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Article *in* The Science of Nature · March 2013

DOI: 10.1007/s00114-013-1034-5 · Source: PubMed

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ORIGINAL PAPER

Climate variability, human wildlife conflict and population dynamics of lions *Panthera leo*

Martina Trinkel

Received: 21 December 2012 / Revised: 28 February 2013 / Accepted: 2 March 2013

Abstract Large carnivores are threatened by habitat loss, declining prey populations and direct persecution. Pride dynamics of eight lion prides in the centre of the Etosha National Park, Namibia are described during a 16-year study. Since the beginning of the 1980s, the number of adult and subadult lions declined continuously to two third of its initial population size, and reached a new equilibrium in the 1990s. Pride sizes decreased from 6.3 adult females in 1989 to 2.8 lionesses in 1997. While the number of adult females declined continuously, the number of adult males, subadult females and subadult males remained constant over the years. A severe drought period, lasting for more than 20 years, led to declining prey populations inside the lions' territory. Besides declining prey populations, conflict with humans at the border of Etosha puts substantial pressure onto the lion population: 82 % of all known lion mortalities were caused by humans, and most of these consisted of adult females (28 %) and subadult males (29 %). I postulate that the considerable decline in the lion population is a response to declining prey populations, and although the human predator conflict is severe, it does not seem to limit the size of Etosha's lion population.

Keywords Lion · *Panthera leo* · Carnivore · Prey population · Predator prey relationship · Etosha

Introduction

Among all carnivores, lions *Panthera leo* have suffered the most dramatic reduction of range and population sizes (Patterson et al. 2004). Before the Pleistocene, the lion was the most widespread terrestrial mammal, ranging from southern Africa to northern Europe, across all of Asia and Northern America (Patterson et al. 2004). In sub-Saharan Africa, lions have been declining since the seventeenth century (Patterson et al. 2004). This marked decline is due to loss of habitat, shrinking prey populations and direct persecution (Nowell and Jackson 1996).

Protected areas offer a potential solution to large carnivore conservation provided they are large enough and conflict with humans on reserve borders is low (Woodroofe and Ginsberg 1998). The Etosha National Park in Northern Namibia includes a 23,000-km^2 semi-desert area and supports the largest lion population in the country. The population for the whole park was roughly estimated as 470–670 lions during 1974–1978, 500 in 1981, 250 in 1985 and 180–200 lions in 1994 (Orford 1988; Berry 1996). The reasons for this decline, however, were unclear (Berry 1996).

Prey availability and distribution is an important selective force on predator densities in that it may modulate group and territory sizes (Macdonald 1983; Van Orsdol et al. 1985; Hayward et al. 2007; Hayward et al. 2009). In semi-desert areas, large predators generally live at low densities, which has been attributed to low prey densities (Stander 1991; Mills 1994). Variability and fluctuations in rainfall are inherent to arid and semi-arid lands, and drought is a common occurrence in such areas (Le Houerou 1996). Prolonged drought periods, however, can lead to a further decrease in primary productivity which causes a subsequent decrease in herbivores. Such a decrease in prey populations is followed by a decrease of carnivores (Le Houerou 1996). Several long-term studies on insects (Polis et al. 1998), birds (Grant et al. 2000) and rodents (Lima and Jaksic 1999) have revealed such bottom-up effects. However, long-term

Communicated by: Sven Thatje

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Published online: 16 March 2013

studies on large predators are generally scarce (Packer et al. 2005; Watts and Holekamp 2008). Trends in the ecology of large carnivores can only be identified with long-term studies, which are therefore of enormous value for the conservation of the species (Polis et al. 1998; Grant et al. 2000). So far, the only long-term data of lions are available from the Serengeti National Park, Tanzania (Packer et al. 2005).

Besides extreme environmental conditions, the conflict with people on reserve borders can cause major mortalities in large carnivore populations, and it was argued that the interaction with people at the periphery can affect their population dynamics throughout a protected area (Woodroofe and Ginsberg 1998; Hilborn et al. 2006). The influence of humans on predator populations was found to be intensified when large carnivores range widely: rather than actual population size, range size was found to increase the risk of extinction of large carnivores (Woodroofe and Ginsberg 1998). In arid and semi-arid areas, ranges of large predators are generally large, leading to conflicts with humans at reserve borders. Under extreme climatic conditions, such conflicts can be intensified.

Here, I analysed long-term records available from the Etosha National Park, where lions in a 2,000-km^2 area have been studied continuously over 16 years. As vegetation increases with rainfall (Coe et al. 1976), herbivore density is related to rainfall (East 1984) and predator density is related to that of their prey (Hayward et al. 2007), I predicted that the prolonged drought would ultimately lead to a reduction in lion density. Furthermore, I show that human-caused mortalities on farmland adjacent to the Etosha National Park do not limit the size of the lion population inside the protected area.

Methods

Study area

The Etosha National Park is situated between three major biotic zones, the southern savannah woodland, the south-west arid zone and the Namib desert (Smithers 1983) in northern Namibia with Etosha's coordinates centered at 19° S, 16° E. The park occupies an area of 22,270 km^2, with a mean annual rainfall of 353 mm measured in the central part of Etosha over 50 years (1960–2010). Our whole study period (1983–1997) fell into a drought period (Fig. 1).

There is a wet season from January to May and a dry season from June to December. Artificial water points and natural springs are the only permanently available water during the dry season. The Etosha pan, a saline desert comprising less than 10 % of Etosha's surface area, is surrounded by short-grass plains (Le Roux et al. 1988). These plains are important grazing areas of springbok *Antidorcas marsupialis*, zebra *Equus burchelli* and blue wildebeest *Connochaetes taurinus*. Plains ungulates in central and eastern Etosha have been declining to persistent low densities during 1960–1994 (Fig. 2, Gasaway et al. 1996). Springbok were reported to increase during the 1970s and then declined during 1982–1987 (Gasaway et al. 1996; Fig. 2). Migratory pattern of plains game is described in detail elsewhere (Berry 1980). In general, during the dry season migratory plain ungulates concentrate along the southern and eastern part of the Etosha pan. During the wet season, there is an influx of migratory prey west of the Etosha pan.

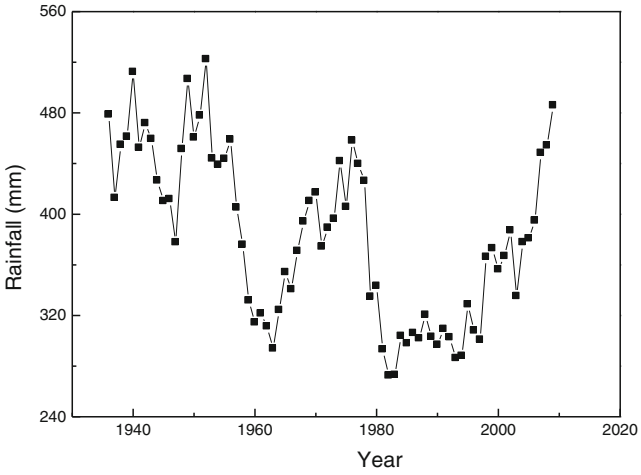


Fig. 1 Rainfall calculated as 5-year moving average measured at Okaukuejo in central Etosha. A moving average was used to smooth out short-term fluctuations and to highlight long-term trends

Our study covered 2,000 km^2 in the central part of the Etosha National Park (Fig. 3). The study area contained grassy plains and adjacent woodland with *Colophosperum mopane* in tree or scrub form (Le Roux et al. 1988). The number of waterholes in the study area was 15 during the 1980s and 13 during the 1990s (Fig. 3). One natural spring (Ondongab) dried up in 1986 (W. Versfeld, personal

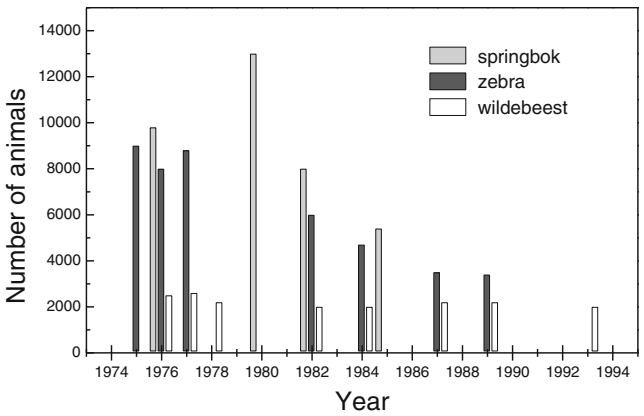


Fig. 2 The number of plain ungulates, i.e. springbok, zebra and blue wildebeest in central and eastern Etosha determined in aerial surveys between 1974 and 1994. Data were taken from Gasaway et al. (1996)

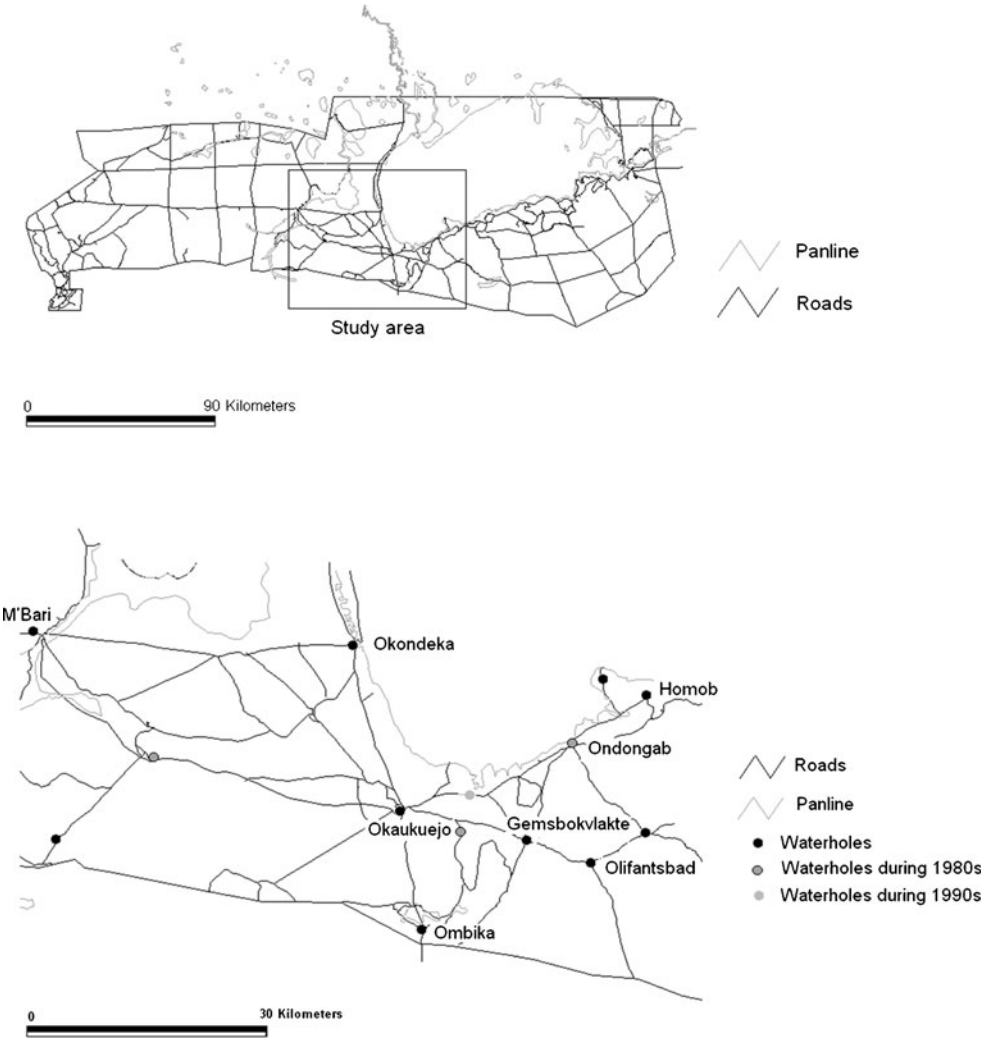


Fig. 3 The study area in the central part of the Etosha National Park. Most of the waterholes (*black dots*) provided water during our whole study period (1983–1997), *dark grey dots* indicate waterholes that provided water during the 1980s, *light grey dots* indicate waterholes that were only active during the 1990s. The eight lion prides (four to six at a time) concentrated around the following waterholes and were named accordingly: M'bari, Okondeka, Okaukuejo, Ombika, Ondongab, Gemsbokvlakte, Olifantsbad and Homob

communication), and one artificial waterhole was closed in 1990 because the high utilization by herbivores puts substantial pressure onto the sensitive vegetation (Osborne and Versfeld 2007). The entire perimeter of the Etosha National Park is fenced and the study area borders on commercial farmland in the south.

Lion population

Between 1983 and 1997, 159 individuals were immobilized and marked with hot brands on both shoulders and buttock (Van Wyk and Berry 1986; Stander and Morkel 1991; Stander 1991). Three additional female lions were identifiable from natural markings. Each lion was aged by tooth eruption, wear and discoloration of their teeth (Smuts et al. 1978), and placed into the following age classes: cubs (0–2 years), subadults (2–4 years) and adults (more than 4 years) (Schaller 1972; Stander 1991). One to two lions in every pride were equipped with radiocollars. Eight lion prides were studied: between 1983–1988 and 1993–1997, each pride was observed on average every 2 weeks, and between 1989 and 1992, each pride was observed on average every 7 weeks. In total, prides were observed 1,357 times with 4,754 observations of known individuals. The study prides were situated around the following waterholes and were named accordingly: M'bari, Okondeka, Okaukuejo, Ombika, Gemsbokvlakte, Ondongab, Olifantsbad and Homob (Fig. 3).

Prey population

The distributions and densities of various prey species were estimated from censuses based on road counts once every month during 1975–1979 and 1995 covering the whole study area. Counts were performed by the Ministry of Environment and Tourism (1975–1979), and by Claudia Auer in 1995 (Auer 1998). In 2000 and 2008, dry season counts were performed by Martina Trinkel. These counts were also used to calculate lion numbers from prey biomass (see below). Road counts are ungulate census techniques that are inexpensive and reasonably accurate (Dasmann and

Mossman 1962; Hirst 1969; Trinkel et al. 2004). Species included in the total count were the migratory prey with springbok, zebra and wildebeest. A strip of approximately 800 m wide on either side of the road was considered as every animal present in this strip could be identified using 8×40 binoculars. It was verified that the resulting density estimates were unbiased by randomly performing transects perpendicular to the road and comparing results. The survey area is a relatively open habitat where visibility bias is low.

Predicting lion numbers from prey biomass

A predator–prey model was used to validate lion numbers from direct observations and to calculate the number of lions for time periods when the lion population was not monitored. The model was adjusted with respect to prey preferences of lions in Etosha (Stander 1991), and describes a highly significant linear relationship between predator numbers and preferred prey species published by Hayward et al. (2007). The relationship between predator density (log10; *x*-axis) and the measure of preferred prey species (log10; *y*-axis) is as follows:

$y=-2.158+0.377x$; $r^2=0.626$; $P>0.001$ (Hayward et al. 2007).

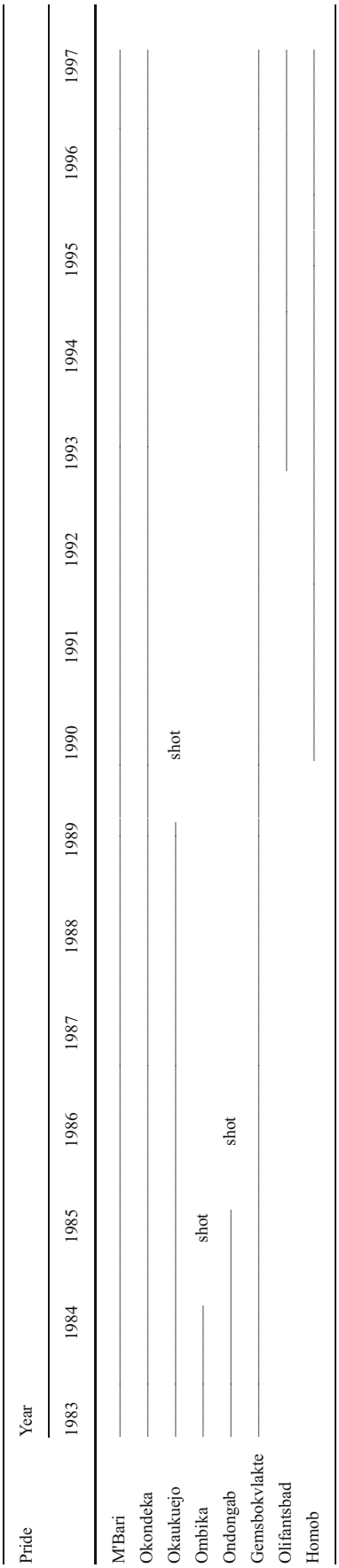
Results

Lion prides

Between 1983 and 1997, eight prides lived in central Etosha, and the number of prides ranged from four to six at a time (Table 1). Three prides (Mbari, Okondenka and Gemsbokvlakte) were present during the whole study period; three others (Ombika, Ondongab and Okaukuejo) were shot on livestock farms bordering the Etosha National Park in 1985, 1986 and 1990. Two new prides (Homob and Olifantsbad) were established in 1990 and 1993 by females that split off from their natal pride (Gemsbokvlakte).

Pride sizes are measured as the number of adult and subadult lions (Schaller 1972) or the number of adult females in a pride (Bertram 1973). In Etosha, lion prides consisted of one to eight females, their dependent offspring and a resident coalition of one to three males. Prides had on average 2.1±0.5 adult males, 1.2±0.6 subadult males (range, 0–7 individuals) and 1.2±0.4 subadult females (range, 0–5 individuals). While the number of adult males, subadult males and subadult females per pride remained stable over the years, the mean number of adult females per pride decreased from 6.3 individuals in 1989 to 2.8 animals in 1997 (Fig. 4). Pride compositions of all prides living in central Etosha in 1984 and 1996 are listed in Tables 2 and 3.

Table 1 Lion prides in central Etosha between 1983 and 1997



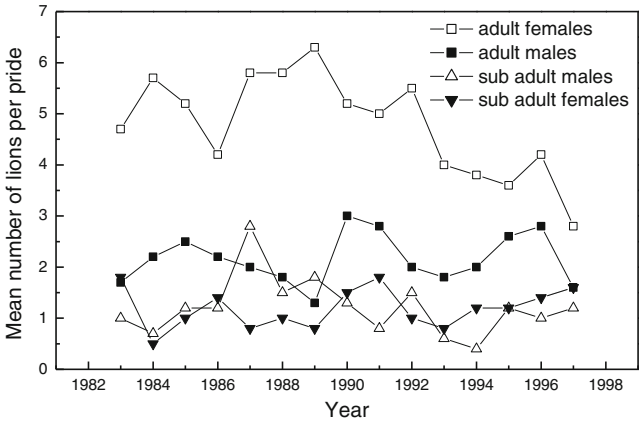


Fig. 4 The mean number of adult males, adult females, subadult males and subadult females per pride in the central study area between 1983 and 1997

Lion population

Between 1983 and 1997, the total lion population in central Etosha fluctuated between 50 and 88 individuals (Fig. 5). The total number of adult and subadult lions, however, decreased over the years and reached an equilibrium of about 42 individuals, which was caused by the decrease of adult females (Figs. 5 and 6). There were three distinctive peaks in population size resulting from a larger number of cubs produced in 1984, 1989 and 1996, which can be related to rainfall: There existed a strong correlation between cubs per female and annual rainfall (Fig. 7).

Mortalities of adult and subadult lions

During the study period, 54 of the known lions died, and 27 lions disappeared and were presumed dead. Thirty-seven out of 54 known lion mortalities were caused by humans: lions were shot or poisoned on livestock farms bordering the Etosha National Park. In three occasions, the whole pride was destroyed on farmland: in 1985, the Ombika pride, living close to the border, moved out of the park and was subsequently shot; the Ondongab pride moved onto farmland after "their" waterhole had dried up in 1986. After the Ombika pride was shot, the Okaukuejo pride moved closer to border of the park, and the whole pride was shot on farmland in 1990. In general, most lion mortalities consisted of adult females and subadult males (Table 4). Seventeen adult females were destroyed on farmland, six females died from natural causes, and one female was destroyed due to poor body condition, after she killed a tourist (Table 4). Twenty-one adult females disappeared and were presumed dead.

Table 2 Pride composition of all prides in central Etosha at the end of 1984

Pride	Adult males	Adult females	Subadult males	Subadult females	Cubs
Gemsbokvlakte	1	5	4	3	5
Okondeka	3	9	0	0	7
M'Bari	1	5	4	3	5
Okaukuejo	2	5	0	0	6
Ondongab	3	3	0	0	5
Ombika	2	6	0	0	5
Mean	2.0	5.5	1.3	1.0	5.5
Standard deviation	0.9	2.0	2.1	1.5	0.8

Table 3 Pride composition of all prides living in central Etosha at the end of 1996

Pride	Adult males	Adult females	Subadult males	Subadult females	Cubs
Gemsbokvlakte	2	3	0	0	8
Okondeka	3	3	0	0	0
M'Bari	3	3	0	0	7
Olifantsbad	3	3	2	3	0
Homob	0	2	1	1	2
Mean	2.2	2.8	0.6	0.8	3.4
Standard deviation	1.3	0.4	0.9	1.3	3.8

Prey abundances

There were monthly fluctuations in migratory herbivore abundance during 1975–1979 (wet period) and 1995 (dry period). In general, the overall monthly number of migratory species was larger in 1975–1979, and monthly fluctuations were more distinct in 1995 (Figs. 8 and 9). Prey abundance during the dry season was found to be the critical limiter of lion density (Van Orsdol et al. 1985).

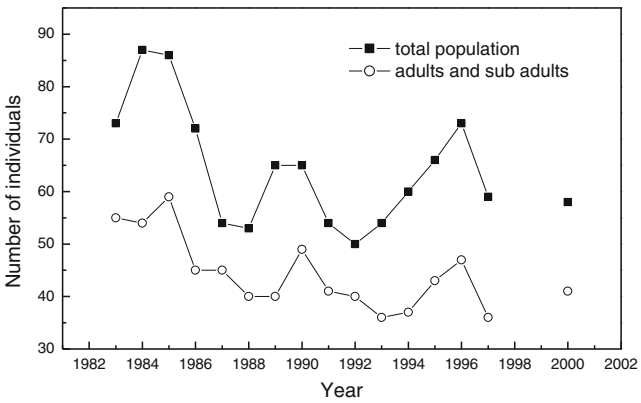


Fig. 5 The total number of lions and the number of adult and subadult lions in the central study area between 1983 and 1997. The total number of lions and the number of subadults and adults in 2000 were determined by A. Burger, T. Burger and C. DuPlessis

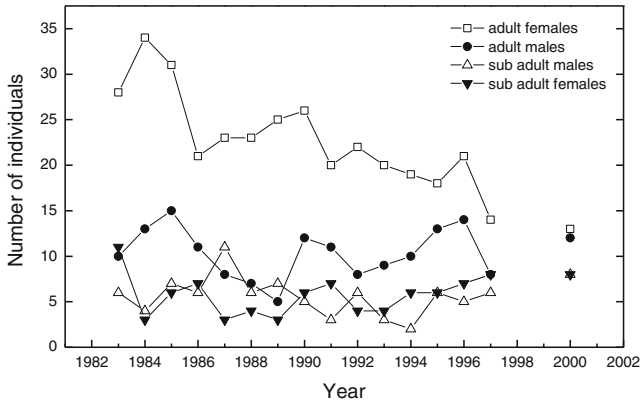


Fig. 6 The total number of adult females, adult males, subadult males and subadult females in central Etosha between 1983 and 1997. The total number of lions and the number of subadults and adults in 2000 were determined by A. Burger, T. Burger and C. DuPlessis

Prey abundances during the dry season (June–December) During 1975–1979, there was a mean number of 4,004±469 springbok, 1,786±566 zebra and 743±179 blue wildebeest in the study area. In 1995, the number of all migratory species was lower, with 2,743±423 springbok, 643±211 zebra and 411±150 wildebeest (Figs. 8 and 9). The differences in dry season prey abundances between 1975–1979 and 1995 were significant (Student's *t* test, springbok, $p<0.001$; zebra, $p<0.001$; wildebeest, $p=0.003$). In 1995, the number of springbok was 32 % lower compared to 1975–1979, and zebra and blue wildebeest numbers were 64 and 45 % lower, respectively.

Prey abundances during the wet season (January–May) During 1975–1979, there was a mean number of 4,058±1,094 springbok, 2,271±781 zebra and 741±252 blue wildebeest. In 1995, there were 4,470±2,115 springbok, 1,376±1,055 zebra and 371±112 wildebeest in the study area. Mean numbers of springbok and zebra did not differ significantly between 1975–1979 and 1995 (Student's *t* test; Figs. 8 and 9).

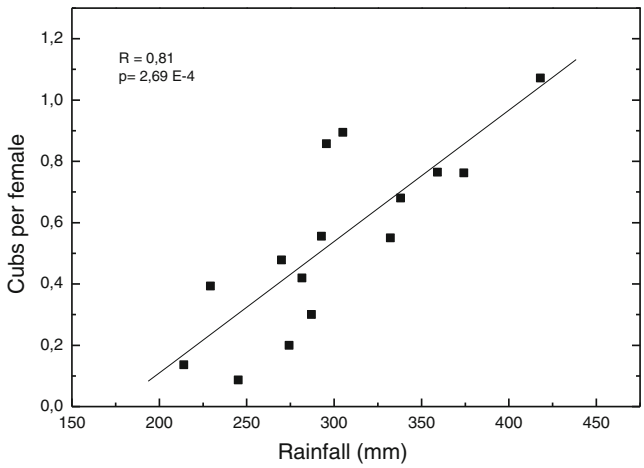


Fig. 7 The number of cubs per female is strongly correlated with annual rainfall

Besides generally lower dry season numbers of plain ungulates during 1995, the relative percentage of prey species changed from 1975–1979 to 1995: the percentage of springbok in the study area increased from 60 to 72 %, while the percentage of both zebra and wildebeest decreased from 29 to 19 %, and 11 to 9 %, respectively.

The dry season counts for 2000 showed that prey populations were comparable to those in 1995: 2,502± 398 springbok, 633±73 zebra and 310±105 blue wildebeest. In 2008, however, the number of springbok (3,535± 465) and zebra (2,212±388) was significantly higher compared to 1995 (Student's *t* test, springbok, $p<0.01$; zebra, $p=0.004$). In 2008, there were 138±72 blue wildebeest in the study area.

Predicting lion numbers from prey biomass

The predator prey relationship for estimating the number of lions presented by Hayward et al. (2007) seems to work well: in 1995 and 2000, when lion numbers from direct observations were 42 and 41 lions, the estimated lion numbers from the predator prey relationship were 43±4 lions and 41±3 lions, respectively. For 1974–1979 and 2008, when the lion population was not monitored, the estimated populations are 56±5 lions and 55±4 lions, respectively (Fig. 10).

Discussion

Since the beginning of the 1980s, the lion population in central Etosha declined continuously to two third of its initial population size and reached a new equilibrium in the 1990s. The population decline might have been caused by a prolonged drought period and thus, declining prey populations.

In central Etosha, erratic rainfall causes movements of migratory ungulates producing major fluctuations in local prey abundance. During the short rainy season, the amount and nutritional value of grass cause large influxes of plain ungulates (Berry 1980, 1981). During Etosha's prolonged dry season, prey abundance in central Etosha is much lower. Drought can cause major reductions in food production for plain ungulate populations (Gasaway et al. 1996). The whole study period of 16 years (1983–1997) fell into a drought period, and I found that prey numbers were only half as high compared to wetter periods (1974–1979). During this wet period in the 1970s, Berry (1981) estimated that the lion population in central Etosha was about 90 adults and subadults compared to the average of 40 adults and subadults during the 1990s. Stander (1991) speculated

Table 4 Mortalities of known lions in central Etosha between 1983 and 1997

	No. of lions during study period	No. of mortalities	Cause of death			
			Shot	Natural	Destroyed	Disappeared
Adult females	60	45	17 (28 %)	6 (12 %)	1 (2 %)	21 (35 %)
Adult males	28	11	3 (11 %)	7 (29 %)	1 (3 %)	0 (0 %)
Subadult females	56	6	4 (7 %)	0 (0 %)	0 (0 %)	2 (4 %)
Subadult males	44	19	13 (29 %)	1 (2 %)	0 (0 %)	5 (11 %)

that Berry (1981) overestimated Etosha's lion population as only few lions were marked in the 1970s. This is in agreement with my analysis: the predictions in lion numbers in the study area derived from the predator prey model described by Hayward et al. (2007) revealed 51–61 adult and subadult lions between 1974 and 1979 (Fig. 10). However, as prey availability during the period of leanest food supply determines lion population sizes (van Orsdol et al. 1985), the decline of the central Etosha lion population might have been caused by the drought and consequently, declining prey populations.

Besides the influence of rainfall on grass growth and thus the number and movements of migratory herbivores, we found that rainfall had a positive effect on the number of cubs produced per lioness: in years of higher (but still below average) rainfall, more cubs were born. However, the lion population did not increase. This might be due to a lack of consecutive "better" rainfall years, as higher rainfall and thus enhanced food availability is known to positively influence cub survival (Berry 1996). Rainfall also seemed to have influenced the recovery of lions in the Serengeti, East Africa: after a significant decline caused by a severe disease, the population remained well below their equilibrium density for years and only started to increase after successive good rainfall years, when migratory prey density inside the lions' territory increased (Packer et al. 2005). Nevertheless, in contrast to other large carnivores such as spotted hyenas (Henschel 1986), lions have the ability to recover quickly after a population decline when environmental conditions are good (Packer et al. 2005; Smuts 1978). This might be beneficial for the lions in Etosha: since 2000, a wet period started with rainfall being much higher compared to the drought period during the 1980s and 1990s. This is in agreement with the lion numbers derived from the predator prey model (Hayward et al. 2007), which revealed 51–59 adult and subadult lions in 2008 (Fig. 10). Furthermore, a recent population estimate for the whole Etosha National Park revealed that the population consisted of 349–428 individuals in 2010 (O. Aschenborn personal communication).

Besides the overall lion population decline, I found that pride sizes declined during the 1990s. During this period, two prides were established by females that split off from their natal pride. The reason for splitting into smaller groups might have been caused by relative changes in prey composition: besides overall lower prey numbers, the relative numbers of small prey such as springbok increased, while the relative numbers of large herbivores, i.e. zebra and wildebeest decreased. Lions generally prey on medium- and large-sized prey (Hayward and Kerley 2005). However, during the 1980s, when pride sizes were still large, Stander (1992) found that springbok was the preferred prey species of lions in central Etosha, whereas zebra and wildebeest were rather avoided. The relative increase of springbok (besides the lower overall prey numbers)

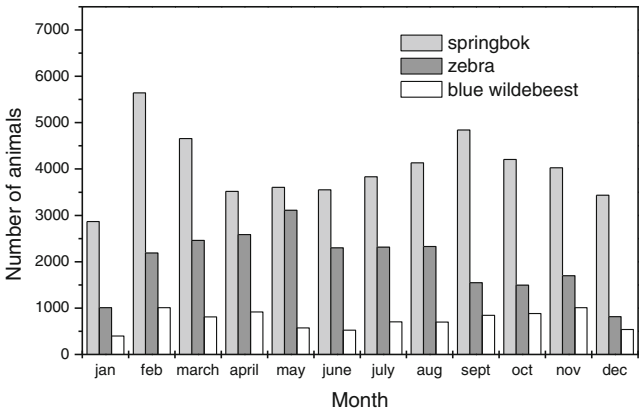


Fig. 8 The average monthly number of springbok, zebra and blue wildebeest in central Etosha during 1975–1979. Road counts were performed by the Namibian Ministry of Environment and Tourism

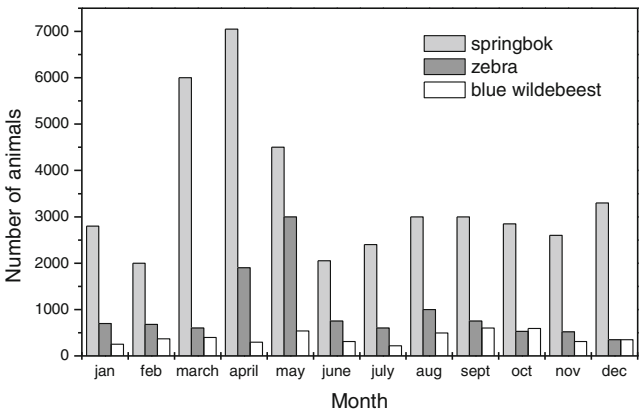


Fig. 9 The monthly number of springbok, zebra and blue wildebeest in central Etosha in 1995. Road counts were performed by C. Auer

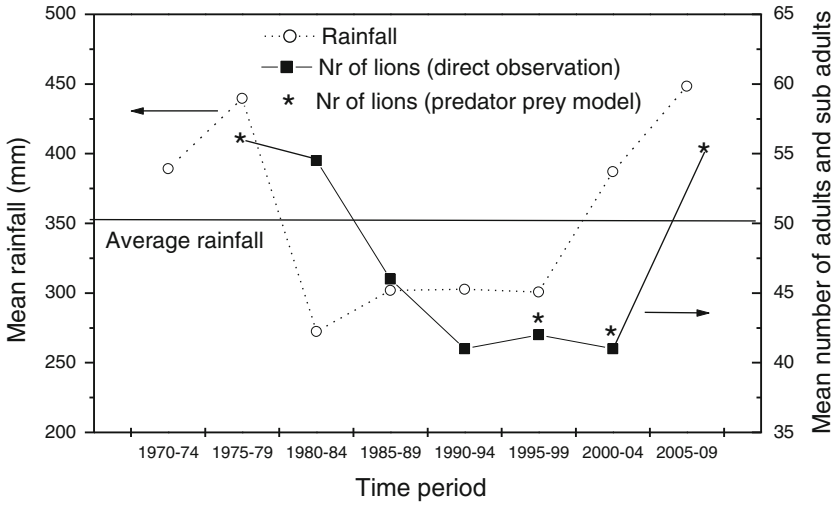


Fig. 10 Mean (5 years) rainfall and mean (5 years) number of adult and subadult lions in central Etosha. Average rainfall over 50 years (1960–2010) was 353 mm. Between 1970 and 1979 (wet period), there were 56±5 adults and subadults in the study area (according to a predator prey model described in Hayward et al. 2007). During our study period (1983–1997), the number of adults and subadults reached a new equilibrium of about 40 lions. From 2000 onwards, mean rainfall started to increase, and lion numbers increased to 55±4 lions in 2008 (according to a predator prey model described in Hayward et al. 2007). Lion numbers in 2000 were determined by T. Burger, A. Burger and C. DuPlessis

intensifies aggression through feeding on small carcasses by large groups, especially in open and short grass plains, where hunting success is low (Stander 1992).

Conflict with people on reserve borders is a major cause of mortality in large carnivores (Woodroofe and Ginsberg 1998). Stander (1992) argued that this human-caused mortality does not limit Etosha's lion population. However, during prolonged drought periods when prey populations decline, interaction with people at the periphery may affect lion population dynamics throughout a protected area: the high number of adult females destroyed on farmland caused a continuous decline in the number of lionesses inside Etosha, which could have adverse effects on the lions' social structure. In polygynous species such as lions, females are the "core" of lion society, and therefore, the decrease in the numbers of lionesses could have adverse effects on the whole lion population (Packer et al. 1988). High mortality rates of subadult males were also found elsewhere as these males are often driven into unsuitable habitat when ejected from their natal pride (Schaller 1972). According to Stander (1990), most subadult males moving onto farmland became specialized stock raiders. In contrast, Stander (1990) found that relatively few adult females were killed on farmland, and these females were mostly "occasional" stock raiders: when the lionesses were translocated back into the protected area, they did not re-enter farmland for years (Stander 1990). In general, carnivores with large home ranges face a higher risk of getting into conflict with people (Woodroofe and Ginsberg 1998). The reason for the high mortality rate of adult females, therefore, might be their large home range of more than 500 km^2 (Stander 1991; Berry 1996). In contrast, the pride system appeared to increase survival of pride males: during our 16-year study period, only three adult pride males were shot on farmland, when they joined their whole pride that moved out the park. However, from the prediction of the number of adult and subadult lions derived from the predator prey model, the lion population recovered after consecutive better rainfall years (Fig. 10). Based on these predictions, I agree with Stander (1992), who stated that the number of lions destroyed on farmland does not seem to limit the size of the Etosha's lion population.

In recent years, there has been an increase in wildlife-based tourism and trophy hunting on both commercial and community farms in Namibia (Göttert and Zeller 2008). This trend from conventional livestock farming to wildlife-based tourism led to a significant increase of wildlife numbers (Göttert and Zeller 2008). For example, through tourism and hunting, the desert lion population in north-western Namibia has been increasing continuously, and consisted of more than 130 individuals in 2010 (Stander 2010). In the case of our study population, one pride (Gemsbokvlakte) moved out of our study area and repopulated a 300-km^2 private game reserve bordering Etosha in 2000. By the end of 2009, several groups had established themselves on this particular wildlife reserve (K. Stratford personal communication). Similar observations were made on a trophy hunting farm bordering Etosha, where lions are frequently sighted in an area which consisted of cattle farms in the past (T. Burger personal communication). The concept of wildlife-based tourism and trophy hunting, therefore, has the potential to provide benefits for both humans and wildlife.

Acknowledgments The project was done under the authorization of the Namibian Ministry of Environment and Tourism, which also provided funding and logistic support. Data were collected by H.H. Berry (253), O. Forge (226), P.E. Stander (209) K. Venzke (116), C. Berry (91) (the number of pride observations is given in parentheses). The following people assisted with data collection (>15 pride observations): Behrens (58), W. Versfeld (51), J.L. Scheepers (26), W.C. Gasaway (23), South (22), H.J.L. Orford (19), B. Fox (19), C. Brain (17), Schenk (15), D. Bartlett (15). Long-term rainfall data were obtained from the Etosha Ecological Institute. All staff members of the Etosha National Park are thanked for assistance, information and advice. The manuscript was improved by the comments of one anonymous reviewer.

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