Rivers, packs of hyaenas scoured the veld and disposed of the rotting carcases. We are also of the opinion that during such adverse times (for prey animals) spotted hyaenas fulfill a most important sanitary role in that the weaker and disabled individuals in the prey community are systematically hunted and killed by hyaenas. In doing so they become a factor in preventing the spreading of epidemic diseases such as anthrax and foot-and-mouth disease.

Prolonged periods of drought in the densely populated areas of the Park impose a particularly severe strain on the large herds of buffalo, such as those inhabiting the Lebombo flats of Crocodile Bridge Section. During such times the herds have to trek considerable distances from watering places to grazing and the young calves and older, disease-ridden individuals are the first to show signs of weakness and lag behind the herd. There is considerable suggestive evidence that hyaenas are mainly responsible during these times, for killing and devouring such physically unfit individuals, although lions also play an important role (Pienaar, 1969 in press). Mortality amongst the youngest segment of the population may be severe, and when conditions are particularly bad, such as prevailed during the dry season of 1965, almost the entire calf crop may be lost.

It is during such periods that heavy predation by hyaenas on weak or debilitated prey animals, prompts one to speculate that even during normal seasons hyaenas do not pull down many adult animals that are perfectly healthy. Hyaenas demonstrate an uncanny ability to select vulnerable members in a herd, and individuals that may appear quite normal to the human eye may in fact have indicated some subtle flaw to the hyaena's superior powers of observation. During drug-immobilization operations on the Lindanda flats, a zebra foal which had only been slightly affected by the drugs was unerringly picked out by a lone hyaena in broad daylight and pursued in a most persistent and determined manner.

As a rule however, spotted hyaeas hunt their larger mammalian prey by moonlight in the manner described by Kruuk (1966), and such communal hunting has been frequently observed locally in areas such as the Kingfisherspruit Section, where adult wildebeest, zebra, waterbuck and kudu are often pulled down and devoured by packs of hyaenas numbering as many as 40 and more. Wildebeest and other prey are often pursued into water and kills have recently been made in the water of the Rabelais and 'Transport' dams. More adult wildebeest are killed than zebra, and these findings confirm those of Kruuk (1966) although this worker points out the fact that zebra are more often pursued in the Serengeti, but with a lower rate of success.

Hyaenas are possessed of immense stamina and can maintain their ungainly and deceptively slow lope for long periods on end. They may thus run down even the most fleet-footed of antelope over a long distance. Eloff (1964) recorded the case where a single spotted hyaena ran down

and killed a young two year old gemsbuck in the Kalahari Gemsbok National Park, and Deane (1962) reported an instance where a lone hyaena chased and killed a three-quarter grown wildebeest. A pack of hyaenas attacked a young hippo calf on dry land and bit off an ear and the tail before the victim took refuge in the Letaba River. Several cases of sick or crippled adult buffalo which had been killed by hyaenas, have been reported during recent years.

In the Kruger National Park hyaenas frequently ambush their prey from thick cover near drinking places, and often also pounce on animals floundering in the mud of receding water holes or dams.

For the first week or so after birth, the young of most prey animals are particularly vulnerable to hyaena predation and a large proportion of the losses sustained during the breeding season of such prey animals as wildebeest and impala could, in our opinion, be ascribed to hyaena predation. Estes (1967) points out the fact that the short peak calving season and the habit of congregating on calving grounds by such species as wildebeest, may in itself be adaptations in the prey population, for the protection of their young against hyaena predation. Instances have been recorded where wildebeest cows successfully defended their new-born young against the attention of single prowling hyaenas.

The extent of hyaena predation on other predators is difficult to assess, but it is probably safe to say that, as in the case of ungulate prey, hyaenas will, when driven by hunger, either singly or in packs, attack any other predator in situations where they have a fair chance of making a kill. Even the lordly lion falls victim to hyaenas when very young, old or unfit. In 1937 the ranger of Lebata Section witnessed a lioness being pertinaciously followed by three hyaenas whom she endeavoured to drive off. The hyaenas persisted however, and the lioness at last took refuge in a tree. She proved to be a very old and emaciated animal, with practically no teeth left, and the observer was certain that the hyaenas would have remained in close attendance until they saw a good chance of finishing her off.

During December, 1948, Ranger Mingard of Shangoni found a young lioness dead, in a river pool near his house, with bad bites in her groin. Two days later he heard a commotion at the same place and arrived there in time to see two spotted hyaenas chase two young lions up a sloping tree. On seeing him, the lions tried to get down, but the hyaenas immediately returned to the attack.

In May, 1959, the ranger of Shingwidzi section observed a hyaena carrying a young lion cub in its mouth, and on several occasions analysis of hyaena dung has revealed the presence of lion claws.

Hyaenas will as a rule take flight in the presence of humans, but when driven by hunger they become bold and dangerous beasts and will

even penetrate human dwellings in search of food. Before the Skukuza rest camp was properly fenced this was a common occurrence at night, and many items of food and personal effects belonging to tourists were carried off by the scavengers. The refuse heaps outside the camp regularly attract large numbers of hyaenas and jackals at night. More recently, a hyaena climbed into the cockpit of a helicopter which was used for census work at Skukuza, and tore out the foam rubber seats and the first aid box.

Several years ago a child sleeping in a tent at Satara rest camp, was bitten on the arm by a prowling hyaena and during the summer of 1966 hyaenas entered the Olifants rest camp and on two occasions attacked sleeping tourists. A young boy and a married woman were both bitten in the face and ghastly wounds were inflicted.

Hyaenas have also taken to begging from tourists along certain roads in the southern sections of the Park, and have snapped at the hands and even cameras of tourists in such situations.

The carcase of a fully-grown young leopard was carried around and worried by a hyaena in the Letaba River-bed, but during the time of observation, it made no attempt to feed on the carcase. Several cases of spotted hyaenas killing and eating jackals have also been recorded, and pet dogs have been carried away at night from rangers' quarters.

Only one instance of cannibalism has been observed — two hyaenas feeding on the hindquarters of a younger one along the Nahpe Road during a night in August 1966.

Considerable numbers of spotted hyaenas are killed annually by lions when the latter are molested at kills, but they are rarely eaten by the lions or by other scavengers. Even vultures are apparently loath to feed on hyaena carcases.

The spotted hyaena population in various parts of the Park have been subject to a number of cyclical fluctuations in numbers. During the early years of the Park's existence, they were intensively hunted, trapped and even poisoned and by 1925 their numbers were reduced almost to extinction. Some epidemic disease, later becoming endemic in the population, may also have played a role here, as their numbers showed a gradual incline during the 1930's despite persistent control measures. Even after the policy of carnivora control was abandoned they remained relatively scarce in certain regions, whereas they became very abundant in other areas, such as the Kingfisherspruit and Tshokwane Sections of the central district and the Malelane Section of the southern district. The population in the far northern part of the Park also experienced an inexplicable decline in numbers during the early 1950's, but has recovered its former status over recent years.

During the severe anthrax epizootics of 1960-61 spotted hyaenas fed on anthrax carcases in large numbers but failed to contract the disease

themselves. A positive case of rabies in a spotted hyaena from Skukuza Section was diagnosed in 1957, however.

Hyaenas are very fond of wallowing in shallow water during hot weather and this habit probably leads to the undoing of some, as crocodiles abound in the permanent and most of the semi-permanent waters of the Park.

A hyaena was found dead in Nwanedzi section with his whole head and neck swollen from the septic wounds caused by porcupine quills which had broken off in his mouth and palate. Spotted hyaenas around Skukuza have also been found to suffer from heavy infestations of the dangerous intra-muscular nematode — *Trichinella spiralis,* which may cause severe emaciation and paralysis of the host.

It has not been possible to arrive at an acceptable assessment of the numbers of spotted hyaenas in the Kruger Park as yet, but it is probably safe to maintain that they are today the most abundant predators in the Park as a whole.

Kruuk (1966) successfully employed the mark-recapture technique and Lincoln index to establish the number of spotted hyaenas in the relatively confined and open Ngorongoro Crater area of Tanzania, but this census method is not feasible under the much more overgrown conditions and in a Park the size of Kruger.

The weight of adult spotted hyaenas measured in the Park varies from 140 - 165 lbs., but Turnbull-Kemp (1967) records the weight of a large female as 190 lbs. The adult sex ratio amongst spotted hyaenas in the Kruger Park may be close to parity but of 209 hyaenas destroyed at random during the control operations of 1954 - 1960, 65.07 per cent were males and 34.93 per cent were females.

(b) *Brown hyaena* (*Hyaena brunnea* Thunberg).

Brown hyaenas are rare in the Kruger Park and the total population probably does not number more than about 150. Of these, the larger proportion inhabits the western areas of the northern district. South of the Olifants River brown hyaenas are very rarely encountered and their impact on the prey community is insignifficant (Pienaar, 1964).

Very little is known about the habits of these nocturnal predators, but judging from the observed carcase remnants of animals killed by them over the years, brown hyaenas are much more aggressive animals and predators in their own right, than their spotted cousins. Despite their smaller build and weight (usually not more than 130 lbs.), they attack a wider range of larger mammalian prey and overpower more formidable ungulate species than do spotted hyaenas (Vide Table 5).

Kudu appear to be by far the preferred prey of brown hyaenas, followed by waterbuck, impala and zebra. Full-grown adults of all these

prey species are run down and killed with ease by brown hyaenas, which normally hunt in smaller packs than the spotted variety.

In addition to the prey species listed in Table 5, brown hyaenas are also reputed to carry off young lion cubs. They also prey on ostriches and other ground birds, their eggs and chicks, reptiles such as tortoises and snakes, freshwater crabs, fish, locusts and wild fruits.

A brown hyaena was once followed by the ranger of Mahlangene Section in his truck for a distance of more than a mile and a half, at speeds ranging from 30 - 35 m.p.h. The hyaena kept ahead of the truck with ease and eventually swung off into the bush.

During the years 1941 - 1943, a family of brown hyaenas took up residence in a number of connected antbear holes on the north bank of the Sabi near Skukuza, and afforded the late warden, Col. Stevenson-Hamilton an excellent opportunity to study their predating and other habits. He commented in his yearly reports for that period, as follows:

1941—"Several wellgrown young ones and at least one pair of adults were present at the den. These hyaenas, which are very rare in the Park, largely kill their own food. Full-grown impala rams were dragged whole to the den, broken up at the entrance, and the meat taken down the holes. Besides impala, of which a considerable number had fallen victims, there was a large and varied assortment of other remains, testifying to the catholic taste of the animals. Among those identified were several full-grown cheetahs, baboons, water tortoises, guinea fowl and even a boomslang about 5 feet long, of which the half-chewed remnants were lying half in and half out of the mouth of one of the holes."

1942—"The family of brown hyaenas again bred in the north bank of the Sabi a few miles east of Skukuza, but changed their breeding holes for others nearer the Sand River junction, their old home having been to a great extent destroyed by some lions which had dug into it extensively to reach the meat which they could smell inside. Established at their new site, these hyaenas continued to kill considerable numbers of animals, and skulls of impala, bushbuck and baboons were found scattered outside, evidently hunted and killed by the occupants of the den."

1943—"The family of brown hyaenas on the north bank of the Sabi continued in their new abode, to take toll of other animals. In addition to the remains of full-grown impala, several baboons and one more cheetah skull was found."

It would have been most interesting to observe how the brown hyaenas succeeded in capturing prey as wary as baboons or as fleet-footed as cheetahs. Unfortunately this has never been witnessed yet and the mystery remains unsolved.

(c) *Jackals.* (*Canis mesomelas mesomelas* Schreber and C. *adustus* Sundevall).

Stevenson-Hamilton (1947) commented as follows on the feeding habits of side-striped jackals, *Canis adustus:*

> "It is not entirely carnivorous, and, in addition to locusts and other insects, it will eat certain wild fruits. I do not think it ever attacks mammals of larger size than a hare, although it becomes a poultry thief when opportunity offers."

The meagre additional information which we have been able to acquire during more recent years is not much more revealing.

Side-striped jackals occur in fair numbers in the northern mopaniveld of the Park, but south of the Olifants River it is not a common animal (Pienaar, 1964). They have not always been rare however, and Stevenson-Hamilton recalls in 1940:

"For a good many years there has been a noticeable decrease of the side-striped jackal. This large species was at one time very numerous in the thickly bushed country south of the Sabi, and in fact right up to the Olifants in the more densely wooded portions. Today it is a rarity and it is an adventure to see one."

Side-striped jackals are more timid, solitary and nocturnal in habit than the saddle-backed species and are not often seen abroad during the day. They also feed on carrion but not to the extent indulged in by their saddle-backed kin. During the hippo-culling campaign along the Lebata several years ago, a few of these jackals regularly visited our camp at night to feed on the hippo skeletons and scraps of offal lying about. In Punda Milia Section lions killed a side-striped jackal at a kill but did not eat the carcase. At Shingomene one was found that had been killed in a fight with other jackals. A pair of side-striped jackals killed a large puff adder at Mcosene, near Numbi Gate. The female killed the snake while the male stood by looking on. In the Shibyeni Spruit of Mahlangene Section a side-striped jackal was drowned when it was overwhelmed by a flash flood.

Side-striped jackals have not been weighed in the Kruger Park, but Wilson (1968) gives their weight as varying from $14\frac{1}{2}$ - $17\frac{1}{2}$ lbs. in Zambia.

In habitats undisturbed by man, saddle-backed jackals, C. *mesomelas mesomelas,* feed mainly on carrion, small mammals such as hares, squirrels, mongooses, rodents, the eggs and chicks of ground-nesting birds (including ostriches), smaller ground-nesting birds themselves, lizards, tortoises, locusts, termites and other insects, wild fruits and other vegetable matter. They have been observed to pluck off tufts of green grass in the manner of domestic dogs.

The new-born lambs of the smaller antelope species are not immune to their attention during the lambing season and even very young wildebeest calves and zebra foals may be overpowered by a group of saddle-backed jackals (Vide Table 6). A young roan calf was killed by a single saddle-backed jackal recently. Adult small antelope such as steenbuck, Sharpe's grysbuck and oribi are also killed by these wily predators.

Isolated instances have been recorded of white storks and secretary birds being killed by saddle-backed jackals.

These jackals congregate in large numbers on the calving grounds of wildebeest herds, but the attraction here is more likely the afterbirths than the calves themselves.

It is a constant finding that saddle-backed jackals are much more numerous in the badly trampled and overgrazed areas of the Park (such as Kingfisherspruit, Lindanda, Lipape, Mlondozi, Tshokwane and Pafuri) than in areas with a more dense vegetation cover. The correlation here probably stems from the fact that denudation of the cover in the habitat makes ground-nesting birds and their eggs, rodents and other small mammalian prey much more vulnerable and easy to hunt. The Kingfisherspruit Section used to be the prime habitat for guinea-fowl and many other ground-nesting birds in the Park. After the severe overgrazing which followed on the erection of the western boundary fence and the successive drought years of 1960-1966, the numbers of guinea-fowl and other game birds in this area dwindled alarmingly, but there was a marked associated rise in the number of saddle-backed jackals in the area. Since the overgrazed part of the section has been protected by a game-resistant fence, the grass cover has come back within two years and there has been a remarkable recovery in the population of ground-nesting birds.

Elsewhere in the Park, saddle-backed jackal populations have also been subjected to cyclical fluctuations such as those experienced by the wild dog and spotted hyaena populations. Periodic declines in the number of these predators were evident in the central and southern districts during the early 1940's and reports were received since 1937, of jackal dying from unexplained causes. The population in Pretoriuskop Section recovered its former abundance by 1948 but declined again during the period 1955-58. During the latter period the number of saddle-backed jackals in Malelane Section and over most of the northern district (with the exception of Pafuri area) also decreased to a very low level. In all these areas there has again been a steady increase in population density over recent years.

At the Rabelais dam in Kingfisherspruit Section it was seen how a group of 8 saddle-backed jackals molested a leopard at a wildebeest kill (which had been made by lions) to such an extent that it abandoned the carcase and slunk away.

The weight of saddle-backed jackals which have been weighed in the Park, varied from 15 - 24 lbs. (average 19½ lbs.)

(vi) *Predation by lesser predators.*

In addition to the major predators and scavenger-predators discussed above, predation by a number of lesser predators also has some bearing on the larger mammalian prey community in the Kruger Park. Included amongst these lesser predators are crocodiles, caracal, serval, baboons, pythons and martial eagles.

Apart from crocodiles and perhaps baboons, the feeding habits of the lesser predators are imperfectly known and do not come within the scope of this paper. It is not intended to catalogue the complete range of small mammal, lower vertebrate and invertebrate prey of the various predators in question, and the lists of prey species in Tables 6 et.seq. provide details in context of predation on larger mammals only.

Crocodiles are undoubtedly the most important of these lesser predators and all the perennial rivers and pools in the Park harbour considerable numbers of these powerful carnivorous reptiles. The muddy waters of the Levubu and Olifants Rivers particularly, are inhabited by large populations and predation by adult crocodiles here must have a definite impact on the prey animals frequenting the drinking places along their length. Crocodiles attain a formidable size in Park waters and specimens of 13 - 14 feet in length are not uncommon. Monstrous individuals exceeding 15 feet in length, and which must weigh well in excess of 1000 lbs., have been encountered in rivers such as the Levubu and Olifants. Despite the fact that these large crocodiles are capable of capturing and drowning even full-grown buffalo and giraffe we found, as did Cott (1961) in Uganda, that adult crocodiles prey rather more heavily on aquatic reptiles such as the terrapin, *Pelusios sinuatus* than on mammals. The stomach contents of a number of large crocodiles, which have been examined here, almost invariably contained portions of water tortoise shells, together with the usual quantity of small stones. On the other hand, remnants of mammalian prey was much less frequently in evidence.

The popular belief that crocodiles do not kill waterbuck is certainly not substantiated by our findings in the Kruger Park, and it will be seen from Table 6 that waterbuck are, in terms of relative numbers, actually the crocodiles' most important mammalian prey species. Impala constitute the bulk of their kills but many kudu and bushbuck are also taken. It was observed how a full-grown giraffe bull, attempting to negotiate the Olifants River, suddenly stumbled, fell and was pulled under by a huge crocodile. An adult buffalo bull wat seized at Nyavutsi waterhole by a 14 ft. crocodile and drowned after a tremendous struggle. Through the years only two cases have been recorded of hippo calves being killed by crocodiles, but several instances of hyaenas, wild dogs and even lions being taken, have been witnessed.

Numerous instances of man-eating have also been recorded and hardly a year goes by without crocodiles killing at least one human along our

rivers. It is also a fact that crocodiles have been responsible, over the years, for the loss of more human lives in the Park, than was caused by all other predating beasts and poisonous snakes combined.

In terms of relative size, caracals are fierce and powerful predators which will more often attack larger mammalian prey species than serval and Cape wild cats. It is known that these sleek, diurnal predators will on occasion kill monkeys, klipspringer, hares, squirrels and rock hyraxes in suitable environments, but in the Park their larger mammalian prey consist mainly of impala lambs, duiker, steenbuck and Sharpe's grysbuck (Table 7).

One case of a caracal killing an adult Cape wild cat has also been recorded. They are sometimes preyed upon by lions however, and the head of one of these spirited animals was found near the Tsende picket, where it apparently disputed the carcase of a waterbuck calf with seven lions.

Serval are much less aggressive in habit than caracal and will rarely attack anything larger than an impala lamb. Their long limbs are built for speed and they run down hares, cane rats and other rodents, as well as game birds, lizards and other small reptiles. They have been observed to feed on frogs and large beetles, but only three cases have been recorded of serval killing young antelope (Table 7).

Cape wild cats, on the other hand, have never yet been incriminated in the Park, with killing mammalian prey larger than hares. The normal prey of these small but savage cats, include rodents, cane rats, squirrels, snakes, lizards, tortoises, game birds up to the size of Kori bustards and various insects.

During the lambing season of many of the smaller and medium-sized antelope, an additional predator appears on the scene in the form of male baboons. Numerous instances have been recorded of big dog baboons snatching and eating the lambs of impala, duiker, bushbuck, nyala and even reedbuck, and young hares are also sometimes caught and eaten by these omnivorous beasts (Table 7).

There are many large pythons in the Kruger Park and these huge snakes also take their toll of larger mammalian prey. The largest prey animals which have been found crushed to death and swallowed by pythons, include bushbuck ewes, a reedbuck ewe, and wildebeest, kudu and waterbuck calves, but impala again feature most prominently in the larger prey category (Table 8).

The only other carnivorous animal preying on the larger mammals of the Park in any significance, is the martial eagle. These large and very powerful raptors are capable of carrying away even adult steenbuck and Sharpe's grysbuck, and also kill impala, bushbuck, and klipspringer lambs, warthog piglets, hares and rock hyraxes (Table 8).

(vii) *Differential predation according to sex and age of prey, and season of the year.*

The data on predation accumulated during the period 1933-1966, unfortunately provide no indication of the age or sex of the individual carcases of prey animals recorded. The gross annual totals of kills obtained were also not analysed for possible variations in predation pressure during the different seasons of the year. Since February, 1966, a new system was adopted whereby all carcases found were classified not only according to species and the predator responsible for the kill, but also in respect of the sex and relative age group of the particular prey specimen killed.

The total annual kills were also subdivided into quarterly periods corresponding with the dry and wet seasons and the main lambing and calving periods of the major prey species. The results of these analyses for the period February 1966 — January 1968 are presented in Tables 19 - 30.

For many prey species the sample of recorded kills is still too small to draw valid conclusions, but for those species which are heavily preyed upon, such as impala, wildebeest, zebra, waterbuck and buffalo, some very interesting manifestations and seasonal patterns of predation have come to light. There seems to be little doubt that a marked seasonal variation in predation pressure exists and which correlates with climatic conditions, degree of concentration or dispersal of prey species, hunting conditions in the habitat and breeding season of the major prey species.

In the case of lions, a very clear-cut pattern in seasonal pressure manifests itself, with a peak during the driest period of August to October, when their prey is concentrated in great masses around the available water supplies and hunting conditions are at a premium.

The kill frequency drops gradually during the early rains and the peak calving period of preferred prey species such as wildebeest and waterbuck (November - January), and reaches its lowest ebb during late summer and early fall (February - April), when the game is widely dispersed in the summer-grazing areas, the vegetation becomes long and rank and hunting conditions are at their worst. Although the lower killing rate during this period may be over-accentuated and more apparent than real, because of diminished visibility and lower recovery rate of carcases by patrols, it is obvious from the behaviour of lions during such times that prey is hard to come by and the kill frequency is decidedly lower than during the dry winter months. It is then that intraspecific competition reaches its maximum intensity, cubs and young lions starve and carcases are attended for much longer periods by the prides than during the dry season. The lower rate of killing by lions during the wet season is an important factor when calculating the kill frequency of individual lions over a period of a whole year, and is a phenomenon which, in the past, has often been overlooked in such estimates by other workers.

In the case of leopards and wild dogs, very much the same seasonal fluctuation in predation pressure holds true as that manifested by lions, but cheetahs make more kills during the lambing season of their major prey species (impala) i.e. during November - January, than during any other period of the year (Vide Table 20). Pregnant females and newly-born young then constitute by far the majority of kills made.

The heaviest rate of predation on young lambs or calves of prey species occur, as would be expected, during the period immediately following the peak breeding seasons of the respective prey species (mostly from Novemer-April) and peters out gradually as the dry season progresses and the new-born young become stronger and more virile. During this time predation on the sub-adult segment of the population increases proportionately and the dry season also represents the period of maximum predation on the adults of most prey species.

An exception to the rule appears in the case of lion predation on impala. Very young impala lambs are not often caught by lions so that the predation rate on the more mature segments of the population is relatively heavier during the lambing season of impala (Vide Table 19).

In the case of all the prey species which are heavily preyed upon by lions (the dominant predators) there appears to be a mechanism in operation which protects the population from excessive decimation by these onslaughts. It will be noted from the data in Tables 19 - 30 that the rate of predation on adult male animals is much heavier than on the breeding female segment of the population. This is true in the case of impala, waterbuck and kudu, and even more so in the case of wildebeest, buffalo and giraffe. Lions, on the average, kill two male buffalo or giraffe for every female. Differential predation on the sexes may in fact be the most important factor responsible for the disproportionate sex ratio which is apparent in the adult segment of the population of the majority of prey species in question (waterbuck — 2.32 ♂ : 1♀; kudu — 2.22 ♂ : 1♀; impala — 2.39 ♂ : 1♀; wildebeest — 2.10 ♂ : 1 ♀).

The greater proportion of adult prey animals killed consist of the more vulnerable territorial males, and as Estes and Goddard (1967) rightly point out, this is a phenomenon which benefits the prey species. In probably every gregarious, territorial antelope species, there are many superfluous fit, adult and young-adult males which cannot reproduce for want of enough suitable territories, so that the continuous removal of territorial or redundant males by predation is of major importance in opening up territories and breeding opportunities for younger and sexually more vigorous males.

Schaller (1967) found that in the Kanha Park in India tigers also killed more male than female sambar deer in spite of the fact that hinds outnumbered stags 3 : 1 in the population and suggests that this highly disproportionate sex ratio of adult sambar deer may be due to selective predation on adult males and possibly also on male fawns.

Of the major prey species of lions the predation pressure on the sexes and the adult sex ratio appear to be more or less equal only in the case of zebra and warthog.

In contrast to lions, predation by leopards, cheetahs and wild dogs is more heavily directed against the female segment of the population and is more in direct proportion with the adult sex ratio. This is particularly true of cheetahs and wild dogs, and a large proportion of females killed are gravid individuals in the period immediately prior to the lambing or calving season of the particular species (Vide Table 20).

(viii) *Predation as a limiting factor of ungulate populations.*

In an objective assessment of predation as a limiting factor of ungulate populations in the Park, some historical background to the subject becomes essential:

26th March 1898 — The Sabi Game Reserve was proclaimed by an act of the Volksraad of the old Z.A. Republic and signed by President Paul Kruger and Dr. Leyds.

1899 - 1902 — The period of the Anglo-Boer War when large numbers of animals were slaughtered in the Transvaal Lowveld by the warring factions and the resident African tribes.

1903—Col. Stevenson-Hamilton, the first warden appointed after hostilities ceased, found the number of game animals in the Old Sabi and Shingwidzi Reserves (Fig. i) very low, but with disproportionately high numbers of carnivora (especially lion and wild dog).

1912—The first estimates of the total number of game animals in the Sabi and Shingwidzi Reserves were made. These are given as ca. 24,000 (of which 4,000 were waterbuck and 1,000 sable) in the Sabi Reserve and about half that number in the Shingwidzi Reserve.

1915—A more detailed estimate of game numbers suggested a total of 23,000 head in the Sabi Reserve and 19,800 in the Shingwidzi Reserve (including 6,500 waterbuck, 3,500 sable, 800 roan antelope (300 in the Sabi Reserve), 1,000 Tsessebe and only 6,800 impala in the whole area). The surprisingly high population of waterbuck during those early times, when compared with the present population, is due to a number of factors. Conservation of waterbuck was launched, in the first place, on a much higher level than that of the other antelope species, as it was not a favoured quarry of the old hunters, in view of its coarse flesh. At the proclamation of the old Sabi and Shingwidzi Reserves these animals still occurred in considerable numbers and were, in fact, at that particular time the most common large ungulate in the Lowveld — so much so, that waterbuck were utilised as rations by the Ranger staff in the olden days. The area covered by the original Sabi Reserve also included large tracts of

land between the present western boundary and the Drakensberg foothills, and the whole area was much more richly endowed with natural water than is the case today. The waterbuck, being a preferred prey of lions and other carnivora, probably also benefited by the stringent carnivora control measures instituted soon after the proclamation of the reserves.

1914 - 1918 — The First World War. Control was relaxed and poaching became an important decimating factor.

1923—A large tract of well-watered country, including the best sable, roan and reedbuck habitats in the old Sabi Reserve, was excised and turned over for African and European settlement (Vide Fig. (i)).

1925—Immediately prior to the reproclamation of the old Sabi and Shingwidzi Reserves as the new Kruger National Park, the total number of game animals in the Sabi Reserve (including the area between the Letaba and Olifants Rivers) was estimated at 100,000 and 30,000 in the Shingwidzi Reserve,

There was thought to be 600 lions in the whole area i.e. 216 game animals for every lion. A progressive decrease in the number of wild dogs was noted. Hyaenas, which were at one time almost exterminated by trapping, were again increasing slightly. Cheetahs were not numerous, but it is claimed that they were never very common.

Extensive burning of the veld in 1925 was followed by a severe drought which caused a famine during which animals such as sable and waterbuck suffered very severely.

1926—The Kruger National Park was proclaimed in its present form.

1930—In his annual report the Warden mentions that sable is again slowly increasing after the havoc of the 1926 - 28 famine.

1932—The remarkable and progressive decrease in the numbers of wild dog which occurred since about 1925 onwards, was ascribed to a possible epidemic disease and brought the population levels in the southern and central districts to a very low ebb.

1945—Col. Stevenson-Hamilton just prior to his retirement in 1946, estimated the total number of game animals in the Kruger Park as 260,000. There was an obvious over-estimation in the number of impala however, and this was subsequently proved by more refined census techniques. The total number of game at this stage therefore, probably did not exceed 160,000.

1954—Warden L. B. Steyn, after a ground census of game animals, concluded that there were in the Park at that time 870 sable, 477 roan antelope, 600 tsessebe, 2,050 waterbuck, 4,280 wildebeest and 5,270 zebra.

1959 - 1960—Two anthrax epidemics caused severe mortality amongst game animals in the northern district of the Park.

1960—The policy of carnivora control, which had been practiced since the earliest days of the Park's existence, was discontinued after representations by the research personnel.

1960 - 1961—The western, southern, northern and portions of the eastern boundary of the Park were fenced by the Department of Agricultural Technical Services, as a deterrent against the spreading of epidemic diseases from game to domestic stock.

1967—Culling of excessive numbers of impala, wildebeest and zebra was commenced in certain over-utilised areas in the central and southern districts of the Park.

1968—The latest estimate of game numbers, based on a series of aerial and ground censuses, provides a total of ca. 182,000 head of larger prey animals in the Park as a whole (i.e. about 180 prey animals for every lion). This total includes 97,400 impala, 14,143 wildebeest, 14,710 zebra, 15,867 buffalo, 5,250 kudu, 3,185 waterbuck, 2,405 giraffe, 1,860 reedbuck, 1,065 sable, 285 roan antelope, 765 tsessebe, 477+ eland (nomadic), 750 nyala, 240 mountain reedbuck and ca. 4,000 warthog.

When it is considered that there are today more impala in the Kruger Park than at any stage since the proclamation of the original Sabi Reserve in 1898 and that their population level has yet to exceed 100,000, according to much more sophistacted census techniques than were at the disposal of the old ranger staff, then it is obvious that previous estimates of impala numbers (variously quoted as between 180,000 and 250,000) were grossly exaggerated, and the total number of game animals in the area today by far exceeds the numbers present at any stage during the history of the Park.

1968—Culling of yearly increase in the numbers of elephant and buffalo populations was commenced.

The mere fact that culling of superfluous herbivorous animals has become necessary to protect the habitat from over-utilisation of both available food supplies and water, and this, after an eight-year period during which no carnivora control was exercised whatsoever, is ample testimony in favour of the concept that in a natural ecosystem predators alone cannot maintain a balance between the herbivorous animals and the natural resources of the habitat, although they may have a variable depressive influence on the numbers of wild hoofed animals.

This also provides further proof for Errington's (1956) supposition that "a great deal of predation is without truly depressive influence. In the sense that victims of one agency simply miss becoming victims of another,

many types of loss — including loss from predation — are at least partly intercompensatory in nett population effect. Regardless of the countless individuals or the large percentages of populations that may annually be killed by predators, predation looks ineffective as a limiting factor to the extent that intraspecific self-limiting mechanisms basically determine population levels maintained by prey."

When it is considered that even a species such as waterbuck, which is obviously the most preferred prey species of lions and many other predators in the Park, managed to increase their numbers from about 2,050 (in 1954) to 3,185 (in 1968), and other preferred prey species such as wildebeest, zebra and buffalo more than doubled their numbers, during a period when carnivora control was discontinued and despite setbacks caused by other agencies such as the drought of 1962 - 65 and the anthrax epidemics of 1959 - 60, then it becomes obvious that predation by carnivores is ineffective in keeping population growth in check, and that the overall decline in the numbers of such species as waterbuck, sable and roan antelope since the early days of the Park must be attributed to other causes. (Vide also Hirst, in press).

After the severe drought of 1910 - 1913 and the very bad one during 1926 - 28, other cataclysmic droughts were experienced in 1933 - 35, 1944 - 48 and 1962 - 65, during which time the populations of particularly sable, waterbuck and warthog were severely decimated.

In the intermediate eras there were temporary revivals in the population numbers during the pluvial conditions prevalent during 1917 - 25, 1936 - 43 and 1954 - 61.

There was a dramatic decline of reedbuck numbers in Pretoriuskop Section during the First World War period, when surveillance was relaxed and poaching became rife. Previously, a large reedbuck population (4,000) was maintained in the old Sabi Reserve despite the depredations of large packs of wild dogs — one of their main enemies. The wild dog population collapsed during the nineteen-twenties and early "thirties", but the reedbuck population was slow to respond. In 1923 the best reedbuck country and some of the best sable and roan habitats were excised from the old Sabi Reserve by the new delimitation of boundaries.

During the two severe anthrax epidemics which hit the northern district of the Park in 1959 and 1960, a large number of ungulates succumbed — amongst others, 877 kudu, 82 waterbuck, and 47 roan antelope. Circumstantial evidence indicates that these regions were also affected by anthrax epidemics during earlier times, although these were not recognised as such. Descriptions of carcases of waterbuck and kudu found are indicative of anthrax during the years of 1911 and 1913 (Shingwidzi and Zoutpansberg districts). and subsequently in 1916, 1923 (Letaba Section), 1933 and 1943.

Over the years, an insidious but progressive dessication of the Transvaal Lowveld became evident. Today many permanent waterholes and

strong springs of former years are much weaker or have dried up completely. Even some of the perennial rivers, such as the Letaba, are today so overtaxed by agricultural and industrial development beyond our borders that they stop flowing during the dry season. The available habitats for water-loving species such as waterbuck and reedbuck have consequently been drastically reduced.

A progressive encroachment of open grasslands by bush and reversion of open savanna to denser woodland-savannas, woodlands or thickets is remarked upon by Stevenson-Hamilton in 1943, and proceeded at an increased rate in such erstwhile open areas as Pretoriuskop during the period 1947 - 54, when all controlled grass burning was prohibited. A concomitant increase in browsing species and decrease in grazing species became evident. Many grazing animals such as wildebeest, zebra, sable, roan and waterbuck emigrated to the more open country in the west, from whence few returned. Habitat regression and bush encroachment also detrimentally affected populations of plains-loving animals such as eland, roan, tsessebe, ostrich and cheetah in other parts of the Park.

Since 1954 an efficient system of fire-breaks was constructed to limit the devastating effect of wild grass fires during the dry season, and a scientific system of grazing management was instituted. Water supplies have also been stabilized and augmented at an increasing rate through sinking of bore-holes and erection of dams and weirs.

The western, southern, northern and portions of the eastern boundary of the Park were fenced during 1960 - 61 in order to curb the spreading of foot-and-mouth disease and other epidemic diseases transmissible from game to domestic stock. The western boundary fence south of the Olifants River finally arrested the age-old east-west migration pattern of game during the dry season, and they had to adapt to the man-made barrier by opening new routes to and from seasonal grazing grounds and water. This was accomplished in a surprisingly short time, and a new north-south migration pattern was established. Before the fencing of the Park's boundaries considerable numbers of game were killed annually by hunters and poachers when they crossed into settled country during the dry season.

Carnivora control was exercised in the Kruger Park to a greater or lesser degree since the earliest days of its existence until as recently as 1960. Prior to 1933 carnivora of all species were systematically destroyed by the ranger staff wherever the opportunity offered, and large numbers of predating animals were shot, trapped and poisoned under the illusion that this would promote a healthy predator-prey relationship. After 1933 control operations were aimed primarily at the larger carnivorous mammals and crocodiles, but considerable numbers were still destroyed in an indiscriminate and often rash manner. Even during modern times (1954 - 60) several hundred head of lion, 229 wild dog, 205 hyaenas, 51 cheetah and 42 leopards were shot in this sanctuary.

The futility of this policy had already dawned on Col. Stevenson-Hamilton where he wrote: "Lions increase in proportion to the animals on which they live. If attempts are made to reduce their numbers artificially, while there is an abundance of game at their disposal, they make up for it by becoming increasingly prolific. In the Sabi Reserve, where a reduced number of now very wary lions were surrounded by great numbers of grass eaters, the lionesses brought forth as many as four and five cubs in a litter, instead of the usual two and three and at the same time the mortality of cubs dropped to almost nil. Thus the big cats increased at about twice their normal rate. Prides of 20 and more, consisting mainly of cubs and half-grown animals, were of everyday occurrence. Little by little the herbivores lost the unnatural advantage which they had enjoyed for some time, and the lions again began to find hunting more difficult. The younger members of the big prides had great trouble getting at a kill, and many of them starved or were killed by the older animals. The lionesses found it no longer as simple a matter to raise their families, and the mortality rate rose once more.

The balance of nature which had been disturbed by man, thus automatically readjusted itself."

Since the fencing of the Park, conditions of overpopulation of prey species in certain habitats have become glaringly apparent, particularly during periods of drought (Pienaar, 1969), and have necessitated steps to cull the annual nett increase of populations such as impala, wildebeest, zebra, buffalo and elephant. Culling of hippo and giraffe numbers may also become necessary in the not too distant future. It is conceivable that these surplus animals had during pristine times fallen victim to primitive man (the super-predator of those days) in stable environmental situations, or were periodically wiped out by epidemic diseases or famines in overcrowded conditions.

It may be concluded that in a natural area the size of the Kruger Park a large predator community is not inimical to the respective prey populations and may exert a definite limiting influence perhaps only in the case of the most preferred prey species such as waterbuck, or where buffer populations of preferred prey species do not offer sufficient protection to low-density populations such as roan, sable and eland.

The stabilization of permanent water supplies, sound grazing management, an efficient fire-break system, control of poaching and drastic epidemic diseases and the manipulation of portions of the habitat to suit the particular requirements of rare prey species, are much more effective and lasting management practices than carnivora control in achieving a stable relationship between predators, prey species and the available natural resources of the habitat.

SUMMARY

Records of carcases found in the Kruger Park during the periods 1935 - 46 and 1954 - 66 have been used as a basis for tables which should provide a clearer insight into predator-prey relationships amongst larger mammals in this area. A margin of error has been allowed and vegetation types, habitats and density of both predator and prey populations have been taken into consideration.

Predators are divided into true predators (lion, leopard, cheetah, wild dog), scavenger-predators (hyaenas and jackals), and minor predators (crocodile, caracal, serval, baboon, python and martial eagle). For each predator the following information is given: numbers in the Kruger Park, range of prey species, preferred prey species, influence of population density of prey species on predation, the estimated kill frequency per annum per predator, hunting characteristics and methods, hunting range, size of pride or pack, and predation as a limiting agency in population increase or decline.

Evidence of differential predation according to sex and age of prey, and season of the year has been found and is discussed.

An historical resume of management practices in the Kruger Park since the earliest days as they affect predators and prey species is given, and the author concludes that,

"a large predator community is not inimical to the respective prey populations and may exert a definite limiting influence perhaps only in the case of the most preferred species. The stabilization of permanent water supplies, sound grazing management, an efficient fire-break system, control of poaching and drastic epidemic diseases and the manipulation of portions of the habitat to suit the particular requirements of the rare prey species, are much more effective and lasting management practices than carnivora control, in achieving a stable relationship between predators, prey species and the available natural resources of the habitat."

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SYSTEMATIC LIST OF PREDATOR AND PREY SPECIES REFERRED TO IN THIS PAPER

PREDATORS AND SCAVENGERS:

Lion	*Panthera (Leo) leo krugeri* (Roberts)
Leopard	*Panthera pardus* (Linnaeus)
Cheetah	*Acinonyx jubatus jubatus* (Schreber)
Caracal	*Felis (Lynx) caracal caracal* Schreber
African wild cat	*Felis sylvestris cafra* Desmarest
Serval	*Felis (Leptailurus) serval hamiltoni* Roberts
Wild dog or African hunting dog	*Lycaon pictus pictus* (Temminck)
Spotted hyaena	*Crocuta crocuta* (Erxleben)
Brown hyaena	*Hyaena brunnea* Thunberg
Saddle-backed jackal	*Canis mesomelas mesomelas* Schreber
Side-striped jackal	*Canis adustus* Sundevall
Baboon	*Papio (Chaeropithecus) ursinus* (Kerr)
Crocodile	*Crocodylus niloticus* Laurenti
Python	*Python sebae* (Gmelin)
Martial eagle	*Polemaetus bellicosus* (Daudin)

PREY SPECIES:

Elephant (African)	*Loxodonta africana africana* (Blumenbach)
Black rhinoceros	*Diceros bicornis bicornis* (Linnaeus)
Square-lipped or White rhinoceros	*Ceratotherium simum simum* (Burchell)
Burchell's zebra	*Equus (Hippotigris) burchelli antiquorum* H. Smith
Bush pig	*Potamachoerus porcus nyassae* Forsyth Major
Warthog	*Phacochoerus aethiopicus sundevalli* Lönnberg
Hippopotamus	*Hippopotamus amphibius capensis* Desmoulins
Giraffe	*Giraffa camelopardalis giraffa* (Boddaert)
Natal or Red Duiker	*Cephalophus natalensis amoenus* Wroughton
Grey duiker	*Sylvicapra grimmea caffra* Fitzinger
Steenbuck	*Raphicerus campestris capricornis* Thomas & Schwann
Sharpe's grysbuck	*Raphicerus melanotis sharpei* Thomas
Livingstone's Suni	*Nesotragus moschatus zuluensis* Thomas
Oribi	*Ourebia ourebi ourebi* (Zimmerman)
Klipspringer	*Oreotragus oreotragus transvaalensis* Roberts
Reedbuck	*Redunca arundinum arundinum* (Boddaert)
Mountain Reedbuck	*Redunca fulvorufula fulvorufula* (Afzelius)
Waterbuck	*Kobus ellipsiprymnus ellipsiprymnus* (Ogilby)
Impala	*Aepyceros melampus melampus* (Lichtenstein)
Roan antelope	*Hippotragus equinus equinus* (Desmarest)
Sable antelope	*Hippotragus niger niger* (Harris)
Tsessebe	*Damaliscus lunatus lunatus* (Burchell)

Blue Wildebeest	*Connochaetes (Gorgon) taurinus taurinus* (Burchell)
Bushbuck	*Tragelaphus scriptus roualeyni* (Gray)
Nyala	*Tragelaphus (Nyala) angasi* Gray
Kudu (greater)	*Tragelaphus strepsiceros strepsiceros* (Pallas)
Eland	*Taurotragus oryx oryx* (Pallas)
Buffalo	*Syncerus caffer caffer* (Sparrman)
Night Ape	*Galago senegalensis moholi* A. Smith
Vervet Monkey	*Cercopithecus aethiops* (Linnaeus)
Baboon	*Papio (Chaeropithecus) ursinus* (Kerr)
Honey badger (Ratel)	*Mellivora capensis capensis* (Schreber)
Civet cat	*Viverra (Civettictis) civetta australis* Lundholm
Antbear	*Orycteropus afer afer* (Pallas)
Scaly anteater	*Manis (Smutsia) temmincki* Smuts
Rock Hyrax	*Procavia capensis* (Pallas)
Yellow-spotted Hyrax	*Heterohyrax brucei ruddi* (Wroughton)
Lowveld scrub Hare	*Lepus saxatilis zuluensis* Thomas & Schwann
Mole rats	*Cryptomys komatiensis* (Roberts) and *Cryptomys hottentotus vandami* Roberts
Porcupine	*Hystrix africae-australis* Peters
Cane rat	*Thryonomys swinderianus* (Temminck)
Grey-footed squirrel	*Paraxerus cepapi cepapi* (A. Smith)
Spring hare	*Pedetes capensis salinae* Wroughton
Swamp rat	*Dasymys incomtus incomtus* (Sundevall)
Angoni vlei rat	*Otomys angoniensis rowleyi* Thomas
Land Tortoises	*Testudo (Geochelone) pardalis babcocki* Loveridge and *Kinixys belliana belliana* Gray
Water Tortoises	*Pelusios sinuatus sinuatus* (A. Smith) and *Pelomedusa subrufa* (Lacépède)
Boomslang (Tree snake)	*Dispholidus typus* (A. Smith)
Ostrich	*Struthio camelus* Linnaeus

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