Predator–prey relationships: the impact of lion predation on wildebeest and zebra populations

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Summary

1. The role of lion *Panthera leo* predation in the dynamics of blue wildebeest *Connochaetes taurinus* and zebra *Equus burchelli* populations was investigated through simulation models. The data used in the models were from intensive observations over 4 years in the south-east of the Kruger National Park.

2. Population estimates of wildebeest and zebra were made from aerial surveys, sex and age ratios from ground counts. Lion numbers were determined from observations of marked and radio-collared animals. Predation was studied by following lions for continuous periods of up to 336 h.

3. Two models were constructed. Model 1 ascertained the number of killing lions (adult females) that could be supported by each prey population while remaining stable. A single model was constructed for the sedentary wildebeest population. A summer and winter model was constructed for the semi-migratory zebra population. The sensitivity of the parameters in the model was tested by changing their value by 10%. In model 2, the kill age structure for each species was changed to determine the number of killing lions the altered prey selection parameters could support.

4. There was no difference in the vulnerability of either species to predation. Zebra foals (<1 year) were killed more frequently than expected. No selection for sex or by season could be found for either species.

5. Model 1 predicted that the wildebeest population stabilizes with 7·7 killing lions, close to the number in the study area. The winter zebra population stabilizes with 6·8 killing lions and the summer zebra population with 19·4. Manipulation of kill rate followed by adult fecundity rate had the greatest effect on population size of both species. In model 2, wildebeest predation was made selective towards calves and zebra predation was made non-selective for sex and age. With these parameters the wildebeest population stabilizes with 10·7 killing lions and the zebra population with 5·4 in winter and 15·1 in summer.

6. The models suggest that lion predation affected wildebeest more severely than zebra during the study. This was through the way in which lions selected their prey, and because of the sedentary behaviour of the wildebeest, as opposed to the semi-migratory behaviour of the zebra.

Key-words: sedentary and migratory prey, populations, model.

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Introduction

The impact of mammalian predators on their prey is a complex and, at times, controversial aspect of predator ecology (Schaller 1972; Smuts 1978a; Peterson 1988). It may have important implications in the management of some species. The data needed to measure this impact include many parameters difficult to measure. These include: the numbers of predators and prey in the area, how the predators select their prey with respect to species, sex, age and condition, how often the predators kill, the fecundity and survival rates of the prey, and the contribution of mortality other than predation in the population dynamics of the prey (Mills 1990). In addition, ecosystems are dynamic and caution should be exercised if results are extrapolated from

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one area to another, or even from one time period to another within the same area.

In the comparatively simple large mammal predator—prey systems in North America, many studies have been conducted to evaluate the effect of predators, mainly wolves *Canis lupus* Linnaeus on their prey. Although these studies have made a significant contribution to the understanding of predator—prey relationships, the interpretation of the results from some of them have given rise to lively debate in the literature (e.g. Bergerud, Wyett & Snider 1983; Van Ballenberghe 1985, 1989; Bergerud & Ballard 1988; Bergerud & Snider 1988; Thompson & Peterson 1988; Messier 1991). The longest running large mammal predator—prey study is the one on Isle Royale in North America, where the relationship between wolves and moose *Alces alces* Linnaeus has been studied for 30 years. It is noteworthy that only after this length of time have important characteristics of this comparatively simple system been revealed (Peterson 1988; Messier 1991).

In Africa, large mammal predator—prey systems are more complex than those in North America, as there are a larger number of species of both predator and prey involved. Few studies have attempted to measure the effect of predation on prey populations. In large, more or less self-contained ecosystems, predation is generally believed to have little effect on prey populations that are migratory, such as in the Serengeti (Schaller 1972; Kruuk 1972; Sinclair, Dublin & Borner 1985) or nomadic, such as in the southern Kalahari (Mills 1990). However, resident populations of herbivores in the Serengeti may be more heavily influenced by predation (Sinclair 1985; Fryxell, Greever & Sinclair 1988). There is also some evidence that predation may regulate the more sedentary gemsbok *Oryx gazella* (Linnaeus) population in the southern Kalahari (Mills 1990). In the Ngorongoro Crater the very high density resident blue wildebeest *Connochaetes taurinus* (Burchell) population was found to be under considerable predation pressure. However, it appeared that the population density was regulated by the amount of herbage available, not by the numbers of predators (Kruuk 1972). These observations largely support the contention of Fryxell, Greever & Sinclair (1988) that predators can regulate resident herbivores at low population densities, whereas such regulation is rare for migratory herds.

The Kruger National Park (KNP), in spite of its large size (19 485 km²), is not a self-contained system and is managed. It is fenced off from the surrounding areas, natural water supplies are supplemented, elephant *Loxodonta africana* (Blumenbach), buffalo *Syncerus caffer* (Sparrman) and, occasionally, hippopotamus *Hippopotamus amphibius* Linnaeus populations are controlled, and the vegetation is burnt on a rotational basis (Smuts 1978a; Joubert 1986). In the central district predation on both migratory and sedentary wildebeest and zebra *Equus burchelli* (Gray) subpopulations was believed to be of major importance in the decline of both during a period of unusually high rainfall. Tall grass conditions and a tendency for herds to fragment may have increased their vulnerability to predation (Smuts 1978a; Whyte & Joubert 1988).

In this paper we examine the role of lion *Panthera leo* (Linnaeus) predation in the dynamics of zebra and wildebeest populations in the south-eastern region of the KNP during a period of normal rainfall. This is accomplished by constructing simulation models based on intensive observations made over 4 years. Although a simple population model has been constructed for the wildebeest population in the central district of the KNP (Starfield, Smuts & Shiell 1976), parameters used to build the model were rather limiting. Our models address two important aspects of predator—prey relationships: (i) the effects of lion predation on a sedentary versus a semi-migratory prey population; (ii) the effects of predator selection of different sex- and age-classes on prey populations.

Study area

The study area was the *Sclerocarya birrea* (A. Rich.) Hochst./*Acacia nigrescens* Oliv. savanna plains, covering 235 km² between the Sabie and Crocodile rivers, bounded by the Lebombo hills in the east and *Acacia welwitschii* Oliv. thickets in the west (see Gertenbach 1983). It is an open tree savanna, intersected by a few well-defined drainage channels. There is a moderate shrub layer and a dense grass layer, comprising mainly *Themeda triandra* Forssk., *Panicum colaratum* L., *Digitaria eriantha* Steud. and *Bothriocloa radicans* (Lehm.) A. Camus (Gertenbach 1983). This landscape type supports the highest density of wildebeest and zebra in the KNP (Gertenbach 1983; P. Viljoen, unpublished data).

Most rain (82%) falls between October and March (Gertenbach 1980). The combined mean annual rainfall at Crocodile Bridge and Lower Sabie during the study (1986—89) was 600·8 ± 100·9 mm, compared with the long-term mean for these stations of 589·4 mm.

Methods

DATA COLLECTION

Wildebeest and zebra numbers

Population estimates of wildebeest and zebra were made from aerial counts conducted during winter and summer months from January 1986 until January 1990, as described by Joubert (1983). Counts were assumed to be total counts which, given the openness of the study area and the large size of the animals

concerned, seems a reasonable assumption. Seasonality of wildebeest and zebra populations in the study area was tested using the Wilcoxon rank sum test.

Lion observations

Lion predation was the most important type of mortality for wildebeest and zebra in the study area. Although spotted hyaenas *Crocuta crocuta* (Erxleben) were common, they rarely hunted, contrary to other areas (Kruuk 1972; Cooper 1990; Mills 1990). Only one observation of an unsuccessful hunt on a zebra foal was made in 132 h observations of hyaenas foraging, and hyaenas were never observed feeding on a carcass of either species that appeared to be their own kill. Furthermore, Henschel & Skinner (1990) recorded only two zebra and three wildebeest kills in nearly 4000 h observations of spotted hyaenas in the same landscape type in the central district of the KNP. Non-predation mortality on adult wildebeest and zebra was also low. Lions were only observed to scavenge one wildebeest which died from causes other than predation during the study, and only one other wildebeest and a zebra were recorded dead from non-predatory causes in spite of the area being intensively patrolled by rangers.

Lions were lured to capture sites in and around the study area at regular intervals, using the mass capture technique of Smuts, Whyte & Dearelove (1977a, b). All lions over 18 months encountered were branded with a small individually recognizable mark. Subsequent observations of lions in this area recorded the location of marked lions, as well as the presence of unmarked lions. In addition, radio-collars were attached to one adult lioness in those prides that most often visited the study area. These radio-collared females were located and followed regularly.

Three types of data on predation were collected based on the duration of the observation period.
1. Radio-location observations, which documented the location of a radio-collared lion, the group composition and, if present, kill information.
2. Short-term continuous observations, when radio-collared lions were followed in a vehicle for periods of 2–15 h, and data on activity, prey encounters and group composition were recorded.
3. Long-term continuous observations, when lions were followed for six periods of 336 h (three each in summer and winter), one of 58 h (summer) and one of 53 h (winter), and the same data as during the short-term observations collected.

The thick bush made it impossible to follow lions at night without lights. To avoid possible interference with prey interactions, the use of lights was controlled. Whenever lions encountered prey the lights were turned off and only switched on again after the prey encounter ended. The end of an encounter

occurred, either after the prey animals had been heard running away, or the radio-signal indicated that the lions had moved on without having made a hunting attempt.

All wildebeest and zebra kills observed were made by adult females. Other lion studies have also found that females do most of the killing (Schaller 1972; Elliott, McTaggart Cowan & Holling 1977; Van Orsdol 1986; Stander, in press), except for very large prey (Packer 1986). Therefore, the models are based on adult females as the killing lions. It is assumed that the number of kills made is related to pride composition (Van Orsdol 1984). Because of differences in food requirements and consumption of lions of different ages and sexes, lion-hours were calculated as the number of hours each lion sex- and age-class was observed. Numbers of observation hours were multiplied by a consumption weighting factor depending on the age and sex of the animals involved, as used by Van Orsdol (1986).

A kill rate per killing lion (adult females) was calculated from the long-term continuous observation data only. Radio-location data were biased towards large prey. Short-term continuous data were opportunistic as the duration of an observation session was partially determined by the state of hunger of the lions and, therefore, the probability that they would kill (Mills, in press).

Although the kill rate data were collected over 3 years we have lumped them into one hypothetical year. This was done because only two to four repetitions (i.e. long-term continuous observation periods) were performed each year, and few wildebeest and zebra kills were made during each one (a maximum of three for either species). Each of the 3 years were similar ecologically, with little variation in rainfall (see Study Area) and numbers of wildebeest and zebra did not fluctuate greatly from year to year (Table 1).

Thus, the kill rate per killing lion in one year was calculated as follows:

kill rate per killing lion year^{-1} = (number of prey killed × number of hours in a year)/number of long-term continuous lion hours.

Prey encounters were classified as: (i) a kill; (ii) a failure (i.e. an attempt was made to kill the prey in that the lions either stalked and/or ran at the prey, but the animals escaped); or (iii) no attempt, where the lions detected prey, but did not attempt to stalk or attack them. Vulnerability of a prey species was calculated as the percentage of all encounters with that species resulting in a kill.

Seasonality (summer/winter) of kills for wildebeest and zebra was analysed using the data from continuous observations, weighted by hours of observation in each season. Age structure of kills was also calculated from continuous observations only and tested against population age structure for

selection. Two age-classes were specified, juveniles (<1 year old) and adults (>1 year). Sex ratio of the adult kills, using both radio-location and continuous observation data, was compared with population sex ratio within the study area. Sex and age classifications of wildebeest and zebra populations were obtained from annual sample ground counts carried out each October in the study area by D. Mason (unpublished data). Vulnerability of prey, differences in seasonality, differences between the age structure and sex ratio of killed prey and the population of the prey, were all tested for significance using χ^2.

THE MODELS

Three kinds of parameters were used in the models: initializing and fixed parameters, and a controlling parameter. Initializing parameters included demographic values obtained from field observations. Thus, the models were initiated with mean values for wildebeest and zebra population size (from the aerial counts), age structure and sex ratio in the study area, during the years of the study (D. Mason, unpublished data). Because the zebra population size fluctuated seasonally, two models (winter and summer) were constructed for this species. All parameters for the summer and winter models were the same except population size. Wildebeest fecundity rates (Braack 1973), zebra fecundity rates (Smuts 1976) and kill rate were fixed parameters throughout the models. Number of killing lions was the controlling parameter used to alter the outcome of the models.

The models simulate the wildebeest and zebra populations in January, following the calving and foaling seasons. The age structure in year i is represented as follows:

j_i = number of calves or foals (juveniles);
y_i = number of yearlings;
$2y_i$ = number of 2-year-olds (zebra models only);
af_i = number of adult females;
am_i = number of adult males.

Fecundity and survival rates are expressed as: affec (adult female fecundity), yfec (yearling fecundity), jsurv (juvenile survival), ysurv (yearling survival), afsurv (adult female survival), amsurv (adult male survival). Perentage of age- and sex-classes in the population are expressed as follows: %j (percentage juveniles), %y (percentage yearlings), %af (percentage adult females), and %am (percentage adult males).

Thus, population size in the following years was determined by the following equations:

j_i = affec × af_i + yfec × y_i × 0·5;
y_i = j_{i-1} × jsurv$_{i-1}$;
$2y_i$ = y_{i-1} × ysurv$_{i-1}$;
af_i = $(2y_{i-1}$ × %af × 2ysurv$_{i-1}) + (af_{i-1}$ × afsurv$_{i-1})$;

$am_i = (2y_{i-1}$ × $(1 - $%$af)$ × 2ysurv$_{i-1}) + (am_{i-1}$ × amsurv$_{i-1})$.

Two sets of models wre constructed.

Model 1

Model 1 was used to describe the wildebeest and zebra populations during the 4 years of the study (see Appendices), and to ascertain the number of killing lions that could be supported by that prey base, while allowing the prey base to remain stable. Stability is defined as the smallest change in population size between year 1 and year 5. Thus, a stability index (SI) was calculated as follows:

SI = (totalpop$_5$/totalpop$_1$) − 1.

The model was structured using the observed kill age structure, with the exception of wildebeest calves, because calf survival rate for wildebeest calculated with only lion predation as a mortality factor, was higher than that observed during the study. Therefore, calf survival rate for wildebeest model 1 was decreased to the mean survival rate of wildebeest calves observed (0·65, D. Mason, unpublished data). The other survival rates were calculated from the age structure of the kills, the kill rate and the number of killing lions in the study area as follows:

jsurv$_i$ = 1 − [(kill rate × number of killing lions × %j)/j_{i-1}];
ysurv$_i$ = 1 − [(kill rate × number of killing lions × %y)/y_{i-1}];
afsurv$_i$ = 1 − [(kill rate × number of killing lions × %af)/af_{i-1}];
amsurv$_i$ = 1 − [(kill rate × number of killing lions × %am)/am_{i-1}];

In order to determine the sensitivity of model 1 to various parameters, a single population parameter was changed, by either increasing or decreasing the value by 10%, while keeping the other observed parameters constant. The model was then run for 10 years to obtain predicted values for the population in year 10.

Model 2

In order to test the effect of age selection on prey, wildebeest model 1 was manipulated by substituting the observed wildebeest age selection for the observed zebra age selection and vice versa for the zebra model 1, to obtain predicted population results after 4 years. The SI in model 2 was again measured to determine the number of killing lions the altered prey selection parameters could support and remain stable.

Results

WILDEBEEST AND ZEBRA NUMBERS

Table 1 gives the results of the aerial counts in the study area. There was no significant difference between the summer and winter wildebeest counts (Wilcoxon rank-sum test $z = -1.18$; $P = 0.239$), but there was between the summer and winter zebra counts (Wilcoxon rank-sum test $z = 3.35$; $P < 0.001$). The zebra population fluctuated in the study area peaking during the summer months, while a segment migrated to the Lebombo Hills and west of the study area, during the winter months (unpublished observations).

LION NUMBERS

Observations of branded and radio-collared lions revealed that two prides, known as the V and M prides, made almost exclusive use of the study area during the 4 years of the study (Table 2). The mean number of adult females, i.e. killing lions, weighted by month in the M and V prides for the 4-year study was 2·3 and 3·6, respectively. For most of the study the two prides associated with four adult males, which divided their time between the two prides. The M pride comprised three adult females and six subadults during 1986, and for most of the remaining period two females raised seven cubs. The V pride comprised four females with six subadults in 1986, three females with no cubs for most of 1987, and three to four females with seven to nine cubs for the remaining time.

In addition to the above-mentioned lions, animals from another four prides, as well as an unknown number of nomads, occasionally entered the study area. Animals from three of these prides were radio-collared in order to see how much use they made of the study area (Table 2). The C and G prides rarely came onto the plains. The L pride, comprising two adult females and five subadults from the Lebombo Hills, began to use the plains in 1989 and had estab-

Table 1. Summer and winter counts of wildebeest and zebra in the study area, March 1986–January 1990

	Wildebeest	Zebra
Summer		
March 86	226	698
March 87	174	495
January 88	321	755
January 89	257	761
March 89	244	433
January 90	181	614
Median	235	656
Winter		
July 86	139	105
July 87	200	90
May 88	150	407
July 88	293	152
July 89	252	346
Median	200	152

Table 2. Percentage of radio-locations of lions from six prides in the study area

Pride	Total number of radio-locations	Percentage of radio locations inside the study area
V	128	96
M	129	97
C	25	14
G	13	15
L	26	38

lished themselves in the north-eastern region of the study area by the end of that year when the study was terminated. No animals from the fourth pride were radio-collared, but they were occasionally seen in the northern tip of the study area. Of 13 sightings of nomadic groups in the study area, 10 were recorded in summer and three in winter.

KILL RATE AND PREY SELECTION

A total of 2126 h of long-term continuous data were recorded for the V and M prides. Applying Van

Table 3. Animals killed by lions during continuous observations

	Adult male	Adult female	Juvenile	Unknown	Total
Impala Aepyceros melampus Lichtenstein	11	7	16	–	34(30·6%)
Zebra	3	3	10	–	16(14·4%)
Wildebeest	5	8	2	–	15(13·5%)
Porcupine Hystrix africaeaustralis Peters	–	–	3	12	15(13·5%)
Warthog Phacochoerus aethiopicus (Pallas)	2	4	8	–	14(12·6%)
Giraffe Giraffa camelopardalis (Linnaeus)	–	–	2	–	2(1·8%)
Buffalo	1	1	–	–	2(1·8%)
Kudu Tragelaphus strepsiceros (Pallas)	–	1	1	–	2(1·8%)
Duiker Sylvicapra grimmia (Linneaus)	1	1	–	–	2(1·8%)
Steenbok Raphicerus campestris (Thunberg)	–	1	–	–	1(0·9%)
Other	–	–	–	8	8(7·2%)
Total	23 (20·7%)	26 (23·4%)	43 (38·7%)	20 (18·0%)	111

Table 4. Vulnerability of wildebeest and zebra to lion predation

	Number of encounters	Kill	Failure	No attempt
Wildebeest	98	14 (14·3%)	46 (46·9%)	38 (38·8%)
Zebra	140	15 (10·7%)	94 (67·2%)	31 (22·1%)

Kills vs. Failures + No attempts/wildebeest vs. zebra: $\chi^2 = 0·687$; df = 1; $P > 0·05$.

Orshol's (1981) weighting factor, this equates to 8757 lion-hours. An additional 783 h of short-term continuous observations were made.

Wildebeest and zebra made up 13·5% and 14·4% respectively of the 111 kills observed during continuous observations (Table 3). During the 8757 long-term lion-hour observations seven wildebeest and eight zebra were killed, giving a kill rate of seven wildebeest and eight zebra per killing lion year^{-1}.

Once encountered there was no significant difference in the likelihood of wildebeest or zebra being killed by lions (Table 4). Neither was there a significant difference in seasonality of kills (Table 5), nor in the frequency with which adult males and females were caught, when the frequencies with which they occurred in the population are considered (Table 6.) For wildebeest there was no difference in the frequency with which adults and juveniles were killed and the observed population age structure. There was for zebra, where lions took mainly juveniles (Table 6).

THE MODELS

Model 1

The initializing and fixed population parameters used in the models are given in Table 7. The most stable wildebeest population (SI = 0·012) was attained with 7·7 killing lions (Table 8). Although the SI is calculated only from the total population size, the survival rates of all sex- and age-classes were consistent for all 5 years (Appendix 1). This concurs with the consistent age structure of the population observed throughout the study. The most stable winter zebra population (SI = −0·006) could support 6·8 killing lions (Table 8, Appendix 2). The most stable summer zebra population (SI = −0·009) could support 19·4 killing lions (Table 8, Appendix 3).

Manipulation of parameters

Manipulation of the various population parameters

Table 5. Number of wildebeest and zebra killed by lions during summer (October–March) and winter (April–September), with number of hours (h) lions were observed during each season

	Summer 1607 h	Winter 1303 h	Summer vs. winter
Wildebeest	10	5	$\chi^2 = 0·779$ df = 1 $P > 0·05$
Zebra	11	5	$\chi^2 = 0·641$ df = 1 $P > 0·05$

Table 7. Initializing and fixed population parameters used in models

Parameters	Wildebeest	Zebra
Initializing		
$\overline{X}$ population size	222	220 (winter) 626 (summer)
% juveniles	29	25
% yearlings	14	13
% adults	57	62
male:female	1:1·34	1:1·33
yearling:adult female	0·41:1	0·32:1
Fixed		
% adult fecundity	92	79
% 2-year fecundity	92	25
% yearling fecundity	34	0
kill rate (year^{-1})	7	8

Table 6. Population and lion-kill sex and age ratios for wildebeest and zebra. The sex ratio kill data are from all lion kills found during the study, the age structure of kills are only from those made during direct observations

	Wildebeest				Zebra			
	Juvenile	Adult	Male	Female	Juvenile	Adult	Male	Female
Kills	2(13%)	13(87%)	10(48%)	11(52%)	10(63%)	6(37%)	5(36%)	9(64%)
Population*	21%	79%	40·3%	59·7%	16%	84%	40·8%	59·2%
	$\chi^2 = 0·519$; df = 1; $P > 0·05$		$\chi^2 = 0·459$; df = 1; $P > 0·05$		$\chi^2 = 24·89$; df = 1; $P < 0·001$		$\chi^2 = 0·151$; df = 1; $P > 0·05$	

* From D. Mason (unpublished data).

Table 8. The number of killing lions required to stabilize wildebeest and zebra populations with model 1 and model 2 parameters

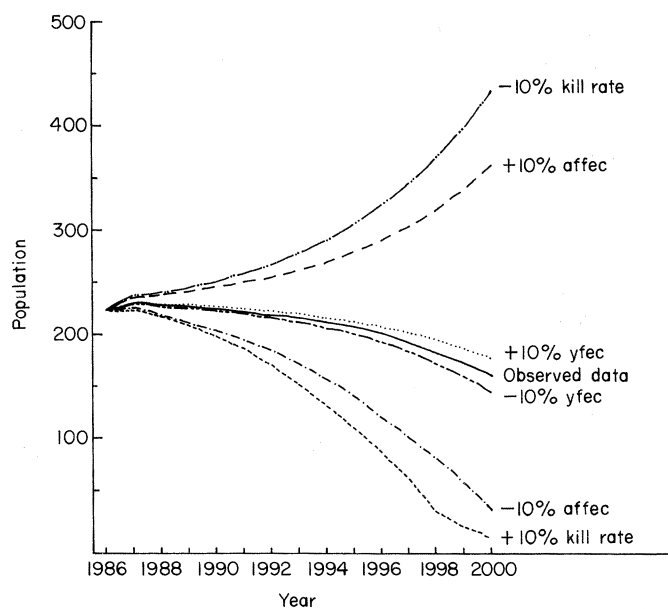| Model	Number of lions
Wildebeest as observed: model 1	7·7
Wildebeest with kill structure biased towards calves: model 2	10·7
Zebra (winter population) as observed: model 1	6·8
Zebra (winter population) with unbiased kill structure: model 2	5·4
Zebra (summer population) as observed: model 1	19·4
Zebra (summer population) with unbiased kill structure: model 2	15·1

Fig. 1. The effects of parameter manipulation on the wildebeest model 1 population.

in model 1 by increasing and decreasing the values by 10% indicated kill rate as the parameter which had the greatest effect on population size, followed by adult fecundity rate (Fig. 1).

Model 2

When the zebra kill age structure was substituted into the wildebeest model 1, and vice versa for the zebra model 1, the wildebeest population could support more killing lions and the zebra population less (Table 8).

Discussion

Studies that have most convincingly measured the effect of large mammalian predators on their prey have been experimental. Predators have been culled in one area and prey number compared with a neighbouring area where no predators were culled (e.g. Smuts 1978b; Whyte 1985 with lions; Gasaway

et al. 1983; Skoog 1983 with wolves). It was not possible to do this in our study, so our approach was to construct simulation models based on intensive observations.

Considerable effort was invested in measuring kill rate. This is a sensitive parameter in the population dynamics of the prey (Fig. 1). Even a 10% change can have a marked influence on a prey population. Accurate calculations of kill rate are notoriously difficult to obtain in areas where it is not possible to follow tracks for extended periods, such as in the snow (Mech 1970), or sand (Eloff 1973). To overcome this we followed lions continuously for periods of up to 336 h, i.e. 14 days.

Even then, there may be several factors which affect kill rate: (i) seasonality (Schaller 1972; Van Orsdel 1982), although in the present study this was not the case (Table 5): (ii) fluctuation of events during repetitions, such as multiple kills (Schaller 1972), (iii) variables that are difficult to control, e.g. predator and prey group size, hunting tech-

nique, bush cover and lunar phase (Van Orsdol 1984; Stander & Albon, in press); and (iv) even random events such as prey encounters in favourable positions for hunting.

In the long term, kill rate may also vary by more than 10% due to changes in ecological conditions. The rapid decline in wildebeest and zebra numbers in the central district of the KNP documented by Smuts (1978a,b), may have been due to high levels of predation. The present study suggests that under more stable ecological conditions predation has a different effect on their populations.

Adult female fecundity is almost as sensitive a parameter in the population dynamics of the prey as is kill rate (Fig. 1). However, this parameter fluctuates little in both populations (Braack 1973; Smuts 1976), and may not be important in practice. In other species in the KNP, e.g. kudu, fecundity was found to drop during drought periods (Owen-Smith 1990).

Model 1 shows that predation affected wildebeest and zebra populations in the study area differently, not because one species was more vulnerable than the other (Table 4), but because of the way lions selected their prey, and the sedentary or migratory behaviour of the prey.

No selection for wildebeest calves could be shown and adult males and females were taken in proportion to their presence in the population. Model 1 suggests that under the observed killing rate for wildebeest, 7·7 killing lions were needed to stabilize this sedentary population. There were at least 5·9 residents from the V and M prides. The kills made by lions from peripheral prides, pride males and nomads moves the number of killing lions closer to 7·7. In addition, the wildebeest population remained stable during the 4-year study period. We conclude, therefore, that lion predation was the main adult mortality factor in the wildebeest population.

We were unable to document the causes of wildebeest calf mortality, mainly because of the low numbers of wildebeest in the study area. They may have been preyed upon at a relatively low intensity by both lions and spotted hyaenas.

In contrast to the wildebeest, zebra predation was selective in that foals were taken more often than expected, whereas adults were killed less often. Using the same methods, Stander (in press) also found a selection by lions for zebra foals, but not for wildebeest calves in Etosha National Park, Namibia. The zebra winter model 1 suggests that the zebra population of numbers comparable to the wildebeest population can support a similar number of lions (6·8) as can the wildebeest population (7·7), even though the fecundity rate of zebra is somewhat lower than that for wildebeest (Table 7). However, if predation was non-selective, the winter zebra population would only remain stable with 5·4 killing lions (Table 8). Predation aimed at young animals

has less impact on population than predation aimed at adults, other things being equal.

Although zebra numbers in the study area were greater during summer than winter, the zebra predation rate did not increase (Table 5). The summer zebra model 1 predicts that 19·4 killing lions are needed to stabilize the population. This is more than were present in the study area, although there may have been an increase in the lion population in summer through nomads entering the study area. The fact that a proportion of the zebra population in the study area is migratory means that for part of the year the prey available to lions is diminished. This may limit the number of lions. When the migrants return to the study area predation pressure is comparatively low. These data support the hypothesis of Fryxell, Greever & Sinclair (1988) that predators can regulate resident herbivores at low population densities, whereas such regulation is rare for migratory herds.

The models presented here are simple but suggest important differences in the impact of predation on wildebeest and zebra. Further manipulation of the data and the construction of more refined models may help to clarify these relationships further.

Different ecological conditions may have different affects on prey populations. During droughts survival rates may drop (Owen-Smith 1990), and during years of high rainfall the kill rate may increase (Smuts 1978a). Changes in the availability of alternative prey may also affect the kill rate. For example, buffalo numbers in the study area are increasing, due to the cessation of culling (I. Whyte, unpublished data). This may lead to an increase in lion predation on buffalo, with a reduction of predation on wildebeest or zebra. Alternatively, it may lead to an increase in the lion population, with no change in predation pressure on the other two species. Continued research in the study area will lead to a better understanding of predator–prey relationships.

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Appendix 1

WILDEBEEST MODEL I

Population results

YEAR	JUV	YRL	ADFEM	ADMAL	TOTAL	AFSurv	AMSurv	YSurv	JSurv	J/100F	Y/100F	%AF
1986	64	32	78	48	222	0·72	0·55	0·90	0·65	68	41	61
1987	72	42	71	41	225	0·70	0·47	0·92	0·65	78	58	63
1988	71	47	68	38	225	0·69	0·44	0·93	0·65	77	68	64
1989	71	46	69	39	225	0·69	0·44	0·93	0·65	77	67	63
1990	71	46	69	39	224	0·69	0·44	0·93	0·65	77	67	63

Appendix 2

ZEBRA MODEL I: WINTER

Population results

YEAR	JUV	YRL	2–3YR	ADFEM	ADMAL	TOTAL	AFSurv	AMSurv	YSurv	JSurv	J/100F	Y/100F	%AF
1986	56	28	20	67	49	220	0·87	0·83	0·87	0·39	84	42	58
1987	56	22	25	67	49	219	0·87	0·83	0·87	0·39	84	33	58
1988	57	22	19	70	50	218	0·87	0·83	0·85	0·40	83	32	58
1989	57	23	19	69	50	219	0·87	0·83	0·85	0·41	83	34	58
1990	57	23	20	69	49	219	0·87	0·83	0·85	0·41	83	34	58

Appendix 3

ZEBRA MODEL I: SUMMER

Population results

YEAR	JUV	YRL	2–3YR	ADFEM	ADMAL	TOTAL	AFSurv	AMSurv	YSurv	JSurv	J/100F	Y/100F	%AF
1986	160	80	58	190	138	626	0·87	0·82	0·88	0·39	84	42	58
1987	160	63	70	191	138	622	0·87	0·82	0·88	0·39	84	33	58
1988	163	63	53	198	142	620	0·87	0·82	0·85	0·39	83	32	58
1989	163	66	54	197	140	620	0·88	0·83	0·85	0·41	83	34	58
1990	163	66	57	196	138	619	0·88	0·83	0·85	0·40	83	34	59