

The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park

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The impact of lion (*Panthera leo*) predation on buffalo (*Syncerus caffer*) and medium-sized ungulates over periods of changing environmental conditions in an area of the Kruger National Park was investigated. Lions were found to prey proportionally most heavily on the resident buffalo and wildebeest (*Connochaetes taurinus*) populations, and less so on the semi-migratory zebra (*Equus burchelli*) population, and have the least impact on the high-density impala (*Aepyceros melampus*) population. The selection was largely in accordance with the abundance of the larger species, but not for impala, which were relatively under-represented in the diet. Zebra and wildebeest were preyed upon more frequently during periods of high rainfall, and less so during drier times, leading to relative population stability. In contrast to wildebeest and zebra, the buffalo population varied in accordance with ecological conditions, with strong evidence for an interaction between drought conditions and lion predation. Male lions preyed more heavily on buffalo than did females, the latter preying mostly on impala, wildebeest, and zebra. However, lionesses did prey on buffalo more frequently during drier periods than during wet periods. Calving and survival rates determined for buffalo were used to parameterize a simulation model, which incorporated ecological conditions and culling pressure on a yearly basis, to predict buffalo population trends. The resultant model closely tracked real population trends, which may be of use in future projections.

Key words: Lions, predation, population dynamics, prey, modelling.

INTRODUCTION

Predator–prey relationships amongst large mammals are complex interactions in systems ecology (Gasaway *et al.* 1983; Erlinge *et al.* 1984; Sinclair 1985; Peterson 1988; Messier 1991; Mills & Shenk 1992), and have important implications for management (Smuts 1978a; Peel & Montagu 1999). African ecosystems involve complex multi-species predator–prey systems (Sinclair *et al.* 1985; Mills & Biggs 1993), further complicated by dramatic fluctuations in environmental conditions, caused by variable rainfall (Smuts 1978a; Viljoen 1993; Mills *et al.* 1995).

Several studies have suggested that predators can regulate ungulate prey populations that both occur at low-density and are resident (Mills 1990; Mills & Shenk 1992; Caughley & Sinclair 1994; Peel & Montagu 1999). Thus resident ungulate prey populations at high densities (*e.g.* wildebeest, *Connochaetes taurinus*, in Ngorongoro Crater)

are controlled by food availability even though they experience high levels of predation (Kruuk 1972). Conversely the massive Serengeti wildebeest and zebra (*Equus burchelli*) population, which are strongly migratory, are regulated by dry season food abundance, and not predation (Sinclair *et al.* 1985). These studies support the argument that predators do not limit high-density resident populations or large migratory populations (Fryxell *et al.* 1988; Caughley & Sinclair 1994).

The role of lions (*Panthera leo*) in predator–prey relationships in the Kruger National Park (KNP) has received considerable attention (Smuts 1978a; Mills & Shenk 1992; Mills & Biggs 1993; Mills *et al.* 1995; Funston *et al.* 1998). Smuts (1978a) showed how populations of wildebeest and zebra in the central region declined during years of high rainfall, and speculated that predation was the cause owing to increased vegetative cover and fragmented herds. Mills & Biggs (1993) looked at a community of large carnivores in the south of KNP, and found that lions were the domi-

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nant predators removing over 50% of the biomass of the prey killed by large predators. A detailed analysis of the influence of lion predation on wildebeest and zebra populations during a period of average rainfall suggested that lion predation affected resident wildebeest more severely than it affected semi-migratory zebra (Mills & Shenk 1992). Here zebra occurred at higher densities than wildebeest, but lion predation was mainly restricted to zebra foals, whereas lions selected for adult wildebeest.

Mills *et al.* (1995) analysed longterm ungulate population trends, rainfall, and predation on buffalo (*Syncerus caffer*) wildebeest, and zebra, and found that buffalo were strongly affected by predation during drought conditions with associated population declines, whereas wildebeest showed some decline during droughts, and zebra experienced the smallest influence.

Our studies in the KNP have revealed that contrary to popular belief, male lions are effective and active predators, but select different prey species than lionesses (Funston *et al.* 1998), their main prey species being buffalo. Thus we expected that predation by male lions could affect the population dynamics of buffalo. Here we examine further the influence of lion predation on its main prey species within KNP.

STUDY AREA

The study was conducted in the southeastern section of KNP between the Sabie and Crocodile Rivers, bordered in the west by *Acacia welwitschii* thickets and in the east by Lebombo Mountain bushveld. The habitat comprises mainly *Acacia nigrescens* and *Sclerocarya birrea* tree savanna, with moderate to dense shrub and dense herbaceous layers (Gertenbach 1983).

High densities of ungulate prey species were found in the area, with impala being particularly common in riverine thickets, and adjacent thicket communities. Buffaloes were present at higher densities than zebras or wildebeests, and comprised most of the ungulate biomass.

METHODS

Rainfall

Annual rainfall records and longterm means were obtained for both Lower Sabie and Crocodile Bridge. It was assumed that rainfall was a good indicator of forage quality and quantity for herbivores (Scholz & Walker 1993). Good ecological

conditions, therefore, were presumed to have existed during average (annual rainfall within 7.5 percentage points of the longterm mean) or above-average (rainfall >7.5% above the longterm mean) rainfall years (high rainfall periods). Years receiving from 7.5% to 25% below the longterm average were classified as below-average rainfall years with moderate ecological conditions. Drought occurred if less than 75% of the mean annual rainfall was received (low rainfall periods) (Fig. 1).

Ungulate populations

The buffalo population was counted annually at the end of the dry season, during helicopter surveys (Joubert 1983). Sex and age ratio estimates were needed for the buffalo model, and were obtained from published records for the study population (Pienaar 1969), and from two intensively studied herds (Funston 1992). Sex and age ratios, however, are not a very sensitive parameter in the model that we used (Starfield *et al.* 1992). Population estimates of the other ungulates were made from fixed-wing aerial counts conducted during winter as described by Joubert (1983) and Viljoen & Retief (1994). Counts were assumed to be total counts owing to the openness of the study area and the narrow width of transects, and no correction factor was applied.

Lion observations

At least one adult lioness in each resident pride and one lion in each male coalition regularly encountered in the study area were fitted with radio-collars. We made longterm direct observations for a minimum of three consecutive nights per session (mean = 3.3 nights, $n = 94$ sessions). Direct observations entailed observing and following a focal animal with the aid of a spot light from a vehicle which generally remained 20–30 metres away from foraging lions, to which the lions were accustomed. During a hunt the lights and vehicle engine were switched off so as not to interfere with its outcome. We observed focal (radio-collared) animals continuously during observation sessions, regardless of changes in group composition. It had previously been found that 88% of lion kills in KNP are made at night (Mills & Biggs 1993). Thus later observations conducted by P.F. were carried out only at night, the nocturnal kill rates thus being adjusted to compensate for the daytime kills that would have been missed.

We recognized three lion group types. Pride

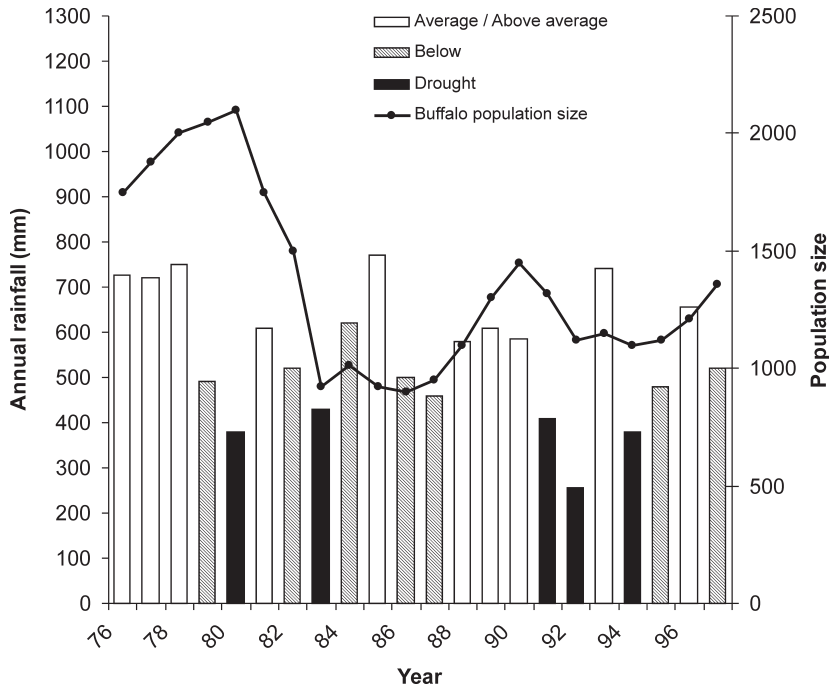


Fig. 1. Buffalo numbers and annual rainfall for the study area over 20 years of differing environmental conditions.

females were defined as a group of adult lionesses including juveniles and dependent subadults. Male groups were those that had dispersed from their natal prides, with non-territorial males being those that did not defend a territory. Kill rates per prey species were calculated for a hypothetical year or season based on the cumulative kill rate per session of that species over three years of observation, and the type of lion group involved.

Constructing the buffalo model

To estimate population trends we used a model developed by Starfield *et al.* (1992) to facilitate management decisions for buffalo in KNP. The model which has an interface to allow for parameter setting calculates the influence of the parameters such as rainfall and cull rate, along with six parameters pertaining to buffalo reproduction and population dynamics, on buffalo population trends. The buffalo parameters are:

1. Survival rates: mortality rates for specific sex and age classes were calculated from data on the number of buffalo of each sex and age class killed by lions (Mills & Shenk 1992; Funston *et al.* 1998).
2. Calf sex ratio: equal numbers of male and female calves were born each year (Visscher *et al.* 2004) in all runs of the model.

3. Monthly birth distribution: in the KNP, buffaloes calve predominantly in the summer months (Pienaar 1969; Funston 1992), and thus equal numbers of births during all summer months was used in all runs.
4. Birth rate: where the number of calves produced per age class of adult females is dependent on the previous year's rainfall (S. Joubert and I. Whyte, unpubl. data).
5. Age at which young bulls first associated in bachelor bull groups: specified as eight years of age (Funston 1992) in all runs of the model.
6. Age structure was based on herds observed by Funston (1992), and was constant in all runs of the model.

RESULTS

Rainfall

From 1972 to 1977 the KNP experienced the most pronounced wet period on record (Gertenbach 1980). This was followed by a dry period with a drought in 1979/80, and again during 1982/83. A definite cyclical rainfall pattern was difficult to determine in the early 1980s (Fig. 1); the 1982/83 drought was followed by two years of high rainfall, which were followed by two years of low rainfall. The late 1980s experienced above-average

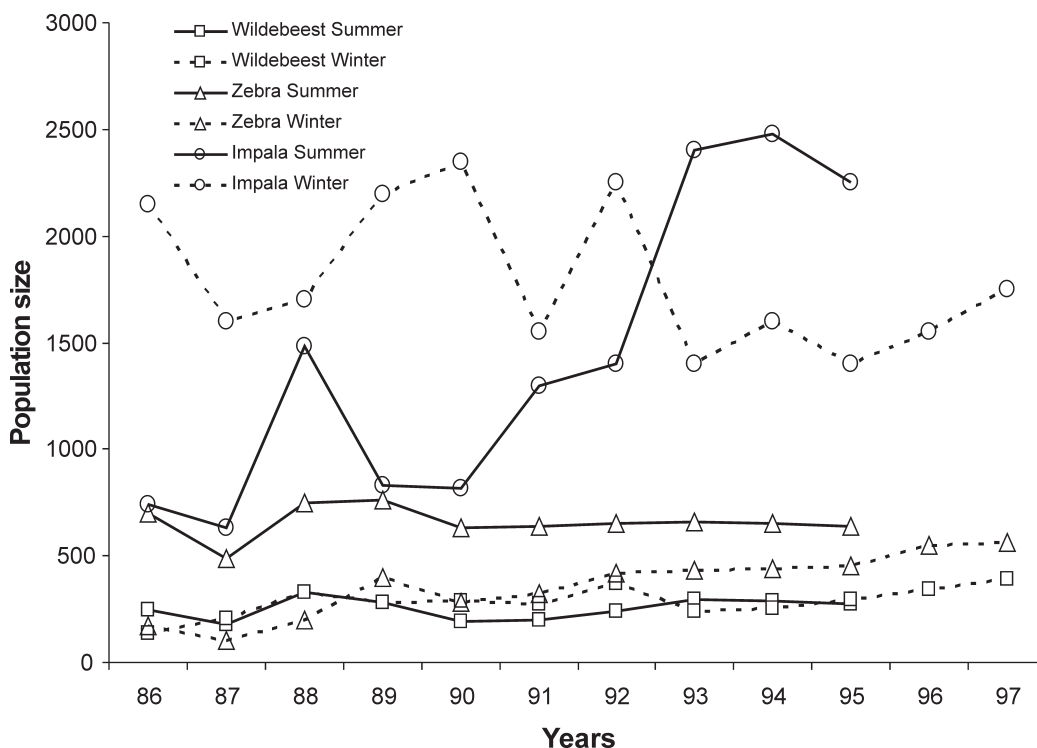


Fig. 2. Population trends for impala, wildebeest and zebra in the study area over an 11-year period that included high and low rainfall periods.

rainfall, and were followed by the 1990 to 1992 drought. This drought was broken by a year of very high rainfall in 1992/93, with subsequent years of low rainfall (Fig. 1).

Lion population

The lion population in the study area remained relatively constant from 1986 to 1995. The number of adult (killing) lions varied from 39 to 54. These comprised two prides permanently resident in the core study (plains) area, with four neighbouring prides that intermittently utilized the plains area (Funston 1999). The mean number of adult females per pride was 3.0 (calculated by averaging monthly total lionesses per pride). From radio-tracking data it was calculated that on average three adult lionesses from the four peripheral prides occupied the plains study area at any particular time. Thus we determined that on average there were 9.0 killing lionesses in the study area between 1985 and 1989, compared to an average of 12.2 killing lionesses in the study area from 1992 to 1995. Several male coalitions were also resident in the area, with an average of 3.7 territorial and 6.7 non-territorial individuals in

the later period. We do not have similar data for male lions from the earlier period.

Ungulate population trends and distribution

The impala and zebra populations remained relatively constant over the duration of the study, and were not adversely affected by the 1991/92 drought (Fig. 2). The tendency of the zebra to leave the basalt tree savanna in the summer months (Mills & Shenk 1992), however, seemed to be less in the period of below-average rainfall (Fig. 2). This was probably a response to food shortages in other habitats. Impala counts were most variable during the high rainfall period, when dense vegetation probably accounted for impala being more difficult to detect. The wildebeest population increased by about 18% during the below-average rainfall period (Fig. 2).

Averaged winter distributions from aerial counts over an 11-year period are presented for impala, wildebeest, and zebra in Figs 3–5. Higher densities of impala were recorded in the Lebombo Mountain bushveld and thicket habitats, and close to the major rivers that bounded the plains (Fig. 3). An inverse distribution was evident for wildebeest,

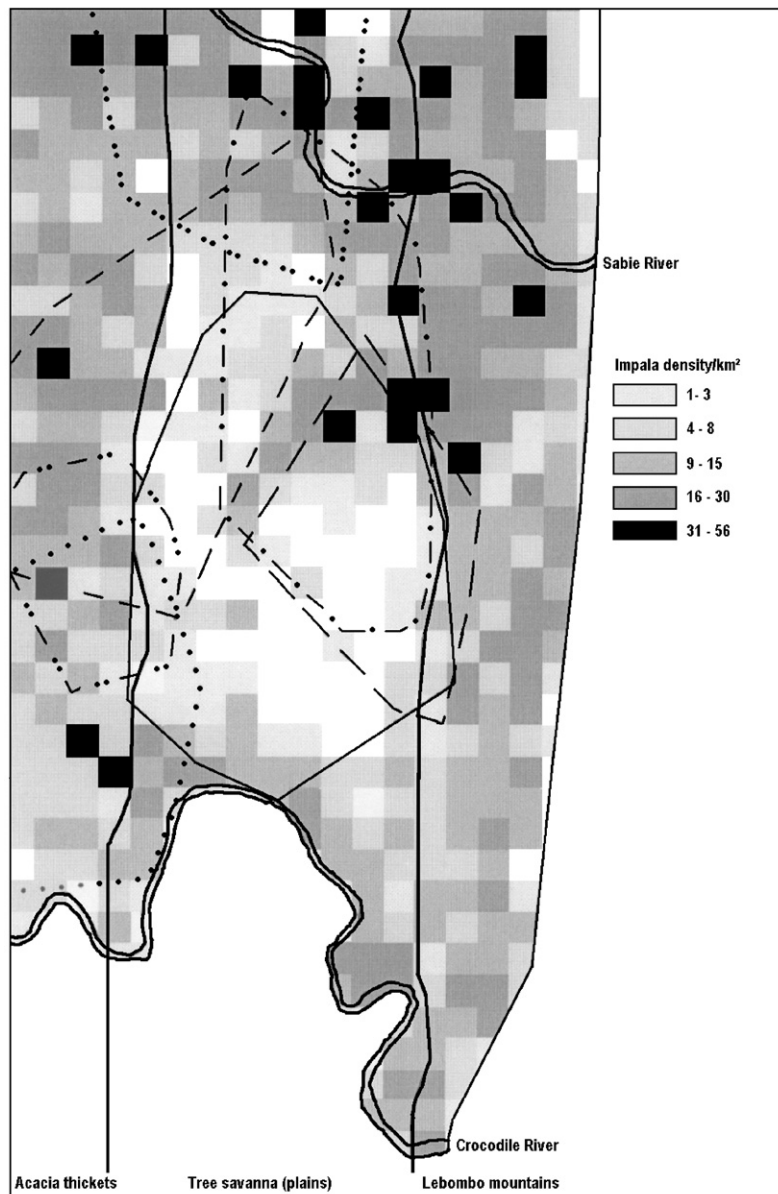


Fig. 3. Mean density/km² and distribution of impala in winter from 1985 to 1993, with the minimum convex polygons of the resident lion prides.

which were at high densities in the central plains area (Fig. 4). During winter the highest densities of zebra were in the Lebombo Mountain bushveld and off the plains where they were at higher densities during summer (Fig. 5).

A total of 1750 buffaloes were recorded in the study area during 1977, and constitute the starting population for runs of the model. From 1977 to 1980 the actual buffalo population increased at

6.7% per year (Fig. 1). This was a period of sharp transition from average to drought conditions. The buffalo population then started to decline (−15.5%) and crashed sharply in the drought of 1982/83 (−34.5%). During the same period the buffalo population was culled by 9% per year, as the population had exceeded the ‘upper acceptable limit’ in the proceeding period of positive growth (S. Joubert, unpubl. data). The combined effect of

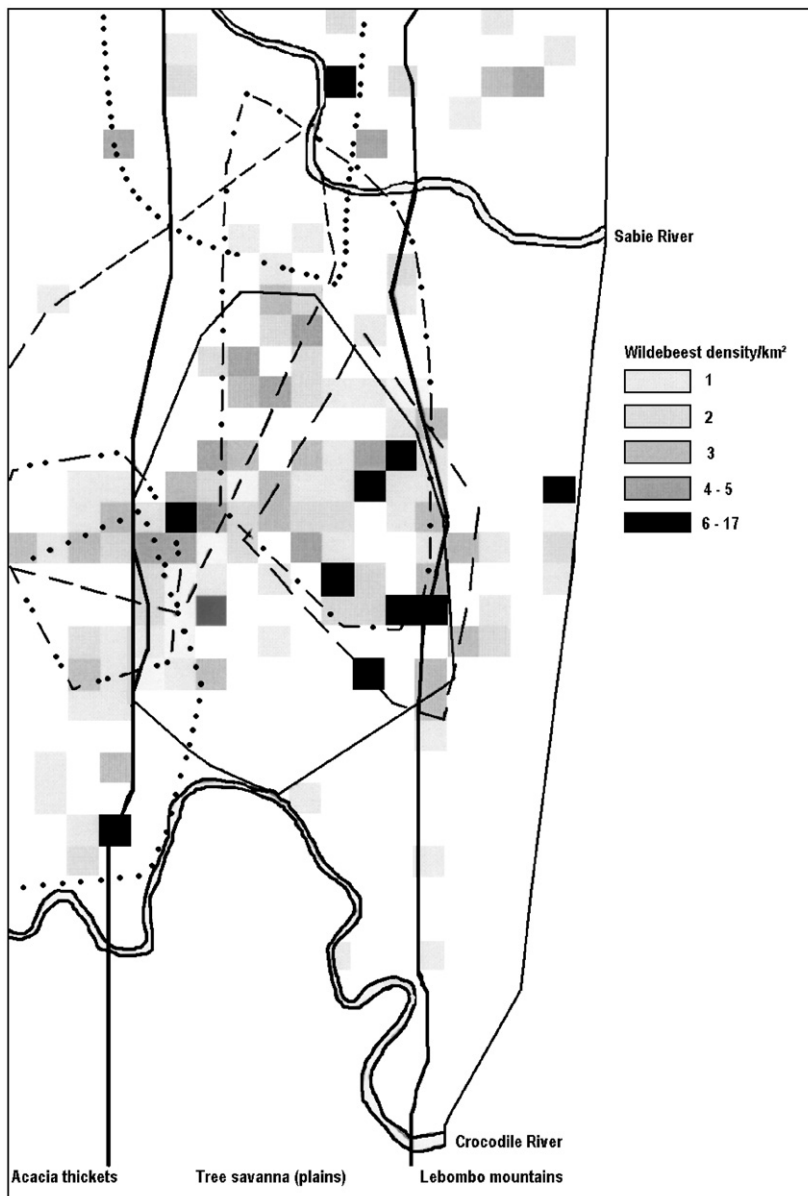


Fig. 4. Mean density/km² and distribution of wildebeest in winter from 1985 to 1993, with the minimum convex polygons of the resident lion prides.

the drought and the cull was a 53% decline in four years (Fig. 1).

The period from 1984 to 1986 experienced below-average rainfall resulting in the buffalo population remaining constant (Fig. 1). During the ensuing average rainfall conditions the population increased at 16% per year in the period from 1986 to 1990. During this period culling ceased, but following the drought years of 1990/91 and

1991/92 the population again declined by 21%. The following years were generally below-average in the study area, resulting in the population remaining stable at around 1100 individuals. During this period we conducted intensive observations of the predatory behaviour of male lions. The buffalo population started to increase again in 1996, following above-average rainfall in the 1995/96 rainfall season.

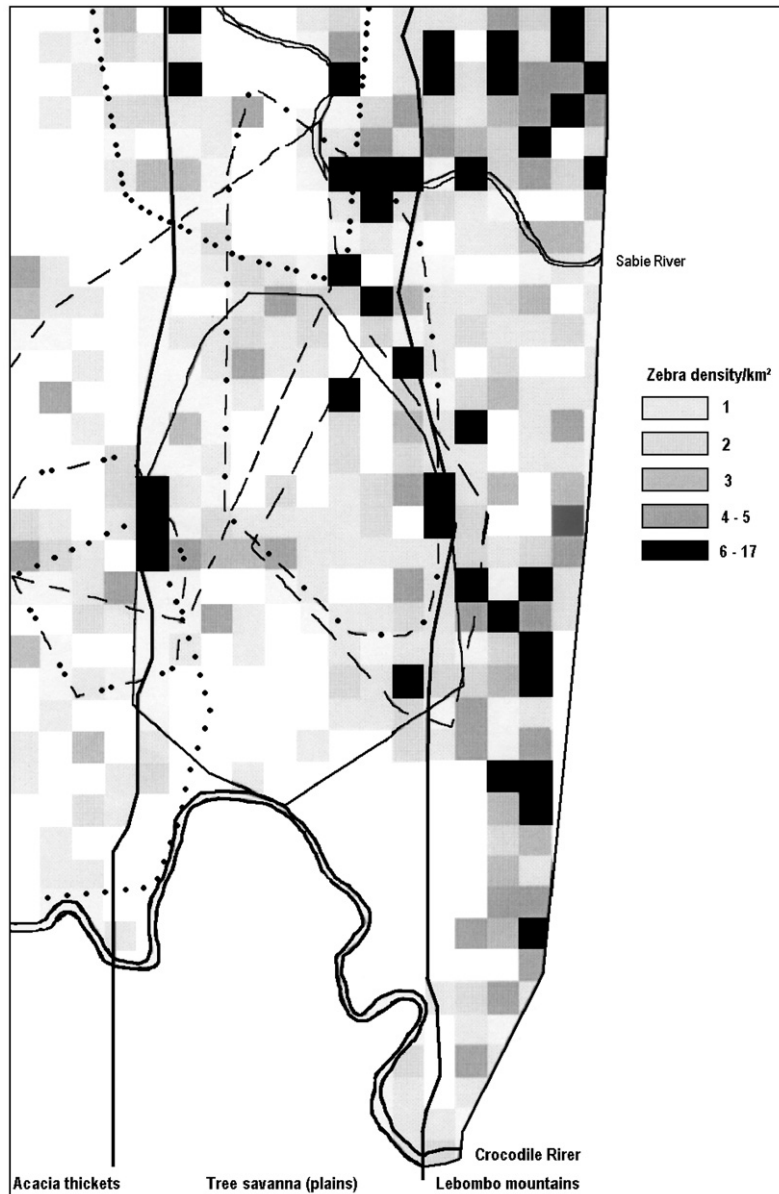


Fig. 5. Mean density/km² and distribution of zebra in winter from 1985 to 1993, with the minimum convex polygons of the resident lion prides.

Kill rate and prey selection

From 1985 to 1989 pride females were observed for 2126 hours of longterm continuous observations, whereas from 1992 to 1995 pride females were observed for 2256 hours. Applying Van Orsdol's (1981) weighting factor, this equates to 8757 lion-hours during the earlier period in which 48 prey animals over 10 kg were captured. During the later period 16 564 lion-hours of observation

were conducted during which 57 prey animals were killed. Estimates of kill rates per prey species per killing lion are presented in Table 1. During the later period 4056 lion-hours of observations of territorial and 7008 lion-hours of non-territorial males, were also made (Table 1). The total number of each major prey species killed per year was calculated by multiplying the kill rate per lion per year by the number of killing lions of each lion

Table 1. Number of each of the four major prey species killed, kill rate per year per killing lion and the calculated proportions of each prey species killed per year from the total population of that species during a period of above-average rainfall (good) compared with a period of below-average rainfall.

Prey species	Ecological conditions	Lion group type	Number killed	Kill rate per lion per year	Number of killing lions	Total population size	Number killed per year (%)
Buffalo	Good	Pride females	2	2.0	9.0	1102	18 (2)
	Below average	Pride females	10	5.4	12.3		67 (6)
		Territorial males	19	23.8	6.7	1103	159 (14)
		Non-territorial males	7	15.1	3.7		56 (5)
							282 (25)
Impala	Good	Pride females	13	13.0	9.0	1992	117 (6)
	Below average	Pride females	15	8.7	12.3		107 (5)
		Territorial males	1	1.3	6.7	1956	8 (1)
		Non-territorial males	7	15.1	3.7		56 (3)
							171 (9)
Wildebeest	Good	Pride females	7	7.0	9.0	236	63 (26)
	Below average	Pride females	8	4.3	12.3		53 (21)
		Territorial males	1	1.3	6.7	248	9 (4)
		Non-territorial males	1	2.2	3.7		8 (3)
							70 (28)
Zebra	Good	Pride females	8	^s 5.3	9.0	^s 665	47 (7)
	Below average	Pride females	10	^w 2.7	12.2	^w 226	24 (11)
				^s 2.8		^s 660	34 (5)
				^w 2.6		^w 455	32 (7)

Summer (^s) and winter (^w) estimates were determined for the semi-migratory zebra population.

group type (Table 1).

Wildebeest were the most heavily preyed species in the study area, with 28% of the population being estimated to be killed per year during the period of below-average rainfall conditions (Table 1). However this predation was almost exclusively by lionesses, with male lions making very few wildebeest kills (Funston *et al.* 1998, 2001). Assuming that lionesses killed adults and calves in equal proportion to their occurrence in the population, the most stable wildebeest population during the earlier period would have been attained with 7.7 killing lions (Mills & Shenk 1992). Thus the 9.0 and 12.3 killing lionesses resident in the area in the respective rainfall periods, as well as the males that were present could possibly have resulted in a population decline for the wildebeest, but this was not supported by the population surveys (Fig. 2).

This is probably best explained by the fact that the model developed by Mills & Shenk (1992) indicated that if the kill rate was biased towards calves, the wildebeest population would have been able to support 10.7 killing lions. This is roughly intermedi-

ate between the estimates of 9.0 and 12.3 killing lionesses on the plains in the respective rainfall periods. Furthermore, although there were more killing lionesses during the drier period, the wildebeest kill rate per adult lioness was lower during this period (Table 1). This probably accounts for the slight increase in the wildebeest population (+18%), and suggests alternative prey (especially buffalo) were more heavily selected during dry periods.

Similarly lionesses also preyed marginally more heavily on zebra in the wetter period, than during the drier period (Table 1), while male lions were never recorded killing zebra. During the wetter period, lionesses also preyed more frequently on wildebeest and zebra in summer than in winter (Mills & Shenk 1992), but this was not evident during a dry period (Table 2). In order to remain stable the winter zebra population would only have been able to support 6.8 lionesses, whereas the summer one could support 19.4 lionesses without declining. As the number of killing lionesses in the plains area never exceeded 12.3, the summer

Table 2. Number of wildebeests and zebras killed by lions during summer (October–March) and winter (April–September) during all continuous observation sessions in above and below-average rainfall periods.

Rainfall	Summer		Winter		Summer vs winter
	Hours observed	Number killed	Hours observed	Number killed	
Average	1607		1303		
Wildebeest		10		5	Chi-square = 0.79, d.f. = 1, $P = 0.37$
Zebra		11		5	Chi-square = 1.17, d.f. = 1, $P = 0.28$
Below average	1028		1340		
Wildebeest		7		8	Chi-square = 0.06, d.f. = 1, $P = 0.79$
Zebra		13		12	Chi-square = 0.74, d.f. = 1, $P = 0.39$

zebra population would not be strongly regulated by lion predation, but the winter population could be. The zebra population remained relatively stable over both wetter and drier periods, and it is thus likely that winter predation by lions on zebra has at least a slight compensatory effect on the population.

Lionesses killed similarly low proportions of impala in both wet and dry periods, with males also killing a relatively small number (Table 1). Impala occur at high densities in the peripheral habitats of the study area and at low densities on the plains area (Fig. 3). Thus, the estimated proportion killed per year may be an under-representation, due to most of our predation data coming from the two central prides. Male lions, particularly territorial ones, utilized areas of thicker bush significantly more than open areas, and were recorded to kill impala significantly more frequently in thick cover (Funston *et al.* 2001).

The largest shift in prey selection occurred with the hunting of buffalo by lionesses: they killed buffalo four times more frequently during a dry than during a wet period. During dry conditions the combined effect of predation by male and female lions was estimated to account for 25% of the buffalo population per year, resulting in the population showing no growth.

Testing the buffalo model

Running the model with the default parameters, no culling, and with actual yearly annual rainfall levels resulted in a pronounced discrepancy between the real and modelled population trends (Fig. 6). The fit of the modelled population was improved only slightly by incorporating culling data (Fig. 6). We investigated the default survival estimates and found that they tended to overestimate survival, particularly during droughts. We thus calculated more realistic survival and birth rate estimates than those provided as defaults with the model, by using data collected from our own predation observations, along with recorded average rates of change of the population under different environmental conditions.

Survival and birth rate estimates

During the drier period the buffalo population comprised an average of 1103 individuals. From our kill rate estimates we determined that only 30% of calves produced survived their first six months and 37% of the remaining calves survived to become yearlings (Table 3). We also calculated survival rates for the other age classes used in the model (see Tables 3 & 4). During this period birth rates were assumed to be 15% lower than during good ecological conditions (S. Joubert and

Table 3. Number of buffaloes killed, proportion of the buffalo population, number killed and survival rate of each sex and age class per year during below-average rainfall conditions.

Sex/age class	Number killed	Proportion in population (%)	Estimated number killed out of the population (%)	Estimated survival rate
0–6 months	17	210 (19)	147 (70)	0.30
7–12 months	8	63 (7)	40 (63)	0.37
Yearlings	4	122 (6)	20 (13)	0.87
Adult bulls	4	283 (25)	20 (7)	0.93
Adult cows	9	488 (43)	43 (9)	0.91

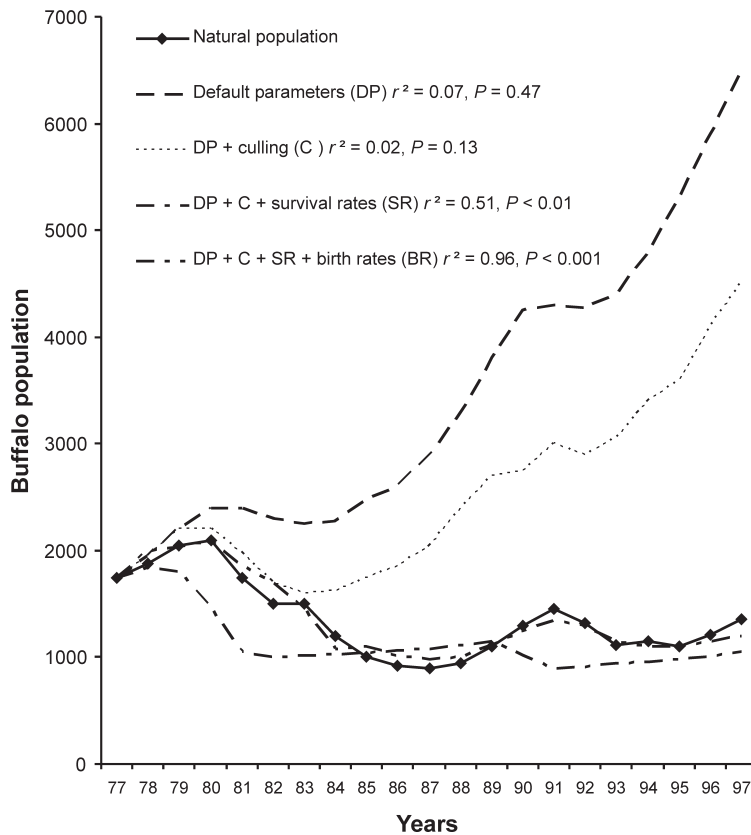


Fig. 6. Yearly buffalo numbers and various modelled estimates of the buffalo population per year.

I. Whyte, unpubl. data). Using these revised estimates, the modelled growth rate accurately reflected observed population trends (Fig. 6).

Under good environmental conditions the buffalo population increased at an average rate of

16%/year. Using the model and census data, we computed the survival and birth rates necessary to attain similar rates of increase by the following means: the proportion of adult cows in breeding herds varied from 33–46% (mean 40%); and

Table 4. Survival and birth rate estimates that produced biologically appropriate growth rate estimates in the buffalo model. Numbers in brackets were the default values.

	Good conditions	Moderate conditions	Drought conditions
Sex/age class		Survival rates	
0–6 months	0.54 (0.80)	0.30 (0.70)	0.20 (0.60)
7–12 months	0.55 (0.90)	0.37 (0.80)	0.30 (0.70)
Yearlings	0.87 (0.90)	0.87 (0.85)	0.70 (0.80)
Adult bulls	0.91 (0.99)	0.93 (0.95)	0.80 (0.90)
Adult cows	0.93 (0.99)	0.91 (0.95)	0.86 (0.90)
Age of cows		Birth rates	
3–4 years	0.60 (0.30)	0.51 (0.30)	0.45 (0.10)
4–5 years	0.75 (0.50)	0.64 (0.50)	0.58 (0.10)
>5 years	0.80 (0.70)	0.68 (0.70)	0.61 (0.60)
Modelled population growth rate per year	+15.5%	–0.1%	–10.3%

under good conditions 80% of adult cows were generally pregnant (Pienaar 1969; Sinclair 1977; Funston 1992). Therefore, at the end of the calving season, in a hypothetical herd of 1000 buffalo there, would be about 320 calves. In order for the ratio of calves : other herd members to decline from 32% to 20%, which was the mean during late winter surveys, 46% of calves would have to have been killed, giving a survival probability of 0.54 for calves (Table 4). Together with the estimates similarly derived for the other age classes (given in Table 4), the model produced a growth rate of 15.5% per year, which was the same as that observed (Fig. 6).

The survival and birth rates during poor ecological conditions were thus estimated in a similar manner: during the 1991/92 drought period only 65% of adult cows were pregnant and calves comprised only 6% of herds six months after the calving period (I. Whyte & C. Wood, unpubl. data). These data resulted in an estimated growth rate of -10.3%, which again closely approximated the observed rates of decline without culling.

When we ran the model specifying yearly rainfall conditions, the percentage culled per year and the revised survival estimates tracked the real population trends relatively closely ($r^2 = 0.51$) (Fig. 6). However, when we incorporated the revised birth rate estimates along with the other variables used in the former run of the model, we found that the model population closely followed the observed population ($r^2 = 0.96$) (Fig. 6).

DISCUSSION

Impala, wildebeest, and zebra populations did not vary as much as the buffalo population did. One of the notable differences in the zebra population from a wetter to a drier period was a decrease in the seasonal movements of zebra in the latter. There was also a slight increase in the wildebeest population from a wetter to a drier period. As expected, predation levels on wildebeest and zebra were lowest in a drier period (Smuts 1978a; Mills *et al.* 1995), with the mechanisms responsible for these trends being elucidated here.

Based on the estimates from the model of Mills & Shenk (1992), levels of predation on wildebeest were likely to limit the population in both wet and dry periods. However, due to lower predation rates, lions did not impact as heavily on the wildebeest population in the drier period. Under either wet or dry conditions the summer 'migratory' zebra population would not have been limited by predation,

whereas the winter population would have been. The low levels of predation on wildebeest and zebra by male lions (Funston *et al.* 1998) were unlikely to further influence the population dynamics of these species. Furthermore the amount of meat that pride females lose to scavenging males is low (Funston *et al.* 1998), and would be an unlikely reason for increased predation rates on these species.

Proportionally the levels of predation by all lion group types on the high-density impala population were low during both study periods, and it is unlikely that lion predation has a significant regulatory effect on their population growth rates. Impala, however, are exposed to continuous levels of predation from a broad, large carnivore guild (Mills & Biggs 1993), the cumulative effect of which might explain why the impala population is also fairly stable between years. Some of the other carnivores also occasionally prey on wildebeest and zebra, especially on juveniles (Mills & Biggs 1993), presumably increasing the fluctuation with rainfall patterns. This is similar to predation patterns in other ecosystems, where a range of predators prey most frequently on one relatively small species, but kill a range of other larger prey when they experience ecological pressure (Erlinge *et al.* 1984).

The buffalo population showed the largest variability over time, which was correlated closely with environmental/rainfall conditions and concomitant levels of lion predation. These fluctuations were accurately predicted by the model, by using predation and other data to calculate mortality (and thus survival) estimates. We concluded that the default model parameters for survival provided by Starfield *et al.* (1992), at least during below-average rainfall periods, were conservative and did not influence the model sufficiently. This seemed to be particularly evident during droughts, when the population did not decline sharply enough. Conversely under high rainfall conditions the population tended to increase too quickly.

By specifying more precisely the survival parameters required by this model, we hope the future use of this model as a research and management tool will be enhanced. Sensitivity analysis revealed that the most important variable to define accurately is survival rate, which is intrinsically linked to the lion predation rate. The survival rate (or kill rate) was also the most sensitive parameter in the model developed by Mills & Shenk (1992). The effects of environmental conditions on buffalo are thus to a greater or lesser extent mediated by lion

predation, but are also influenced by other factors including culling. In Manyara National Park, lion predation was also found to be the chief proximate cause of death amongst buffalo, accounting for 88% of observed mortality (Prins & Iason 1989). Without culling the decline observed in the KNP buffalo population in our study area during the period from 1980 to 1983 would not have been as sharp.

Most studies dealing with predation on buffalo are based on the number of carcasses located (Pienaar 1969; Schaller 1972; Prins & Iason 1989; Mills *et al.* 1995), and have probably underestimated the level of predation on calves because these carcasses are completely consumed. McBride (1984), however, also observed that lions preyed predominantly on young buffalo in Botswana where 63% of buffalo kills made by lions were calves. In Serengeti it was estimated that 49% of buffalo calves die in their first year, predation by lions probably being the main cause of this mortality (Sinclair 1977). Considering the relative infrequency of below-average or drought periods in the Serengeti ecosystem, this gives us confidence in the mortality estimates that we determined for periods of good ecological conditions. Buffalo populations have the potential to increase while enduring these levels of predation, provided that adult mortality is low.

We showed that during below-average ecological conditions predation on calves was relatively high but with relatively low levels of predation on adults. Ecological conditions during these periods probably do not result in adult buffaloes losing condition sufficiently to become ready victims to lions, or for herds to fragment, which may lead to increased predation levels. During droughts, however, even adult buffaloes become easy victims of lions, and along with having lower birth rates, buffalo herds tend to split into smaller herds which are known to be more vulnerable to lion predation (Prins & Iason 1989), and thus experience pronounced population declines (Mills *et al.* 1995). Lions have been found to show clear switches in prey selection between wet and dry cycles, with wildebeest being the wet-cycle prey, and buffalo the dry-cycle prey in Kruger (Mills *et al.* 1995). The continued presence of large buffalo populations during droughts would probably result in degradation of the herbaceous vegetation in an ecosystem, and thus reduce the chance of survival of low density, selective grazers.

During our study, buffalo population declines associated with droughts were followed by periods

of zero growth associated with concomitant below-average ecological conditions. Thus buffalo populations seem to only have the potential to increase only during periods of average to above-average rainfall. Our study shows that in KNP buffalo are an extremely important prey species for lions, making up the largest portion of their diet by biomass, particularly during low rainfall periods.

While the findings of this study confirm once again that large self-regulating ecosystems like KNP establish predator-prey relationships that keep the system functioning within a stable but dynamic equilibrium, can the same be true in smaller fenced reserves that are not self-regulating and require some degree of management? Even in large parks like KNP certain circumstances have exacerbated inappropriate managerial actions in conjunction with extreme environmental variations or perturbations (Smuts 1976, 1978b; Harrington *et al.* 1999; Grant *et al.* 2002). The reintroduction of large carnivores, especially lions, into smaller reserves is in its infancy (Hunter 1998) and wildlife managers are still coming to terms with how to assess and manage the influence of predation in these reserves. It is important for wildlife managers to be aware that the dynamics of specific animal populations cannot be separated from those of associated populations or from the environment as a whole (Smuts 1978a), and that by implication most of these reserves can support only resident ungulate populations.

Management practices easily compound the complexity of these relationships. Little attention has been given to these aspects in smaller conservation areas and game ranches that have begun reintroducing large carnivores (Hunter 1998; Peel & Montagu 1999). Peel & Montagu (1999) showed that a declining blue wildebeest population exposed to lion predation and a live game removal programme would decline under this management regime unless all removal was halted and the number of lions was maintained at a reduced level. Thus it is our desire that this paper, while contributing to our understanding of predator-prey relationships in larger reserves, will also contribute both to an improved understanding and more informed management decisions in smaller reserves and game ranches.

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