PREDATION ON LARGE MAMMALS IN THE KAFUE NATIONAL PARK, ZAMBIA

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INTRODUCTION

Faunal areas in Zambia may be managed with a variety of aims in view. Whether the object is to produce a maximum yield in a game cropping area, to eliminate tsetse fly or to produce a wild life spectacle in a National Park it is necessary to understand the role of the predators which are present. It is not possible to decide whether or not they are beneficial to the immediate project or whether some control is necessary without adequate information concerning their food and feeding habits.

This paper is a summary based on information collected on nearly 650 kills in the Kafue National Park. It concerns primarily predation on ungulates by the major carnivores but a few records of other groups are included. The picture, at this stage, is far from complete but sufficient information has been collected to allow an assessment of the present state of our knowledge and to guide future research.

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THE STUDY AREA

The Kafue National Park has provided the bulk of the material on which this paper is based. Smaller quantities have come from the two adjoining Controlled Hunting Areas, the Mumbwa West and the Sichifula. The park itself covers 8,600 square miles whilst the total study area is in the region of 11,000 square miles. The park and the former Controlled area lie entirely within the basin of the Kafue river with the watershed separating Zambia from Barotseland as the western boundary. South of the park the Sichifula controlled area spreads westwards into the Zambesi basin.

The Kafue River has cut its bed down into the underlying granite rock so that the bulk of the area lying within the Mumbwa and North Namwala districts is on sandy granite soils. The granite was overlain by Karoo sediments and these, in turn, by Kalahari sands. The Karoo outcrops in the Musa-Nkala interfluve whilst the bulk of South Namwala, as well as the entire

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western boundary of the Park is covered with Kalahari sand. In the Kasempa district geological formations of the Katanga system, again mostly sandstones, are present. The remarkable Busanga plain of some three hundred square miles is formed by the flood plain of the Lufupa river before it reforms into a normal incised channel.

The great bulk of the above areas carry woodlands of the *Brachystegia-Julbernardia* complex with characteristic open drainage lines carrying grass savannas with aquatic grasslands in the wetter patches. The Busanga plain and strips of flood plains along all the major rivers support well developed aquatic grasslands.

In the south the valleys of the Nanzhila and of the Siamatanga which drains the Sichifula controlled area are characterised by a waterlogged clay soil which supports a savanna woodland of *Colophospermum mopane*.

THE COLLECTION OF INFORMATION

The study of predation became a major project in the Park after mid 1960 following a series of general reports which had been submitted since 1958. The majority of the 649 records of individual kills on which this report is based were made between 1st June, 1960 and 31st May, 1963 covering a period of three complete years. The entire staff of the Park were concerned with the collection of field data.

When a kill was located the skull was collected where possible but, from remote areas, often only the lower jaws were retained. The specimens were labelled for locality, date and predator. Only fresh kills were recorded; predators of older kills could not be identified. Where possible a condition rating was made on the femur marrow of the kill, as described by Riney (1954).

The age of prey specimens was determined by examination of the teeth. The younger age groups are characterised by the state of the eruption of the molars and the replacement of deciduous milk teeth by permanent adult teeth. The dental replacement of the duiker *Sylvicapra grimmia* has been worked out by Riney and Child (1960). Child has worked out the impala *Aepyceros melampus* and the warthog *Phacochaerus aethiopicus*. Robinette has studied lechwe *Kobus leche* and Mitchell hartebeest *Alcelaphus lichtensteini*. Buffalo *Syncerus caffer* have not yet been studied but ageing has been grouped somewhat arbitrarily according to the dental replacement of ranch cattle as given by Miller and Robertson (1937).

The following categories have been used.

(1) Calf, lamb, foal or piglet less than 12 months old.
(2) Yearling.
(3) Two year old. This group cannot be recognised in smaller species.
(4) Young prime. Full permanent dentition but teeth having only light wear.
(5) Prime. Full permanent dentition with medium wear.
(6) Past prime. Old animal with teeth showing heavy wear.

The skulls were subsequently deposited with the Rhodes-Livingstone Museum or the National Museum, Bulawayo.

The predator in each case was identified either by being found in possession or alterna-

tively by recent tracks. It is, of course, not always certain that the predator found feeding on the dead animal had killed it. Some animals, hippo *Hippopotamus amphibius* in particular, die as a result of intraspecific fighting and both lions and leopards will take carrion. This source of error is believed to be small in the overall picture which emerged from the present study. Other errors may have arisen where identification was by tracks only. In particular, it is difficult to distinguish between the tracks of leopard and cheetah, especially if they are a day or two old and if the surroundings have been flattened by vultures. But again such errors were probably few.

The striking fluctuation of monthly kills by all predators (Table 1) was due to differences in our ability to locate them at different times of the year. This was easiest in the dry season after fires when not only was visibility better, but Park staff were able to cover greater areas than during the wet season when the grass was tall and most roads impassable. The movements of vultures are an important indicator of carcasses but we believe that when the woodland is in full foliage and the grass long, vultures also have difficulty in locating food. On 11 February, 1962 four lions killed a prime hartebeest male some ten miles south of Ngoma and it was almost completely consumed by the following afternoon. In spite of this on 22 February, eleven days later, several vultures were still sitting around the skeleton.

During July and August vultures will sometimes forsake a carcass within a few hours of the withdrawal of the lions and it is during these dry months that these birds are feeding their young. Benson (personal communication) says "Of the 68 egg-laying records of the Aegypiidae for the Rhodesias and Nyasaland all fall within the period April to August with a peak in June. I think one could reasonably assume that the period when the nestlings are making the greatest demand on their parents for food would be when they are three to four weeks old, as has been shown with eagles. This would be in the July-August period." Another obvious point is that the larger the prey the more conspicuous it is and the longer it will last and consequently the more vultures it will attract. Therefore the figures for the prey are likely to be loaded in favour of the bigger species.

We have divided the year into two six-month periods, June to November when some or

TABLE 1. NO. OF KILLS ALL SPECIES FOUND BY SEASONS

Predator	Wet Season Dec.–May	Dry Season June–November	Ratio Wet to Dry Season
Lion	160	250	1 : 1·56
Leopard	40	56	1 : 1·40
Cheetah	9	24	1 : 2·66
Wild dog	49	47	1 : 0·96
Crocodile	2	9	1 : 4·5
Eagle	1	2	1 : 2
Totals	261	388	1 : 1·49

TABLE 2. PREDATION: GRAND TOTALS FOR ALL SPECIES

Prey	Lion	Leopard	Cheetah	Wild Dog	Crocodile	Martial Eagle	Totals
Buffalo	125				1		126
Bushbuck	1	4	1	6			12
Bushpig	8						8
Duiker	1	11	1	25			38
Eland	12			1			13
Grysbuck		4				1	5
Hartebeest	67	9	3	15	2		96
Hippo	6						6
Impala	8	8	2	2			20
Kudu	4	3	1	4			12
Lechwe	2	3		1			6
Oribi		3	1	2		1	7
Puku	4	15	15	3	4		41
Reedbuck	8	19	4	24	1		56
Roan	23				2		25
Sable	21			4			25
Warthog	39	2	2			1	44
Waterbuck	24			2			26
Wildebeest	25	1	2	4			32
Zebra	30		1		1		32
Baboon		2					2
Vervet Monkey ..		3					3
Civet		1					1
Genet		1					1
Serval		1					1
Porcupine	2	1		1			4
Cane Rat		1					1
Spring Hare ..		2					2
Hare		1					1
Lion..				2			2
Catfish		1					1
Totals	410	96	33	96	11	3	649
No. of spp.	19	22	11	15	6	3	

all of the country is burnt and December to May when trees are in full foliage, the grass long and visibility correspondingly reduced. Our results are recorded in Table 1.

However, it is apparent that the actual figures presented here cannot be accepted without reservation. Existing facilities are inadequate to allow material to be collected by a random statistical sampling method, and the data must therefore be considered in the light of the above sources of error. A further limitation is that no figures are yet available to indicate the populations of any species or the total biomass present in the area.

Lion *Panthera leo*, leopard *P. pardus*, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus* and hyena *Crocuta crocuta* are all present in the area as actual or potential predators whilst the crocodile *Crocodilus niloticus* and martial eagle *Polomaetus bellicosus* also account for some ungulate deaths. Table 2 gives a list of all kills recorded and indicates the degree to which various prey species are used by the predators, showing where competition or complementary usage occurs.

PREDATION BY LION

A total of nineteen prey species have been recorded, buffalo being the most important. In the Kafue National Park there is a strong seasonal trend (Table 20) with more being killed during the dry season than during the rains. At present the explanation of this appears to be related to the complete change in the habitat caused by the bush fires in the dry season. When the grass is long and cover dense, hunting conditions for lions are apparently easy and they can satisfy themselves with easily killed species, warthog *Phacachaerus aethiopicus*, in particular. However, after burning many grazing species move out on to the plains to the new flush of grass and then lions find hunting more difficult and are forced to turn to buffalo which continue to spend much time in thicket and woodland country.

Hartebeest *Alcelaphus lichtensteini* are the next most important food species, others being roan *Hippotragus equinus*, Sable *H. niger*, waterbuck *Kobus defassa*, wildebeest *Connochaetes taurinus* and zebra *Equus burchelli*. Puku *Kobus vardoni* comprising only one per cent of total kills are unexpectedly low on the list considering that they are so numerous in many areas. All except the very smallest species of the Bovidae have been recorded as prey to lions.

TABLE 3. PREDATION BY LION BY MONTHS

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Buffalo	2	5	4	9	7	3	10	21	23	27	12	2	125
Bushbuck ..				1									1
Bushpig			2		1			4	1				8
Duiker			1										1
Eland			2	1		1	4	2	1			1	12
Hartebeest ..	1	10	1	2	7	6	12	4	7	11	3	3	67
Hippo							2		3	1			6
Impala			2			2	1		1	1	1		8
Kudu		1		1		1	1						4

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Lechwe									2				2
Puku			4										4
Reedbuck ..		1	2			1	1		1	1		1	8
Roan	1	1	2	1	6		5	1	2	2	2		23
Sable	2	3	4	3	2	1	1		1	2		2	21
Warthog ..	5		3	2	5	5	1	1	5	5	5	2	39
Waterbuck ..	1		4	3	3	3	2	1	2	4	1		24
Wildebeest ..	1	3		4	2	4	1	2		4	2	2	25
Zebra	2	6	1	2	1	7	4		1		1	5	30
Porcupine ..				1								1	2
Total 19 spp. ..	15	30	32	30	34	34	45	36	50	58	27	19	410

Table 3 records the manner in which lions distributed their predatory activities by months and Table 4 gives a summary of the size of recorded lion prides for a period of nearly six and a half years. One of us (J. C. M. Uys) with extensive knowledge of the area is certain that during recent years, there has been an influx of lions into the study area on account of excessive hunting pressure in areas surrounding the Park, although there are no actual figures to support this belief. This may be a real factor and might be a cause of the steady decrease in the size of litters of cubs from 1958 to 1963 as shown in the table.

TABLE 4. LION: SUMMARY OF PRIDE SIZE

Year	No. of Records	Average Males	Average Females	Sex Ratio	Average Litter	Average Pride	Maximum Pride
1957	4	1·5	1·0	1 : 0·66	3·3	5·0	7
1958	8	1·37	2·0	1 : 1·45	4·5	4·75	12
1959	35	0·86	2·4	1 : 2·87	3·4	5·14	15
1960	20	1·7	1·5	1 : 0·89	3·3	4·35	10
1961	25	1·2	2·12	1 : 2·83	2·57	4·0	10
1962	39	1·3	1·37	1 : 1·83	2·7	4·6	13
1963 .. .. .. To May 31	9	1·0	1·33	1 : 1·33	2·0	4·5	14

Overall Sex Ratio to 31 May 1963, 176 Males : 290 Females; mean sex ratio whole period 1 : 1·73.

PREDATION BY LEOPARD

With twenty-two recorded prey species this cat shows a very wide choice of food ranging from fish to hartebeest. Five full grown hartebeest and a past prime kudu *Tragelaphus strepsi-*

ceros are the largest recorded kills whilst reedbuck *Redunca arundinum*, puku, duiker and impala have been taken in the largest numbers. There is no evidence of any seasonal differences in the species taken.

TABLE 5. PREDATION BY LEOPARD BY MONTHS

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Bushbuck ..					1	1		1			1		4
Duiker	1	2	2		1	1			2	1	1		11
Grysbuck ..		1			2						1		4
Hartebeest ..	1	1	1				1	1	2	1	1		9
Impala		1	1	3		2				1			8
Kudu		1					1			1			3
Lechwe									1		1	1	3
Oribi							2					1	3
Puku				1	1	5	2		2	2	2		15
Reedbuck ..		1	2	2	1	2	1	3	2	2	2	1	19
Warthog								1		1			2
Wildebeest ..								1					1
Baboon				1	1								2
Vervet Monkey ..			1			1		1					3
Civet		1											1
Genet		1											1
Serval				1									1
Porcupine ..						1							1
Cane Rat ..										1			1
Spring Hare ..	1	1											2
Hare					1								1
Catfish						1							1
Total 22 spp. ..	3	10	7	8	8	14	7	8	9	10	9	3	96

It is known that, on occasions, both lions and leopards consume enormous quantities of meat but information is never complete. It may be recorded that two lions killed a hartebeest weighing some 300 lb. and consumed it in twenty-four hours but there is no evidence as to how long they had been without food nor is it certain that other lions were not present during the night. Reliable evidence on this subject is not easy to obtain. However some information is available. The Livingstone Game Park is exactly one square mile in extent and contained at the time about one hundred and eighty-five individuals of seventeen species, the majority being animals which we have recorded as being important leopard prey. Some 70 head were duiker, reedbuck or bushbuck.

On the night of 10 February 1963 a wild leopard came in over the fence and remained within the Park until it was shot 20 days later. During that period it killed and ate two reedbuck females weighing approximately 130 lb. each, a young bushpig *Potamochaerus porcus* weighing some 25 lb. and a female duiker of say 32 lb. (Robinette 1963). A twenty-two month old kudu male was also killed but was found and removed before being eaten. The total weight of the animals eaten would be in the order of 317 lb. which would "dress" down to approximately 160 lb. of edible meat. Thus the leopard must have been feeding at the rate of over 50 lb. of meat per week.

The record of a catfish *Clarius* sp. being taken by a leopard may refer to a particular animal which was liberated in the Kafue National Park after having been rescued on one of the temporary islands in the Kariba lake. When trapped on the island it was apparently entirely on a diet of fish to which it had become adapted living under unusual conditions. This again points to the high adaptability of the leopard, as is reflected in the extent of its distribution not only geographically but also in the wide range of habitats in which it occurs.

PREDATION BY CHEETAH

Only 11 prey species are recorded for cheetah though doubtless this figure will be increased when more data are accumulated. Puku comprise 45·4 per cent of all kills, whilst the figure for reedbuck is surprisingly small. Cheetah do not venture on to extensive open plains but occupy savanna woodlands, tree savannas and smaller grasslands.

TABLE 6. PREDATION BY CHEETAH BY MONTHS

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Bushbuck					1								1
Duiker					1								1
Hartebeest ..		1								1	1		3
Impala										1		1	2
Kudu					1								1
Oribi									1				1
Puku			1			1	7		2	1	1	2	15
Reedbuck ..			1			2	1						4
Warthog				1					1				2
Wildebeest ..									2				2
Zebra										1			1
Total 11 spp. ..	—	1	2	1	3	3	8	—	6	4	2	3	33

PREDATION BY WILD DOG

Fifteen prey species have been recorded. All the smaller Bovidae are doubtless taken as well as calves of many of the larger species. Common duiker comprise 26 per cent of recorded kills,

reedbuck 25 per cent and hartebeest 15·6 per cent. There is no evidence of a seasonal difference as far as duiker are concerned but there is possibly an increase in predation on reedbuck during the dry season. The reedbuck habitat is largely wet during the rainy season and this may afford this species temporary protection. The fact that wild dog are strictly seasonal breeders, dropping their pups early in the dry season, suggests that for this predator hunting is easier at that time of the year. There are two cases on record of wild dogs killing and eating old lionesses.

TABLE 7. PREDATION BY WILD DOG BY MONTHS

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Bushbuck ..	1		1			1		1	2				6
Duiker	2	3	2	2	1	3	2	1		5	1	3	25
Eland			1										1
Hartebeest ..	3	1	3	1				1		2	3	1	15
Impala	1		1										2
Kudu	1	1							1			1	4
Lechwe												1	1
Oribi		2											2
Puku							2		1				3
Reedbuck ..	4		1				1	2	1	6	5	4	24
Sable										1	3		4
Waterbuck ..					1					1			2
Wildebeest ..		1		1						2			4
Porcupine ..					1								1
Lion	1			1									2
Total 15 spp. ..	13	8	9	5	3	4	5	5	5	17	12	10	96

PREDATION BY HYAENA

Hyaena are not common in the area although they are somewhat more numerous in the north. No definite instances of ungulates being killed by this species are on record. It is possible that the hyaena could become an important predator if the general condition of the antelope population was severely lowered due to some adverse factor such as overcrowding, drought or disease but this does not apply in the Kafue National Park at the present time.

PREDATION BY CROCODILE

Six species only have been recorded as being killed by crocodiles but this figure must be affected by the difficulty of locating kills in the rivers and the short time they are available. Other than lion, crocodile is the only predator recorded as taking buffalo. The sample of kills is small but puku head the list. It is likely also that lechwe on the Busanga are also taken.

PREDATION BY MARTIAL EAGLE

Three records only are vailable all referring to small juveniles of grysbuck *Raphicerus sharpei*, oribi *Ourebia ourebia* and warthog.

SEX RATIO OF PREY SPECIES

Tables 8 and 9 give the details of the numbers of animals of each sex which have fallen victim to the various predators. Except in the case of cheetah the predators have all taken a greater number of males than females.

TABLE 8. SEX RATIO OF PREY SPECIES

	Lion		Leopard		Cheetah		Wild Dog		Crocodile		Eagle		Ratio	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Buffalo ..	56	36							1				1 : 0·63	
Bushbuck ..			1	1	1		4	2						
Bushpig ..	3													
Duiker ..			5	2		2	9	7						
Eland ..	5	5						1						
Grysbuck ..			2	2								1		
Hartebeest ..	31	26	2	3	1	2	7	4		1			1 : 0·88	
Hippo ..	2													
Impala ..	5	1	5	3	1	1	1	1						
Kudu ..	2	2	3			1	2	2						
Lechwe ..	2		1	2			1							
Oribi ..			1	1		1	1	1						
Puku ..	2	2	7	8	5	9	2	1	2	2			1 : 1·22	
Reedbuck ..	5	2	6	7		1	8	11	1				1 : 0·05	
Roan ..	10	6												
Sable ..	6	8					1	1						
Warthog ..	24	7	1			1							1 : 0·32	
Waterbuck	8	9					1							
Wildebeest	5	7												
Zebra ..	3	18												
Lion ..								2						
Others ..			2	3										
Totals ..	169	129	36	32	8	18	37	33	4	3		1		
Sex Ratios	1 : 0·76		1 : 0·88		1 : 2·25		1 : 0·89							

Overall Sex Ratio of prey is 1 : 0·84.

TABLE 9. SUMMARY OF SEX RATIOS OF PREY

Predator	Sex of Prey: Males Total	Males %	Females Total	Females %
Lion, Leopard, Wild dog and Crocodile ..	246	55·5	197	44·5
Cheetah only	8	30·8	17	69·1
Total	254	54·3	214	45·7

This excess of males is likely to be due to the fact that females, especially those accompanied by a juvenile, are considerably more alert than the opposite sex particularly if the males are solitary or in small parties. The result of the excess mortality of males will be reflected in the sex ratios of the herbivores.

CLASSIFICATION OF PREY BY AGE GROUPS

Tables 10, 11, 12 and 13 classify the prey by age groups of lion, leopard, cheetah and wild dog.

TABLE 10. CLASSIFICATION OF PREY BY AGE GROUPS: LION

Age Group	1	2	3	4	5	6	Total
Buffalo	12	4		13	21	11	61
Bushbuck						1	1
Bushpig	2	3				1	6
Eland	1			1	1	2	5
Hartebeest	7	8	2	14	12	8	51
Hippo	5						5
Impala	2			2			4
Kudu					1	1	2
Lechwe				1			1
Puku	1					1	2
Reedbuck					1		1
Roan	4			5	1	7	17
Sable	4	1	1	3	5	2	16
Warthog	6	3	3	2	7	2	23
Waterbuck	4			4	2	3	13
Wildebeest	4	1	1	1	7	3	17
Zebra	8	—	1	2	10	6	27
Totals	60	20	8	48	68	48	252

TABLE 11. CLASSIFICATION OF PREY BY AGE GROUPS: LEOPARD

Age Group	1	2	3	4	5	6	Total
Bushbuck				1	2		3
Duiker	4	1		1	4		10
Grysbuck	1			2	1		4
Hartebeest	4			3	1	1	9
Impala	1	2		1	1	2	7
Kudu	1	1				1	3
Lechwe				1			1
Oribi	1				1		2
Puku	1	3		3	3	2	12
Reedbuck	5	1		2	1	1	10
Warthog	2						2
Wildebeest	1						1
Totals	21	8		14	14	7	64

TABLE 12. CLASSIFICATION OF PREY BY AGE GROUPS: CHEETAH

Age Group	1	2	3	4	5	6	Total
Bushbuck				1			1
Hartebeest	1				1	1	3
Impala		1					1
Kudu				1			1
Oribi	1						1
Puku	2	2		5	1	2	12
Reedbuck	1	1			1		3
Warthog	1				1		2
Wildebeest	1						1
Zebra	1						1
Totals	8	4		7	4	3	26

TABLE 13. CLASSIFICATION OF PREY BY AGE GROUPS: WILD DOG

Age Group	1	2	3	4	5	6	Total
Bushbuck				3	1		4
Duiker	6	3		6		1	16
Eland	1						1
Hartebeest	5	4	1		1	3	14
Kudu	1			2		1	4
Lechwe		1					1
Oribi				1			1
Lion						2	2
Puku				2	1		3
Reedbuck	8	3		4	2		17
Sable	2				1	1	4
Waterbuck	1			1			2
Wildebeest	2						2
Totals	26	11	1	19	6	8	17

Table 14 is a summary of the age grouping of the prey of all species expressed as a percentage of the total.

TABLE 14. CLASSIFICATION OF PREY: SUMMARY OF ALL SPECIES

Age Group	1	2	3	4	5	6	Total %
Predator							
Lion	23·8	8·0	3·2	19·1	27·0	19·1	100·2
Leopard	32·9	12·5	0·0	21·9	21·9	10·9	100·1
Cheetah	30·8	15·4	0·0	26·9	15·4	11·5	100·0
Wild Dog	36·6	15·5	1·4	26·8	8·5	11·3	100·1
Mean	27·9	10·4	2·2	21·3	22·3	16·0	100·1

Predation is shown to be heavy on the juvenile group, is reduced on yearlings whilst the sub-adult group is hardly taken at all. This is doubtless due to the vigour and alertness of this age group. The young prime and prime groups are used equally whilst the figures drop off for the past prime animals, suggesting that predation in the area is so heavy that few animals are given the opportunity to reach old age. It will be noticed that whilst with leopard, cheetah and wild dog the age groups taken are remarkably uniform, lion have definitely taken fewer juveniles but have concentrated on prime animals.

CLASSIFICATION OF PREY BY CONDITION

Tables 15, 16, 17 and 18 classify by condition the prey of lion, leopard, cheetah and wild dog respectively. Condition was in many instances assessed from the state of the marrow in the femur. It is not often that a carcass is found sufficiently freshly killed to obtain an estimate of condition based on the quantity of body fat. The marrow test operates only at the lower end of the condition scale and therefore does not give a very sensitive picture.

TABLE 15. CLASSIFICATION OF PREY BY CONDITION: LION

Condition	Good	Fair	Poor	Total
Buffalo	6	4	9	19
Eland	3			3
Hartebeest	10	1		11
Lechwe	1			1
Roan	4			4
Sable	5			5
Waterbuck	4	2	1	7
Wildebeest	3			3
Zebra	2	1	1	4
Total	38	8	11	57

TABLE 16. CLASSIFICATION OF PREY BY CONDITION: LEOPARD

Condition	Good	Fair	Poor	Total
Duiker	3	1		4
Hartebeest			1	1
Kudu	1	1		2
Oribi	2	1		3
Puku	3			3
Reedbuck	5	2		7
Warthog	1			1
Total	15	5	1	21

TABLE 17. CLASSIFICATION OF PREY BY CONDITION: CHEETAH

Condition	Good	Fair	Poor	Total
Bushbuck	1			1
Hartebeest			1	1
Impala		1		1
Puku	5	1		6
Total	6	2	1	9

TABLE 18. CLASSIFICATION OF PREY BY CONDITION: WILD DOG

Condition	Good	Fair	Poor	Total
Bushbuck	1			1
Duiker	4	1		5
Eland	1			1
Hartebeest	1			1
Impala		1		1
Kudu	4			4
Lechwe	1			1
Puku	1		1	2
Reedbuck	5			5
Total	18	2	1	21

Table 19 is a summary of the condition of the prey of all species expressed as a percentage of the total.

TABLE 19

Condition	Good	Fair	Poor	Total %
Predator				
Lion	66·7	14·0	19·3	100·0
Leopard	71·5	23·8	4·8	100·1
Cheetah	66·6	22·2	11·1	99·9
Wild dog	85·8	9·5	4·8	100·1
Mean	71·3	15·8	13·0	100·1

The proportion of prey in good condition is high for all species, lion killing a higher proportion of poor condition animals than any of the other predators. These poor condition animals are almost all buffalo. It is considered that the good condition of the prey as a whole must again reflect the general condition of the herbivores in the area which, indeed, do maintain reasonable condition throughout the year. This again may be another indication of the heavy predation which is in operation.

PREDATION ON BUFFALO

Apart from an old bull taken by a crocodile the only recorded predators of buffalo were lion. More buffalo kills (126) than for any other species were recorded. This is partly due to the numbers present but the figure is weighted by the fact that being the largest prey species, with the exception of hippo, the location of kills is easier than for the smaller species.

Buffalo comprised 18·1 per cent of all recorded lion kills during the wet season as compared to 38·4 per cent of kills located during the dry season. As already mentioned we believe that it is easier for lions to obtain other food during the rains when there is plenty of cover than after the grass is burnt.

There is one record of an old lioness being killed by buffalo and two records of a buffalo pulled down by lions being abandoned when charged by the herd. Attwell has reported three buffalo bulls routing two lions which were stalking the herd. There is no doubt that buffalo are dangerous for lions to hunt but lions apparently favour buffalo as prey for they persistently follow the buffalo herds. It would appear therefore that if cover is plentiful lions may content themselves with easier prey, warthog in particular, but that after the grass fires have been through the country many herds of antelope move out on to the open plains for the fresh green nibble. In the absence of adequate cover, hunting of these species becomes much more difficult so that lions are forced to take more buffalo.

TABLE 20. PREDATION BY LION ON BUFFALO

Sex	Calf	Yearling	Two years	Young prime	Prime	Past prime	N.D.	Total
Male		1		5	9	3	36	56
Female	3	2		6	5	5	17	36
N.D.	9	1		2	7	3	11	33
Total	12	4		13	21	11	64	125

Sex	Condition Good	Condition Fair	Condition Poor	Total
Male	2	2	5	9
Female	4	1	2	7
N.D.		1	2	3
Total	6	4	9	19

CALENDAR MONTHS

Sex	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Male				4	5	3	5	9	14	12	4		56
Female	2	3		4	1		3	7	4	7	5		36
N.D.		2	4	1	1		2	5	5	8	3	2	33
Total ..	2	5	4	9	7	3	10	21	23	27	12	2	125

Sex	Wet Season December–May	Dry Season June–November	Total
Male	9	47	56
Female	10	26	36
N.D.	10	23	33
Total	29	96	125

When a large herd of buffalo is grazing, the animals in the lead are mainly cows and younger animals whilst a bunch of bulls normally brings up the rear. Single bulls and small parties of old males frequently lag behind the main herd. It is possibly as a result of this formation that males comprise such a high proportion of the kill. A higher proportion of buffalo attain past prime condition than in any other prey species. This must mean that the average life span is comparatively greater than for the others and reflects the difficulty of hunting due to the strength and ferocity of the animal.

PREDATION ON HARTEBEEST

Of ninety-six recorded kills lions were responsible for 67 (69·8 per cent), wild dogs for 15 (15·6 per cent), leopard for nine (9·4 per cent). Cheetah and crocodile also attack this species.

Thus with five recorded predator species, hartebeest ranks as one of the most important food animals in the area. There is a difference in the age groups taken by the primary predators, wild dog concentrating on juveniles and past prime animals whilst lion concentrate on the mature groups. There are two records suggesting that female hartebeest had been killed by lions whilst in the act of parturition.

Unlike wildebeest, hartebeest will not stand up to wild dogs and the herd will scatter at the approach of a pack so that the calves become an easy prey. On one occasion a hartebeest, being pursued by wild dogs, took refuge amongst a herd of wildebeest. The latter packed together whilst single bulls chased the wild dogs and kept them at bay. The wildebeest tried unsuccessfully to evict the intruder but the hartebeest refused to leave. After about a quarter of an hour the wild dogs gave up and departed.

TABLE 21. PREDATION BY LION ON HARTEBEEST

Sex	Calf	Yearling	Two Years	Young Prime	Prime	Past Prime	N.D.	Total
Male	2	4		7	7	2	9	31
Female	2	4		6	4	6	4	26
N.D.	3		2	1	1		3	10
Total	7	8	2	14	12	8	16	67

Sex	Condition Good	Condition Fair	Condition Poor	Total
Male	8	1		9
Female	2			2
N.D.				
Total	10	1		11

CALENDAR MONTHS

Sex	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
Male	1	5	1		5	4	2		2	7	3	1	31
Female		1		1	2	2	7	3	5	3		2	26
N.D.		4		1			3	1		1			10
Total ..	1	10	1	2	7	6	12	4	7	11	3	3	67

Sex	Wet Season December–May	Dry Season June–November	Total
Male	13	18	31
Female	6	20	26
N.D.	5	5	10
Total	24	43	67

PREDATION ON REEDBUCK

A total of fifty-six reedbuck kills are on record, again with five predators involved. Reedbuck also rank as one of the important food animals. Wild dog and leopard are the main enemies but they have also been taken by lion, cheetah and crocodile. Examination of Tables 10 to 13 show that nineteen reedbuck have been killed in age groups 1 and 2 against only sixteen in the adult age groups, only one past prime occurring. Predation on this species must be very heavy indeed and the population turn-over very rapid.

There is one record of a reedbuck outrunning a pack of wild dogs after a two-and-a-half mile chase as well as two records of this species escaping by taking sanctuary in water. Three reedbuck were once observed standing in some bushes at the edge of a flood plain. Three wild dogs suddenly appeared running in to locate the reedbuck of whose presence they were obviously aware. The antelope stood fast until the dogs were within about 12 or 15 yards of them when a young male broke and ran followed by the pack. It was interesting to see the other two buck remain standing firm although the dogs were within a very few yards of them. The dogs were two hundred yards away before they became aware of the presence of the observer and moved off.

PREDATION ON PUKU

Puku with forty-one recorded kills is another species used by five predators. In spite of the scarcity of cheetah in the Kafue National Park and the general abundance of puku we have as many records of puku killed by *Acinonyx* as by leopard and puku comprise more than 50 per cent of all recorded cheetah kills. Apart from puku being a suitable size both prey and predator occur in similar habitat. Correlated with their good eyesight and speed cheetah occur most commonly on open grasslands and tree savanna. The typical puku habitat is the alluvial flood plain of a permanent river which supports a fertile aquatic grassland bordered on one side by savanna woodland and usually on the other by a strip of riparian forest. It is this gallery forest which harbours the other main predator, the leopard. Our figures do not show any differences in age groups taken by these two cats.

The number of kills made by lions is remarkably small as is also the number made by wild dogs. This is doubtless due to the proximity of permanent water in which puku run for protection. The sanctuary of the river may, however, have its own hazards. Game Guards have reported seeing a puku hard pressed by wild dogs take to the water only to be killed by a crocodile. On another occasion Game Guards witnessed two puku rams fighting. Their skirmishing took them into shallow water where one was seized in the back leg by a crocodile. It immediately started to bleat loudly. The other ram, encouraged by the cries of his adversary, charged him with such vigour that the startled crocodile let go and the puku escaped.

Owing to the slender chances of locating crocodile kills, it is likely that predation on puku by this reptile is considerably higher than indicated by our records.

PREDATION ON WARTHOG

Of the forty-four recorded kills, only five have been made by a predator other than lion. Two juveniles have been taken by leopard, a piglet and one adult by cheetah and a tiny suckling by martial eagle. The condition of the adult taken by the cheetah was not recorded. In spite of its relatively small size the warthog is evidently too formidable to be tackled freely by any of the smaller predators. On account of the comparatively small size of the carcass as compared to buffalo and the consequent difficulty in the location of kills it is probable that warthog is an even more important food animal for lion than is suggested by the figures. All age groups are taken. During the rainy season, when the ground is soft, lions sometimes dig them out of their burrows.

DISCUSSION

The two main factors determining whether a predator will kill a particular prey species appear to be opportunity and physical possibility. Opportunity involves sharing the same habitat and possibly being active at the same period during day and night. Relative size must be the main factor determining the possibility of killing any particular animal, and must certainly prevent the adults of the larger prey species being taken by predators other than lion. Without estimates of the total populations of the various species in the area, it is not possible to assess predator preferences. The smaller prey such as bushbuck and duiker appear to be ignored by lion but size alone cannot explain the small number of puku taken by lion, as they stand considerably higher than warthog, one of the lion's favourite foods. Again it is difficult to see why cheetah take so few reedbuck which inhabit what appears to be suitable cheetah country.

The general position in the Kafue National Park is that hunting conditions are easy and predation consequently heavy. Except in the case of buffalo few animals reach old age whilst the condition of ungulates remains good throughout the year. Hyaenas are scarce and take no part in predation.

In contrast is the position of the lechwe on the Kafue Flats as described by Mitchell and Uys (1961). Here lechwe live in shallow water on vast open plains which makes hunting very

difficult, and a considerable proportion of them reach old age. There is an annual period of stress during which the herds lose condition badly and many die of poverty. The hyaena is present in greater numbers than the true predators and, in fact, is responsible for killing most lechwe. Hunting conditions on the Kafue Flats are such that the true predators cannot possibly cope with the ungulate food supply. The latter can multiply to very large numbers and overstocking can result. The scavengers are then in a position to reap a full harvest. There is thus no fixed ungulate biomass per unit predator but there exists a local availability factor which plays an important part.

In the Kafue National Park, increase of pressure on buffalo by lion during the dry season allows a corresponding reduction of pressure on the smaller species. This supports the suggestion made by Wright (1960) that the degree of predation can be manipulated by management of the habitat. Extensive early burning in the park may reduce predation on the smaller species of lion prey at the expense of buffalo.

A point which is likely to have an important bearing on predator prey relationships and which must receive attention in future studies is the degree of territorial behaviour exhibited by the ungulates and the predators. The populations of species such as lechwe are not limited by territorial behaviour and can multiply to very high numbers capable of doing damage to the habitat. Other species such as hartebeest appear to be strictly territorial and are consequently unlikely to be able to increase excessively. Predator control will not have the same results when applied to these two groups.

SUMMARY

Some 650 kills, mainly of lion, leopard, cheetah and wild dog have been analysed over a period of more than three years.

The leopard with 22 prey species has a broader food range than lion with 19, wild dog with 15 and cheetah with 11. Leopard and wild dog appear to be indirect competition for the same prey. The hyaena is not a significant predator. The sex ratio of the kills is one male to 0·84 females.

Hartebeest, reedbuck and puku are used by five predators and are killed in considerable numbers. Buffalo and warthog are used extensively and almost exclusively by lions. Buffalo comprise 18 per cent of recorded lion kills during the rainy season compared to 38 per cent after the grass fires. Predation by lion can therefore be influenced by manipulation of the habitat.

In Kafue National Park hunting conditions are easy and predation very heavy. The general condition of the prey remains good throughout the year and few animals reach old age. Hyaenas are scarce. The formidable buffalo is the only species which reaches old age in any numbers.

The local territorial distribution pattern of both predator and prey species is likely to be an important factor in the intensity of predation.

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