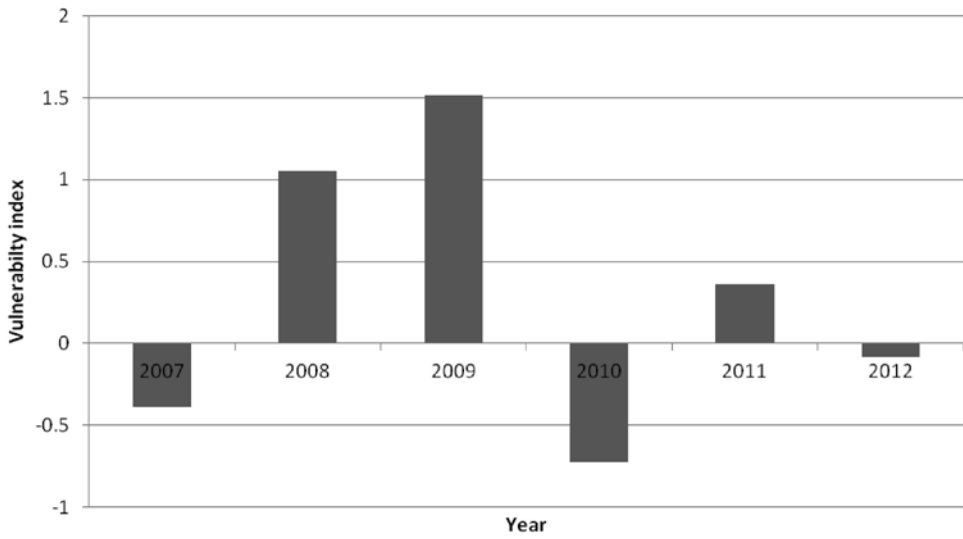


Figure 2.5
Amboseli lion Vulnerability Index to drought 2007-2012.

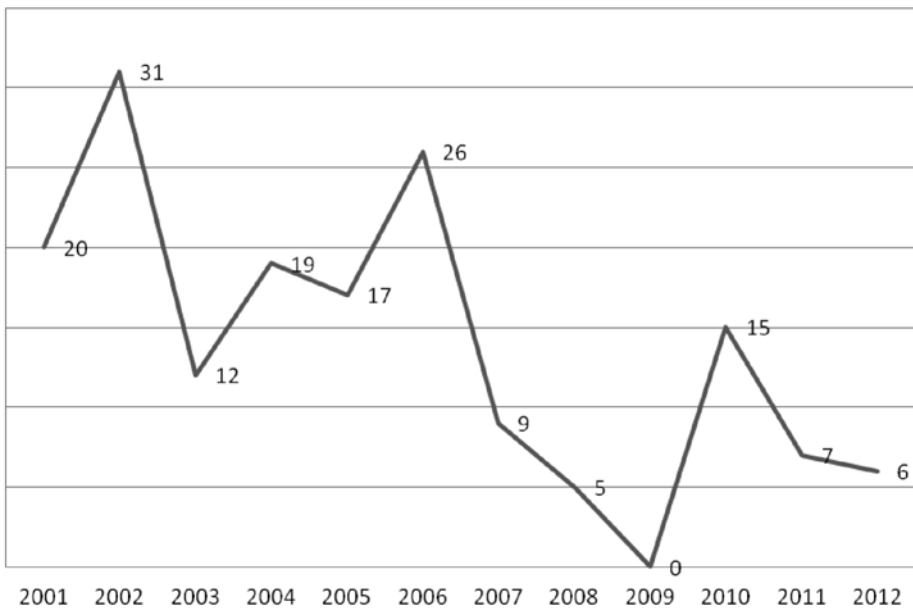


Figure 2.6
Retaliatory lion killing in Amboseli National Park and neighbouring community areas (Sources: KWS occurrence report book 2001-2012)

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

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

Table 2.1

Changes in lion population density (Total lions per km², Adult lions per 100 km²), sex ratio (Male: Female) and sex ratio (Juvenile: Adult) and estimated lion pride size between 2007 and 2012 in Amboseli NP, ($P > 0.05$) NS indicates non-significance.

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

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

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

2.4 Discussion

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

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

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

When excluding the two disturbed years with outliers in lion mortality (2009 and 2010), we found a significantly lower lion mortality in the period

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

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

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

We observed, that although drought also affected livestock, people moved with their livestock and returned after the rains. Other livestock owners restocked their farms with livestock bought from elsewhere. Our study found a serious problem in prey availability during the first wet season after the drought year (2010) showing changes in diet, sex ratio and group size as well as extremely high mortality. There may also be positive effects of drought for lion populations, shown by enhanced reproduction immediately after. Previous studies have established strong relationships between herbivore abundance and rainfall (Ottichilo et al., 2000) and showed that

extreme drought had adverse impacts on predator biomass (Georgiadis et al., 2007). Rainfall variability, therefore, is considered important as it influences the dynamics of African ungulates and thereby may alter carnivore population structure and abundance.

2.4.2 Effect on lion sex ratio

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

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

2.4.3 Effect on lion social structure and group size

The changes in social structure, with smaller group size after the drought, are an indication of a disturbed social structure as a result of scarcity of food. The study found a serious problem in prey availability during the first wet season after the drought year (2010) showing changes in diet, sex ratio

and group size as well as extremely high mortality. There may also be positive effects of drought for lion populations, like enhanced reproduction immediately after the drought.

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

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

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

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