

PREDATOR-PREY RELATIONSHIPS AMONGST THE LARGER MAMMALS OF THE KRUGER NATIONAL PARK

by

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INTRODUCTION

During recent years a number of precise and well-founded studies on hunting and other behavioural aspects of Africa's larger mammalian predators have shed much light on the food habits and bionomics of such carnivorous mammals as the lion (Guggisberg, 1961), leopard (Turnbull-Kemp, 1967), wild dog (Estes and Goddard, 1967), spotted hyaena (Kruuk, 1966), and cheetah (Schaller, 1968).

In the absence of reliable census data and sufficiently large samples of kill records it has, however, not always been possible to obtain a true perspective of predator-prey relationships in the particular study areas. Other aspects of predation such as differential mortality rates amongst sexes and age groups of prey species, prey selection, seasonal variation in predation pressure and the possible limiting influence of predation on prey populations have also been difficult to assess, and popular notions regarding these have often been misleading or misrepresented.

Since the earliest years of the Kruger Park's existence records have been kept of the kills found in the area by organized patrols. Unfortunately, many of these records have been lost from our archives, but it has been possible to compile a complete series of carcass data for the periods 1933-1946 and 1954-1966. This probably represents the most extensive register of carcass data for any one area in Africa, and includes a total of 46,181 kills by 13 different species of predators.

The Kruger National Park is an area not only richly endowed with a diversity of herbivorous large and small mammals but, because of this broad spectrum of available prey species, also harbours substantial populations of many small and large predators (Pienaar, 1963 and 1964).

It is the main objective of this paper to provide through the carcass data compiled in this area, a clearer insight into the intricate relationships between the more important large indigenous predators and their larger mammalian prey species.

MATERIAL AND METHODS

For the purpose of the tables provided at the end of this paper only kill records which could be assigned with reasonable certainty to a particular carnivorous species were considered. With proper training it has been found that our Ranger staff (both European and African) soon became adept at recognizing from the remains of a carcass, the manner in which it was slaughtered and the surrounding sign, the predator which was responsible for the particular kill. It is quite true that some of the kills ascribed to a particular predator may in fact have been killed by a lesser or more skilful predator and then been appropriated by a more powerful predator or group of predators. Hyaenas, for instance, are particularly adept at taking over prey killed by wild dogs, cheetahs, leopards and even lions, after the manner described by Estes and Goddard (1967) and this has been witnessed on numerous occasions in the Kruger Park. Other instances of commensal predation have also been recorded in the literature and will be further commented on below.

It also appears probable that the accuracy of the final kill totals in the tables are questionable because of certain species being over- or under-represented. It is reasonable to assume, for instance, that impala and other medium- or small-sized prey, as well as the young of larger ungulates may be under-represented in the kill samples in view of numbers being consumed without leaving a trace. Other species with sedentary habits and localized distribution, such as waterbuck, may again be over-represented in the sample, as most of the patrols by the field staff, particularly during the dry season, follow the water courses and other watering places rather than the surrounding country.

In view of these unavoidable limitations in the sampling technique some of the kill percentages and preference ratings in the tables may be more apparent than real.

With prior knowledge of the possible errors in the technique, it does seem possible however, that with more refined methods of studying the predating habits of particular groups or individual predators (such as by radio-telemetric tracking), a correction factor may be calculated which will provide a more authentic picture of food preferences of the different predators in question. The errors imposed on the present data are at least of a fairly constant nature and an analysis of the yearly records indicates a remarkable consistency in the kill totals and percentages for the respective prey species.

The composite data presented in Tables 1-4 provide tallies of kills by lions, leopards, cheetahs and wild dogs in the respective sections and districts of the Kruger Park, with an indication of the total number of animals killed by the particular carnivorous species and the relative percentage of each prey species featuring in the total kills. The data for the two periods 1936-1946 and 1954-1966 are presented separately, as considerable changes

in the composition and distribution patterns within the prey community had occurred in the intervening years. Significant deductions may thus be made from the differences in predation pressure during each of the two periods.

The boundaries of the Kruger Park have not changed much since its proclamation as a National Park in 1926, but prior to this the old Sabi and Shingwidzi Reserves were subjected to considerable boundary changes in 1923, when a large portion of very good game country was excised from the Sabi Reserve. The boundaries of the respective ranger sections have also changed over the years, and these are illustrated in figs (i)-(iv).

The available carcass data have been broken down to individual sections and districts of the Park because of major differences in the topographical and vegetational aspects, as well as in the composition of the respective predator and prey communities. For a detailed description of the ecological differentiation of game habitats in the Kruger Park, the reader is referred to a previous publication (Pienaar, 1963). For the purpose of this paper it is sufficient to refer to Table II and to mention that the area north of the Olifants River is mainly covered by mopani or mixed mopani-combretum woodland, with more open grassland and woodland-savannas along the eastern Lebombo flats of Klipkoppies, Shingwidzi and Punda Milia Sections, and denser woodland and woodland-savannas in the western sections (Letaba, Mahlangene, Shangoni and Punda Milia). The north-western portion of Punda Milia Section is covered by denser woodland and deciduous forest and there is a true riverine forest along the fringes of the Levubu River (the main habitat of the rare Nyala antelope). The northern district of the Park is also the major elephant habitat of the Park and also affords sanctuary, in suitable environments, to the entire eland population and the major portion of the roan antelope and tsessebe populations in the Park. Substantial buffalo, zebra, waterbuck and sable populations occur but impala are relatively less numerous and wildebeest and giraffe rather uncommon. The central district, which lies between the Olifants and Sabi Rivers and is the major wildebeest, zebra and giraffe habitat of the park, comprises primarily fairly open *Sclerocarya caffra*-*Acacia nigrescens* savanna to woodland-savanna on the eastern Lebombo flats of Nwanedzi, Satara and Tshokwane Sections and denser Combretum and Acacia woodlands in the western sections (Kingfisherspruit and Tshokwane). This is also the basic vegetational demarcation of the southern district except the central area, which is mainly dense Acacia woodland and thickets (the major impala habitat of the Park), and the higher-lying extreme western half of Pretoriuskop Section, which is a broad-leaved and deciduous woodland-savanna with tall fire-induced grasses (and is the most important reedbuck habitat of the Park).

The Kruger Park covers an area of some 7,340 sq. miles, of which the northern district comprises 3,850 sq. miles, the central district 2,130 sq. miles and the southern district 1,360 sq. miles.

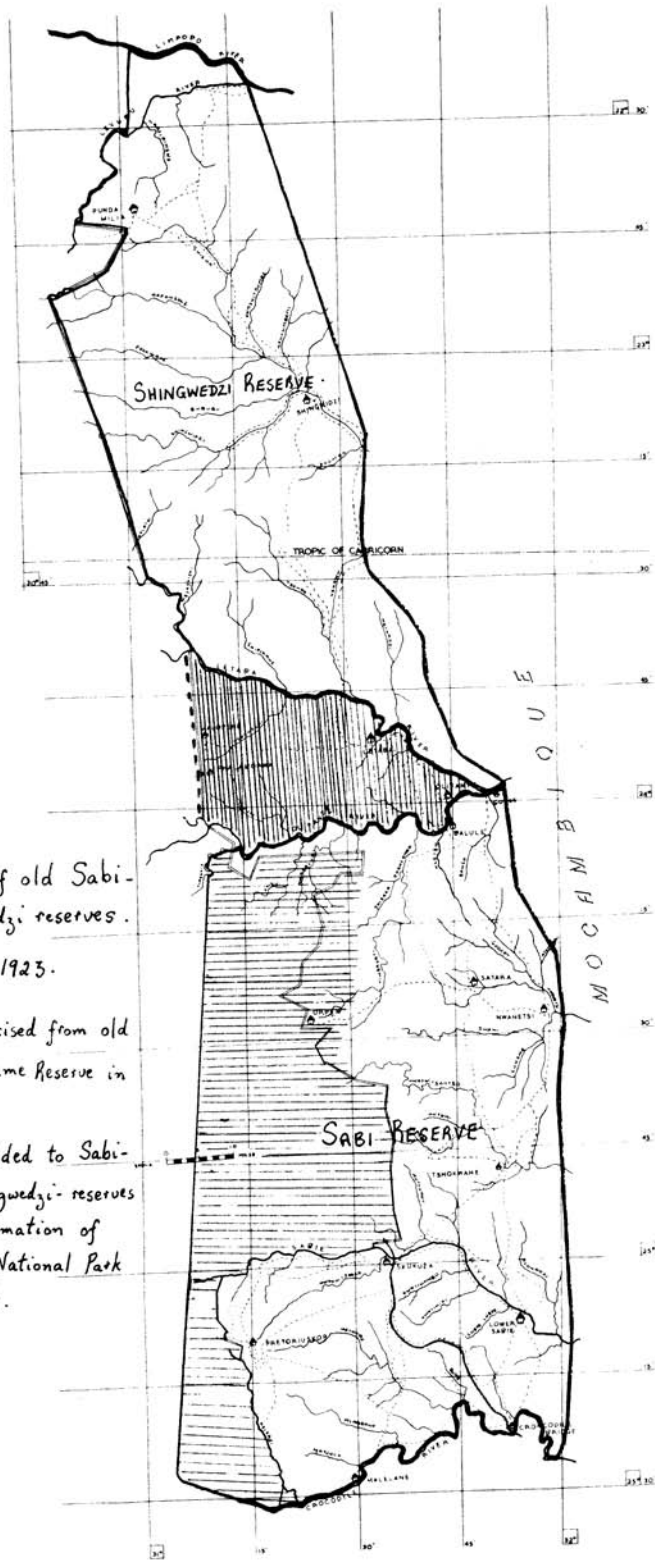




Fig. 1
 Boundaries of old Sabi-
 and Shingwedzi reserves.
 1903 - 1923.

 - Area excised from old Sabi Game Reserve in 1923.

 - Area added to Sabi- and Shingwedzi- reserves at proclamation of Kruger National Park in 1926.

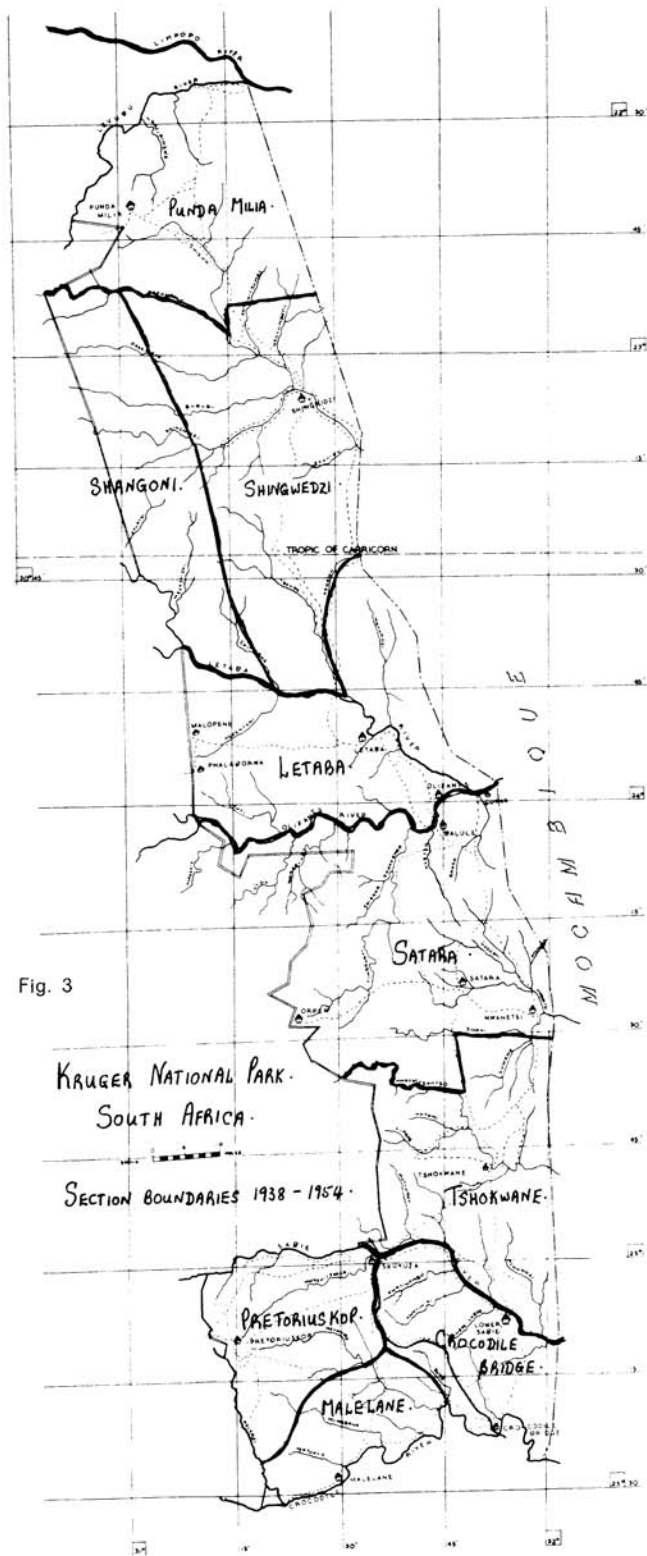


Fig. 3

It is unfortunate that no information was provided in the older kill records other than the species of the animals killed. The old system was only replaced in January 1966 and the new carcass returns provide specific mention of the sex, approximate age and condition of the killed prey species. The data accumulated during 1966 and 1967 have been analysed separately (vide Tables 17-30), and provide very interesting information on differential predation, seasonal variation in predation pressure and other aspects which will be discussed below.

The kill totals by hyaenas (brown and spotted), black-backed jackals, crocodiles, caracals, serval, baboons, pythons and martial eagles are not considered large enough to merit treatment similar to that of the major carnivores (lions, leopards, cheetahs and wild dogs), and mere lists are provided of the totals of all prey species found killed during the two periods in question (vide Tables 5-8).

The census totals and relative abundance of the different prey species presented in Table 11 were derived from a combination of recent total aerial counts of species such as buffalo, wildebeest, zebra, giraffe and sable, and an exhaustive series of differential ground counts on a grid pattern, from which natural ratios in the prey community of the various sections were established.

The estimates of the total number of lion, cheetah, leopard and African hunting dog were deduced annually from a register system whereby accurate records are kept of all single individuals, prides or family groups of the particular predator, as observed by the field staff throughout the year. A predator log is kept and the sight records are pin-pointed on a special grid-map to indicate numbers and distribution patterns.

A satisfactory census method for hyaenas, jackals and other more strictly nocturnal carnivores has not yet been perfected for the relatively dense woodland conditions of the Kruger Park. In the more open grassland savanna of the Serengeti and Ngorongoro crater of Tanzania, Kruuk (1966) obtained promising census results of the hyaena population by marking a number of hyaenas throughout the study area and by employing the Lincoln index count subsequently.

In the Kruger Park road strip counts at night do provide some indication of relative abundance when the numbers of hyaenas and other nocturnal predators are compared with the numbers of lions counted.

DISCUSSION

Any attempt at ascertaining natural trends in prey selection or particular prey preferences should be founded on reliable census data of both prey and predator species. In the absence of such acceptable estimates of totals of herbivorous animals in the Kruger Park for the period 1936-1946, no attempt has been made to establish prey preference ratings for that period.

For the later period of 1954-1966 census data are available and we have calculated the preference rating of a prey species for a particular predator as in a previous paper (Petrides and Pienaar, in press):

$$\text{Preference rating} = \frac{\text{Kill frequency of prey}}{\text{Relative abundance of prey.}}$$

These preference ratings (vide Tables 13-16) provide a true indication of the real food preferences of a particular predator irrespective of the density of its various prey species.

For the purpose of this discussion predators will be divided into the four major true predators, for which reliable census figures are available (lion, leopard, cheetah and wild dog), the scavenger-predators for which no reliable population density estimates could be calculated (brown and spotted hyaenas and black-backed jackal), and the minor predators which prey on the larger mammals or their young merely incidentally as part of their normal diet (crocodiles, caracal, serval, baboons, pythons, martial eagles).

(i) *Lion predation.*

After the reign of primitive man (and the modern hunter) was ended at the end of the last century, with the proclamation of the old Sabi and Shingwidzi Reserves, and a tight curb was applied to poaching activities, the lion became the dominant predator in the sub-tropical Lowveld savanna of the Transvaal. It is also the most successful predator, and an analysis of the available carcass data indicates that in the Kruger Park it preys on no less than 37 species of large and smaller mammals as well as ostriches, crocodiles and tortoises (vide Table 9). Of all carcasses of larger mammals killed by predators during the period 1933-1966, lions accounted for 65.83 per cent of the total (46,181).

The latest estimate of the number of lions in the Kruger Park (1964) was 1,120, of which 506 were in the area north of the Olifants River, 394 in the central district and 220 south of the Sabi River.

Lions are the most important predators in this area of blue wildebeest, Burchell's zebra, waterbuck, kudu, buffalo, giraffe, sable antelope, roan antelope, eland, tsessebe and warthog (vide Table 12).

During the period under discussion lions have been encountered at the carcasses of three young elephant calves, i.e. in the Shangoni, Letaba and Klipkoppies sections of the northern district. In the absence of reliable evidence that the lions had actually made the kills themselves, these records have not been included in the tabulated kill data.

Elsewhere in Africa authentic records have proved that lions do occasionally attack and kill young elephants. An elephant of about 5 feet high and with tusks 9 inches long, was the victim of lions in the Luangwa valley

some years back. The calf was first hamstrung and then killed by biting into the lower part of the throat. According to Pitman (1945), young elephants are not infrequently killed by lions in Uganda, which has a very large elephant population. The famous old hunter, Selous did not consider it impossible that lions might sometimes even attack sub-adult cows.

On the other hand, elephants are intolerant of lions and in the Kruger Park they have frequently been witnessed to display open hostility towards them, particularly when meeting at waterholes.

As a rule lions and adult white rhinos show little interest in each other, but during October 1965 lions attacked a full-grown adult white rhino bull, recently introduced into Pretoriuskop section from Natal, and mauled it so severely that it had to be destroyed. Subsequently, lions also killed and devoured a very young white rhino calf near Gomondwane, in Crocodile Bridge section. These are the only instances, to date, of lions accosting white rhinoceri in the Kruger Park, but instances have been cited by observers such as Wahlberg and Taberer of lions attacking and killing full-grown black rhinos in East Africa.

It is well-known that lions frequently prey on young and even adult hippopotami in areas where these beasts are particularly numerous. Thus, according to Bourlière (1955), young hippos, out grazing at night in the Parc National Albert, are among the lions' favourite victims in that area. Such instances are rare in the Kruger Park, and over the years only 6 cases have been recorded of lions successfully attacking hippos on dry land. Four of these were weak and emaciated animals which were caught along the Olifants River during a period of very severe drought.

Of the larger mammalian prey of lions in the Kruger Park blue wildebeest is the most important, constituting 23.72% of the overall kills by lions over recent years (Table 13). When the carcass data is considered separately for the various sections and districts of the Park, it becomes apparent that although the wildebeest is undoubtedly a very important prey species wherever it occurs, the mortality rate due to predation is very much density dependant. Thus, in the southern district of the Park, where wildebeest constitute only 2.47 per cent of the prey community (Table II) they are superseded in the kill totals by impala, which take over as the staple prey species of lions in this region. In the northern mopani-veld, where wildebeest comprise only an insignificant proportion of the prey community (0.53 per cent), the most important prey species of lions are the numerically much more abundant Burchell's zebra (20.4 per cent of recorded kills), waterbuck (17.82 per cent), kudu (16.67 per cent) and buffalo (14.69 per cent) (Table 13).

Similarly, buffalo which are an important constituent of the prey community in such areas as Crocodile Bridge, Mahlangene and Letaba Sections, feature prominently in the lion kill tallies, confirming also the findings of Mitchell, Shenton and Uys (1965) in the Kafue National Park, Zambia,

whereas relatively few buffalo are caught by lions in the low density areas (for buffalo) such as Pretoriuskop, Malelane and Satara sections.

In terms of actual preference however, the lion's major prey species in the Kruger Park is the waterbuck, with the highest preference rating of 6.05 (Table 13). This is a constant finding, irrespective of predator density, abundance of other prey species, or habitat type, in all areas where waterbuck comprise a significant constituent of the prey community. It is also a phenomenon which has been maintained with remarkable consistency since the earliest years of the Park's existence. Because of this top rating on the prey preference scale of lions, waterbuck is probably the one ungulate species for which lion predation is a factor of some consequence in regulating the population level. The particular vulnerability of waterbuck probably stems from its relatively sedentary habits and localized distribution — always frequenting areas near permanent water, and displaying reluctance to disperse over a wider range even during the rainy season. It is significant therefore that recent studies indicate heavy predation by lions on waterbuck throughout the year, and there is considerable suggestive evidence that the predation rate on waterbuck relative to its associated prey species in the habitat may even increase during the wet season.

Despite this heavy predation by lions on waterbuck the mortality thus induced cannot be regarded as the only limiting factor regulating population growth. There is abundant evidence that declines in the growth curve of the waterbuck population of the Kruger Park are linked rather with density-independent factors such as prolonged droughts or with disease epizootics such as anthrax, and that there is a progressive, albeit slow incline of the growth curve during normal seasons, despite the heavy predation on the species by lions and other predators.

Considering the Park as a whole, the next most important prey species of lions (in terms of relative abundance) is kudu, with a preference rating of 3.82, followed closely by wildebeest and giraffe (with preference ratings of 3.06 and 3.01 respectively). Other important prey species of lions in order of preference include sable antelope (2.62), eland (2.04), zebra (1.98), roan antelope (1.62) and buffalo (1.06) (Table 13).

Impala, numerically the most abundant of all potential prey species of lions, rank very low on their preference scale (0.37), and even in an area such as the southern district of the Park, where more impala are killed by lions than any other species, 8 other prey species have higher preference ratings than impala.

Although the relative frequency of wildebeest in all recorded lion kills is by far the highest in the central district of the Park, where these animals occur in great nomadic herds and are heavily preyed upon by lions, they still do not represent the lion's most sought-after victims in this area. The less abundant waterbuck again has the highest preference rating, followed by kudu, giraffe and wildebeest in that order.

Where the density level of a preferred prey species such as wildebeest declines in an area, in view of some other limiting factor such as drought, diseases etc. it has been found that lions may still prey heavily on the survivors and predation may then become a definite limiting factor retarding the recovery of the population. This is at present true of the wildebeest population in Malelane section, which still has not recovered from the disastrous droughts of the 1926-35, 1944-48, 1950-53 and 1962-65 eras.

In such cases where the numbers of a prey species decrease below a critical level, the chance loss through predation of even one or two of the remaining few becomes a calamitous phenomenon, and the loss so magnified that it does not represent a true reflection of prey preference. An example in question is the killing by lions of some of the remaining few roan antelope in the Batavia area of the central district (vide Table 13).

When comparing the relative frequency figures of the different prey species in the total kills by lion for the two periods 1936-1946 and 1954-1966 some very interesting differences come to light (vide Table 1). This apparent shift of predation pressure (the gross totals did not vary much), is obviously correlated with increased abundance of certain species and decline in the numbers of others. The relative frequency of impala in the kill totals is somewhat higher for the period 1954-66, which is to be expected, considering the great increase in the numbers of this species which followed in the wake of progressive encroachment by woody growth of much of the open savanna regions during this period. This is also true for another browsing species, kudu, and even more so for giraffe, which may have doubled their numbers during this time. The very much reduced rate of predation on wildebeest apparent in the figures for 1954-66 is entirely due to the great exodus of wildebeest (and zebra) from the heavily populated Pretoriuskop and Malelane Section to areas outside the borders of the Park, after the temporary cessation of rotational burning in this area during the period 1947-1954. Wildebeest kills recorded dwindled from 2,638 in Pretoriuskop section and 718 in Malelane section during the 1936-46 period to 339 and 237 respectively during 1954-66.

Over the years, a series of severe droughts and disease epizootics made serious inroads on the numbers of waterbuck in the Park, and because of this reduced availability the rate of predation on this preferred prey species also decreased during the more recent period of 1954-66. Buffalo, on the other hand, have increased tremendously over recent years and lions are preying more on them. The predation rate on Burchell's zebra has decreased somewhat in contrast, despite a very definite increase in numbers during the later period. The only explanation for this apparent discrepancy is that in the Kruger Park zebra is not a really preferred prey species of lions (vide its low preference rating), and lions find it easier to stalk and kill prey less wary and formidable than these sagacious beasts.

The importance in the habitat of an abundance of preferred prey species, such as wildebeest, as buffers against predation on less abundant

or rare prey species is well demonstrated when the status of sable antelope is considered. In Pretoriuskop and Malelane sections, where there is a low density of the preferred prey species of lions (i.e. wildebeest and waterbuck), the rate of predation on sable is significantly higher than in the central district (with more or less the same number of sable antelope), where there is an abundance of both wildebeest and waterbuck. There would therefore be considerable survival value for sable and other rare prey species if the numbers of wildebeest could be built up in both these erstwhile famous wildebeest habitats through mass translocation of surplus animals from the central district. This represents a management practice which we would strongly recommend, provided that the population of wildebeest is not built up to a level where sable antelope and other more fastidious grazing species are adversely affected by interspecific competition for grazing, water or 'Lebensraum'.

In the northern district, where the numbers of wildebeest are low, in view of the unsuitable nature of the habitat, the buffer-effect is shared by waterbuck, zebra, kudu and even buffalo. In sections where the numbers of these buffer species are high (e.g. Letaba section) the rate of predation by lions on associated less abundant prey species such as sable, roan and eland is significantly lower than in areas where the buffer species are relatively less common (vide Mahlangene and Shangoni section).

Bourlière (1963) stated that 'carnivores actually only prey upon herbivores of about the same size and weight'. While such a generalization is open to dispute, it is certainly true that in the case of lions animals of lesser weight than these predators contribute only a small proportion to their total annual kill.

Although it is quite possible, as has been pointed out before, that the actual kills recorded of such medium- and small-sized prey is an under-representation in view of their total consumption on many occasions by a pride of lions, it is a fact that the numbers of such prey species as impala killed by lions is nowhere nearly correlated with the abundance of these prey species. Impala constitute 53.41 per cent of the larger mammal community preyed upon by lions, but the relative frequency of impala in the total recorded lion kills for the period 1954-66 is only 19.85 per cent. Apart from impala, warthog is the most important of the lion's lesser prey species in the Kruger Park but other small- and medium-sized antelope contribute only in very small measure to the annual kill tallies of lions (Table 13).

Despite the fact that lions normally do not hunt the lesser prey species in significant numbers it is nevertheless safe to say that most species of small mammals within the lion's area of influence may fall prey to him at one time or other. This is particularly true in the case of young lions learning to hunt or old individuals which are no longer capable of hunting their larger prey. Such nocturnal prey species as antbears and scaly anteaters are hunted at night when ranging abroad or are dug from their warrens

during the day. Certain prides become particularly adept at digging up warthogs that have taken refuge in old antbear holes. Sometimes whole families are eliminated in this manner. Lions often hunt porcupines at night although many sustain nasty or even fatal wounds in the process. During lean times lions are not averse to digging up grass rats and gerbils and avidly pursue cane rats and even hares, which they kill with a quick blow of the paw. Lions also kill more baboons than they are generally credited with and during the period under discussion 7 baboon kills by lions were reported. Ostriches and other ground birds are also preyed upon where the opportunity arises and even wily and secretive animals such as bush pigs are sometimes surprised and killed.

Lower vertebrates are also occasional victims of lions, and of these tortoises and crocodiles are the most important. The latter sometimes dispute lion kills which have been made near water, and two cases have been recorded during recent years where crocodiles were killed in such battles and eaten by the lions.

Many years ago, a lion in the Kruger Park bit in half a large python which attacked it, and ate a portion of the giant snake.

When pools or dams dry up during severe winters, lions in the Park have been seen to throw some of the struggling barbel (catfish) from the shallow mud with a swipe of the paw. A case has been recorded where lions visited the camp of a gang of workmen at night and fed on chunks of mealie meal porridge which they discarded near their tents. Where large swarms of flying termites or locusts appear lions have on occasion been observed to feed on them. They are also attracted to carrion and will eat the most putrid of meat with about equal relish to that of a freshly killed animal. A case comes to mind where two male lions approached the decaying carcase of an elephant bull which had been destroyed and fell into the Sabi River near Skukuza. Numerous crocodiles were tearing at the carcase and this gruesome spectacle deterred the one lion from venturing nearer. The other lion waded boldly through the shallow water, avoiding the snapping jaws of the crocodiles and commenced gorging himself with the rotten meat.

Lions are confirmed cannibals and the urge here is not necessarily hunger. Fights often ensue at a carcase and may end in the death of one or more of the contestants. The victors will then promptly set to devouring the vanquished. Intraspecific competition resulting in mortal fights around a carcase is of more frequent occurrence during lean times than during pluvial periods and young lions naturally suffer most. Many cases have been recorded however, where adult males may even kill one of their own mates during such disputes and eat part of the dead lioness. There are also records of lionesses eating members of their own sex, but cannibalism seems to be less prevalent with them than with males.

The lion is the dominant species in the predator hierarchy of the Kruger Park and often preys on lesser predators or will appropriate the carcasses of prey killed by them. In old age or crippled condition they fall prey themselves to hyaenas and even wild dogs. Many cases have been recorded over the years of lions relieving leopards of their prey after these wily hunters have made a kill. Lions will even climb up the perpendicular trunks of trees to a surprising height in order to get at the carcasses of animals which leopards have wedged in a forked branch.

Many other cases of inter-specific competition involving lions have also been recorded. Along the Lower Sabi Road a lioness was seen chasing a hyaena for almost 100 yards before catching it and proceeding to devour it. The hyaena was pursued for no apparent reason — there being no kill, nor was it worrying the lion. Although hyaenas are often killed by lions when mobbing a feeding pride they are rarely eaten in such situations. Several years ago a cheetah was cornered by two lionesses along the Nahpe Road and severely mauled before it managed to escape.

During the period under discussion lions were reported to have killed 39 hyaenas, 6 leopards, 2 cheetahs, 12 jackals, 2 civet cats, 2 honey badgers, 1 caracal and two crocodiles. Many of these victims were partially eaten.

Since the proclamation in 1898 of the original Sabi Reserve however, only about a dozen cases of man-eating have been recorded in the area that comprises the present Kruger Park.

The kill frequency or number of animals killed by a lion during a unit period, is the subject of considerable controversy. Undoubtedly no generalization could be made here, as the killing rate is determined by so many variable factors, such as the age and skill of the predator, the size of the pride, presence or absence of cubs, availability of prey, season of the year, condition of the habitat etc. Adult male lions in the Kruger Park have been found to weigh as much as 485 lbs. and adult females around 300-320 lbs. Several authors such as Kirby and Lyell have stated that a full-grown lion can eat as much as 40-50 lbs. of meat during one meal. Lions will gorge themselves when the opportunity arises and may fast for several days subsequent to such a huge meal. Depending on their hunting success however, lions may often go without food for days, particularly during the wet season, when their prey is dispersed over a wide area and hunting conditions become difficult because of the rank vegetation. Such knowledgeable authorities as Stevenson-Hamilton (1947) have estimated that an individual lion would kill about 26 head of prey a year. (At a later stage this author modified his estimate to 10-12 head per annum.) The killing rate of individual lions have been variously put down as 35 head of prey per year by Talbot and Talbot (1963), 36.5 by Wright (1960), and from 19-20 by E. Hubert, E. Wells and Guggisberg (1961).

Until more sophisticated studies provide the precise information required on this particular aspect of lion predation, we are inclined, from our own