

FOOD ECOLOGY OF THE KALAHARI LION *Panthera leo vernayi*

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Abstract – Aspects of the food ecology of the lion were researched in the Kalahari Gemsbok National Park. A survey based on 195 periods of 24 hours each, indicated that porcupines represented 32,3% and gemsbok 25% of lion kills. Because so many small or young mammals are being caught, a single Kalahari lion probably makes as many as 50 kills per year — considerably more than anywhere else in Africa. The Kalahari lion covers a distance, on average, of 11,8 km per night in search of food. The hunting success of the Kalahari lion, the ecological division of predators, and the effect of food on mortality is discussed. Predation by lions seems to play an insignificant role in the regulation of prey population numbers.

Introduction

The food ecology of a predator covers a wide variety of activities. In this article about the Kalahari lion its diet, its food intake, some of its activities concerned with obtaining food, and its hunting success will be considered.

An article on aspects of the Kalahari lion's food ecology was published in 1973 (Eloff 1973). It was based on observations made over a period of three years and covered all the activities of individual as well as groups of lion during 91 nights. The activities of another 104 nights have been added since 1973. All the data are discussed in this article.

The same methods were applied for both parts of the project, which ensured that all kills, regardless of the size of the prey, were recorded (Eloff 1973).

Diet

It is known that lions have a catholic taste. According to Pienaar (1969), *Panthera leo krugeri* of the Kruger National Park feeds on at least 37 different species: 34 types of mammals, as well as ostriches, crocodiles and tortoises.

The situation in the Kalahari Gemsbok National Park is indicated in Table 1. This table is based on 195 nights' activities and indicates that porcupines represent 32,3% and gemsbok 25% of lion kills. Together they represent 57,3% of all Kalahari lion kills.

Table 1

Lion kills encountered in the Kalahari Gemsbok National Park between July 1970 and January 1983

Species	No. killed	Percentage of total kills	Note
Eland	1	1,0	adult
Gemsbok	24	25,0	12 adults 6 subadults 6 calves
Red hartebeest	8	8,3	4 adults 4 calves
Blue wildebeest	3	3,1	3 adults
Springbok	10	10,4	6 adults 4 lambs
Duiker	1	1,0	
Steenbok	1	1,0	
Porcupine	31	32,3	
Springhare	1	1,0	
Aardvark	3	3,1	
Lion	1	1,0	
Brown hyaena*	1	1,0	
Honey badger*	1	1,0	
Bat-eared fox	3	3,1	
Suricate*	1	1,0	
Ostrich	4	4,2	
Kori Bustard	1	1,0	
Secretary Bird*	1	1,0	

* not eaten

Apart from these kills, it was also recorded that three females broke and ate one ostrich egg out of a nest of five. This is not the first record of lions eating ostrich eggs. Judith Rudnai (1971) described how two females found an ostrich nest and enjoyed a giant omelette.

Carrion

It is known that lion will rob food from other predators and will also eat carcasses which are in an advanced state of decay. The Kalahari lion is no exception. Cases of lion chasing away leopard or spotted hyaena from a carcass and taking it for themselves, have been recorded.

Cannibalism

Cannibalism often occurs and a lion killed in a fight is sometimes eaten by its opponent or, if he was a member of a group, by others of the group.

Cubs are also killed and eaten by lions. Various cases in the Kalahari Gemsbok National Park were brought to my attention. A cub suffering from rachitis was the only case of which I have personal knowledge. He could hardly walk and his mother had to carry him long distances. He was later eaten by his mother and father. It is not sure whether the male or female killed the cub, or both did, or whether the cub was already dead when it happened.

Other carnivores

Lions often kill other carnivores, but seldom eat them. In the Kalahari several cases are known of lion killing spotted or brown hyaena, but not once have these animals been reported as eaten. Most of these incidents did not happen at carrion, but while the hyaena were lying at their burrows. Sometimes these animals are only mutilated and left to die a painful death.

Other carnivores killed by lion in the Kalahari are the honey badger, bat-eared fox and suricate. The bat-eared fox is sometimes eaten, but not always. It is often caught and usually devoured completely, but, in isolated cases simply abandoned.

Consequently other carnivores are not an important source of food for the lion, except maybe the bat-eared fox which might be an important emergency ration for the Kalahari lion. Strangely enough the black-backed jackal is not caught by lion in the Kalahari, although it is often caught and eaten by leopard.

Small mammals

One of the most remarkable aspects of the Kalahari lion's food ecology is the high frequency of small mammal kills.

In the Kruger National Park small mammals represented less than one per cent of all lion kills recorded over a period of 25 years and covering more than 25 000 kills (Pienaar, 1969). The same applies to the Serengeti area. Schaller (1972) listed 1 180 items eaten by lion, and only two of these were small mammals — a pangolin and a hare.

In the Kalahari Gemsbok National Park small mammals and young animals (calves and lambs) represent 57,6% of all recorded lion kills. To see this in perspective, one must bear in mind that small mammals are in most cases under-represented in figures given for lion kills as a result of the method used to identify lion kills. Usually small mammals are devoured completely without leaving any traces and are never, or at least very seldom, recorded. This has been accentuated by various researchers in their evaluation of lion kills (Hirst 1969; Pienaar 1969; Schaller 1972).

According to the method applied in the Kalahari, every kill, even if only a springhare, is observed and recorded. This may be the main reason why so many small mammals appear on the Kalahari lion's menu. In any event, I believe that the Kalahari lion anyway kills more small mammals than other lions, because he sometimes has nothing else to eat. Although small mammals are unimportant in terms of bio-

mass, they may play a significant role as a maintenance diet during periods of insufficiency.

Another remarkable aspect of the Kalahari lion's food ecology, is his partiality, or at least his dependence, on porcupines. In other parts of Africa, including the Kruger National Park, porcupines are also caught by lion, but only in exceptional cases; Schaller (1972) said about the porcupine: "Lions rarely kill it." In this respect the Kalahari lion is probably unique.

Age and sex of prey animals

The gemsbok is the only prey animal of which a significant sample exists. Unbelievable as it may sound, the 24 gemsbok kills consisted of six adult bulls, six adult cows, six young animals (one to two year old) and six calves, in other words 12 adult and 12 young animals. Fifty per cent of the young component consisted of calves, that is 25% of all kills, which is remarkably high considering the gemsbok's habit of concealing their calves. When hidden the calves lie completely flat and do not flee from man or animal. I have observed lions passing within five metres from such a calf without detecting it.

I do not have sufficient figures for different age categories, and so I am unable to draw any conclusions about the vulnerability of the various age groups. It is interesting that 83% of blue wildebeest kills in the Kruger National Park were identified as adult animals. Eighty per cent of all zebra, and 84% of the buffalo were adult. In comparison only half the gemsbok caught in the Kalahari Gemsbok National Park are adult animals. The Kalahari lion either kills relatively more young animals, or young animals and calves in particular are under-represented in the numbers for the Kruger National Park, an inherent shortcoming of almost all data concerning lion kills.

In this connection I refer to Bertram (1978) who maintains: "A greater proportion of very young animals are taken from most prey species than would be expected on the basis of their relative numbers in the live population."

Although the numbers available on springbok and red hartebeest are inadequate to be conclusive, it is interesting that 50% of the latter, of which the age could be determined, were adult, and the other 50% were young. Six of the ten springbok killed were adult and the other four young, in other words 60% were adult; thus the young component is much higher than in other areas.

Activities

Now that we know what the lion's diet consists of, we can look at the activities necessary to obtain food. These include not only the actual hunting, but all activities during every 24-hour period.

The question may arise what daily activities have to do with food. Not all the lion's activities, such as sleeping, resting, running, and so on have something to do with food. It might be just to drink water, or to communicate with each other. But at night lions mainly move in search of food. The lion is an opportunist. He will move inside his hunting area, and it depends to a great extent on the presence of prey animals and his own acumen whether the night's hunt will be successful.

Like all other lions, the Kalahari lion's hunting activities are mainly nocturnal. Thanks to our Bushman trackers a step by step report on the Kalahari lion's nocturnal activities was recorded. These activities during 123 24-hour periods, from January 1973, indicated that groups and individual lions covered an average of 11,8 km per night. Unfortunately too few observations were made during winter, so the activities during winter and summer cannot be compared. Some other conclusions can be drawn from this information.

It seems that females cover greater distances than males. The greatest distance covered during a single night was 41,2 km covered by a female. The next greatest distance covered in a single night was 33,6 km by a group of six females and a young male two to three years old.

The greatest average daily distance covered over a period of more than one night, was achieved by three females, which travelled an average of 22,34 km over eight nights. Second place goes to a female (the champion mentioned above) which covered an average distance of 16,2 km over 10 nights. Two males covered an average of 15,1 km over six nights.

It should be mentioned that the three females referred to above did not make a single kill during a period of eight nights and this influenced the distance covered, since lions remain at a big carcass for up to two days and do not walk far on a full stomach.

Cubs do not influence the distance covered by groups, because when they are big enough to accompany the mother on hunts, they are left behind at a certain stage and fetched again as soon as a kill has been made.

Young lions are remarkably tough and have surprising endurance. A young lion of about six months old accompanied four females for 10 nights and covered an average distance of 9,4 km per night. One night she (it was a female) covered 16,9 km.

Cubs of eight weeks old are usually left behind when the adults go hunting, but this does not always happen, and I would like to mention one incident to illustrate this point.

One cub of about eight weeks old accompanied his mother in a group consisting of a male and three adult females. The cub's age could be calculated with reasonable accuracy, because another female and three cubs of a known age were present in another part of the research area at the time. Over a period of nine days the cub accompanied the group on all their excursions and covered a distance of 68,4 km. On one single night he covered a distance of 13 km. During these nine days, when the heat was intense, the group drank water three times and killed a young gemsbok, two porcupines and a kori bustard — not much food for four adult lions.

The courageous little cub kept up with them all the time. One night the group started trotting and carried on for two kilometres. The cub accompanied them. When they slowed down to a walk again, the cub remained behind. The group continued and 3,5 km further on killed a young gemsbok. Usually the mother returns to fetch her cub, but not in this case. Whether she called him or whether he followed them on his own initiative, is not known, but he joined them at the kill. His tracks indicated that he walked alone for 3,5 km in a direction parallel to that of the adults. Sometimes he ran, and he had to cross numerous sand dunes and force

his way through dense grass and shrub in an area where hyaena, honey badger and other predators abound.

Hunting success

How successful is the Kalahari lion as a hunter? Hunting success is not only measured by the hunter's abilities, but also by the prey animal's dexterity. It also varies from place to place and from one season to another, depending on ecological conditions.

There is no sense in comparing the hunting success of the Kalahari lion with that of Schaller's Serengeti lions or Pienaar's Kruger Park lions, because the prey animals and the conditions under which hunting takes place, make such a comparison absurd.

Even in the Kalahari it is difficult to measure hunting success. Does the killing of a porcupine and a bat-eared fox reflect hunting ability to the same extent as the killing of a gemsbok? I will, in any case, give the figures concerning the recorded hunting attempts, from a springhare to an eland. I will later present it in terms of particular prey species.

Fifty-seven of the 148 hunting attempts recorded were successful: in other words, there was a hunting success of 38,5%. It is interesting to note that the results would have been totally different if the attempts of two groups were omitted. I followed three females who made nine unsuccessful attempts, while a single female succeeded in three out of 33 attempts. If these attempts are disregarded, the hunting success would have been 49,5%.

These figures do not have much meaning. Schaller (1972), who observed more than 500 hunts, discusses the hunting success of lions in different types of habitat, the success of nocturnal and diurnal efforts, the correlation between hunting success and the number of lions taking part, the degree of success with regard to the different prey species, and the role played by other factors such as climate, wind, etc.

Unfortunately I did not record all the hunting efforts from the start, but since I have started doing so, the following information on the hunting success in respect of three prey species, namely aardvark, porcupine and gemsbok, has been collected.

Three out of 22 hunting attempts on aardvark were successful. This gives a hunting success of 13,6%. Twenty-three out of 27 hunting attempts on porcupines were successful, in other words 85%. Only six out of 39 hunting attempts on adult gemsbok were successful, *i.e.* only 15%. I must add that a single, inexperienced female was responsible for 16 out of the 33 unsuccessful attempts on gemsbok. If this female is ignored, which, naturally, cannot be done, the successful attempts would number 6 out of 23, in other words 26% instead of 15%.

The hunting success regarding aardvark, *i.e.* 13,6%, is particularly low compared with the hunting success of 85% involving porcupines. The habits of the prey animal, as well as its anti-predator behaviour, must be kept in mind. We know very little about nocturnal animals such as the aardvark and porcupine, but it seems that the aardvark seldom loiters further than 200 metres from its burrow. When pursued by a lion, it takes a shortcut to its burrow which is usually close enough to

offer escape from its pursuer. The aardvark is also much faster than the porcupine and when a lion is pursuing it, it can avoid the lion by twisting and turning and when the lion runs past, it can reach its burrow.

I tried to find a correlation between the size and composition of the group on one hand, and prey partiality on the other, but could not find any meaningful relationship, maybe as a result of too little information being available.

Most groups of lion kill a variety of animals, but interestingly enough the largest group (consisting of 13 lions) which I have ever followed, caught only gemsbok — five (two adults and three calves) over a period of five nights.

A female which hunted alone caught only porcupines — four in four nights — and a group consisting of one male and two females also caught only porcupines — five in ten nights.

Food intake

From the article previously mentioned (Eloff 1973), I arrived at the conclusion that the daily food intake of a female is 4,7 kg, while that of the male is 7,2 kg. These figures are very close to those mentioned by Schaller (1972).

The research also indicated:

- a. About a third of the carcass is not eaten.
- b. The Kalahari lion can eat at least one fifth of its body mass in one meal. According to Schaller (1972) it can be one quarter, and according to Kruuk (1972) a spotted hyaena can eat one third of its body mass at a time.
- c. The Kalahari lion kills more animals per year than lions in other parts of Africa.

According to various authors, lions kill 12 to 36 prey animals per year. Pienaar sets it at 15 in the Kruger National Park. In the Kalahari the number is about 50, which is much higher than any of the figures given above. This is the result of the many small mammals killed by the Kalahari lion, and it also accentuates the fact that it is not even worth debating the point because of the large variation in size and mass of the prey animals killed. These numbers provide a distorted picture because a gemsbok and a porcupine are equal on a list of kills, although the first provides ten times more meat.

Discussion

Ecological division of predators

Since the ecological division of predators is presently being researched in the Kalahari Gemsbok National Park, I would like to make the following comment on the subject. In the previously mentioned article on the food ecology of the Kalahari lion (Eloff 1973), I mentioned that: "There appears to be more overlap in the prey species of the Kalahari's four main predators than anywhere else in Africa and this is probably mainly due to the smaller range of prey species available."

Today I doubt whether this statement is true. The hypothesis that different predator species can co-exist because each one hunts a different set of prey animals, seems basically plausible, but it might be taking it too far. Overlapping of prey species of predators living in the same habitat is much more common than it might seem at first glance.

Pienaar's (1969) information on the Kruger National Park indicates that 22 out of the 24 species eaten by cheetah are also found on the lion's menu. There is, in other words, an overlap of 92%. Twenty-five of the 31 species eaten by leopard are also eaten by lion, an overlap of 80,6%, and all 12 items eaten by spotted hyaena, are also eaten by lion. Lion, leopard, cheetah and spotted hyaena to a great extent share the same resources in the Kruger National Park, but by concentrating on different segments of the prey population, competition is kept to a minimum. If greater competition occurs among the four large predators in the Kalahari Gemsbok National Park than elsewhere in Africa, it is not as a result of greater overlapping of prey populations, but rather as a result of the smaller variety of prey species available.

Maybe there does exist a unique situation in the predator-prey relationships of the large predators in the Kalahari, but the puzzle has not yet been resolved.

The effect of food on mortality

Adult lions

No positive information is available on this topic, but one can speculate that food scarcity caused by a lack of prey animals during certain periods in arid country, such as the Kalahari, might well have an influence on the mortality rate of adult lions, and old, sickly animals in particular. I know of two cases where lions died as a result of wounds caused during skirmishes with porcupines. These animals did not die immediately; in fact, they actually died of starvation and hardship after suffering long and bitterly.

Cubs

Starvation is probably one of the most important factors of cub mortality in the Kalahari as a result of the Kalahari lion's habits and the type of habitat.

The Kalahari lion's partiality for and dependence on smaller prey animals were probably forced on him by the scarcity of larger prey species during certain times of the year. Especially during times of scarcity the Kalahari lion is forced to be more dependent on small mammals than anywhere else in Africa. In our research area it was found that small prey animals are completely devoured by adult lions and that literally nothing is left for the cubs in the group. Schaller (1972) noted that Thomson's gazelle are below the optimum size for lion and added: "When only small gazelle are available, cubs get little or no food." According to him one out of every five cubs die of starvation at Seronera.

The same applies to the Kalahari, and when only small prey animals are being killed, the cubs and young lions have to go without food for long periods. A female, which has small cubs to feed, needs more than a small portion of porcupine or any other small prey animal to keep up her milk production.

Under these circumstances small cubs which are completely dependent on the mother's milk, or older cubs which are partially dependent on meat to supplement their food supply, will die of starvation, and as a result of the particular circumstances in the Kalahari this is a mortality factor of extraordinary importance.

Lions sometimes have to cover great distances to obtain food; a distance of 41 km

has been recorded. Cases are known of pregnant females which had to go without food and water for seven days. This inevitably affects the mother's milk supply.

If females with cubs are unsuccessful in their hunting attempts, they do not return to the cubs on the same night. In one case the mother stayed away for five nights and on her return two of the three cubs had died of starvation and the third was in a poor condition.

At a certain stage of their lives young lions must take in enough calcium and phosphorus for the development of the bone structure. If not, they contract the deficiency disease rachitis (rickets). Because the small prey animals are completely devoured by adult lions, cubs do not only starve, but also suffer of rachitis and we have records of two cubs who died of rachitis. Other cases were observed by Elias le Riche (*pers. comm.*).

The impact of predation on prey populations

The impact of predation on prey population is one of the most controversial subjects in modern ecology.

Information on predator-prey relationships differs to such an extent that generalisations are impossible. While predation may restrict the growth of a prey population in one area, it may have no visible effect in another. In this regard many examples can be mentioned from Serengeti, Ngorongoro Crater, Nairobi Park, Kruger National Park, and other parts.

In Errington's (1956) hypothesis on the factors restricting the numbers of the higher vertebrate populations, he stated that predation as a regulative factor is of little value if the level of the prey population is determined by other influences. Errington's hypothesis might be applicable in the Kalahari where the population levels of antelopes and other herbivores are to a great extent determined by factors such as food supplies, shelter and the extreme environment conditions. Predators may play a small role in the regulation of prey population numbers under certain circumstances. It seems that the number of lions is restricted by their own food supply, as maintained by Lack (1954).

The vulnerability of the prey is to a great extent determined by the type of habitat. In the Kalahari with its open areas and lack of effective shelter, it can act as an important factor restricting the predator population. Habitat conditions may play an important role in the selection of the prey and the tempo of predation on all the different prey species, which may reduce the modifying effect of predation by lion.

By means of seasonal migrations, which sometimes assume enormous proportions, the Kalahari's prey populations seem to remain within the limits of their food supply and so maintain a reasonably well-balanced population level. Under these circumstances predation by lion may play an unimportant role in the regulation of prey population numbers.

One wonders whether a stable biotic interaction can develop to such an extent that it has a controlling effect in a community where predator-prey interactions are of an opportunistic nature.

It is true that predators have an influence on prey population numbers, but in the Kalahari, in particular, where the amount and distribution of rainfall has a great influence on the available food, the food supply might be the eventual regulatory factor.

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