# 10 The Cheetah

With its small round head, deep chest, trim waist, and long slender legs the cheetah is the most atypical of the cats, an animal built for speed rather than for power. Man has tamed cheetah for centuries and hunted antelope with them for sport. For example, Akbar the Great, Moghul emperor of India in the sixteenth century, kept 1,000 cheetah with which to hunt blackbuck antelope, a sport which survived in that country until the middle of this century. Considering the long intimate contact which man has had with cheetah, remarkably little became known of its habits. When I began work in the Serengeti, the literature consisted mainly of cursory popular accounts (Denis, 1964) and lists of prey animals killed by these cats (Mitchell et al, 1965). Graham (1966) attempted to analyze the social structure of cheetah, but "as practically all the information recorded by the survey was drawn from people's memories many mistakes could have been made." Recently Eaton (1969, 1970a, b, c, d) studied cheetah for 4½ months in Nairobi Park and McLaughlin (1970) did so for 1½ years in the same area. Valuable information on tame but freeliving animals was obtained by J. Adamson (1969).

With published information scanty, I attempted to learn as much as possible about cheetah in the Serengeti. Most cheetah there are exceedingly shy, sometimes fleeing from a car at distances of up to 1 km, but several have become used to vehicles and permit themselves to be approached to within 10 to 15 m. Two sisters became so indifferent to persons and vehicles that they commonly used a car's hood as a vantage point from which to spot prey and on one occasion permitted me to approach on foot to within 3 m. Although my contact with cheetah was limited to about 150 hours of direct observation, other persons, particularly my wife, Kay, D. Baldwin, A. Braun, A. and J. Root, S. and L. Trevor, and A. Laurie spent many hours with them and generously reported their findings to me.

## Distribution and Numbers

Within historic times cheetah were found in arid regions from India westward through Iran to Arabia and over most of Africa, except in the driest deserts and dense forests, a distribution similar to that of the lion. The cheetah became extinct in India in 1952 but remnant populations of the Asiatic subspecies may survive in parts of Turkmenistan, Afghanistan, Iran, and possibly in northern Saudi Arabia (Simon, 1966). Cheetah in North Africa are rare (Hoogstraal et al., 1966–67) but south of the Sahara they are found sparsely from Chad and Sudan through parts of East Africa to Rhodesia, Angola, Southwest Africa, and South Africa where the Vaal River is at about the southern limit of their distribution. They are most widespread in wooded steppe, grass steppe, and undifferentiated woodlands, using the terms as defined by Keay (1959).

Cheetah occur throughout the Serengeti ecological unit but they prefer the plains and the woodlands-plains border, judging by how seldom I saw them in the Corridor and Northern Extension. In contrast, the cheetah in Kafue Park "do not venture on to extensive open plains" (Mitchell et al., 1965). Their distribution in the Serengeti seems to be less influenced by the vegetation than by the movements of Thomson's gazelle. With the onset of the heavy rains in 1967, cheetah disappeared from Seronera, together with the gazelle, and none were there from March 28 to July 4. After that date and until December they were again common. With the renewed rains both species moved to the plains, and I saw no cheetah around Seronera between December 8, 1967, and June 7, 1968. Their appearance and disappearance correlates with the gazelle migration (see fig. 37).

The extensive movements of cheetah in and out of my study area made it difficult to census the animals, especially since some undoubtedly traveled out of the park to the Salai plains and other areas. The cats were uncommon in the woodlands, and even on the plains I often spent many days without finding any. Occasionally cheetah concentrated temporarily in a locality, but such aggregations bore no relation to their density in the park as a whole. On May 14, 1967, for instance, I found 14 large cheetah around the Gol kopjes, and on December 19, 1967, I counted 10 there in contrast to most other days when none were seen. I guess that there are about 200 to 250 cheetah in the ecological unit, or about one animal per 102 to 127 sq km, as compared to one animal per 72 sq km in Kruger Park (Pienaar, 1969). The densest known cheetah population existed in Nairobi Park whose



115 sq. km were used at one point in 1969 by 15 adults and 11 cubs (McLaughlin, 1970). At the other extreme, Lamprey (1964) made only 11 cheetah sightings in four years in the 20,800 sq km Masai steppe of Tanzania, and he estimated a population of "less than 20."

## Movements

As mentioned earlier, many cheetah follow the movements of Thomson's gazelle but I have no information on the total extent of their wanderings. One female had a litter in the Masai kopjes in July, 1967. As soon as the young were mobile, she moved toward Seronera and remained for about 1½ months within an area of 10 sq km. The family disappeared on December 8, having spent the season within an area of about 60 sq km. On June 26, 1968, the mother and two cubs reappeared in their old haunts where they roamed widely between Mukoma Hill and Seronera, using at least 65 sq km of terrain. The cubs separated from their mother in mid-October but all remained in the area until early December. On February 14, 1969, I found one of the grown cubs near the Barafu kopjes, 40 km east of Seronera. One of the cubs was seen back at Seronera on about April 20, the second cub in mid-May, and the mother in June. The mother was accompanied by a new litter, and one of the cubs had a litter about 10 km from the place at which she was born. Both remained within the area they had occupied the previous two seasons, at least until late September. These observations indicate not only that some cheetah tend to remain localized after migrating off the plains, but also that they may return to the same area each year. In Nairobi Park, cheetah occupied permanent and overlapping ranges. One female with cubs used 76 sq km of terrain, another 82 sq km, and two males roamed together over 102 sq km (McLaughlin, 1970).

Other cheetah remained for a few days or weeks within a small area but then moved away without returning. This was particularly true of subadults which had just become independent of their mother. For example, one group of 3 such animals stayed at Seronera from late January to early March, 1967, another group of 3 was there from mid-July to early August, 1967, and a third group, again of 3, from mid-June to mid-July, 1969. One female with two cubs, 3 months old, was first observed on August 24, 1968. She remained in the same locality until December, then disappeared until April 18, 1969. After her return she was seen almost daily, but suddenly vanished on about May 12.

Several cheetah occupied the same general area around Seronera during the dry season, some as temporary residents others only as transients. In mid-July 1969, for instance, a total of 2 males, 5 females, and 8 cubs, singly and in groups, frequented at one time or other the area lying between the Seronera River and Mukoma Hill; of these only 2 females with cubs were resident for the season. Cheetah merely avoided contact when they saw each other, and there was no evidence for any form of territorial defense. The animals spaced themselves out by centering their activity in a locality not much used by others at the time and by avoiding meetings both by visual and olfactory means (see below). In Nairobi Park, where cheetah are resident, Eaton (1969) saw no evidence of territoriality either. He wrote: "It appears that there are loosely-defined boundaries to a home range. In a two-day period, 13 cheetah of three groups used the same area, indicating how the home ranges overlap."

## Population Dynamics

For convenience I divided cheetah into several age classes. The pelage of newborn cubs is black with spots only faintly visible; in addition, there is a long blue-gray mantle of hair on the head, neck, and back, a distinct natal coat unique to cheetah among cats.[1] The mantle begins to disappear and the black coat gives way to the tawny black-spotted one of adults when the young are about 3 months old. Cubs grow rapidly; by the age of 6 months they are half the size of their mother and by 12 months over two-thirds her size. The deciduous canines are replaced by permanent ones at about 240 days of age (J. Adamson, 1969). Young aged 0 to 3 months were designated as black cubs, those aged 3 to 6 months as small cubs, and those 6 to 12 months as medium-sized cubs. Cubs older than 12 months were termed large cubs until they separated from their mother. These cubs could be distinguished from an adult mainly by their more slender build and a small ruff on the nape.

Males tend to be larger and stockier than females. Three males measured by Shortridge (1934) were 236, 221, and 220 cm long, and one female was 190.5 cm long; the length of 3 males reported by Stevenson-Hamilton (1954) varied from 193 to 211 cm. The weights of 4 males ranged from 58 to 65 kg and that of one female was 63 kg (Meinertzhagen, 1938); one male reported by Wilson (1968) weighed

1. I am unable to explain the adaptive significance of this coat.



54 kg, another by Pienaar (1969) 45.5 kg. None of the adults I was able to observe closely were old, judging by tooth wear, even though the potential longevity of cheetah is at least 15½ years (Crandall, 1964).

### Population Composition

I was able to sex five litters of black cubs but only after some young had already disappeared. The survivors consisted of 4 males and 7 females. Nine out of 11 cubs sexed by McLaughlin (1970) in Nairobi Park were males. There were 11 males and 7 females in 7 captive litters (van de Werken, 1968; Manton, 1970). I further sexed 14 different litters of small to large cubs and these comprised 10 males and 18 females. An equal sex ratio at birth seems probable, but more data are needed to confirm this.

It was difficult to obtain an unbiased sex ratio of adult cheetah because the animals around Seronera would be represented too often and because females with cubs were easier to identify at a distance than solitary individuals. Consequently I excluded all Seronera cheetah from the computations and considered females with young separately. Among the cheetah tallied were 58 males, 92 females, and 94 unidentified ones. Assuming that the ratio of males to females in the unidentified sample is the same as in the identified one, the total adds up to 94 males and 150 females. In addition, 68 females with litters were encountered. Females thus outnumber males 2:1, but whether this is due to a differential death rate or is merely the result of emigration of males into areas surrounding the park could not be determined. In contrast, 58% of 471 cheetah sexed in Kruger Park by Pienaar (1969) were males. My sample also included 68 litters totalling 146 young, all less than 16 months old. Thirty-one percent of the females, including a small number which were not yet reproductively active, were accompanied by cubs. The population as a whole consisted of 21% males, 47% females, and 32% young. Some 44% of the young were large ones, 12 to 16 months old.

### Reproduction

One of Akbar the Great's numerous captive cheetah is said to have had a litter of 3 cubs. No other captive births were reported until 1956, when a litter was born in the Philadelphia zoo. Since then a dozen others have been born in various zoos (for summary up to 1967 see van de Werken, 1968).

One tame but free-living female conceived for the first time at the

age of 22 months (J. Adamson, 1966). Of two Serengeti females born in July, 1967, one had her first litter on about July 10, 1969; it was conceived in April when she was 21 months old, assuming a gestation period of 90 to 95 days (Asdell, 1964; Spinelli and Spinelli, 1968). Her sister courted on May 19, 1969, at the age of 22 months.

The size of 10 captive litters varied from 1 to 4 with an average of 2.7 (van de Werken, 1968; Manton, 1970; San Diego zoo, pers. comm.). The tame Adamson cheetah had litters of 3, 4, 4, and 4. Foster and McLaughlin (1968) mentioned litters of 4 and 5 in Nairobi Park, Eaton (1970a) noted 5 litters of 5 cubs each in the same area, and McLaughlin (1970) reported on 6 litters which ranged in size from 3 to 6 cubs with an average of 4.3. Graham (1966) cited several litters of 8 large cubs but these observations need to be confirmed. One newborn Serengeti litter consisted of 4 cubs. The average number of cubs in 14 other litters of black cubs was 3.0 with a range of 1 to 5, but some young probably had already died. The true average probably lies between 3 and 4. Fourteen litters of small cubs averaged 1.9 animals in size, 12 litters of medium-sized cubs averaged 2.0, and 23 litters of large cubs averaged 2.1, indicating that some one-third to one-half of the cubs died between the ages of about 5 to 6 weeks and about 3 to 4 months; after that, their mortality was low. These observations were confirmed by direct observation. For example, one female had 3 black cubs when seen for the first time on September 16, 1967. By September 25 one cub had disappeared, but she raised the remaining two. She appeared with another litter of three on June 6, 1969, but within a month one weak cub that lagged behind the group vanished. The daughter of this female had 4 cubs on about July 10, 1969. One of her cubs disappeared between August 15 and 19, a second one between September 4 and 16. Pienaar (1969) noted that cub mortality in Kruger National Park is about 50%, a figure close to the 43% given by McLaughlin (1970) for Nairobi Park. One tame but free-living cheetah lost 2 of her 4 litters within the first weeks of life, one possibly to hyenas (J. Adamson, 1969).

A female may come into estrus again soon after losing her litter. The Adamson cheetah once mated within 3 weeks after her 6-week-old litter disappeared and once within about a week after her 13-day-old young vanished. Estrus is held in abeyance while cubs are small, although a captive female came into heat 4 months after the birth of a litter (Spinelli and Spinelli, 1963). One female raised her cubs to an age of 16 months before mating again (J. Adamson, 1969). Foster and McLaughlin (1968) wrote: "Two male cheetah, survivors of a family of four born to a female in May, 1966, separated from her in July, 1967. In November, 1967, she gave birth to another five cubs," an interval of 15 months between birth and the next conception. Other birth intervals in the same area included 17, 18, and 19 months (McLaughlin, 1970). One Serengeti female conceived again 18 months after giving birth.



My sample of 14 litters of black cubs is too small to show a breeding season. Birth months were evenly distributed between January and August, but no litters were known to have been born between September and December. According to Eaton (1970d), births in East Africa "mainly occur from March to the end of June."

## Mortality

As noted earlier, about half of the cubs die within the first few months of life, but the causes of death remain largely unknown. Turner told me that one litter died in a grass fire. Several cubs were sick, judging by their slow movements and unsteady gait. Four cheetah young from Nairobi Park showed postmortem findings similar to those found in domestic cats suffering from infectious feline enteritis, a fatal viral disease (Murray, 1967). Pienaar (1969) noted that "malnourished or vitamin-deficient cheetah cubs" are frequently found in Kruger Park. Small young are also vulnerable to a variety of avian and mammalian predators, and in fact Eaton (1970a) postulated that most deaths in Nairobi Park were caused by lion, leopard, and hyena.

The cheetah population in the park is surprisingly low considering the available prey and the success the cats have in catching it (see below). While the number of cheetah around Seronera may have increased in recent years (Turner, pers. comm.), there is no evidence that the park population as a whole has done so. The fact that almost 15% of the population consists of large cubs 12 to 16 months old indicates not only that reproduction is adequate but also that mortality of adults is high, assuming a stable population. Possibly cheetah move out of the park and are shot and snared. While this may account for a few animals, other factors no doubt help to decrease the size of the population and finally keep it depressed at a level below the one which the park can support. The same is true in Kruger Park. That an area can tolerate a fairly high cheetah density is shown by Nairobi Park. I have no data that would help to account for high adult mortality. Turner (pers. comm.) found a cheetah that had been killed and stored

in a tree by a leopard. One young adult female in emaciated condition, weighing only 23 kg, was killed by lions; there were many *Rhipicephalus carnivoralis* ticks on her. Pienaar (1969) found that cheetah in Kruger Park may die of anthrax. Murray (1967) noted bacillary particles, identical to *Eperythrozoon felis* which causes hemolytic anemia in domestic cats, in a cheetah from northern Kenya. The same animal was infested with a spiruroid nematode, *Spirocerca lupi*, which may cause damage to and rupture of blood vessels.

## Social Structure

In this section I describe, first, cheetah group structure, a point about which published information is confusing, and then those aspects of communication and other interactions between individuals which are of particular interest for comparison with what is known about lions.

### Group Size and Composition

Taking the sample of 244 individuals not accompanied by cubs which I used in the computations of sex ratio, 52% were solitary, 31% were in groups of 2, 14% in groups of 3, and 3% in groups of 4. I once saw a female with 4 large cubs and once one with 5, and such individuals would all have been labeled as adults by the casual observer. A female with young was never accompanied by other adults or by her cubs of the previous litter. I never saw adult females together except once after two had met inadvertently. One or more adult males were seen with a female three times when courting and twice for a cursory visit only. Adult males, on the other hand, may form companionships in the manner of lions. Most occur in pairs, but in Nairobi Park four adult males hunted together in 1965 and 1966 (Foster and Kearney, 1967). All other groups consisted of litters which had broken away from their mother but had not yet split up. Such groups were either of the same or of mixed sex. Females probably leave such groups and become solitary before their first estrus, but males may remain together. One such group consisting of two males and one female were together most of July but late that month the female left. Two female cubs left their mother on October 18, 1968, and were still together on November 17. On February 14 one was seen alone and in April it conceived. The sisters never again associated, to my knowledge, nor did they have contact with their mother even though all three used the same area. These observations show that adult females are unsociable, except when



in estrus and when they have cubs, but that adult males may form social bonds with others of their sex.

My data differ strikingly from some published ones. According to Pienaar (1969), "cheetah are more sociable creatures than leopards, and although single cheetahs are sometimes seen, they are more often encountered in pairs or in family groups up to 8 in number." Of 1,794 adult cheetah unaccompanied by young, tallied by Graham (1966) from questionnaires, 27% were solitary, 34% were in groups of 2, 19% in groups of 3, and 20% in groups of 4 to 12; he also found that 63% of litters were accompanied by one adult, 21% by 2 adults, and the rest by 3 and 4 adults. In Nairobi Park, one group of 3 adult males and 2 adult females hunted together, as did one of 2 males and 1 female, according to Eaton (1970c); however, McLaughlin (1970) reported no such associations. If cheetah in these areas have a different social system from those in the Serengeti, or if the discrepancies are the result of careless observation, cannot be decided without further research.

### Communication

Many gestures and facial expressions of cheetah are so similar to those of lions that further description would be redundant, but several patterns are worthy of note.

*Gestures and postures.* During agonistic interactions with other cheetah or with other species of predator they use the head-low posture in the manner of lions. Slapping, which in lions is usually with a sideways motion, consists in cheetah of such a rapid and forceful downward thrust either with one paw or with both in unison that on several occasions the animal hit the ground with a thump.

Head rubbing, a method of greeting prominent in *Felis* and *Panthera*, was not observed in free-living cheetah although one may touch the face of another with its nose or cheek. However, Leyhausen wrote me that the gesture occurs in captive ones.

Around Seronera the cheetah were harassed by tourists to such an extent that even tame individuals began to avoid vehicles by hiding. A lion in such a situation crouches and a cheetah usually does too, but on two occasions one lay flat on its side in high grass; A. Root observed similar behavior. On another occasion, a female had just killed a gazelle when she saw a lion 150 m away. She reclined immediately on her side in the open, only her head raised.

*Vocalizations.* Cheetah use two distinct vocalizations with which they communicate at a distance. One is a chirp, reminiscent of a bird call or the distant yip of a small dog, given repeatedly and with varying intensity. It consists of a single modulated note with a frequency range between 1 and 3 kHz and a duration of about .2 seconds (fig. 22[I]). The sound can be heard for several hundred meters in spite of its ephemeral quality. Females chirp when separated from their cubs after a hunt, and cubs use the vocalization when looking for their siblings or their mother. Once, for example, a cheetah with two cubs left a third one asleep in the shade of a tree. It woke up when the others were 150 m away and chirped. The female returned and led it to the others. Cheetah also chirp when excited, as when, for instance, two adults meet, when they court, and when cubs are around a kill. The sound resembles the miaow of a lion cub spectrographically, and indeed it possibly should be classified as such.

The chirr is emitted once or several times in succession. It is a staccato sound, spectrographically reminiscent of the lion's growl, and it may last from .3 to 1.0 seconds at a frequency of up to 4 kHz (fig. 22[H]). This sound is often given in conjunction with the chirp. One female called her cubs thus: 5 chirps, 1 chirr, 2 chirps, 1 chirr, 18 chirps, 1 chirr, and so forth. At other times chirrs predominate. The function of the two calls seems to be similar, denoting "Here I am," except that the chirp can be heard farther than the chirr. In this respect the two calls are analogous to the soft and loud roars of the lion except that the calls are discrete rather than graded.

On one occasion small cubs emitted nasal bleats interspersed with chirps when separated from their mother, and two cubs bleated and hissed when fighting. A female gave several growly bleats as she circled a male lion after he had taken a kill from her. It is probable that a bleat denotes distress, just as it does in lions.

Cheetah purr loudly in the manner of house cats when they lick each other or when cubs rest contentedly by their mother.

In agonistic situations, cheetah growl, snarl, hiss, and cough but they do so infrequently. Growling at kills, for example, is rare, and hisses are directed mainly at lions and hyenas when they approach a kill on which a cheetah is feeding. Cheetah also moan, a loud *uuuu*, which they emit when approached by a lion or leopard. A female also moaned at a cub from another litter. The vocalization, sometimes given in the head-low posture, functions mainly as a threat. According to Eaton (1970b), cheetah mothers emit an *ughh*, which deters cubs from following, as she sets out on a hunt. Although I was often close to cheetah in such situations, I never heard this sound.



*Marking.* Male cheetah, and also females on occasion, lift their tail and squirt fluid against tree trunks and tufts of grass. Once a male rubbed his face in the moist area, and animals frequently sniffed the scent after depositing it, something seldom done by lions. According to Eaton (1969), "groups of cheetah on the move mark the same trees that they have on prior days . . . when cheetah come across a marking, they spend several minutes smelling the marked area before they mark it themselves." In fact, Eaton (1970a) felt that groups tend to orient their movement according to the location of marking sites. Cheetah may scrape soil alternately with their hind paws, and Eaton (1970a) noted that two males then "defecated just a small amount and/or urinated onto the scrape." I have several times seen cheetah defecate on termite mounds but it was not clear to me whether the behavior was deliberate or fortuitous. But once I watched a cheetah detour 20 m to a termite mound and defecate on it. Pienaar (1969) noted that cheetah defecate on isolated boulders, and Hanström (1949) observed two animals climb 4 m into a tree and deposit their feces on a branch. Cheetah also claw tree trunks on occasion.

## Interactions between Adults

Adults watched each other on several occasions at a distance of 200 to 600 m without joining or retreating. A mother and her daughter, both with cubs, spent several weeks in the same area and sometimes saw each other but to my knowledge never associated. On September 2, 1968, a male approached a female with two large cubs and briefly sat 3 m from them without eliciting a response. On September 20, at 0835 the same male was 300 m from the family. By 1730 he had moved to within 8 m of it, according to Kay, who watched the event. He sniffed the ground then advanced a step at a time, his lowered forequarters supported on his elbows, a posture resembling one used by hyenas in submission (Kruuk, 1972). One cub lunged at him. He then stood broadside 2 m from the group, and when a cub moved closer he charged it. He sniffed the ground, circled the others, and reclined 3 m from them. By the following morning he was alone again. McLaughlin (1970) observed that males fought with family groups on 4 out of 6 encounters.

At 0840 on July 21, 1969, a female with 2 cubs about 3 months old

killed a gazelle. She called until her cubs came. Suddenly she crouched and sneaked away. Attracted by the chirps, another female, also with two 3-month-old cubs, arrived. One of her cubs ran to the others and mingled with them freely. However, the new female advanced in the head-low posture to within 2 m of the first female which sat and chirped loudly. The new female then left at a trot followed by her two cubs. A cub from the other litter chased after them and attacked a cub. The new female rushed to the defense of her young which in turn caused the other female to trot closer. At this the new female fled with her cubs—as well as with a cub from the other litter. The first female returned to her kill, ate, then rested, seemingly oblivious to the fact that one of her cubs was missing.

The new female noted that she had an extra cub but was unable to distinguish her own from the stranger. Each time a cub came near her, she slapped it with one or both paws, hissed at it, or lunged at it with bared teeth. After being hit several times, all three cubs cringed and crept around the female just out of reach of her attacks. By 1140, she was 130 m from the cubs. She chirped occasionally but crouched and faced any cub that came near, then fled again. The cubs recognized the stranger, for they hissed at it and sometimes exchanged blows with it. At 1715, the female called the cubs once more but hit one hard when it ran to her. Somehow during the night the families sorted themselves out, for each female had two cubs on subsequent days.

One or more males may court an estrous female. Akbar the Great is said to have trapped six males in pursuit of one female (Ali, 1927). Once I saw two males follow a female closely, and I presumed that she was in heat. On another occasion I saw two males briefly rear up and slap each other while a female stood nearby, but all fled when they perceived the car; a fourth cheetah, possibly another male, stood in the distance. Males have been known to kill each other in such fights (Stevenson-Hamilton, 1954). Eaton (1969) wrote that "there was no aggression between three males which all copulated with the same female," but no further information about this incident is given. A 14-month-old cub tried to mount his mother but was deterred by a slap (Eaton, 1970a).

I observed courtship only once, at 1000 on May 19, 1969, but since the animals chose the Seronera airfield for this activity they were constantly interrupted. The male sat 13 m from the female and both chirred and chirped constantly. When she walked, he followed closely; when she reclined beneath the wing of an aeroplane, he lay 2.5 m from



her. When several persons rolled a barrel past them at 10 m, the male retreated 50 m but she remained. When the male returned, the corners of his lips far retracted, she slapped him gently and rolled on her back. Disturbed again by people working in his vicinity, the male stayed 70 m from her until 1755. At that time both entered the hangar. She rolled on her back in front of him, dashed away only to approach again and paw him. But when he advanced, she raked both forepaws past his face while he chirred intensively. She left the hangar with him trailing 1.5 m behind and climbed on the hood of my car and sat there while he waited at 5 m. They left at darkness and I could not find them the next day.

### Interactions between Mother and Young

Females hide their newborn young well. For example, one female had a litter in a kopje densely overgrown with shrubs and another gave birth in tall grass but moved her young to a thicket two days later. Births were observed on January 13, 1966, and December 14, 1966, in a private zoo (Florio and Spinelli, 1967; Spinelli and Spinelli, 1968). In the first litter, consisting of a single cub, the birth lasted 2 hours, from the first contraction to the expulsion of the young. The placenta was discharged immediately and was eaten by the female. The cub weighed 300 gms. "It crawled soon after birth, stood up unsteadily at the age of one week. It started to walk 12–13 days after birth, but often fell down. Its eyes did not open until four days after the birth." The three cubs of the second litter were born at 0935, 1000, and 1020, and the female broke the fetal membranes of each one with her teeth. The weight of the young ranged from 250 to 280 gms. Their umbilical cords fell off at the age of 4 to 5 days, on the tenth day their eyes opened and they also stood up, on the sixteenth day they walked, and on the twentieth day the first teeth appeared. Similarly, J. Adamson (1969) found that cubs can stand at 9 days of age, that their eyes open at 11 days, and that they can walk well at 21 days.

I saw a heavily pregnant female on July 9, 1969, and three days later her four young were found in a patch of grass. The eyes of the cubs were closed. They tried to crawl away and emitted soft chirring sounds when I handled them. The female had just moved one cub to a thicket 300 m away and she returned at a trot, picked up a second cub by the back, and carried it off too. The third was handled in a similar manner, but the fourth and last cub was carried by the upper arm, a rather haphazard method of transport reminiscent of the one used by wild

dogs rather than the precise grip used by lions. After moving her cubs, the female returned once more, sniffed silently around the site, walked 30 m toward her cubs, then checked the former resting place a final time. The cubs remained in that thicket until August 15, although S. Trevor told me that he saw the cubs following their mother unsteadily on August 7. On August 19, at the age of 5½ weeks, the female took the cubs to their first kill. The gazelle was not dead and the cubs were frightened of it, according to S. Trevor who witnessed the event.

"At the age of 18 days the cubs started to eat donkey meat regurgitated by the female" (Florio and Spinelli, 1967). Similarly, J. Adamson told me that she observed a cheetah feed her cubs with regurgitated meat. I never saw such behavior. It seems likely that regurgitation is practiced by a female only when her cubs are less than 6 weeks old, too small to follow her to a kill. Regurgitation, a canid trait, has not been reliably reported for other cats. Spinelli and Spinelli (1968) noted that their captive litter was weaned at 5 months of age. I never saw cubs older than 3 months suckle, indicating that cheetah young are fully weaned at a much younger age than lions. However, J. Adamson (1969) noted that a cub almost 14 months old attempted to suckle on its mother.

Once they are fully mobile, cubs follow their mother at all times, becoming separated from her only when she chases prey. Their contacts are remarkably free from friction, compared to those of lions, and aggressive interactions are rare even when a group feeds on small prey. One cub grabbed a meaty bone from its sibling and 5 minutes later the former casually took it back. After a meal the mother often licks the face of her cubs and sometimes two animals lick each other mutually, a utilitarian as well as perhaps a social gesture. Yet in spite of the fact that a mother and cubs constitute a closely knit social unit, the animals give the impression of remaining aloof, of lacking the intense social orientation of lions.

Cheetah cubs play occasionally in the morning and evening and while traveling from one rest site to another. Solitary play consists of dashing along in a zigzag run, tail raised, and of climbing a meter or two up the trunks of trees and bushes. Although some social play involves crouching, stalking, and pouncing, most of it consists of chases with one swatting at the flanks and rump of the other in the typical manner of an adult bringing down prey. Such play was first seen at the age of 11–12 weeks in a captive litter (Encke, 1960). Occasionally two cubs face each other and hit with rapid downward thrusts of a paw. Wrestling, a common form of play in lion cubs, is only occasional and brief in cheetah. A female may paw her cubs gently, and once I watched a mother and two large cubs dash around for several minutes as each chased first one and then another.



> 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 10 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 (Schaller, 1968).

Two female cubs, born in July, 1967, were still closely associated with their mother on October 17, 1968, at 1815. The next day at 1825, when Kay found the cheetah again, the cubs had separated from their mother. They never came together again to my knowledge. They were 15 months old at the time. The abrupt severing of social bonds was dramatic, especially since I was unable to anticipate the break by such behavioral means as an increased level of aggression or temporary separations prior to the final one. Other families behaved similarly. One female was with her two large cubs on June 19 but not on June 21; another family split between August 17 and September 23. McLaughlin (1970) noted the abrupt separation of two litters both at the ages of 16 to 17 months. The sudden transition from dependence to independence in the cheetah is strikingly different from the gradual one in lion and leopard.

The litter of the tame but free-living cheetah observed by J. Adamson (1969) behaved differently than the Serengeti litters. At the age of 11 months the young wandered away from the female for as long as 2 to 3 hours, and by the age of 16½ months they remained away for longer periods than that. The final break with the mother occurred when the cubs were 17½ months old.

During their 15 to 17 months of association with their mother, cubs must learn to hunt well. In this they pass through three broad stages. At first they ignore the hunting postures of the female while they play around her and trot ahead, thereby alerting prey at times. She in turn may reduce such interference by her behavior, as one hunt illustrates.

> The female stalks slowly toward some gazelle 300 m away. Her three cubs, 9 weeks old, run playfully ahead of her. She sits. When the

cubs return and cluster by her, she immediately advances, but the youngsters once again range in front. She sits 5 minutes and the cubs settle by her side. The gazelle have drifted behind some bushes. She walks rapidly, trailed by the cubs, to within 100 m of the gazelle, suddenly sprints, and advances to within 50 m before the gazelle become aware of her and flee. She pursues an adult female, almost loses her when she dodges, and then both paws flash out and miss. After another 35 m she slaps the flank of her quarry and it crashes on its side. She overshoots 5 m, dashes back and grabs the throat. She drops the gazelle after 2 minutes and pants after her 270 m run. Then she pulls the gazelle by the throat or flank about 50 m toward her cubs. But a lioness trots up and takes the carcass.

Cubs 3 months old or older usually remain behind their hunting mother either walking slowly or waiting until the kill has been made. Small cubs may be introduced to live prey by their mother: "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" (Schaller, 1968). Similarly, Laurie (pers. comm.) watched a cheetah bring a fawn to her cubs which mauled it for 10 minutes before it died.

By the age of about 8 to 12 months cubs may initiate stalks and capture prey by themselves. A female may even provide cubs with the opportunity to capture prey by refraining to take part in the chase herself (Eaton, 1970b). I watched two 1-year-old cubs catch a gazelle fawn, but most such hunts ended in failure because of ineptness. For example, on August 21, 1968, a 13-month-old cub knocked a gazelle fawn down several times until finally the mother cheetah ran up and killed it. In three subsequent hunts observed, the female did the killing. On October 1, the same cub, now over 14 months old, again failed in its attempt to kill and the female finally dispatched the fawn. In spite of these failures, this cub and her sister separated from their mother on October 18. On October 28, one of these cubs caught a gazelle fawn, but it escaped and another 100 m of pursuit were required to bring it down. Suddenly a hyena ran up and appropriated the kill. The two cubs became very lean in the month following the separation from their mother. Obviously cubs are far from experienced hunters when they become independent, yet their learning proceeds rapidly for I found no evidence of death from starvation in that age class.



## Predation

Most information on predation was collected around Seronera, an area which provided me with 70% of the kill records as compared to 3% for the woodlands and 27% for the plains. There were usually many Thomson's gazelle around Seronera when cheetah were there, and this together with the open terrain had undoubtedly a marked influence on food habits and hunting behavior. In a preliminary paper (Schaller, 1968) some aspects of cheetah predation were described. This account includes an additional two years of data.

### Food Habits

A total of 261 kills were found, 91% of them Thomson's gazelle and the rest Grant's gazelle, wildebeest, impala, hare, and several others (table 63). Thomson's gazelle obviously are the most important prey of cheetah in the area. Similarly, of 23 kills reported by Kruuk and Turner (1967), 13 were Thomson's gazelle and 6 were wildebeest. The preponderance of gazelle kills reflects the seasonal movements of cheetah in pursuit of that species. Of 1,092 kills reported by Pienaar (1969) from Kruger Park, 68% consisted of impala, and among the 23 other kinds of food items were two young giraffe, two young buffalo, aardvark, porcupine, jackal, and other cheetah. Impala, Grant's gazelle, Thomson's gazelle, and hartebeest, in that order of importance, constituted some 85% of the kills of cheetah in Nairobi Park (McLaughlin, 1970).

Size of prey was an obvious factor in its selection. Excluding Thomson's gazelle, which seldom weigh more than 20 kg, all wildebeest, the hartebeest, one Grant's gazelle, and one topi kill were less than 2 months old; adult prey included four female Grant's gazelle, two female impala, and a male and female reedbuck, all weighing less than 60 kg each. However, large prey may be attacked, especially if two or more cheetah hunt together. Two male cheetah killed a yearling topi weighing about 90 kg. N. Tinbergen (pers. comm.) observed three cheetah wait beside a sick adult zebra at least four hours and one once darted in and bit its anus. Kruuk and Turner (1967) mentioned an adult female wildebeest, a male hartebeest, and yearling zebra as having been killed by cheetah. Foster and Kearney (1967) noted the following kills in Nairobi Park: "1 zebra, 7 Grant's gazelle, 1 Thomson's

gazelle, 4 impala, 1 waterbuck, 5 kongoni and 1 ostrich. All of the large prey were killed by 4 male cheetah which hunted together."

The preference for small species or young of large ones weighing 60 kg or less is related in part to the difficulty cheetah may have in subduing large prey. Tracks in the sand showed that a cheetah and reedbuck scuffled for some 25 m before the latter was vanquished. Kruuk and Turner (1967) observed a cheetah attack a male 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." Adult prey may also defend itself or its young. Kay watched a cheetah knock down a topi calf but an adult attacked and drove the cat off; when it made another attempt, two topi drove it away. Trevor (pers. comm.) saw wildebeest behave similarly.

Table 64 shows the ages of 228 Thomson's gazelle kills. These consist of 55% fawns (classes I–IV), as compared to about 35% of them in the living population. However, small young are usually not represented fully in a kill sample. One female we watched intermittently throughout the day for 26 days killed 24 gazelle in that time of which 62% were fawns. The actual hunt was observed in 66 of the 228 kills (excluding 10 unaged and unsexed ones) and the results were as follows:

| *Age class* | *Killing seen* | *Killing not seen* |
|---|---|---|
| I–IV | 80% | 45% |
| V–X | 20% | 55% |

The number of small young in a kill sample will vary with the season, but judging from these figures it is likely that at least two-thirds of the gazelle a cheetah captures are less than a year old, a higher proportion than expected. McLaughlin (1970) noted that 52.4% of all kills in Nairobi Park consisted of juveniles. Table 78 compares yearling and adult kills with a sample from the living population. The figures show that classes IV and V are relatively invulnerable to predation, that classes VI to VIII are taken about as often as expected, and that old animals (IX and X) are killed slightly more often than expected.

If cheetah prey unselectively on the sexes, and 22% of the population consists of adult males and 28% of adult females, then about 44 males and 56 females should occur in a sample of 100 kills (classes VI-X). The actual figures were 35 males and 65 females, about 25% fewer males than expected. As table 64 shows, predation was more or less



equal on the sexes in all age classes except in the two oldest ones. In those classes more females than males were taken ($P = <.05$), but if this was because they were more vulnerable or because there is a disproportionate sex ratio of old animals in the population I do not know.

Two gazelle and a wildebeest kill were heavily infected with sarcoptic mange. The other prey appeared to be healthy, and during the hunts I observed none of the pursued animals showed evidence of being in poor condition, which, of course, may merely indicate that the cheetah could detect slight weaknesses which I could not. The marrow of five adult gazelle was checked in the dry season of 1969 and three were depleted of fat.

In contrast to other predators, cheetah were not seen to scavenge, although Pienaar (1969) reported several instances of it in Kruger Park. Being low in the interspecific predator hierarchy, cheetah are probably too timid to investigate possible sources of meat in most instances.

### Killing Frequency and Food Consumption

From October 13 to November 5 and from November 14 to 19, 1967, a female cheetah with two cubs, 3–4 months old, was kept under intermittent observation throughout the day for 26 days to obtain some idea of how often cheetah kill. She was not observed at night, but, judging by the fact that she was usually located in the morning in the same place where she was the previous evening, she did little or no traveling at night. During the period she killed 24 Thomson's gazelle and one hare. She failed to capture prey on three days but on each of two days she caught two gazelle (Schaller, 1968). A. Laurie watched the same female from July 10 to 15, 1969, when she had another litter of two cubs, about 3 months old. In that period she failed to kill on two days, but captured a total of two adult female gazelle and two fawns on the others. Between August 13 and 15 she caught three adult female gazelle, one each day. Thus in 35 hunting days, this female captured 31 gazelle and a hare. Her grown daughter with three small cubs was observed for 6 days in August and in that period she killed a gazelle on each of five days and on the sixth one she was so persistently bothered by tourists that she was unable to hunt (Trevor, pers. comm.). I observed a female with two large cubs for five days between August 21 and 28, 1968. Six gazelle were caught in that period. In the Seronera area, female cheetah accompanied by cubs kill almost at a rate of one gazelle per day, or about 341 per year. I have no precise information

on how often solitary cheetah kill but McLaughlin (1970) found out that they do so every 2 to 3 days or about 150 kills a year.

An estimated 200 to 250 cheetah use the ecological unit. Of these, 28%, or 57 to 70 of them, are solitary, each killing at a rate of 150 animals per year. The rest are in about 54 to 72 groups, some consisting of females and cubs and others of independent young or adults, each group killing at the rate of about 341 prey per year. Thus a total of 26,964 to 35,052 animals a year are taken by cheetah. Around Seronera and on the plains most of their food consists of Thomson's gazelle, but impala, dik-dik, topi young, and others may contribute much to their diet in the woodlands. Possibly 60% of all kills are Thomson's gazelle, which would indicate an annual kill of 16,178 to 21,031.

The average amount of food actually consumed by a cheetah over a period of days could be calculated from the kill record of the female that was observed for 26 days (Schaller, 1968):

> 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 3,650 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).

Assuming that an adult has on the average 4 kg of edible food available each day and a cub 2 kg, including meat of large kills that is wasted, and that a third of the 200 to 250 cheetah are cubs, then these animals used a total of 243,090 to 292,950 kg per year. About 40% of a large prey and 30% of a small one consists of inedible portions and the amount actually killed is therefore about 35% higher than that which they have available as food, or about 373,985 to 450,692 kg.



Since these figures are based on several assumptions, they are at best of the correct order of magnitude.

### Hunting Behavior

Cheetah spend most of the day resting. Around Seronera, where prey is usually plentiful, they seemingly wait for it to wander into their vicinity rather than roam in search of it. They seldom travel more than 3 to 5 km in a day, but in Nairobi Park they are said to move almost 8 km on the average according to Eaton (1969) and 4.3 km according to McLaughlin (1970). Their various forms of activity, including stalking, feeding, and walking at their normal speed of 3 to 4 km per hour, usually require less than 4 hours of the day. Although cheetah are primarily diurnal, they may also travel and hunt on moonlit nights. The 147 exact and estimated times of killing prey as well as the times of 32 unsuccessful attempts are combined in figure 44 to show that the animals may hunt at any daytime hour between 0600 and 1900 with peak activity periods between 0700 and 1000 and 1600 1800. In addition, once cheetah were on a kill that was made in the dark at about 1930, and on another occasion a gazelle was captured in moonlight at 0200.

Around Seronera, gazelle are typically scattered over the plains in small groups of 2 to 20 individuals, with cover during the dry season consisting mainly of occasional shrubs and patches of grass. Cheetah typically hunt for prey either by walking alertly over the plains, sometimes climbing into the low branch of a solitary tree or on a termite hill to scan, or by waiting until a gazelle walks by. When a cheetah tried to approach prey undetected or ran after it, I considered it a hunting attempt. I observed 48 such attempts of which 16 failed before a rush could be made, eight runs were unsuccessful in spite of the fact that the cheetah pursued at great speed, and 24 (50%) ended in a kill. Other observers told me the outcome of 55 actual chases they witnessed. The 16 hunts that were terminated prior to the rush failed for several reasons: in 8 instances the cheetah bounded or trotted several meters toward gazelle then halted, presumably because it did not see a vulnerable individual; in 4 instances it stalked then ceased to do so for no obvious reason; in 3 instances it stalked but the prey sensed danger and looked up; and once prey moved inadvertently out of the cheetah's reach.

A complete hunt can be divided into an approach, chase and capture, and finally the kill. A cheetah may approach prey in several

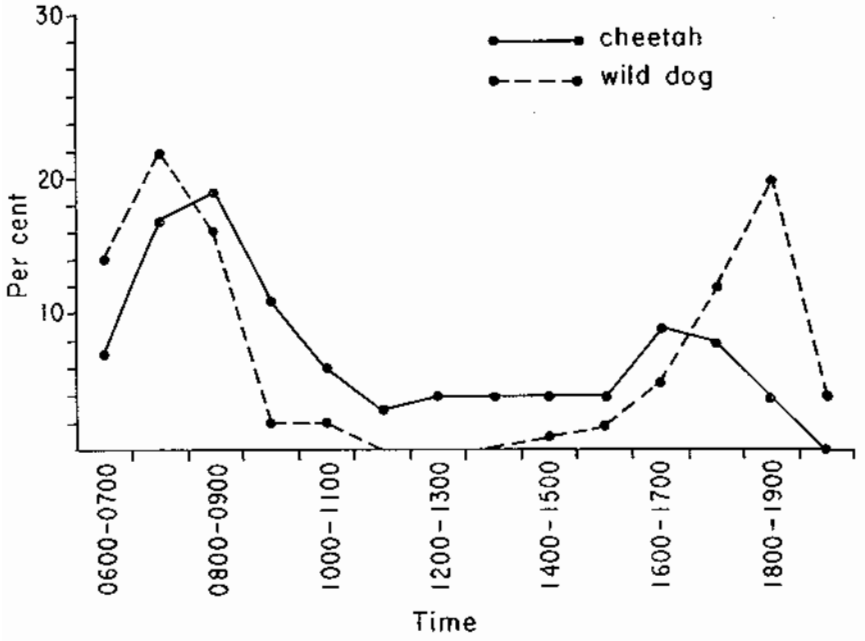


Fig. 44. The time of day when cheetah and wild dog killed their prey.

ways. Occasionally it walks toward gazelle without concealing itself. The gazelle may stand and watch and even trot closer, to within 60 m to 70 m. The cheetah may then run at one or another group, giving the impression of searching for a suitable quarry. Another kind of approach is to bound toward an unsuspecting herd from at least 100 m, and by the time the prey becomes aware of danger the cheetah is close enough to select an individual. If a cheetah sees a small fawn it may begin its pursuit from as far away as 500 m to 600 m, according to Root who saw two such hunts. Many hunts involve a variety of techniques from walking closer, waiting and stalking, to actual pursuit at various speeds. Cover is used for concealment but no attention is paid to wind direction. Eaton (1970a) stated that "the cheetah does not crouch like most cats," but it does so readily in the Serengeti. If a gazelle looks up from its feeding, the cheetah may halt, standing motionless until the animal lowers its head again.

In 17 successful hunts which I observed from beginning to end, the cheetah began its approach from an average distance of 180 m (50–300 m). On 7 of these it stalked closer for an average distance of 125 m



before rushing, on 3 of these it walked and trotted some 60 m to 130 m closer, and on the remaining 7 hunts it ran closer without preliminaries. Usually a gazelle spotted the cheetah immediately and fled, but on three occasions the animals did not see the cat until it was 20 m, 30 m, and 50 m away, respectively. Six unsuccessful hunts began from an average distance of 125 m.

Cheetah can attain a speed of about 104 to 112 km per hour (65–70 mph) according to Howell (1944), and even 114.6 km per hour on a race course (Demmer, 1966). The fact that these cats can readily capture gazelle, which I have clocked as they ran beside the car at 70 to 80 km per hour, suggests that they may certainly reach a speed of 95 km per hour. However, a cheetah can use its full speed only to draw close to a gazelle, and after that it has to follow at a reduced rate in order to follow each twist in the unpredictable route of its quarry. With danger imminent, the gazelle may zigzag but seldom does so more than 3 to 4 times. When close enough, the cheetah slaps the hindleg, thigh, or rump of its prey with a sideways or downward sweep of its forepaw; occasionally a cheetah attempts to hit a gazelle with both paws in unison. Eaton (1970b) noted that large prey such as hartebeest may also be slapped on the foreleg. The slap may leave a cut in the skin, presumably caused by the large dewclaw. When hit, the gazelle crashes to the ground or it may even flip over in mid-air. One Grant's gazelle apparently broke a foreleg in such a fall and another Grant's gazelle a hindleg. "Racing up alongside its quarry the chita springs with unerring aim at the throat or on the back" according to Stevenson-Hamilton (1954) but such behavior was not observed.

Many runs begin at a moderate speed while a quarry is being selected, and after that the cheetah accelerates to a final burst which never exceeded a distance of 300 to 400 m. The total distance of the chase varied from 35 to 460 m. Small fawns (classes I and II) were caught after an average run of 190 m in 12 hunts observed, but 11 runs after large fawns and adults required an average distance of 290 m. Ten unsuccessful runs after adults were 270 m long.

Once a cheetah slipped and fell when making a sharp turn after a gazelle, on another occasion a hunt failed because the cheetah was unable to select an individual from the compact herd, and on a third occasion the cheetah lost sight of its prey after it mingled with others. Twenty-three other unsuccessful runs terminated when a cheetah gave up the chase after 200 to 300 m, particularly after it failed to follow a sharp turn by a gazelle. It seemed exhausted, panting at a rate of some

150 breaths a minute, and seldom attempted another rush for at least half an hour unless it spotted a small fawn.

Hunting success varies with the age of the gazelle selected. Of 31 runs after small fawns (class I and II), 100% were successful. This figure does not include three crouched fawns that were snapped up nor does it include one instance, related to me by a visitor, in which a cheetah caught a fawn but then released it alive when a lion approached. Of 56 runs by cheetah 14 months old and older after large fawns, yearlings, and adults, 30 (53.5%) were successful. The success rate for gazelle of all ages was 70%. These percentages do not include stalks and other hunting attempts which failed to culminate in fast pursuit. McLaughlin (1970) saw 236 chases of 25 m or more after a variety of prey with a success rate of 37%.

Several factors play a role in the selection of a particular gazelle. (1) Small fawns are selected undoubtedly because a cheetah is assured of a meal, even if a small one. (2) Cheetah prefer prey which is separated from others of its kind. When, for instance, a gazelle veered from a fleeing herd, the cheetah pursued it. It was my impression that groups of two and three gazelle were favored by cheetah over large aggregations. (3) Gazelle which are near cover, behave inattentively, or are situated in such a way that the cat can approach undetected are often chosen; final selection depends on size and on distance from the cheetah, but not primarily on the animal that flees first as has been suggested by Kruuk and Turner (1967) and Walther (1969). (4) Fleeing animals seem to be chosen more than stationary ones, so that territorial males, which tend to stand and watch the cheetah rather than escape immediately, may be passed by. In many instances a quarry is not selected until both predator and prey have run a distance and the physical condition of the latter may, by then, have influenced the cheetah's final choice.

On several occasions a female assisted her cub when it was unable to subdue a fawn. Trevor (pers. comm.) once watched a large cub bound at several gazelle; while their attention was drawn in one direction the female sprinted in from another and caught one. But such cooperation seemed fortuitous, and communal efforts in securing prey as practiced by lions and wild dogs were not observed.

Three examples of hunts provide a more complete picture of the behavior than presented so far.

(1) A female approaches several gazelle through high grass for 130 m in a stalking walk, but they spot her when she is 45 m away and she gives up her attempt. Twenty-seven minutes later she sees about 15 gazelle at 250 m, approaches slowly to within 150 m and suddenly runs toward them, the first 130 m moderately fast as she chooses a victim, and then 160 m at full speed after a yearling. She slaps but misses as the gazelle dodges, and the hunt is a failure.

(2) A female climbs 3 m into a tree and looks around. She spots 10 gazelle 230 m away and walks 140 m toward them with head held low and then lies watching for 5 minutes. One female grazes somewhat separated from the herd; the cheetah rushes her and is within 35 m before the gazelle turns and flees. After a chase of 160 m including a 180° turn, the gazelle suddenly flips forward, hind feet in the air, apparently tripped by the cheetah which lunges in and grabs her throat.

(3) A female sees about 12 gazelle grazing on burned stubble 175 m away. She first walks toward them 100 m then bounds, chasing the herd at moderate speed for 175 m before selecting the smallest individual. She sprints after it, follows three zigzags closely, and after 130 m catches it in a cloud of dust. She holds its throat for 5 minutes before it dies.



One or both forelegs and the chest may be used to hold the struggling animal down. The cheetah tries to grab the throat of its quarry, usually remaining behind the animal, away from the sharp hooves, while doing so. In 21 detailed killings observed, 20 were with a throat hold, the cheetah either standing, sitting, or lying; one small fawn was bitten in the nape (plate 38). Although the skin was often punctured by the canines and occasional chewing movements were made by the cheetah, death in most instances seemed to be due to strangulation. An average of 4.5 minutes (2 to 11) elapsed before the gazelle ceased to move. Occasionally the cheetah dropped the body, but when the animal continued to kick it was picked up again and held by the throat several additional minutes. If a bush or a tree is near, the body may be dragged or carried as far as 250 m into the shade with the cheetah holding the carcass by the throat, nape, back, rump, or thigh. The hunt and the moving of the kill seem to exhaust a cheetah so much that it may rest half an hour before eating. Cubs less than 3 months old are often unable to cut through the skin of prey and the mother may do so first and then rest while her offspring feed.

Cheetah usually eat the meat off of one thigh and then off of the abdomen and ribcage before starting on the other thigh, the forelegs, and on the liver and heart. Blood in the body cavity may be lapped up, useful behavior in areas where water is scarce. (Cheetah around Seronera

drank at the river irregularly in daytime as well as at night.) All that typically remains of a gazelle is the articulated skeleton with most of the skin attached as well as the digestive tract. Most bones and skin of a small fawn may also be eaten. Meat from a Thomson's gazelle is seldom wasted, but a considerable amount may be abandoned when an adult Grant's gazelle or other large prey is killed. Cheetah were never observed to take more than one meal from a prey. When one or more large cheetah feed on a gazelle fawn, the remains are abandoned within 15 to 35 minutes, but a female with small cubs may eat on such a kill for as long as 70 minutes. A female with two small cubs required a total of 50, 65, 75, and 120 minutes, on four occasions, to consume adult gazelle. According to J. Adamson (1969) cheetah may scrape dirt over the carcass after eating.

Cheetah feed rapidly, stopping occasionally to look around, as if nervous, probably because other predators frequently appropriate the kill. Of 238 kills, 20 were known to have been taken by lions before the cheetah was finished with the meal (plate 38), 11 by hyenas, and one by leopard, a loss of 12%. On at least 11 of these occasions lion and hyena were attracted by vultures that descended to the kill. In fact, on two occasions a solid phalanx of white-backed vultures advanced to within 1 to 1.5 meters of a cheetah, which abandoned the remains before finishing. Usually, however, the cheetah ignores vultures or rushes at them, occasionally leaping into the air and swatting at an escaping one. Jackals, too, may be chased from the vicinity of a kill, and in one instance a female pursued one 100 m and slapped it. Hyenas meet little resistance when taking kills from cheetah although in one instance two hyenas were attacked and driven off and on another occasion a cheetah hit a hyena in the face as it took the kill. More typical, however, was the following sequence of events.

> A female cheetah sees several gazelle 200 m away, among them a small fawn. She trots, then bounds, some 175 m toward them, then chases the fawn 100 m, her tail held almost vertically, and catches it. As she holds it by the throat, a hyena lopes up. She drops the fawn, jumps back 3 m and hisses while the hyena carries the carcass 50 m and eats it in 10 minutes. A few minutes later she spots another fawn 170 m away and catches it, thereby providing the same hyena with another meal.

Cheetah have no defense against lions, and whenever one approaches a kill, they either retreat immediately or circle the lion at distances of 10 to 20 m while growling, moaning, hissing, and occasionally lunging.