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

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Abstract

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

4.1 Introduction

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

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

To better understand how or why a predator selects a prey species, it is important to know the prey availability. If a prey species is killed more often than would be expected according to chance, it is considered a preferred

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

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

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

4.2 Study area: The Amboseli Ecosystem

The Amboseli ecosystem is situated across the border of Kenya and Tanzania (Figure 4.1). The area is generally arid to semi-arid with an average of 340 mm rainfall per annum (Moss et al., 2011). The ecosystem has bi-annual rainfall, short rains starting in October-November and long rains in March until May. Within the ecosystem, there are variations in its agro-ecological zones. The ecosystem is more suitable for pastoralism and for conservation of wildlife and tourism enterprises than for crop farming (Moss et al., 2011). Administratively, the Amboseli ecosystem consists of Amboseli NP (392 km²) and the surrounding six group ranches (6,000 km²) namely; Kimana/Tikondo, Olgulului (North, East, South and West), Selenkei, Mbirikani,

Kuku, and Rombo. These group ranches cover an area of about 5,063 km² in Kajiado County (Figure 4.1). The Amboseli ecosystem also includes the former 48 private ranches located in the foothills of Kilimanjaro, which are now under rain-fed crop production, and no longer utilized by wildlife.

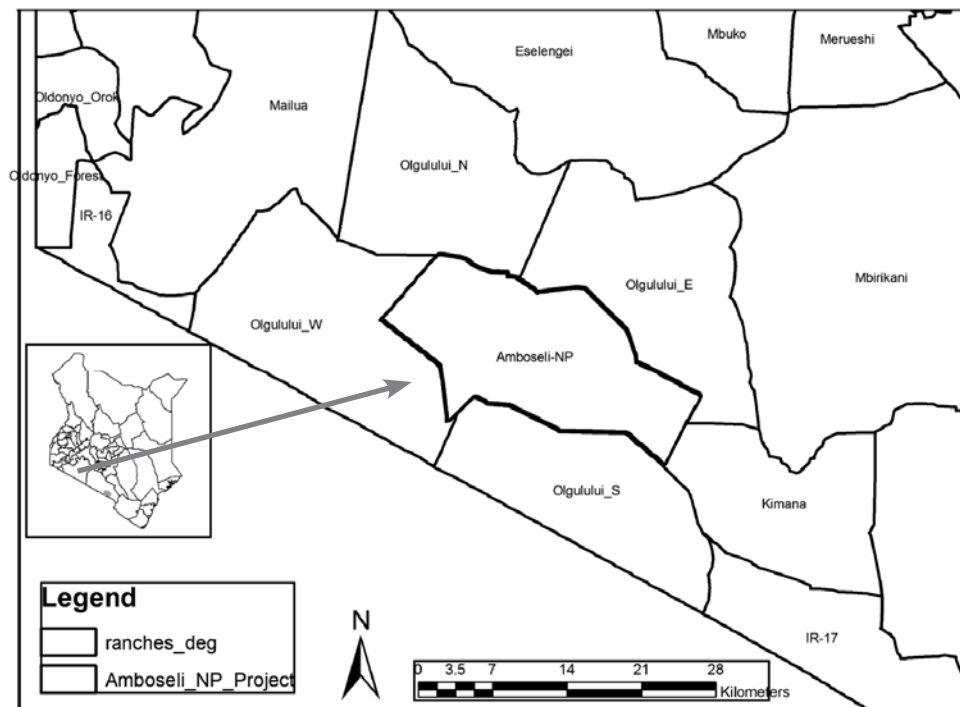


Figure 4.1
Amboseli National Park and surrounding group ranches which together form Amboseli ecosystem

4.3 Methods

4.3.1 Assessment of rainfall variability

Rainfall is seasonal, with bi-modal rainfall interrupted by dry months. The long rains (March-June) are when most plant growth is expected and prey and predators reproduce. The short rains (October-November) are often sporadic and extended periods of dryness are not unusual, disturbing both wild animals and domestic stock. For the Amboseli Ecosystem, we relied on the rainfall records kept at the baboon research station inside the park. We used 35 years of data on rainfall to calculate the deviations from the long-

term mean. From the long-term rainfall deviations from the mean, we were interested mainly in the years 2007-2009 (which corresponded with severe droughts) and 2010-2012 (recovery years). The year was divided into wet and dry seasons of six months each. All prey killed by lion was recorded for each season and seasonal lion prey composition for each year was compared to find if there was any variation in prey composition.

4.3.2 Seasonal prey composition

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

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

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

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

In the fourth sampling strategy, we conducted 60 annual and seasonal transect prey counts (Table 4.1, Figure 4.2), to determine the distribution and density of potential lion prey. Five transects (2×1 km) along a park track (500 m on each side) were semi-randomly selected to cover a number of habitats, to include short and tall grasslands, alkaline plains, *Acacia* woodlands, Phoenix mixed woodlands and freshwater Papyrus swamps (Moss, 2011). The transects covered a total of 10 km², which were representative for the rest of the park (396 km²). Their locations are marked in the map of Amboseli NP (Figure 4.2).

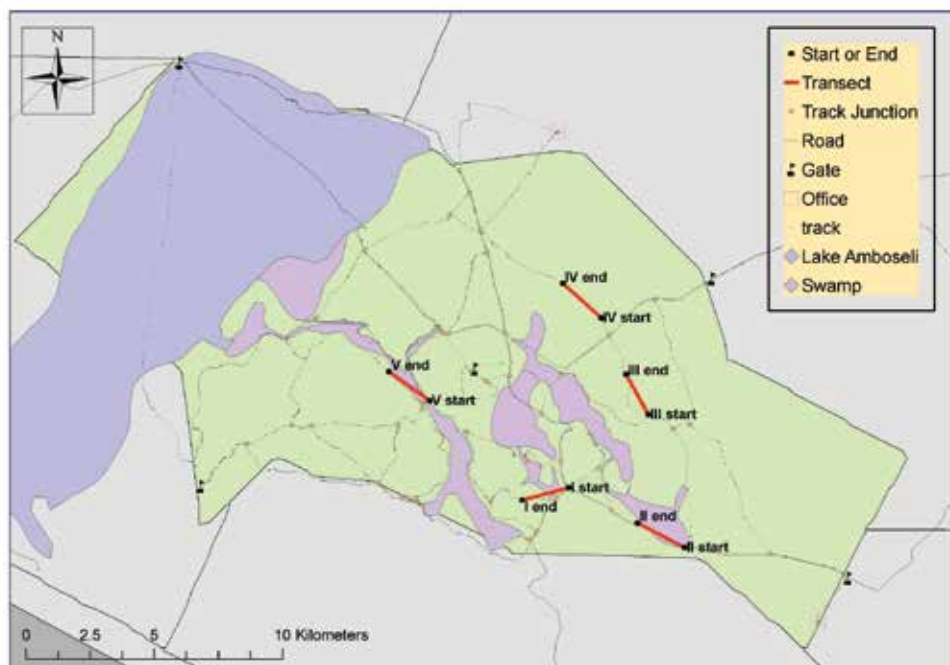


Figure 4.2
Transect locations inside Amboseli National Park

By using distance measured in meters (Bushnell Yardage Pro Trophy Rangefinder) during the transect counts the exact distance of the herbivores was determined within the distance of 500 meter. These transect counts were, conducted once every week, when possible at the same time, alternating between 08:00-10:00 and 16:00-18:00 hours, both during the wet and dry season. These times were chosen so that animals seeking shade during the warmer periods of the day were not overlooked. All herbivores larger than ~5 kg were recorded. Additional data included numbers of ne-

onates within the group, habitat type, and weather and grass conditions. Complementary data from counts conducted by the KWS and previous studies were added to assess the size of the wild prey population and how this changed over previous years. Transect counts data were used to classify prey species in weight/size groups to estimate the available biomass of prey species in the national park (Hayward et al., 2005).

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

4.3.3 Scat analysis

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

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

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

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

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

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

4.3.4 Data management

Transect data were extrapolated to estimate the abundance of each species. Species number and weight class categories were estimated according to Estes (1991). To establish abundance of prey species from the transect counts, daily average animal density per km² was consolidated for all herbivore species counted in the whole park. We used this data to an average animal density per species per month for the five transects.

Animal densities of prey animals were calculated as follows:

- 1 Total Number of Transect Counts (TC) = 247
- 2 Months of observation = 30 months (approximately 3 years)
- 3 Total Transect Area (TA) per month = 5 transects * 2 count periods * 2km²;
- 4 Total Month's Average Count (MAc) = Σ individual animals counted per month

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

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

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

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

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

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

4.3.5 Data analysis and statistics

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

4.4 Results

4.4.1 Rainfall variability and severe drought

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

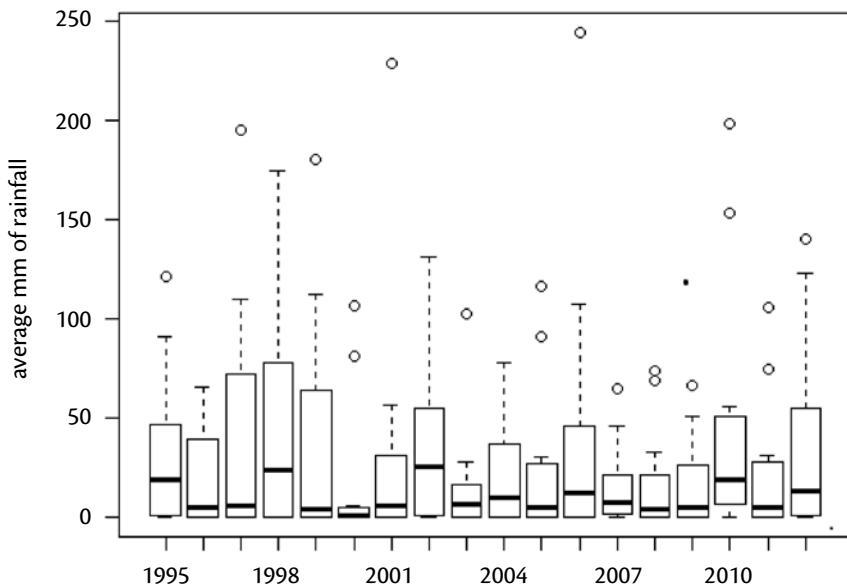


Figure 4.3

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

4.4.2 Herbivore density and seasonal fluctuation

There were large differences in herbivore density in Amboseli National Park between the period before/during the drought (2008–2009) and after the drought (2010–2012). The fluctuations were both annual and seasonal (Table 4.1). There was a heavy decline in densities of wildebeest, zebra and buffalo populations during the severe drought in 2009. The estimated zebra population was significantly reduced from densities of 42.5 per kilometer in 2009 to densities of 9.54 per km² in 2010 and 0.2 per km² in 2012. The wildebeest population was found to show an extreme decline from densities of 73.9 per km² in 2009 to 9.87 per km² in 2010 and to 3.4 per km² in 2012.

Table 4.1

Ammboseli National Park herbivore transects counts from April to July 2012 and density (per km²) from 2007 till 2012.

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

4.4.3 Lion prey composition

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

Table 4.2

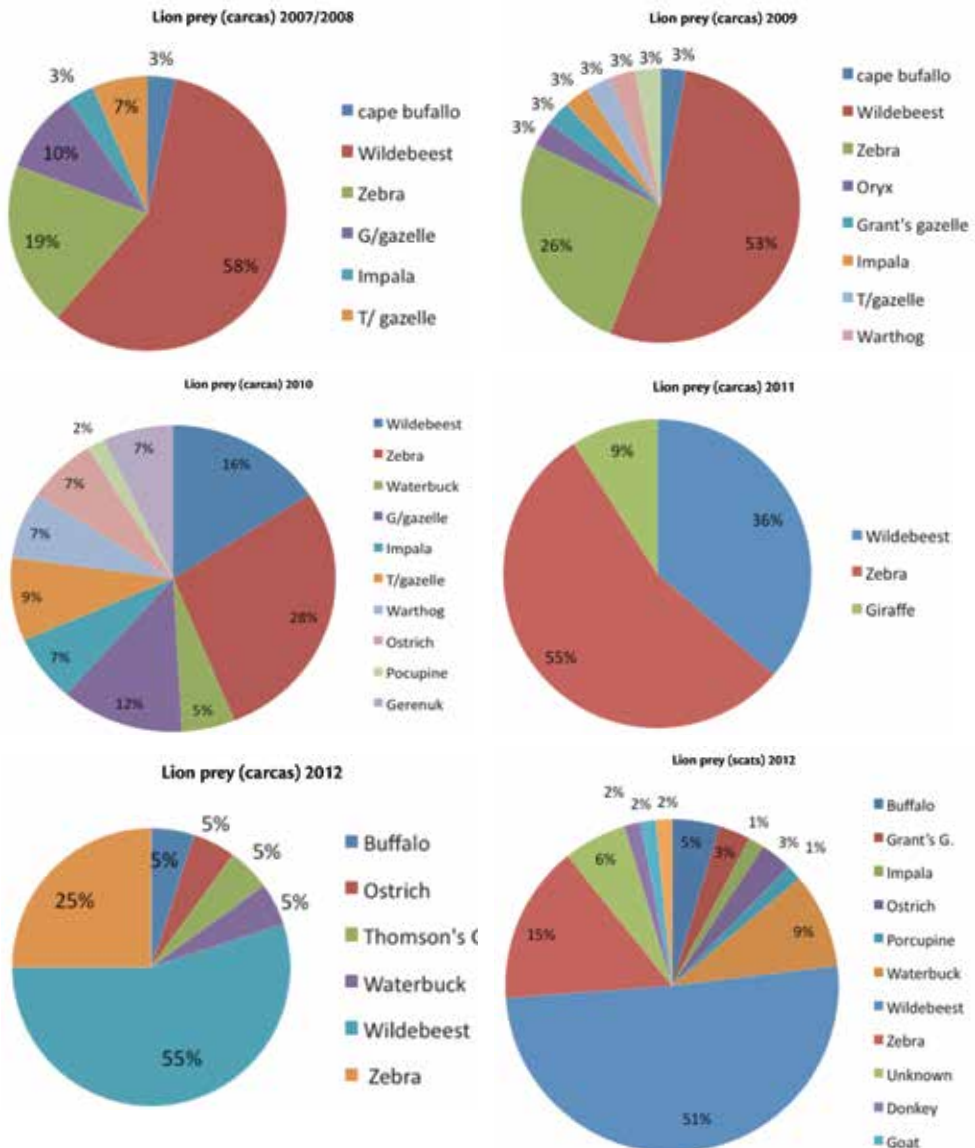
Analysis of seasonal lion prey composition in wild herbivore weight categories (Small, medium and large) – class distribution 2007-2012.

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

4.4.4 Changes in diet composition

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

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

**Figure 4.4**

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

4.4.5 Prey preference and selectivity

The Jacobs index was analysed for different years and periods before or after drought. The Wilcoxon test on periods shows that there was a significant difference between feeding preference in the period before and

after drought (p -value $<2.2e-16$). We conducted a pairwise Wilcoxon test on both years and period (Table 4.3). Table 4.3 shows that 2008 and 2009 are significantly different ($p=0.0029$). Similarly, year 2009 and 2010 are also significantly different ($p=0.0264$). We summarized the differences below, where years with the same letter are similar and years with different letters are significantly different in terms of lion feeding preference: 2008 (“a”) 2009 (“b”) 2010 (“a”) 2011 (“ab”) 2012 (“ab”) 2007 (“a”).

Table 4.3

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

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

P value adjustment method: Bonferroni

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

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

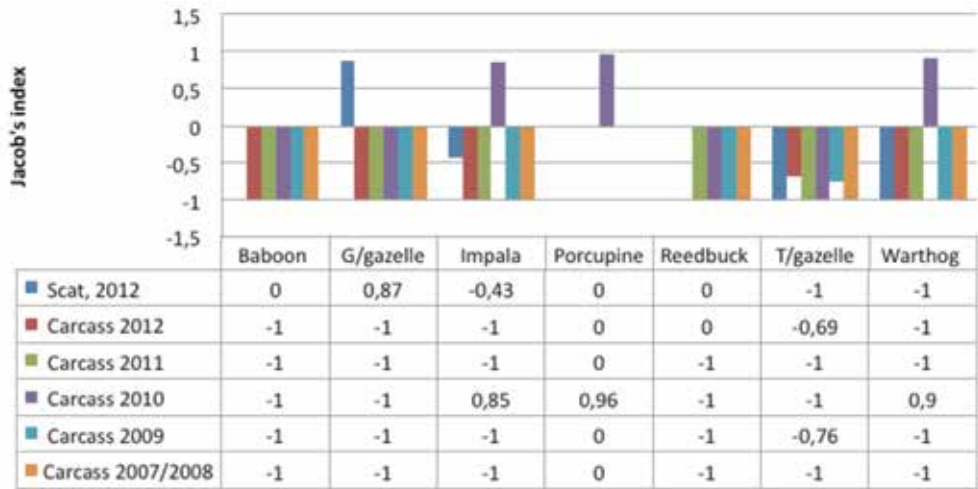


Figure 4.5a

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

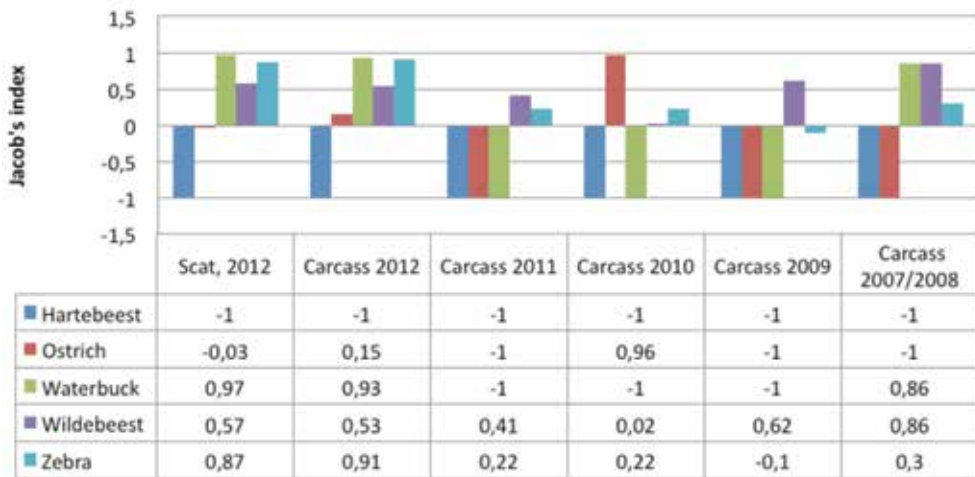
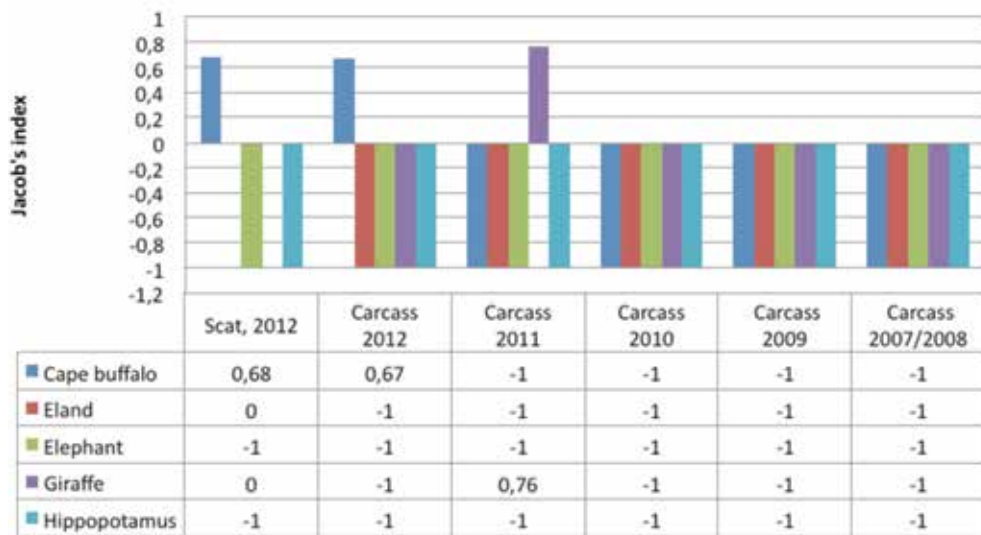


Figure 4.5b

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

**Figure 4.5c**

Large size herbivores lion prey preference index from carcass (2007-2012) and scat (2012) in Ambose-li National Park.

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

4.5 Discussion

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

events such as drought by adapting their diet. This was also suggested by Hayward & Kerley (2005).

4.5.1 Impact of rainfall variability on prey densities

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

4.5.2 Prey distribution and density

We found strong fluctuations in the density (per km²) of the wildebeest and zebra population from 2007 till 2012, with a significant reduction in densities during 2010-2012.

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

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

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

4.5.3 Lion diet composition and preference

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

increases their abundance by a factor of two or three) or during the calving period may be another reason for this preference (Ogutu & Dublin, 2002; Hayward & Kerley, 2005).

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

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

The fact that the scat analysis showed a larger range of species in the lions' diets suggests that this method if used in combination with carcass appropriate compared to carcass counts alone. There are various methods for determining diets from scat analysis (Klare et al., 2001) and these methods can be classified as qualitative (frequency of occurrence per scat) or as quantitative (biomass calculations per scat). The qualitative methods overestimate the contribution in the diet of small-sized prey, compared to larger-sized

prey, because the presence of both is weighed equally even though there are differences in surface area to volume ratio (Marker et al., 2003). A requirement for a successful quantitative method is to conduct feeding trails to convert the frequency of occurrence into relative biomass and number of individuals consumed (Breuer, 2005).

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

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

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

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