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Abstract: Lions, leopards, cheetahs and wild dogs in the Serengeti area attack different prey size and use different hunting techniques. The diet can change according to the individual (in leopards) or sex (in lions). For lions, the number of hunted prey is a function of their size, however this is not true for hyenas. Thomson's gazelle represents the principal prey attacked by these predators, with the exception of the lion that prefer wildebeests, for that it is responsible of only 1.2% of its natural mortality.

MAMMALIA

COMPARATIVE NOTES ON PREDATION BY LION, LEOPARD, CHEETAH AND WILD DOG IN THE SERENGETI AREA, EAST AFRICA

by

H. KRUUK * and M. TURNER **

Les méthodes de chasse et de sélection des proies diffèrent pour chacun des prédateurs étudiés, même lorsqu'ils s'attaquent à la même espèce (gazelle de Thomson). La taille des gibiers recherchés est également variable.

Le régime alimentaire peut différer suivant l'individu (chez les léopards) ou le sexe (lions). Le nombre de prédateurs par proie peut être soit fonction (cas des lions), soit indépendant (cas des cynhyènes) de la taille de celle-ci.

La gazelle de Thomson constitue la base de l'alimentation des prédateurs étudiés, à l'exception du lion dont la proie principale est le gnou. Le lion n'est cependant responsable que de 1,2 % de la mortalité naturelle de ce dernier.

I. INTRODUCTION

In spite of the store of knowledge built up by many observers of large African predators, the published reliable information on their ecological niches and their hunting and feeding is still surprisingly poor. Furthermore, an insight into the part played by the various predators will be important for our ultimate understanding of the selection pressures that operate amongst the many species of plains game and is imperative already now if we are to formulate a sound management plan directed at the conservation of these vast numbers of animals. These are the needs which have prompted the present paper.

Certainly the most numerous predator in the area discussed is the Spotted Hyaena *Crocuta crocuta* (Erxleben) ; but this species will not be considered here because it is the subject of a special

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study (Kruuk, 1966). Here we want to deal with problems of prey-selection by the other four common big carnivores — the lion *Panthera leo massaica* (Neumann), the leopard *Panthera pardus pardus* (Linnaeus), the cheetah *Acinonyx jubatus raineyi* (Heller) and the wild dog *Lycaon pictus lupinus* (Thomas). We will consider observations on their food preferences and on their hunting methods and we will try to explain, at least in part, the differences in their diets.

It is clear that the predator-prey relationship is determined not only by the actions of the predator, but also by the behaviour and ecology of the prey ; how complicated such an interaction can be has been shown in another situation (Kruuk, 1964). We are not yet able to evaluate the importance of the behaviour of the prey, but will confine ourselves to outlining some of the predators' behaviour patterns which may explain some of the differences in diet and which may enable us at a later stage to link up with observations on the behaviour of prey-animals.

In the following sections, first a very short account will be given of the area and the numbers of game present in it. Then observations on hunting methods and the diet of each predator in the different habitats will be presented, and in the discussion the 4 predators will be compared with each other, after shortcomings of our methods have been briefly considered. Finally, some remarks on the ecological importance of each predator will be made.

Our data are based on direct observations of predators either seen hunting or found with their kills. They were gathered by M. Turner from 1957 till mid-1964 and from then on by both authors until the end of 1965. For statistical evaluation, non-parametrical tests were used with tables from Siegel (1956).

II. HABITATS AND ANIMAL NUMBERS

Our observations have been carried out in the area covered by the annual migrations of the most common species of plains game, about 8,000 square miles. This is the present Serengeti National Park and the rest of the Serengeti Plains to the east of this ; the Grumeti, Ikorongo and Maswa Controlled Areas are also included. Descriptions of the geography and vegetation of the

region have been presented by Pearsall ( )56) and Grzimek & Grzimek (1959, 1960). The country consist for about a third of grass plains with occasional rock outcrops the « kopjes » ; the rest is made up of different types of bush ountry, varying from dense thorn-scrub to plains with widely sc ttered trees. Through both plains and bush run a number of rive -valleys which, at the edge of the plains and in the bush-countr , have a fairly dense vegetation of tall trees and shrubs, very clea ly demarcated against the surrounding vegetation.

It is clear by now that migration and seasonal reproduction cause considerable fluctuations in the number of animals of different species in the area and also there are large fluctuations in numbers over the years. Hence absolute figures of game counts are only valid over a relatively short period. Three such counts were carried out during our period of observation, the results of some of which are presented in table 1.

TABLE 1

Numbers of some ungulates in the Serengeti

	1958 (Grzimek, 1960)	1961 (Stewart & Talbot, 1962)	1963 (Turner & Watson pers. comm.)
Wildebeest	99,481	221,699	338,000
Zebra	57,199	151,000	over 160,000
Gazelle	194,654	480,000 - 800,000	
Topi	5,172	15,766	
Buffalo	1,813	15,898	
Kongoni	1,285	1,379	
Eland	2,452	4,900 - 7,350	

The differences between the three counts are partly due to different areas being covered. Grzimek's count included the Ngorongoro area (which made little difference for the species mentioned, see Turner and Watson, 1964) but excluded the bush-covered northern part of the range. This area has many buffaloes, but, in the season in which the count took place, few of the other ungulates mentioned. Apart from this, most of the differences between the three counts must be due to changes in populations and/or counting errors. For our purpose, it is important to note that the ratio of wildebeest to zebra (about 5 : 3 ; 4.5 : 3 and 6 : 3 respectively) is fairly constant and that both these species are outnumbered by gazelle.

Estimates of the number of predators in the area are rare; Stewart and Talbot mention the figure of 300-400 lions; Adamson (1964) counted the lions in only part of the Serengeti and assessed their numbers at 450; we feel that there must be at least 700 in the whole area. There may be perhaps a hundred cheetah, several hundred leopards, possibly 150 wild dogs — but these figures are no more than inspired guesses. The number of spotted hyaenas runs into several thousands; attempts are being made to arrive at an estimate through a mark-recovery scheme.

Within the area, seasonal movements and reproduction of the ungulates cause, throughout the year, large local differences in the availability of prey. Wildebeest have their calves out on the open plains in January/February and most of the zebra-foals are also born in that period. Fawning of the Thomson's gazelle is less restricted in time and place. These phenomena influence their availability to predators but since most lion, cheetah and wild dog appear to follow the movements of the concentrations of plains game, this influence on availability is less than might be expected. Only for the predator with a restricted habitat (leopard) will we have to take the above into consideration, when comparing its diet with the others.

III. PREDATION

(a) Lion

(i) *Hunting techniques.*

Guggisberg (1962) summarises the available data from literature and his own observations and states that the lion catches its prey after a stalk of varying length, using cover as much as possible. Then, depending on the terrain and the behaviour of the prey, it makes a final, very fast dash towards the victim. If the prey is not caught at once, the lion does not pursue it further than 50 to 100 meters, with few exceptions.

These statements are corroborated by our own observations. Of 8 observed lion hunts which resulted in a kill (usually of medium size prey), 5 consisted of a stalk followed by a longer or shorter dash at running speed, 2 were made from an ambush (the lion lying still watching the game move past and running a short distance towards the prey) and once 2 lions were seen drag-

ging a warthog out of a hole. In the 7 observ
missed its quarry, the stalk-run technique was used 3 times (once
alternately stalking and running towards the prey several times)
and the run from ambush once. Twice a group of lions was seen
stalking game together in a sort of formation, approaching the
game whilst keeping some distance apart from each other. Finally
3 lionesses were once seen walking at a steady pace through dense
shrub along the river some ten meters apart when a reedbuck jum-
ped up just in front of one of them ; one lioness immediately leapt
up at it but missed.

Thus the lion's hunting starts with a search, not directed at any particular animal or group of animals but scanning the environment either from a sitting position or in a slow walk with the head forward. While stalking or lying in ambush, the lion stares intently at a potential victim, lying down or moving slowly with the body held low to the ground, occasionally swishing its tail. Progress during stalking may be in bouts, alternated with periods of « freezing », or is just a very slow continual forward movement. During the run too, the body may be held rather low, yet such a run is very fast, sometimes reaching up to 50 km.p.h. (30 m.p.h. Guggisberg, 1962). The actual grabbing and killing of the victim have been described by Guggisberg (however, see also Eloff, 1964) and our observations largely confirm these descriptions. The prey is usually grabbed from the side or from behind, with one paw on the back and one on its flank or chest ; it is then dragged down, the lion biting at the throat or muzzle whilst pulling down the animal by its own weight, killing it through suffocation. We never saw the predator break a victim's neck.

Although it is possible to detect some frequently occurring behavioural trends in the lion's hunting, it is also clear that it is highly adaptable to varying circumstances. The lion is able to catch his prey in almost all habitats of the area, and although largely nocturnal, it does hunt during the day as well.

We do not have any indications that, when a pride of lions is hunting together, anything more than « accidental » co-operation occurs between them, and the references to organised co-operation between two parties viz. one or more lions deliberately stampeding a herd of game in the direction of other members of the pride lying in ambush (Guggisberg, *op. cit.*) are not based on sufficient

data to rule out coincidences. Of course this does not imply that a system like this cannot exist but more systematic observations would be required to prove that lions when hunting together behave differently from lions hunting alone. So far, it would seem most likely that each lion goes his own way to catch and kill a victim ; if one member of the pride stampedes a herd, other lions may make use of this, as they also do when cars cause a herd to run away.

TABLE 2

Relation between prey-size and number and sex of lions on the kill

Prey Size (for definition see table 4)	Average number of lions per kill	% kills with one lion only	Number of kills with one female	Id. with one male
Large	4.4	11	0	3
Medium	3.0	37	6	18
Small	1.2	76	12	2

The size of the prey of the lion appeared to increase with the number of lions present (table 2) ; this was statistically highly significant (median test : median number of lions = 2 ; $\chi^2 = 17.0$; df = 2 ; $p < 0.001$). A large prey would take longer to kill and be consumed, and our figures did not show whether the relation between prey-size and number of lions is due to large prides selecting large prey, or to other lions joining later either during or after the killing of a large animal. We had the impression that all three situations did occur. Further, if only one lion was present on a kill, it was more likely to be a male when the prey is large and a female when it was small ($\chi^2 = 12.6$; df = 1 ; $p < 0.001$) ; in fact no single females have been found at all with a large kill.

Male lions are more likely to chase a female off her kill than are other females (Guggisberg, *op. cit.*) ; this chasing away is more probable if the prey is larger and this might explain part of the relationship between sex and prey-size. Although we have no figures on this point, we do not believe that this is a major source of error, since in so many of our observations we found just the one lion with his prey, with no trace of another lion anywhere near. We believe, therefore, that our figures represent a real sex-difference in the lion's hunting.

In some cases, animals are killed without immediately being consumed. Thus, one male lion was found with two giraffe victims and a female was observed to kill four Thomson's gazelle in one morning (two of them in one rush) but only eating one. On the other hand, lions will often stay for days on their kill, thus utilising it to the utmost for hyaenas are only infrequently able to take a bite while the lions are still there.

Lions are scavengers to a much greater extent than is generally assumed ; we have several observations of them taking over kills from hyaenas especially, but also from leopards. Some of the carrion they find by watching vultures alighting near it, then running up to it from distances of over one km.

(ii) *Lion's prey selection.*

From the beginning of 1957 till the end of 1965, lion kills that we came across in the Serengeti were entered in the Warden's diary. However, only over the last 1½ years of the period was this done really indiscrimantly ; over the first 7½ years notes were not always kept of the two most common prey species, the wildebeest and the zebra. We have, therefore, separated the observations of the two periods, presenting lion kills from the whole observation period in table 4 (which therefore presents a biased view of the lion's diet) and our observations from June 1964 onwards in table 3, which we can compare directly with the diet lists of the other predators.

The most important phenomenon expressed in table 4 is the occurrence of relatively large game animals in the lion's diet, and in this the lion differs from the other predators discussed. From table 3 it is clear however that large animals are not very important compared with the frequency with which medium sized prey is encountered ; wildebeest make up half of the prey species, and zebra another quarter. These data are remarkably similar to those of Wright (1960), who found that in the Serengeti and Nairobi National Parks 5 % of the lion kills encountered were buffalo, 49 % were wildebeest, 15 % zebra, 10 % gazelle, 2 % Kongoni and fewer than 1 % ostrich. His figures are dealing with a slightly different prey population.

All the large game animals mentioned in table 3 and 4 were killed in the bush which is for all of them their sole, or most fre-

quently used, habitat. The lions on the plains are much more dependent on medium sized game and to a lesser extent on small game ; in fact it is clear that they follow the large concentrations of plains game.

TABLE 3

Lion kills encountered between June 1964 and December 1965

		Bush	Mixed	Plains	Total	% of total
Large	Buffalo	3	—	—	3	8 %
Medium	Zebra	2	3	5	10	26 %
	Wildebeest	1	4	14	19	49 %
	Kongoni	—	—	1	1	3 %
	Ostrich	—	—	2	2	5 %
Small	Grant's gazelle	—	1	1	2	5 %
	Thomson's gazelle	—	—	2	2	5 %
		6	8	25	39	101 %

TABLE 4

Lion-victims : total number of observations 1957-1965

Large (> 500 kg.)	Buffalo	19
	Giraffe	6
	Eland	2
Medium (100 to 350 kg.)	(Wildebeest adult)	(38)
	(Zebra adult)	(26)
	Topi adult	10
	Kongoni adult	1
	Defassa Waterbuck	1
	Ostrich	3
Small (20 to 100 kg.)	Grant's gazelle	2
	Impala	2
	Warthog	1
	Thomson's gazelle	12
Very Small (< 20 kg.)	Porcupine	1
	Leopard cub	1
		125

(c) CHEETAH

(i) *Hunting techniques.*

Various authors have speculated on the speed of which the cheetah is capable : Guggisberg (1962) estimates it at 55 m.p.h. (90 km.p.h.) maximum and our observations corroborate this figure, although it may be that an even higher speed is attained during short bursts. This predator seemed to be mainly active during the day and most of our observations have been made on the open plains. We have twice seen it take a young wildebeest-calf. On one of these occasions, the cheetah was walking through a large herd of wildebeest, apparently entirely disinterested, whilst all the wildebeest were watching it at some 50 meters distance. It suddenly broke into a very fast run and after about three hundred meters, knocked over a small calf with a forepaw and grabbed it by the throat. In the other case, a cheetah was lying on the plain and, while we were watching, it suddenly got up, walked a few paces and then ran at full speed toward a herd of wildebeest about two hundred meters away. It sized a calf in a cloud of dust, and rolled on to the ground with it whilst biting it in the throat. In two other instances we saw cheetah take a Thomson's gazelle, one adult female and one small fawn. The adult tommy was one of a large herd, of which all members were watching the slowly approaching cheetah. The male Thomson's gazelles allowed the predator to come much closer than the females, as near as 50 metres ; the females were all more than 80 metres away. The cheetah broke into a very fast run when some of the females in the back of the herd started fleeing — after a chase of about 200 metres, directly after those females which had run first, the cheetah overtook a pregnant female, put a forepaw on its back and when it overturned at full speed, grabbed it by the throat. A few days later we saw the same cheetah with two cubs, again chasing Thomson's gazelle. The adult cheetah walked slowly over the plain, the cubs following ; now and then she made a short run in the direction of a herd of tommies but stopped when the gazelle started running. This happened five times but on the sixth occasion, she broke into a fast run and caught a young fawn about 50 metres further on in a cloud of dust. The cheetah emerged carrying the fawn by the

head, walked back to the cubs and there dropped her prey in front of them. The gazelle was not dead, however, and jumped up and away, the cubs running after it and the mother cheetah watching. Twice the cubs managed to hit the fawn with a paw over the back but both times they were unable to grab it after bowling it over and the fawn escaped by zigzagging in a large circle. But after two minutes the adult cheetah made a short quick dash at it again, put her front paw on its back and grabbed it in the throat, this time killing it.

Once we saw a cheetah running towards a herd of Grant's gazelle ; it grabbed a large male and tried to drag it to the ground whilst biting it around the muzzle, the Grant meanwhile butting at the cheetah with his large horns. The fight lasted several minutes and ended by the cheetah suddenly leaving its victim, maybe frightened away by our presence. On two occasions a cheetah was seen chasing smaller antelopes, once a dik-dik and once an oribi. Both got away by reaching cover in time ; in the case of the dik-dik, especially, it was clear that its quick turns around trees and shrubs enabled it to gain ground on the cheetah.

We never saw a cheetah stalk its prey although it might appear to make use of high grass for getting nearer to a herd of antelopes. When the cubs were playing together or chasing jackals, they might approach their « victim » by a detour from behind an anthill, often lowering their body while doing so ; as in many carnivores, this play-behaviour could reflect hunting methods. But in general, the stalking part of the hunt seemed virtually absent in this species. It walked over the open plain towards a potential prey, which was often watching it all the time, and after a sudden very fast run which took the cheetah over several hundred meters, it knocked the prey down with a forepaw and bit it in the throat. Once while a cheetah-cub was chasing another cub, it tripped up its victim by slapping a forepaw against the hindlegs but we never saw this method used in hunting.

Usually the cheetah killed alone, although one or two companions might join later : on 23 kills, the average number of cheetah was 1.6. There seemed no relation between the size of the kill and the number of cheetah found on it.

After eating their fill, cheetah usually did not stay for any length of time on the kill and they were also easily chased off it,

especially by spotted hyaenas. They utilised their kills to a lesser extent than the other carnivores mentioned in this paper.

Summarising its hunting methods, we can confirm that in cheetah stalking plays a minor role, if any, and that a very fast chase after which the victim is knocked over with a forepaw is the characteristic way of hunting. The fast run usually develops from a slow walk in full view of the prey, and its onset is probably often stimulated by the running away of the quarry. The victim is killed by suffocation through a bite in the throat or around the muzzle.

(ii) *Prey selection by cheetah.*

All the cheetah kills which we observed have been presented in table 6. Most of the victims were small (78 %), 12 % were medium sized and only twice was a very small prey found (8 %). Adult Thomson's gazelle was by far the most important item in

TABLE 6

Victims of the cheetah

		Bush and mixed habitat	Plains	Total	% of total
Medium	Wildebeest ♀	—	1	1	4 %
	Kongoni ♂	—	1	1	4 %
	Zebra yearling	1	—	1	4 %
Small	Thomson's gazelle (adult)	6	6	12	52 %
	Wildebeest (juvenile)	—	5	5	22 %
	Kongoni (juvenile)	1	—	1	4 %
Very small	Hare	—	1	1	4 %
	Thomson's gazelle (juvenile)	—	1	1	4 %
		8	15	23	98 %

the diet (52 %), followed by the young of medium sized antelopes (26 %). The diet of the cheetah would have been largely the same in wooded areas and on the plains if it were not for the fact that the wildebeest calved almost exclusively on the plains and thus provided the cheetah with 33 % of its diet. Because of this, although the Thomson's gazelle made up 75 % of the cheetah victims in

the wooded areas, it only did so for 47 % on the plains ; if we consider the cheetah victims on the plains without the wildebeest calves, it appears that 70 % were Thomson's gazelle.

It is interesting to consider the sex of the cheetah's prey as well. Of 7 Thomson's gazelle victims which were sexed, 6 were females. If these figures would prove consistent, they might well be very tentatively explained by the fact that female Thomson's gazelle have a much larger fleeing distance from all large predators, including cheetah, than male gazelle (confirmed by Walther, pers. comm.). This means that in mixed herds the females flee first on the approach of a cheetah, and as shown above there is evidence that this may stimulate the cheetah to run, and to select one of those fleeing animals as a quarry.

(d) Wild dog

(i) *Hunting techniques.*

Both Van de Merwe (1959) and Lang (1963) described observations on hunting by packs of wild dogs, and Kühme (1965) studied their hunting and other behaviour around a denning site. Our observations confirmed those of the above authors ; in this section we will draw a general picture of the very stereotyped way in which this species catches its prey, obtained from 11 complete observations of successful hunts, 17 unsuccessful ones and some observations of only the final stage of a chase.

For most of the year, wild dogs roamed around over the plains and in the bush, usually not staying in the same place for more than a day. They were rarely alone but almost always in groups, the size of their packs varying as shown in table 7, with an average pack-size of 9.2. Kuhme (*op. cit.*) described how the wild dogs hunted strictly in the first and the last hour of daylight and, with

TABLE 7

Observations on pack-size of wild dogs

N°. in pack	1-5	6-10	11-15	16-20	21-26
N° of observations	10	13	4	6	1

A small antelope is usually very quickly eaten but quite often the dogs have to share with hyaenas and jackals.

(ii) *Prey selection by wild dogs.*

The different victims with which we found the wild dog have been tabulated in table 8. Medium sized antelopes make up only a small part of the diet (17 %) ; the rest are small antelopes, headed by the Thomson's gazelle with 64 %. The great difference in diet composition between wooded areas and the plains has been discussed above.

TABLE 8

Victims of the wild dog

		Bush and mixed habitat	Plains	Total	% of total
MEDIUM	Wildebeest (adult)	4	1	5	12 %
	Topi (adult)	2	—	2	5 %
SMALL	Impala	1	—	1	2 %
	Grant's gazelle	—	4	4	10 %
	Thomson's gazelle	—	27	27	64 %
	Wildebeest calf	—	3	3	7 %
		7	35	42	100 %

Of the 27 Thomson's gazelle, 3 were young animals and the remaining 24 consisted of 10 females and 14 males. Thus, the difference in occurrence of the two sexes is only very small.

IV. DISCUSSION

(a) METHODS

Before discussing our results, we will have to consider the value of our method, i. e. direct observations of predators with their prey. The obvious advantage of collecting data in this manner is that of any direct method ; other, indirect methods (like faecal analysis) involve the difficult identification of prey-remains, and the laborious calculation of correction factors in order to

arrive at the diet-composition (Lockie, 1959). Moreover, the collecting of faeces of some predators is a difficulty in itself. However, the direct method used by us does have a number of serious drawbacks as well. First of all, the chance of finding a killed animal depends to some extent on the size of that animal — the smaller the victim, the sooner it has disappeared. Thus, in our tables, smaller prey is under-represented. Similarly, habitat accessibility might influence the figures ; and there may be other pitfalls. It is clear then that we have to be extremely cautious with our interpretations.

The danger pointed out above becomes directly apparent when considering the data on lion-food. Although in table 3, the Thomson's gazelle only makes up 5 % of the lion's diet and wildebeest and zebra together 75 %, there are times of the year when a proportion of the lion-population lives in areas where Thomson's gazelle is virtually the only ungulate present, and all the evidence points to the fact that it makes up almost the entire diet for a considerable length of time. But, for a lion, catching and eating a gazelle is a matter of half an hour or less, and is therefore observed only rarely. The 5 % is almost certainly an under-representation. The lion's data for wildebeest and zebra should, however, be perfectly comparable with each other. The ratio of 19 wildebeest to 10 zebra is not very different from the ratio in which these animals occur in the area. This probably means that there is little or no discrimination by the lion between the two species, although it is still possible that the lion prefers one of the two but is met by a more effective defence of that species.

The leopard also takes a good number of very small species and probably the same applies here as has been said for the lion's diet. Several observers report leopards catching rats, and prey of that size would stand a very good chance of being unnoticed by us.

(b) Common trends and differences in predation

Bearing in mind the restrictions of our methods, we believe that we are justified in drawing a number of conclusions from our material. First of all, we will consider some differences in hunting methods as outlined in table 9.

It appears that those predators which rely on stalking are

chiefly nocturnal, whereas the runners hunt by daylight. Except for the lion, they are either stalkers or runners exclusively ; the lion is both and thus has more possibilities for adapting its hunting to different situations and the variety of habitats in which it occurs.

TABLE 9

Hunting methods of lion, leopard, cheetah and wild dog

	Lion	*Leopard*	*Cheetah*	*Wild dog*
Time of activity	Nocturnal	Nocturnal	Diurnal	Dusk and dawn
Habitat	All habitats in the area	Dense vegetation	Plains, open woodland	Plains, open woodland
« Sociability »	Solitary or in prides	Solitary	Almost entirely solitary	Packs
Hunting behaviour :				
Stalk	Well developed	Very well developed	Almost absent	Absent
Run	Relatively short but well developed	Almost absent	Very fast over not very long distances	Fast, over very long distances
Kill	Throatbite or otherwise	Throatbite	Throatbite	Tearing apart

Only the wild dogs are without a special behaviour pattern for killing their prey, which is undoubtedly related to their habit of hunting in packs — once a gazelle is caught, it is seized by so many mouths that it no longer stands a chance of fleeing or defending itself.

It is clear from table 9 that fundamental differences in hunting methods exist between all predators and hence, even if all 4 of them are preying on one and the same prey species, one would expect them to select from this stock in different ways. In fact, the scanty evidence we have on this point — with regard to Thomson's gazelle — indicates that this is actually the case. For leopard, cheetah and wild dog, we presented evidence on the sex ratio of

omson's gazelle kills ; statistically, the figures are just significantly different between leopard and cheetah ($p < 0.025$) and between cheetah and wild dog ($p < 0.05$, Fisher's exact probability test with Tocher's modification).

Above we have already indicated possible mechanisms for these differences and the figures suggest clear differences in prey selection which will probably also hold true as regards age, fitness etc. of the prey.

However, although the lists of prey-species in the diets show considerable overlap, on the whole the differences are more striking than the similarities. Only lions took prey which fall into our « large » category, although medium sized animals formed the mainstay of the diet. Leopards preferred small and very small prey, and both cheetah and wild dog took mainly small animals but also some medium sized ones. The small animals caught by leopards were often those from wooded habitats ; 27 % of the prey animals were Thomson's gazelle, 29 % were impala, reedbuck or bushbuck. For cheetah and wild dog, however, the Thomson's gazelle was much more important, and made up 56 % and 64 % of their respective preys. In fact these last two predators showed greatest overlap in diet, but when we take habitats into consideration, differences become apparent again. In the bush areas, wild dogs clearly preferred medium sized game, whereas the cheetah took small prey as on the plains. While on the plains, the cheetah ate 6 Thomson's gazelle and 9 other animals, the wild dogs took 27 Thomson's gazelle and 8 other animals which is statistically a just significant difference ($\chi^2 = 4.9$, $p < 0.05$).

It is thus clear from the above that generally speaking the four predators are not competing directly as far as food is concerned, and that wherever they do prey on the same species, they probably select from this stock in very different ways.

When trying to explain these variations in diet by differences in hunting methods, gregariousness, habitat selection etc., it is clear that there is more to it than size-differences of the predators corresponding with size-differences of the prey (Bourlière 1963), although obviously the size of the predator plays a role as well. The habitat is of major importance as has been shown for each predator separately. In lions, the size of the pride and the sex of the predator seemed to influence the choice of prey very strongly,

mption are met only partly, the lions' offtake from the large herds is only a very small one. Talbot and Talbot (1963) calculated a considerably higher mortality of wildebeest through lion predation than we found ; the difference is due to the fact that, based on field estimates, they assumed lions to eat about three times as much as the figure we have used.

TABLE 10

The yearly consumption of the lion population

Prey species (see table 3)	Numbers eaten	Weight in kg.	Total weight consumed in kg.	Calculated numbers consumed yearly by 700 lions	Estimated real numbers consumed yearly
Buffalo	3	495	1,485	492	600
Zebra	10	247	2,470	1,640	2,000
Wildebeest	19	169	3,211	3,116	3,800
Kongoni	1	140	140	164	200
Ostrich	2	110	220	328	400
Grant's gazelle	2	56	112	328	400
Thomson's gazelle	2	22	44	328	400
	39		7,682	6,396	7,800

The lion's most frequent prey is wildebeest ; according to the above calculation lions would kill 1.2 % of the 330,000 wildebeest annually. If adult mortality of wildebeest is still 8 % per year (Talbot & Talbot, 1963), it is clear that the lion's share in this is not a very big one. The same will probably also hold true for the other prey species of the lion.

None of the other predators occurs in large enough numbers to assert any considerable mortality pressure on the most common ungulates. It may well be that some of the less common species are suffering a high mortality through those predators, for instance reedbuck from leopards. But at present we have insufficient data to throw any light on this.

Considering the importance of different prey species, it stands out that the Thomson's gazelle makes up the bulk of the food for three of the four predators ; as for the fourth one — the lion — the Thomson's gazelle can be very important during certain periods of the year. The wildebeest is also important, and so are impala

, reedbuck, esp. for the leopard.

but this could not be shown for the others. Leopards seemed occasionally to develop very individual tastes and this may well have been so for the others but would be difficult to show. Our observations suggest that the very stereotyped hunting methods of each species played a very important role, like their reactions to fleeing behaviour of the game, the different extents to which they used stalking, the speed with which they ran and their perseverance in this. It is not yet clear to what extent the differential reactions of the game to predators influenced prey selection, but observations on this are in progress.

(c) Predation pressure

Only for the lion can we make an estimate of numbers present and figures have also been published on their average yearly consumption. It might be interesting, therefore, to make a very tentative calculation as to the total numbers of game which are killed each year by lions in this region.

We assessed the weight of the prey species according to Ledger (1963, for Thomson's gazelle), Watson (pers. comm. for Serengeti wildebeest), our own estimate (for ostriches) and Lamprey (1964 for all remaining species). As calculated in table 10, this brings the total weight of animals we have seen eaten by lions to 7,682 kg. According to Wells (1933) the yearly ration of meat for lions in the wild is under 4,000 lbs (1,800 kg.) and his figures are corroborated by other authors (see summary in Guggisberg, *op. cit.*). If we assume that our lion population numbered 700 heads, the total annual consumption of this population would be 1,260,000 kg. Hence to calculate the actual numbers of different prey animals, we will have to multiply our observed numbers by a factor

$$\frac{1{,}260{,}000}{7{,}682} = 164.0$$

In this way, we arrived at the figures in the fourth column of table 10. These figures have been increased by an arbitrary one-fifth and rounded off (fifth column) to allow for wastage etc., and they should give an approximation of the lions' yearly toll. It appears that even if our assumptions on numbers and annual con-