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Abstract: Eighty-nine per cent of 136 cheetah kills in the Serengeti National Park consisted of Thomson's gazelles, the most abundant and readily available species in the size category (60 kg or less) preferred by the cheetah. Fifty-four per cent of the Thomson's gazelle kills were subadult; among the adults all age classes were represented. One female cheetah captured 24 Thomson's gazelles in 26 days, a killing rate of 10kg/day. The actual food intake of this female was about 4 kg/day. The hunting success of cheetah pursuing large subadults and adult Thomson's gazelles was about 50 per cent. The hunting methods - including the various means of approaching prey - are described as are the typical ways of killing and feeding. Twelve per cent of the cheetah kills were appropriated by lions and hyaenas.

## HUNTING BEHAVIOUR OF THE CHEETAH IN THE SERENGETI NATIONAL PARK, TANZANIA

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### SUMMARY

Eighty-nine per cent. of 136 cheetah kills in the Serengeti National Park consisted of Thomson's gazelles, the most abundant and readily available species in the size category (60 kg or less) preferred by the cheetah. Fifty-four per cent. of the Thomson's gazelle kills were subadult; among the adults all age classes were represented. One female cheetah captured 24 Thomson's gazelles in 26 days, a killing rate of 10 kg/day. The actual food intake of this female was about 4 kg/day. The hunting success of cheetah pursuing large subadult and adult Thomson's gazelles was about 50 per cent.

The hunting methods—including the various means of approaching prey—are described as are the typical ways of killing and feeding. Twelve per cent. of the cheetah kills were appropriated by lions and hyaenas.

### INTRODUCTION

Although a number of publications (Wright, 1960; Mitchell *et al.*, 1965; Graham, 1966; Kruuk and Turner, 1967) present data on food habits and hunting behaviour of the cheetah (*Acinonyx jubatus* Schreber), detailed information on such topics as prey selection, killing frequency and daily food intake is not available. In the course of studying the lion (*Panthera leo* L.) in the Serengeti National Park, observations on cheetah were made whenever possible for comparative purposes. In addition, one female cheetah with two small cubs was followed more or less continuously for nearly one month to obtain a record of prey killed during that period.

### FOOD HABITS

A total of 136 cheetah kills were found between June, 1966 and November, 1967. Of these 121 (89 per cent.) were Thomson's gazelle (*Gazella thomsonii* Günther), and the remaining 15 (11 per cent.) consisted

of wildebeest (*Connochaetes taurinus* (Burchell)), Grant's gazelles (*G. granti* Brooke), hare (*Lepus capensis* L.), reedbuck (*Redunca redunca* Pallas), topi (*Damaliscus korrigum* (Ogilby)), kongoni (*Alcelaphus buselaphus* Pallas) and dik-dik (*Rhynchotragus kirkii* (Günther)) (Table 1). Of 23 kills reported from the Serengeti National Park by Kruuk and Turner (1967), 56 per cent. were Thomson's gazelles and 26 per cent. wildebeest.

TABLE 1

Cheetah kills, Serengeti National Park, June, 1966-November, 1967

| Species           | Number    |
|-------------------|-----------|
| Thomson's gazelle | 121       |
| Grant's gazelle   | 3         |
| Wildebeest        | 3         |
| Hare              | 3         |
| Reedbuck          | 2         |
| Topi              | 2         |
| Kongoni           | 1         |
| Dik-dik           | 1         |
|                   | <hr/> 136 |

The Thomson's gazelle is obviously by far the most important prey item of the cheetah in the area. However, all except 13 of the 159 kills in the two studies were found in the plains or along the edge of the woodlands. A larger kill sample from the woodlands, which cover three-fifths of the park, would undoubtedly reveal that such species as impala (*Aepyceros melampus* Lichtenstein) are also taken. For example, in Kruger National Park, Brynard and Pienaar (1960, quoted in Bourlière, 1963) found that 47 (73 per cent.) of 65 kills consisted of impala.

#### PREY SELECTION

The size, availability and vulnerability of the prey influence the food habits of the cheetah. Thomson's gazelle are small, the average adult male weighing 20.4 kg, the average adult female 16.2 kg (Sachs, 1967), less than half as much as an adult cheetah. The three wildebeest, the kongoni, one Grant's gazelle, and one topi mentioned in Table 1 were young, one month or so old. Two Grant's gazelle, the dik-dik, and the two reedbuck were adult. The largest kill, made by two male cheetah, was a yearling topi weighing about 90 kg. These data indicate that the cheetah selects as prey primarily small species or the young of large species. Kruuk and Turner (1967) mentioned an adult female wildebeest, a male kongoni, and a yearling zebra (*Equus burchelli* Gray) among the kills, but such large victims seem to be uncommon. On the other hand, the selection for Thomson's gazelle may not necessarily reflect a preference for prey in that size category. The main prey in Kruger National Park is impala (Brynard and Pienaar, 1960, quoted in Bourlière, 1963), which weigh about twice as much as a Thomson's gazelle. In general, cheetah seem to select prey weighing about 60 kg or less when hunting alone. With their relatively small jaws and teeth, they probably find it difficult to subdue large prey, unless two or more attack together.

From December to June approximately one million ungulates frequent the plains of the Serengeti National Park and adjacent areas, over half of them Thomson's gazelle. Wildebeest and zebra also occur in large herds, but only the young of these species fall into the size category preferred by the cheetah. The wildebeest show a strong birth peak, and this limits the period during which

small young are available to the cheetah. Zebra foals appear to be rarely taken, perhaps because they are difficult to attack in the cohesive herd to which they belong, and also because adult zebra possibly defend young against cheetah just as they do against hyaenas (*Crocuta crocuta* Erxleben) and hunting dogs (*Lycaon pictus* Temminck). During the dry season from June to November, the plains are almost devoid of prey except for some Grant's gazelle and scattered herds of Thomson's gazelle. The latter species is, therefore, the most abundant and most readily available food source in the plains throughout the year, a fact reflected in the kill sample.

Of 116 Thomson's gazelle kills aged, 65 (56.0 per cent.) were subadult (teeth in various stages of eruption) and 51 (44 per cent.) were adult (all permanent teeth erupted). A cheetah selects a particular animal before attempting to catch it with a final burst of speed. In most hunts observed, the cheetah pursued a small fawn when available, suggesting strong selection for that age class. About one-third of the subadults caught were fawns a month or less old, and few were older than about four months. The ease with which prey can be captured seems to be more important to the cheetah than the ultimate size of the meal, and small fawns, because of their lack of speed and endurance, are particularly vulnerable. Large fawns and adults eluded pursuing cheetah in about half of the hunts observed, whereas small fawns are almost invariably captured as the following figures on hunting success by single cheetah illustrate:

|            | No. chases<br>observed | %<br>captured |
|------------|------------------------|---------------|
| Small fawn | 11                     | 100           |
| Others     | 29                     | 48            |

The amount of wear on the teeth in the lower jaw of 34 adult Thomson's gazelles indicated that animals of all age classes fell prey. The wear on the molars of three kills was light (all infundibuli present); the wear of 23 kills was moderate (one or both infundibuli were worn off the first molar and wear on the second molar was noticeable); and wear of eight kills was heavy (the infundibuli were worn off the first and second molars and occasionally off the third). It is not possible to determine if adult gazelle

of certain ages are preyed on more heavily than others without information on the distribution of tooth wear classes in the living population. However, there seem to be proportionally fewer young adults in the sample than might be expected.

With the exception of two adult male Thomson's gazelle which suffered from sarcoptic mange, all animals killed appeared to be healthy.

Adult male Thomson's gazelle may adhere for days to a limited territory; they often wander alone along thickets, and they permit a predator to approach more closely before fleeing than do females and subadults, all traits that would seem to make them highly vulnerable to predation. Adult males constitute about 20 per cent. of the living population. In a sample of 121 kills, 24 adult males are expected if the cheetah selects randomly from both sexes. The actual kill record was 22 males, 26 females, and three

unsexed individuals, indicating that only as many males as expected were caught. In contrast, of 63 Thomson's gazelle kills found stored in trees by leopard (*Panthera pardus* L.) in the Serengeti National Park, 34 were adult males, about three times as many as expected.

#### KILLING FREQUENCY AND FOOD CONSUMPTION

From October 13th to November 5th and from November 14th to 19th, 1967 a female cheetah with two cubs, 3-4 months old, was kept under intermittent observation throughout the day for 26 days. During this period she confined herself to a tract of about 10 km<sup>2</sup> of burned grassland. The prey population, consisting primarily of Thomson's gazelle and a few Grant's gazelle and topi, varied from sparse to abundant. The cheetah killed 24 Thomson's gazelle and one hare in 26 days (Table 2), an average of about one kill/day. She failed to capture prey on three

TABLE 2

*Record of consecutive kills by an adult female cheetah*

| Date        | Time      | Species                  | Comments                  |
|-------------|-----------|--------------------------|---------------------------|
| October 13  | 1000—1100 | Thomson's gazelle (fawn) |                           |
| " 14        | —         | —                        | No observation            |
| " 15        | 1720      | T. g. (adult female)     | Scavenged by lion         |
| " 16        | 0700—0800 | T. g. (fawn)             |                           |
| " 17        | 0900—1000 | T. g. (fawn)             |                           |
| " 18        | 0710      | T. g. (fawn)             |                           |
| " 19        | 0742      | T. g. (adult female)     |                           |
| " 20        | 0800—0900 | T. g. (adult female)     | Scavenged by lion         |
| " 21        | 0910      | T. g. (fawn)             |                           |
| " 22        | 0803      | T. g. (fawn)             |                           |
| " 23        | 1412      | T. g. (fawn)             |                           |
| " 24        | —         | —                        | No observation            |
| " 25        | 0700—0800 | T. g. (fawn)             |                           |
| " 26        | 0825      | T. g. (fawn)             |                           |
| " 27        | 0827      | Hare                     |                           |
| " 28        | 0         | 0                        | No kill; one attempt seen |
| " 29        | 1600—1700 | T. g. (adult female)     |                           |
| " 30        | —         | —                        | No observation            |
| " 31        | 0740      | T. g. (fawn)             |                           |
| November 1  | —         | —                        | No observation            |
| " 2         | 0712      | T. g. (fawn)             |                           |
| " 3         | 1000—1100 | T. g. (adult male)       |                           |
| " 4         | 0         | 0                        | No kill; one attempt seen |
| " 5         | 0700—0800 | T. g. (adult female)     | Scavenged by hyaena       |
|             | 1400—1500 | T. g. (adult female)     |                           |
| November 14 | 0         | 0                        | No kill, one attempt seen |
| " 15        | 0900—1000 | T. g. (fawn)             |                           |
|             | 1600—1700 | T. g. (fawn)             |                           |
| " 16        | 0800—0900 | T. g. (adult female)     |                           |
| " 17        | 1400—1500 | T. g. (fawn)             |                           |
| " 18        | 0800—0900 | T. g. (fawn)             |                           |
| " 19        | 0755      | T. g. (adult female)     |                           |

days, but on each of two days she caught two gazelle. If her killing rate remains constant, she would account for 337 gazelle in a year.

By using the average weights of adult male and female gazelle presented by Sachs (1967) and by estimating the weights of fawns visually, it was determined that the total weight of prey killed by the cheetah was 261.3 kg, an average of 10.0 kg/day or 3650 kg/year. However, only about 8.8 kg/day were available to the cheetah because a lion scavenged her kill twice and a hyaena once. Part of each kill is not eaten, primarily the digestive tract and its contents, most bones, and most of the skin. The weight of an adult female Thomson's gazelle averages 16.2 kg. The remains of two females weighed 6.4 kg and 6.8 kg, respectively, after the cheetah finished eating. About 60 per cent. of the weight of an adult female Thomson's gazelle is therefore consumed, and a similar amount seemed to be taken from adult males and from large fawns; perhaps a somewhat higher percentage is eaten from small fawns. Although the cheetah had 8.8 kg of prey per day available, they ate only 5.3 kg. Each cub took probably at least 0.5 kg, leaving 4.0 kg/day for the female. This rate of food consumption is over twice the 1.3 to 1.8 kg/day needed to keep a cheetah in healthy condition in a zoological garden (Crandall, 1964).

#### HUNTING BEHAVIOUR

In areas where prey is moderately abundant, the cheetah spends much of the day lying in the shade of a bush, in a patch of grass, or on a termite mound, seemingly waiting for prey to wander into the vicinity. Occasionally it moves 100 to 200 m to another site but, on the whole, little effort is expended in search of a victim. The female cheetah whose daily activity was followed remained several times in the same place until late afternoon before beginning to hunt. On most days this cheetah travelled a total distance of only 1 to 2 km during daytime and little, or not at all, during the night; at least she was usually located in the morning near the same spot she was in the previous evening.

The cheetah may hunt at any time of the day, but does so predominantly in the early morning and late afternoon. The

time of killing was determined 76 times, either by observing the actual hunt or by estimating the time elapsed since the capture from the partially eaten carcass. Fifty-nine per cent. of the kills were made between 0600 and 1000 h, 14 per cent. between 1000 and 1400 h, and 27 per cent. between 1400 and 1800. In addition, a cheetah killed a Thomson's gazelle at 0200 h in bright moonlight.

A cheetah may approach its prey, such as a herd of gazelle, in several ways. Occasionally it walks toward the animals with no attempt at concealment. The gazelle watch the cat alertly and usually permit it to advance to within 60 to 70 m before fleeing a short distance. But then they usually halt, and some may trot closer. The cheetah in turn often trots or makes brief rushes toward the gazelle and afterwards just stands and looks: it gives the impression of searching for a suitable victim. If one or more gazelle separate from the herd, these are usually pursued. However, sometimes the selected animal mingles with the fleeing herd and the cheetah loses sight of it. Perhaps it is because of the difficulty of capturing a particular animal in a large herd that cheetah tend to be found not in the centre of large prey concentrations but rather around the periphery where herds are small and scattered. Another method of approach is to bound toward an unsuspecting herd from a distance of 100 to 200 m. By the time the animals become aware of the danger and flee, the cheetah is usually close enough to select an individual and pursue it at full speed.

Although Kruuk and Turner (1967) stated "that in cheetah stalking plays a minor role, if any," most hunts for Thomson's gazelle observed during this study were preceded by a careful stalk sometimes exceeding a distance of 100 m. The cheetah usually approaches a foraging gazelle herd with body and head held low, using the available cover but paying no attention to the direction of the wind. If a gazelle looks up from its feeding, the cheetah becomes immobile and remains so until the animal lowers its head. Sometimes the cat crouches, body pressed to the ground, a position it may retain for ten or more minutes. If by chance the gazelle face away from the cheetah, or if they move briefly out of sight in a depression or behind a termite mound, it often trots quickly some 10 m closer and then drops to the ground motionless. Finally, after a stalk that may last half

an hour and bring the cheetah to within 30 m of a gazelle, it suddenly rushes at its intended victim.

The cheetah is generally considered to be the fastest land mammal over short distances, attaining a speed of about 95 km/h (Guggisberg, 1963). The fact that cheetah can readily overtake fleeing Thomson's gazelle—which on several occasions were clocked at 70 to 80 km/h when running parallel to the car—lends support to this estimate. For much of the chase, however, the cheetah runs only as fast as the gazelle it is trying to catch. While the gazelle dodges and zig-zags, the cheetah attempts to follow each turn in the unpredictable route. When close enough, it slaps a hindleg, flank, or rump with a forepaw, leaving at times a cut in the skin which is presumably caused by the large dewclaw. Thrown off its stride, the gazelle usually crashes on its side and, in one instance, turned a somersault in the air. The gazelle is grabbed by the throat immediately or, in the case of a small fawn, sometimes by the head or nape.

As indicated earlier, about half of the pursuits after adult Thomson's gazelle end in failure. The cheetah seems to be able to maintain a high speed for only about 200 to 300 m, and it tends to stop, apparently exhausted, if it has not caught the prey in that distance. In 14 of 15 unsuccessful hunts observed, the cheetah failed to follow a sudden dodge by the gazelle and seemed to lose too much ground to continue the chase, and once it slipped and fell when making a sharp turn. Usually no further pursuits are attempted for at least one hour after an unsuccessful hunt.

Gazelle are killed by strangulation, a method that may require ten minutes. The cheetah either lies, sits, or walks while holding the animal by the throat until it ceases to struggle. Frequently the body is then moved to a bush or tree to be eaten, in one instance a distance of 250 m. Adult gazelle are held by the throat or nape and dragged, but small prey is often carried by the head, neck, back, or rump. As many as 30 minutes may elapse between the time of killing and the time the cat begins to eat. At first it often just lies by the carcass, panting from the exertion of the hunt (breathing rate usually 120-150/min).

A typical hunt went as follows: A female cheetah lies by a shallow ravine between

0645 and 0800h, her two cubs, three months old, beside her. Scattered Thomson's gazelle forage 250 m away. At 0803 h, the female followed by the cubs trots in a semi-crouched position through scattered patches of tall grass to within 100 m of the gazelle without being seen. After halting briefly, she advances 20 m, crouches, moves another 20 m, still followed by the cubs, and crouches again. Closest to her and separated somewhat from the others is a male fawn about five months old. She waits two minutes until the gazelle grazes facing completely away from her. Suddenly she bounds forward and after a chase of about 230 m, during which the gazelle dodges sharply three times, the hunt ends in a cloud of dust from which the cheetah emerges holding her victim by the throat. The cubs, which have remained sitting during the final phase of the hunt, run up and tear at the body as she drags it 100 m to the base of a tree. She drops the gazelle, but it still kicks; she grabs the throat once more and holds it until the animal dies at 0812 h. The cheetah lie beside the kill until 0830 h. At that time the female chews through the skin on the flank, exposing the muscles, and the cubs eat while she rests another ten minutes.

D. Baldwin and my wife watched a cheetah carry a small Thomson's gazelle to her two cubs, four months old. When she dropped the fawn, it jumped up and fled. While the female watched, the cubs pursued it and once knocked it down, but they were unable to catch it. The female then killed it. Kruuk and Turner (1967) also related an instance of a cheetah providing her cubs with the opportunity to chase a gazelle fawn.

Three cubs, about 15 months old, were seen playing with a young Thomson's gazelle. When the cubs found the fawn hidden in the grass, they crouched around it, their faces 15 cm from that of the gazelle. It fled after a few seconds. One at a time, a total of 18 times, the cubs swatted the fawn and bowled it over, yet it continued its attempts to escape. The mother cheetah suddenly rushed up, bit the fawn in the neck, but then released it. Again the fawn tried to run away but, after being knocked over twice more, it merely crouched. The three cubs surrounded it and one grabbed its throat.

The cheetah characteristically eats the meat off one flank first, and then, moving forward, that off the abdomen and off the the ribcage including the soft part of the

ribs themselves. The blood collects in the body cavity, much as in a bowl, and this the cat sometimes laps up, useful behaviour in a predator that inhabits semi-desert country in which water is often scarce. The cheetah eats rapidly and occasionally stops to look around, seemingly nervous. Attracted by the vultures that usually land near a kill, lions and hyaenas sometimes investigate and appropriate the carcass. Eleven (8 per cent.) of the 136 kills were taken away by lions and five (4 per cent.) by hyaenas. About one to two hours after killing, the cheetah finishes the meat on an adult Thomson's gazelle and leaves the vicinity of the carcass. All that typically remains is an articulated skeleton with most of the skin attached and the digestive tract.

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