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Abstract: The sex ratio among adults in the two observed areas Nairobi National Park and Amboslie Game Reserve was about 2:1, in the litters 1:1. In Nairobi National Park, impala, Grant's gazelle, kongoni and waterbuck occur most frequently in the cheetah's diet. 12 of 30 aged kills were adults, 18 juveniles. Details on group size while hunting and of the herd size of the hunted species, prey selection, the cheetah's energy budget and the interaction of cheetahs with other species are presented.

POPULATION PARAMETERS

Robinette et al. (1961) used weight and length to describe a growth curve for young cougar. Bobcat are aged with the cementum layers in the canine teeth. The only method that has been used to age cheetah is a system of five general age classes based on how large cubs are relative to an adult (Graham and Parker, 1965; Graham, 1966).

Some characters are distinctive to certain age classes. Shortridge (1934:108) related the sharpness of claws to age, and Stevenson-Hamilton (1947) noted the age of first climbing. Age criteria that depend on capturing animals are undesirable when visual measures are possible from a distance.

Two-week-old cubs are covered on their upper parts with blue-gray fine hair, while the sides, tail, belly, and legs are covered with dark, solid spots. At three months cubs begin losing the long gray hair and dark spots become apparent all over the body (Fig. 3-1). Morris (1965:323) says that the mane, which Stevenson-Hamilton (1947:199) described as being lost in the third month, disappears after the tenth week at the same time that the cubs lose the ability to retract their claws. The cubs are blind at birth and the spots are present under the gray fur (Shortridge, 1934:108; Sterndale, 1884:203). These observations were confirmed by Adamson (pers. comm.,

1969) and her observations on maturation are summarized in Table 3-1.

It is appropriate here to theorize why I believe the stripe, or tear line as it is sometimes referred to, has evolved in the cheetah face. It could be important to identify members of the species and I have experimentally verified this using mounted specimens of cheetah and leopard at Lion Country Safari. In addition, it seems reasonable to suppose that the stripe breaks up the continuity and shape of the head (Fig. 3-2). It detracts especially from the large eyes. A human observer or a potential prey animal has its perceptual expectancy disrupted by the stripes. The cheetah is a diurnal predator and when it hunts it never takes its eyes off of the prey, often holding the head up in clear view above the vegetation while stalking. The stripes are really only obvious when the observer looks straight on at the cheetah's face and this is exactly the view that prey get when being stalked. Also plausible is the function of reducing glare.

TABLE 3-1 MATURATIONAL DATA DERIVED FROM ADAMSON (1969)

Age	Morphological or Behavioral Changes
5 days	Eyes shut, orient to sounds and respond by "spitting"
9 days	Cubs standing, greet mother
11 days	Eyes open
12 days	No teeth, staining
14 days	Climb well, cling to roof of cage (Stevenson-Hamilton, 1947)
21 days	Walk steadily, "chirp" call attracts mother
28 days	Teeth erupting
190 days	Permanent molars
240 days	Canines, last of first set of teeth, lost
245 days	Lower incisors erupt

The stages following the loss of the gray outer fur and dark undersides are more or less continuous through the adult stage. The only differences apparent to an observer are size. Elephants Laws, 1966:31) are aged by relative size comparisons. In the Serengeti, Scaller (1972) classed cubs by age as follows: 0-3 months—black cubs; 3-6 months—small cubs, one-half size of mother; 6-12 months—medium size, two-thirds size of mother; and older than 12 months—large cubs, distinguished from mother by more slender build and small ruff on the nape. To develop a suitable system of aging animals in the field, it is necessary to have known aged animals that can be weighed, measured, and photographed weekly during development. Sets of diagrams or illustrations could then be used in the field to age animals without having to capture them. Herman (1972) should be able to offer such a system based on the development of captive cubs at San Diego Wild Animal Park.

The use of "cap-chur" equipment to immobilize ("dart") animals for

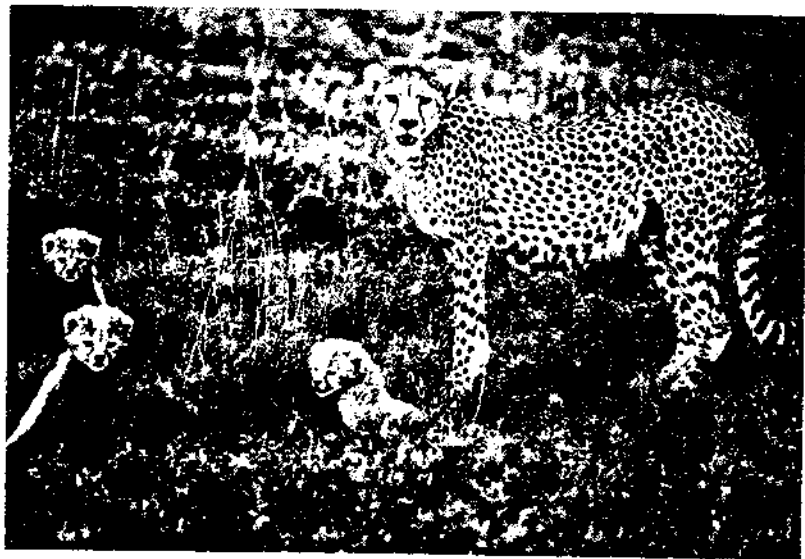


Figure 3-1 Cheetah cubs have a silver gray mantle until about three months old. (Photo: N. Myers.)

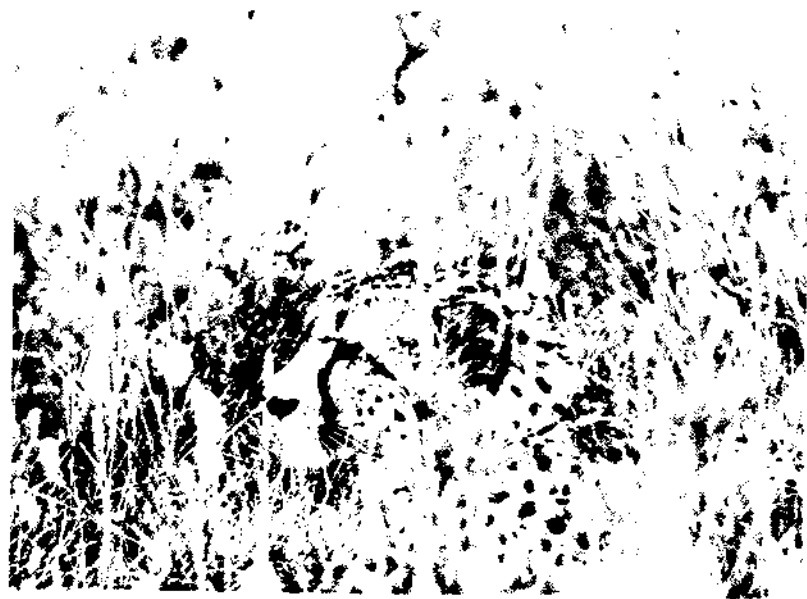


Figure 3-2 Hunting in tall grass, Nairobi Park. (Photo: R. L. Eaton.)

weight and measures of length could be employed to provide a series of measurements so that estimates of age would improve in accuracy. However, drugging inevitably leads to some losses and usually the knowledge gained counterbalances such losses. But in an endangered species the use of any technique that entails only occasional losses can hardly be justified. There are additional considerations with the use of drugs for capture. Unless an entire family is captured at one time, which is in itself very difficult, a cub, once recovered from the effects of the drugs, may get left behind in which case it would die. In my field study it would have been very useful to capture cheetahs with drugs and place radio transmitters on them so they could be located readily. Only one group can be kept track of at one time and each time I wanted to observe a different group it had to be searched out. Because of the hazards of immobilizing techniques, the idea was abandoned. However, York (1973) of Lion Country Safari has carefully established dosages of several drugs that can be safely used to immobilize cheetahs, and Herdman (1973) had similar success. Neither lost any cheetahs.

There are very little data on sex and age ratios. Graham (1966:51) gives sexes and groupings for 47 adult cheetahs, unaccompanied by young. The ratio of males to females for these groups is almost exactly 5:1 (males:females). In addition the Cheetah Survey (Graham and Parker, 1965:3) provides the sexes of 17 adult cheetahs that were shot, poached, or killed. There were 12 males and 5 females, bringing the ratio from the combined data to 4:1 in favor of males. The ratio appears unusually high. Schaller (1972) said the sex ratio in the Serengeti was 1:2 while Eloff reports (pers. comm.) a 3:1 in Kruger Park. We have no idea why such diverging sex ratios obtain in different areas, if in fact they do.

Graham and Parker (1965:2) compiled 1225 sightings of 2785 individual cheetahs. Of 2095 adult animals 1794 or 85% were adults, 301 or 15% were adults accompanied by litters. Of the 253 litters seen with adults, 160 or 63% were seen with one adult, 62 or 26% of the litters were seen with more than one adult, and, 31 or 12% were not seen with adults.

I think that most of the 31 litters not seen with adults must have had an adult female mother that was probably not recorded due to being present but not observed, and more likely was off hunting. Although Graham and Parker (1965:3) do not have data on the sex of the 160 single adults seen with litters, I am sure that almost all of these adults were females. Of the 62 litters seen with one or more adults (141), 62 adults can be assumed to be female mothers and 79 to be adults in groups comprising roughly 64 males and 15 females in which the males of the groups were pursuing mothers in "heat."

In the Serengeti, Schaller (1972) observed 244 individuals not accompanied by cubs; 52% were solitary, 31% were in groups of two, 14% in groups

of three, and 3% in groups of four. As in Nairobi National Park, Schaller never observed a female with young accompanied by other adults or a second litter. Serengeti females are unsociable except when mating or when they have cubs, and males may form social bands with other males (Schaller, 1972), just as I observed in Nairobi Park.

In Nairobi Park I found seven males and four females among resident adults and an adult male and one female among nonresident adults. In the Amboseli area I observed three males and one female among adults. For both areas the sex ratio for adults was about 2:1.

Sex ratio data in the Cheetah Survey (Graham and Parker, 1965) are probably biased by observational factors related to movements and activities of cheetahs, which are quite different for adult groups compared with family groups. In some areas such as Nairobi National Park, observers see adult groups more readily than litters, while in the Serengeti more frequent sightings of litters means fewer sightings of adult males and the total sex ratio is biased in the female direction. Why group compositions vary between areas is unknown unless higher early litter mortality discriminates against the latter formation of male groups.

Data on sex ratios in young are relatively rare. Graham and Parker (1965) record the sex of one litter. Very young cubs are not individually marked and it is hard to know just which cub one is observing. For this reason it is difficult to sex an entire litter, that is unless the observer can see the genitalia of all cubs at the same time!

In one litter of four cubs, I saw two males and one female but was never able to sex all four at the same time. In another litter of four cubs there were two males and two females. Another litter had two males and three females. For 13 wild cubs, 12 were sexed and the ratio was 1:1. In the litter recorded in the Cheetah Survey (Graham and Parker, 1965:9) there were originally five cubs. After one cub disappeared, there were two males and two females. These data all point to an even sex ratio for wild litters, but it is important to know sex ratios at birth and all these cubs were several months old.

Schaller (1972) sexed five 0-3 month old litters from which some cubs had already disappeared. He found 4 males and 7 females. McLaughlin (1970) in Nairobi Park found 9 of 11 cubs to be males. In older cubs, Schaller reports 10 males and 18 females, and says, "an equal sex ratio at birth seems probable."

All the cheetahs I sexed were at least five months old. In many species it has been found that there is differential infant mortality of the sexes. This possibility cannot be accounted for in the cheetah.

Longevity is an important factor when considering population dynamics and productivity. More important than longevity is period of reproductive activity. Nonreproductive members of the population can be important in

other ways than actual reproduction. They can be valuable for survival of other individuals, for example if they are leaders of groups. In carnivores such as the mountain lion (Young and Goldman, 1946:87; Hornocker, 1970), learning from conspecifics, the mother in felids, is important and the value of older, more experienced individuals cannot be overestimated.

When advocating the existence of altruism or self-sacrifice in a species the problem is to determine the selective advantage to the altruistic individual's genes. In cheetahs, adult females do stay with young a short while after they have learned to hunt effectively. Continued teaching of the cubs should not counterbalance the advantage to the female in rearing still more young. The 14–16 months that a female spends with a litter indicates that learning is an important aspect of female-young relationships.

Adaptive modification of behavior (learning) gives selective advantage only to those males that can remain alive to pass on their genes and to females to remain alive, reproductive, and functioning as a parent. Burton (1962:187) gives up to 16 years for life span. Flower (1931) gives three ages for cheetahs in captivity: 13 years, 6 months; 14 years; and 15 years, 7 months in captivity. He also says that cheetahs seldom live more than six years in captivity, but Crandall (1964:398) says it is even less. Graham and Parker (1965:17) give seven years for a captive cheetah. In 1970 I discovered a pet cheetah in southern California that was 19 years old. In the wild, mortality appears much greater in cubs than in adults. Their attempts to defend kills against hyena, leopard, lion, and wild dog are usually futile. The cheetah's great fear of lions implies their vulnerability to other predators. Indeed, even adult cheetahs are killed by other predators, especially lions. Average life span of adults in the wild may be relatively short. Selection forces appear to have increased litter size and frequency of birth compared with other larger cats, implying that length of reproductive life may be relatively short, or mortality of young is high, which is fairly obvious.

Robinette et al. (1961:212) and Hornocker (1970) point out that in mountain lions, as in cheetahs, the female stays with her cubs for about two years. Mountain lions have two or three cubs per litter and give birth at about two year intervals in absence of litter mortality. The cougar has a smaller litter size and reproduces less frequently than the cheetah. Its lower reproductive potential correlates with less mortality from other predators, and apparently cougars are seldom inflicted with disease (Hornocker, 1970). Hornocker (1970) has found that the training period of the cubs is prolonged and rigorous, more so than earlier believed.

Cheetahs average at least four cubs per litter and often come into estrus while the litter is still being raised. Females with litters mate as soon as 10–12 months after parturition in the absence of litter mortality. Allowing

for a three months gestation period, births are sometimes 13–15 months apart, a higher frequency than any other big cat. Since mating by females with cubs often occurs more than three months prior to the time when the first litter strikes out on its own, there may be delayed implantation of the embryo which is known to occur in cougars (Robinette et al., 1961:216) and house cats (Asdell, 1964:168).

The only wild individuals on which I have dates for determining longevity is a group of males in Nairobi Park. Park records, photographs, and Graham and Parker's data all lead to the conclusion that a group of four males were mature in July, 1964. In fact, they must have been more than 14 months old since they were exceptionally large at that time. A photograph of a nearly mature litter (Fig. 3–3) with the mother shows how the young adults are not as heavy in build though they are 14–16 months old.

Putting the four brothers' age at a minimum of 16 months in July, 1964, their age (only two of them were present in February, 1967) at the termination of the field study was 47 months. They appeared to be in peak physical condition, were the largest cheetahs I ever saw, and were the most effective hunters. Their teeth appeared perfect and they dispatched and ate prey easily. It appears that four years is prime age for males.

Pippa, Joy Adamson's cheetah, was four and one-half years old in July, 1968. She was apparently quite healthy and certainly was reproductively active. Pippa conceived the first time at about 22 months. Age of sexual maturity in females is given by Varaday (1966) who also kept a pet cheetah that he let run free on his farm in South Africa. His female came into her first estrus at two years. In the Serengeti, one female conceived at 21 months, and another exhibited behavioral estrus at 22 months (Schaller, 1972). Cheetah females apparently mature sexually at an earlier age than mountain lions (Robinette et al. 1961) or lions (Asdell, 1964) in which 30–36 months is usual; however, the earliest record of age at first birth is 24 months, for a lioness at Lion Country Safari (Eaton, 1972).

The age composition of a population is crucial if one is to understand population trends. Natality and mortality have considerable influence on the age composition and vice-versa as Alexander (1958:136) sets forth.

To really understand a population's trends and to be able to predict its future one must have data over several years. With the cheetah it is desirable to evaluate the annual cyclic environmental changes and how they effect productivity. The age makeup of a population at any point in time should be present in the data of 2785 cheetah observed in East Africa. The age composition of these cheetah was 2095 adults and 690 immatures or 75% adults and 25% immatures, an adult to young ratio of 3:1. This ratio appears entirely too large.

Cheetahs are more difficult to observe the younger they are. As they



Figure 3-3 A family group of a female and four nearly mature young (14-16 months) shows that the mother, second from the right, is larger and heavier. One male cub took over leadership of the entire family but was not allowed to mate with his mother when she came into heat. (Photo: R. L. Eaton.)

mature they are much more active and are larger, both of which should increase observability. Beyond about six months of age observer bias should decrease since cubs then begin hunting with the adult at least some of the time, and are more active and less secretive.

Graham and Parker (1965:5) present data on the age groups of the immatures observed. Litter size increased with progressive age until the four to seven months category. It is hardly imaginable that numbers of litters should increase with age. They should stay the same or decrease with age. Again, more data on the fate of litters from birth are necessary.

The only way that a 3:1 age ratio can be productive is if there is hardly any mortality between birth and reproductive age. That this is not the case is obvious. Level of mortality in the reproductive or postreproductive part of the life span is unknown. Mortality may be higher for females as indicated by the exaggerated sex ratio in adults in some areas.

The postreproductive age mortality is probably quite high for the few cheetah that may live this long. There appears to be selection favoring only the reproductively active individuals in the population; however, there are no aging techniques for adults, and there is no information that relates mortality to adult age.

Since many adult groups are well recognized and known to have remained together in nearly every case, it is believed that mortality to members of all-adult groups is relatively low. Adult groups are almost always males, and females should suffer higher mortality due to rearing young. The nature of social organization in cheetahs appears to account for the high sex ratio. Where cub mortality is low, for example where other predators are less numerous, groups should be larger and males might be expected to predominate in the local sex ratio which would be even more exaggerated since observers see adult groups more readily than single females or females with cubs. In those areas where adult groups are not common, sex ratios should be lower and more accurate since solitary individuals should be encountered equally regardless of sex. Data on sex ratios in different regions are sparse. In Kruger Park where lions and hyenas are not abundant, the sex ratio is largely (3:1) in favor of males. Nairobi Park, low in hyena, has a high sex ratio. In the Serengeti, where other larger predators are most dense, there appears to be a sex ratio in favor of females. The missing link in these speculations is whether or not males separate and live singly as adults in some areas, for example where availability or size of prey would favor a modified social life. Ecological conditions could easily account for such social artifacts; however, we simply lack data from several long-term studies carried out in different regions.

PREDATOR-PREY ECOLOGY

Equatorial Africa has the richest mammalian fauna in the world. "Nowhere else in the world is there to be found so many species of wild ungulates, many of which have extremely large populations" (Bourliere, 1963). Because of this great array of both individuals and species of wildlife, this area has great aesthetic value. In order to preserve the wildlife of Africa in the face of rapid population growth many biologists have advocated the use of surpluses of natural animal populations for food rather than

attempting to replace them with domestic livestock (Bourliere, 1963; Darling, 1960). The wise management of the wild animal resources can be carried out effectively only if the ecology of these species is thoroughly understood.

Ecologists are studying these natural communities, especially the ungulate herbivores since they make up the great potential for human food. Until recently less attention has been paid to the larger carnivores. Vesey-FitzGerald (1960) suggests that in the Rukwa Valley predators (lion, leopard, and hunting dog) are not important in limiting prey but rather the alternating seasons of flood and drought and its effects on the herbage. On the other hand, the Talbots (1963) argue that on the Serengeti-Mara Plains of East Africa the lion is limiting the numbers of wildebeests by taking up to a third of the population per year. Bourliere (1963) presents data from the Ruindi-Rutshuru Plains and Nairobi and Kruger National Parks to support his hypothesis that carnivores (lion, leopard, cheetah, and wild hunting dogs) play an important role in controlling the size of herbivore populations, at least for several of the prey species.

The diversity of opinion on the role of predators in controlling prey populations is not new. Errington (1946) for example has argued from years of work on muskrat (*Ondatra zibethicus*) ecology that losses due to predation are incidental and that habitat conditions are what limits the herbivore. Laboratory experimentation and theoretical speculations, on the other hand, have suggested that many herbivores are predator-limited, not food-limited. At least for Africa this question is of vital importance for the continued survival of the large predators in any kind of management scheme.

Investigations by Kühme (1965), Guggisberg (1963), Wright (1960), and Schenkel (1966) have added information on the African lions ecology and mating behavior. The first full-scale field studies have just been conducted by Schaller (1972) and Eloff (1973) on the lion. Kruuk (1972) has conducted a long-term study of the hyena (*Crocutus* c.). Estes and Goddard (1967) studied the hunting dog (*Lycaon pictus*), and Wyman (1967) the jackal (*Canis mesomelas*). Observations on the leopard are relatively rare (Bourliere, 1963b; Schaller, 1972), due to the fact that they live mostly in riverine bush where observation is difficult. Because the lion has attracted the attention of sportsmen and biologists, much more is known of its general ecology (Fig. 3-4). Schaller's long-term study (1972) adds greatly to an overall understanding of the lion and its role in the community.

Previous conclusions on cheetah biology should be evaluated with skepticism. Most observers have marveled at the cheetah's speed and relative ease with which it should procure a meal; but purely on the basis of deductive inference from evolutionary theory, can it therefore be surmised that the cheetah has adapted to small, swift antelope but that the



Figure 3-4 The lion has been the subject of several studies in East Africa. (Photo: N. Myers.)

antelope are helpless? If this were true then we would expect the cheetah to overeat its prey, which it does not. The prey, as Klopfer (1964) states, usually adapts as a function of the predator's capabilities, and one goal of the field biologist is to unravel the intricate behavioral adaptations that have evolved between hunter and hunted in their never-ending race of adaptation.

A number of excellent recent studies (Bourliere, 1963; Foster and Kearney, 1967; Graham, 1966; Hornocker, 1969; Kruuk and Turner, 1967; Schaller, 1972; Wright, 1957; Joslin, 1973; Eloff, 1973; Muckenhirn and Eisenberg, 1973) have contributed to our knowledge of the predator-prey ecology and behavior of the big cats.

It was pointed out that to describe a predator's energy budget, it is not sufficient to give the percentage of occurrence of each prey species in the predator's diet. Wright (1957, and pers. comm.), for example, lost much valuable information in his pioneering study of African predators in that he located carcasses usually long after the animal had been killed and largely consumed by predators and scavengers. Foster and Kearney (1967:118) point out a similar limitation in their study: "The smaller species are probably always under-represented due to the rapidity with which they are eaten." Young prey with soft, edible bones are either more

quickly or more completely eaten, and both cases lead to biases in data which are gathered by examination of prey remains (Fig. 3-5).

In many studies on carnivores in African parks, much of the data are collected by indirect and nonrandom means, such as using vultures which locate kills in more open areas, and on reports of visitors and park personnel who largely frequent the more accessible areas. Round-the-clock observation of a predator provides important information by which data gathered in other ways can be more objectively evaluated to determine the factors related to successful predation by cheetah and to examine regional differences and similarities in food habits, prey selection, and hunting techniques. This same principle emerges from Schaller's (1972) study of cheetah predation in the Serengeti, where the ages of prey varied significantly when Schaller (or others) actually observed killing as opposed to examining prey discovered after it was killed.

FOOD HABITS

A total of 27 species have been recorded as cheetah kills in East Africa (Graham, 1966). Pienaar (1969) listed 24 species for Kruger National Park, and 9 species are recorded as prey in the Serengeti (Schaller, 1972). The variety of prey ranges from hares and newly born warthogs to adult wildebeests and zebra—a weight range of less than 5 to 600 pounds (weights after Bourliere, 1963). Impala, Grant's gazelle, and Thomson's gazelle, which as adults average 120-160, 130-155, and 40-50 pounds respectively, comprise about two-thirds of all recorded kills in East Africa (Graham, 1966). In the Serengeti, a lot of cheetah kills were Thomson's gazelles, by far the most abundant prey species. (Schaller, 1972).

TABLE 3-2 WEIGHTS OF KILLS OF NAIROBI NATIONAL PARK CHEETAH GROUPS

Group	N	Range (Lbs.)	Mean Weight (Lbs.)
1	17	10-150	75
2	7	30-150	124.2
3	3	10-600	185.0
4	3	10-130	67.0
			$m = 112.8$

The average field-estimated weight of all cheetah kills observed was 113 pounds. The average for each group varied from 67 pounds for group 4 to 185 pounds for group 3 (Table 3-2).

In Nairobi National Park, impala (*Aepyceros melampus*), Grant's gazelle



Figure 3-5 A family group feeding on Thomson's gazelle in Amboseli, Kenya. (Photo: H. Patel.)

(*Gazella granti*), kongoni (*Alcelaphus buselaphus*), and waterbuck (*Kobus ellipsiprymnus*) occur most frequently in the cheetah's diet. A preference

quotient, $\frac{\text{relative frequency in diet}}{\text{relative frequency of abundance}}$ shows a value of 1.0 or

higher for impala, Grant's gazelle, and waterbuck but less than 1.0 for kongoni (Table 3-3). Reedbuck (*Redunca redunca*) show the high value of 18 but they are relatively rare and unimportant overall as cheetah prey. It should be noted that McLaughlin (1970) found Thomson's gazelle to be more important prey in Nairobi Park than I did, but this was not unexpected since his study was longer than mine. Further, after my study, water was made available year-round in the park, thus keeping "Thommies" there. Unlike Grant's gazelles, Thommies require water daily. Moreover, the entire critical result of my analysis of predation (Eaton, 1970) was that intergroup variation was high, and can be expected to vary over time with new specializations or preferences of succeeding generations. Students of carnivores should thus be cautioned to expect striking differences in individuals and groups in the same area, and also in different populations.

Observations by ten observers (pers. comm.) in Nairobi Park during my study total 23 kills (Table 3-4). Of the 14 aged kills, 13 were adults,

TABLE 3-3 INDEX OF PREFERENCE OF CHEETAH PREY SPECIES IN NAIROBI NATIONAL PARK*

Species	Relative Frequency of Abundance	Relative Frequency of Diet	Diet/Abundance Index
Kongoni	.26	.10	.38
Impala	.16	.433	2.7
Grant's Gazelle	.13	.166	1.2
Thomson's Gazelle	.092	.033	.35
Waterbuck	.024	.133	5.5
Wildebeest	.067	.00	—
Reedbuck ^b	.0018	.033	18.0
Warthog	.041	.10	2.4
Zebra	.126	.00	—
Ostrich	.025	.00	—

* Relative frequency of abundance computed from Foster and Kearney, 1967.

^b Species not listed in Foster and Kearney but Nairobi National Park censuses in October and November, 1966, average = 7.

compared with my observations of 12 adults and 18 juveniles. Ten of the 12 adults were females. When lumped, the two sets of data show a preponderance of adults and a near-even sex ratio.

Of 16 species in the park known to be cheetah prey, ten were hunted and seven were killed. Park records, visitor's observations, and photographs show that of the three species not killed in my observations, zebra and wildebeest have been taken in the park while steinbuck (*Raphicerus campestris*) kills were not recorded; however, they were hunted.

Group 1 hunted seven species and killed all but one—steinbuck. Group 1's hunt/kill ratio was 5:1. About one-half of its kills were impala, 3:1. Grant's gazelle, second most important in diet was second in hunt/kill, 5:1. Thomson's gazelle and kongoni were hunted frequently but show a high hunt/kill ratio (that is, low success).

The adult female's eight impala kills (Table 3-5) include four adults; the only male was weak and apparently quite old. Observations by others give adult females and juveniles for six of seven kills.

Group 2 hunted five and killed two species. Their overall hunt/kill is 3.5:1.0. They were especially effective with waterbuck, hunt/kill = 2.0:1.0. A preference quotient shows waterbuck highly vulnerable to this group. All the waterbucks were subadults and the impalas were adult females.

Group 3 hunted four species, killing kongoni and warthog. The group originally consisted of four males, thought to be brothers, and are known to have killed adult zebra, wildebeeste, waterbuck, ostrich, and Grant's gazelles. The Nairobi Park records and two of my observations show kongoni as most important in this group's diet. They show a hunt/kill of 2:1 for all prey. All kills in park records are listed as adults, sex unknown. The warthog was newly born and killed by one of the group when the two separated temporarily. Both kongoni kills from which I collected skulls and

additional kills aged by M. Gosling (pers. comm.) were subadult males about 14 months old.

Group 4 hunted five species, killing three. Their hunt/kill was 4:1. Their three kills included a newly born warthog, an adult female Grant's gazelle and a juvenile male impala.

HUNTING BEHAVIOR

There is much disagreement on the hunting behavior of the cheetah. Kruuk and Turner (1967:21) conclude that cheetah are "almost entirely solitary" hunters in the Serengeti. On the other hand Bourliere (1963)

TABLE 3-4 A. COMPILED KILL DATA FROM TEN OBSERVERS IN NAIROBI NATIONAL PARK DURING THE PERIOD OF THE STUDY

	Adult			Juvenile			?	Total
	Male	Female	?	Male	Female	?		
Impala	1	2	—	—	—	—	3	6
Grant's Gazelle	2	1	—	—	—	—	1	4
Thomson's Gazelle	3	—	—	—	—	—	1	4
Kongoni	—	—	—	—	—	—	2	2
Waterbuck	—	—	—	—	—	—	1	1
Warthog	—	—	—	—	—	1	—	1
Wildebeest	—	—	1	—	—	—	—	1
Zebra	—	—	1	—	—	—	—	1
Reedbuck	—	1	—	—	—	—	1	2
Ostrich	—	1	—	—	—	—	—	1
Total	6	5	2	—	—	1	9	23

B. MY OBSERVATIONS OVER THE SAME PERIOD

	Adult			Juvenile			?	Total
	Male	Female	?	Male	Female	?		
Impala	1	7	—	2	3	—	—	13
Grant's Gazelle	—	2	—	2	—	1	—	5
Thomson's Gazelle	—	1	—	—	—	—	—	1
Kongoni	—	—	—	2	—	1	—	3
Waterbuck	—	—	—	2	1	1	—	4
Warthog	—	—	—	—	—	3	—	3
Wildebeest	—	—	—	—	—	—	—	—
Zebra	—	—	—	—	—	—	—	—
Reedbuck	1	—	—	—	—	—	—	1
Ostrich	—	—	—	—	—	—	—	—
Total	2	10	—	8	4	6	—	30

TABLE 3-5 THE IMPALA KILLS OF THE SINGLE ADULT OF GROUP 1

Impala	Sex	Adult	Juvenile	Estimated Weight	Condition
1	m	x		120	poor
2	m		x	20	good
3	f		x	40	good
4	f	x		100	good
5	f	x		100	good
6	f		x	40	good
7	?		x	40	good
8	f	x		100	good
Total	5 f 2 m 1 ?	4	4	m = 70 pounds	

states, "Only those predators like . . . the cheetah . . . that hunt their prey in organized groups may succeed in overcoming animals much larger than themselves. . . ."

Schaller (1968:98-99) reports hunts by a single hunting female with cubs only, and makes no mention of adult group hunting. Estes (1967a:46) says that cheetahs are "open pursuit" and "solitary" hunters as opposed to "stalk-pounce" and "gregarious" hunters. Walther (1969) observed 88 hunts by single cheetah in the Serengeti. De Vore and Washburn (1963:364) observed five cheetahs kill an impala in Nairobi Park. Graham and Parker (1965:19) say, "In the adult segment of the population unaccompanied by immatures, single animals are the most common grouping everywhere except Nairobi Park, where twos are the most common . . . except the Serengeti Park where singles are most frequent." Pienaar (1968) reports that cheetahs are seen in groups (at least two) or families in Kruger Park more frequently than singly.

Conclusions about the structure and size of hunting cheetah groups are misleading due to regional differences in ecology and consequently litter and adult group sizes. The above divergent views reflect the differences that do exist from area to area.

The differences in prey size and species preyed upon in any area is in part a function of the size of the hunting group. Kruuk and Turner's (1967) data on 23 kills, when fitted to prey weights, show an average prey size of 83.5 pounds, about 30 pounds less than the average of 30 kills in Nairobi National Park. Schaller's (1968:95-96) kill data show an average prey size even smaller since 121 of the 136 kills were Thomson's gazelles in his data.

The fact that Thomson's gazelle is the most abundant cheetah prey in the Serengeti may make it uneconomical for anything but single cheetah to hunt this area's most predictable prey item. Cheetah prey most on Thomson's gazelle in the Serengeti (Graham, 1966; Kruuk and Turner, 1967;

and H. F. Lamprey, pers. comm.). Selection may disfavor group hunting there; however, it is reasonable to suppose that selection favors group hunting of larger species, and that other ecological factors, such as predation on litters, limit group size and therefore prey size.

I observed hunting by 15 cheetahs comprising the four groups in Nairobi Park. They offered a variety of sex and age compositions for comparison (Table 3-6). Because of the cohesiveness of adult or family groups each group can be considered functionally as a separate, distinct hunting unit. Nearly all hunting was done by the entire family or adult group, only rarely by single individuals. At no time did one group cooperatively hunt with another, though cooperation within groups did occur.

Descriptions of hunting vary widely. Graham and Parker (1965:13) analyzed 40 eyewitness accounts of cheetahs making kills; all except two involved either a direct approach or stalking of the prey followed by a rush. The gap between predator and prey was usually 70-100 yards.

In the Serengeti, Walther (1970) relates that cheetahs approach to hunting distance, 150-250 meters, lie down, sit, or stand, then attack. Stalks were rarely seen as opposed to open approaches. Kruuk and Turner (1967:13) say, ". . . the stalking part of the hunt seemed virtually absent in this species. It walked over the open plains towards a potential prey . . . and caught the prey after a chase of several hundred meters." They often observed cheetah cubs stalking in play. Schaller's (1968:9) observations of 40 hunts by an adult female show that stalking was an important element of this (Serengeti) cheetah's hunting behavior.

Pienaar (1968) relates that cheetahs do stalk in Kruger Park. There, impala, which prefer wooded savanna, are the principal prey, and stalking is to be expected.

The hunting technique of open pursuit is probably more common in the Serengeti than in Nairobi Park. Cheetahs hunting in habitats that offer cover, such as most of Nairobi Park, stalk the prey, but in open short-grass plains, for example part of Nairobi Park and much of the Serengeti area,

TABLE 3-6 HUNT-TO-KILL RATIOS FOR NAIROBI NATIONAL PARK CHEETAH GROUPS

Group	Hunts	Kills	Hunt/Kill
1	115	17	6.1/1.0
2	24	7	3.5/1.0
3	6	3	2.0/1.0
4	12	3	4.0/1.0
Totals	4	157	30
			m = 5.2/1.0 (for all observations)*

* Unweighted mean hunt/kill for all groups = 3.8/1.0.

open pursuit is employed. In Masai Amboseli Game Reserve's open, flat plains, where ground cover is scarce, a cheetah with cubs stalked by crawling on the ground before attacking. Since cheetah cubs stalk in the Serengeti but adults seldom do, stalking must be a portion of the innate predatory sequence but later "drops out" with hunting experience.

In areas conducive for only open pursuit hunting, where prey are also usually aware of the predator, the cheetah's role is more one of a natural culler of less fit individuals from prey populations. In such areas, cheetahs appear to prey more selectively by making a greater number of hunts per unit time and kill, and thereby sample prey herds for less fit animals more effectively. Schaller's (1972) study of cheetah in the Serengeti indicates that old animals are killed slightly more often than expected. His data agree with Walther's (1970) in that a disproportionately greater number of adult females are taken.

A hunt can arbitrarily be divided into a stalk and an attack. This division is artificial in that a hunt may consist of a stalk or an attack but not both. For instance, prey have stumbled onto resting or hiding cheetah and an overt attack occurred without a prior stalk. Also, cheetahs, in spite of a careful stalk, were often discovered by the intended prey and an attack was not made. Here a hunt is described as either a stalk or an attack or both, a kill being a successful hunt.

Factors related to hunting success are many—prey species (sex, age, condition, etc.), herd size, cover type, prey responses before attack, prey responses during attack, number of hunting cheetahs, distance of cheetah's attack, cheetah-prey distance when prey ran, and cheetah-prey distance when cheetah attacked. A hunt-to-kill ratio is applied to each of these factors in order to evaluate their importance.

For the four groups in Nairobi Park, the cumulative data show a hunt-to-kill ratio of 5.2:1.0 (Table 3-6). The individual groups show differences, which on the basis of hunts per kills indicate an order from most to least successful: 3, 2, 4, and 1.

SIZE OF PREY HERDS, HABITAT AND OTHER FACTORS

There are no data available as to frequency of herd size for the species in Nairobi Park, only monthly censuses (Foster and Kearney, 1967). When hunted herds are arbitrarily divided into sizes (Table 3-7, it is seen that of 157 hunts, 136 were of herds numbering 30 or less. One to five is the most commonly hunted herd size, with 1-5, 6-10, 11-20, 21-30, having an average hunt/kill ratio of 5.1:1, about equal to the ratio for all herd sizes, 5.2:1. The single hunting female of group 1 hunted herds of 1-30 70% of the time. She hunted Grant's gazelle, Thomson's gazelle, impala, and

TABLE 3-7 GROUP HUNT/KILL RATIOS RELATED TO PREY HERD SIZES

Herd Size	Group				Total
	1	2	3	4	
1-5	7:1(28:4)	4:1(16:4)	4:1(4:1)	2.5:1(5:2)	4.8:1(53:11)
6-10	5.1:1(26:5)	2:1(4:2)	—	2:0(2:0)	4.6:1(32:7)
11-20	8.7:1(26:3)	2:1(2:1)	—	3:1(3:1)	6.1:1(31:5)
21-30	5:1(15:3)	2:0(2:0)	1:1(1:1)	2:0(2:0)	5:1(20:4)
31-40	4:0(4:0)	—	—	—	4:0(4:0)
41-50	6:1(6:1)	—	1:1(1:1)	—	3.5:1(7:2)
51-100	7:0(7:0)	—	—	—	7:0(7:0)
101+	1:1(1:1)	—	—	—	1:1(1:1)
Total	115:17	24:7	6:3	12:3	5.2:1(157:30)

kongoni 60% of the time. These species appeared in herds of 1-30 animals frequently.

Seventy-five percent of Group 2's hunts and 57% of their kills were of herds numbering 1-5. Waterbuck, this group's principal prey, were seen most frequently in small bands. Group 3 hunted 1-5 animals four times; its kongoni kills were from herds of 21-30 and 41-50. Several kongoni kills (M. Gosling, pers. comm.) were from hunts of large herds. Group 4 hunted herds from 1 to 30; one of its three kills was a warthog, a species found in family groups of 1-5.

Acacia-grassland savanna is about equal in total area with open grassland plains in Nairobi Park. All groups' home ranges overlapped. Of four cover types (Table 3-8) there were, for all groups, 83 hunts and 13 kills in Acacia-grassland savanna, 52 hunts and 12 kills in open grassland, 12 hunts and 4 kills in heavy bush, and 10 hunts with one kill in marshy habitat.

Group 1, the female with small cubs, hunted mostly in Acacia-grassland savanna where it made 9 of its 17 kills. This group was the only one to hunt in either heavy bush or marsh. The mother's hunts were particularly successful just inside heavy bush areas adjacent to savanna or plains (Fig.

TABLE 3-8 HUNT/KILL RATIOS IN THE HABITAT TYPES OF NAIROBI NATIONAL PARK

Group	Acacia-Grassland Savanna	Open Grassland Plains	Heavy Bush	Marsh	Total
1	7.7:1(70:9)	7.7:1(23:3)	3:1(12:4)	10:1(10:1)	115:17
2	—	3.4:1(24:7)	—	—	24:7
3	2:1(4:2)	2:1(2:1)	—	—	6:3
4	4.5:1(9:2)	3:1(3:1)	—	—	12:3
Total 4	6.4:1(83:13)	4.3:1(52:12)	3:1(12:4)	10:1(10:1)	157:30

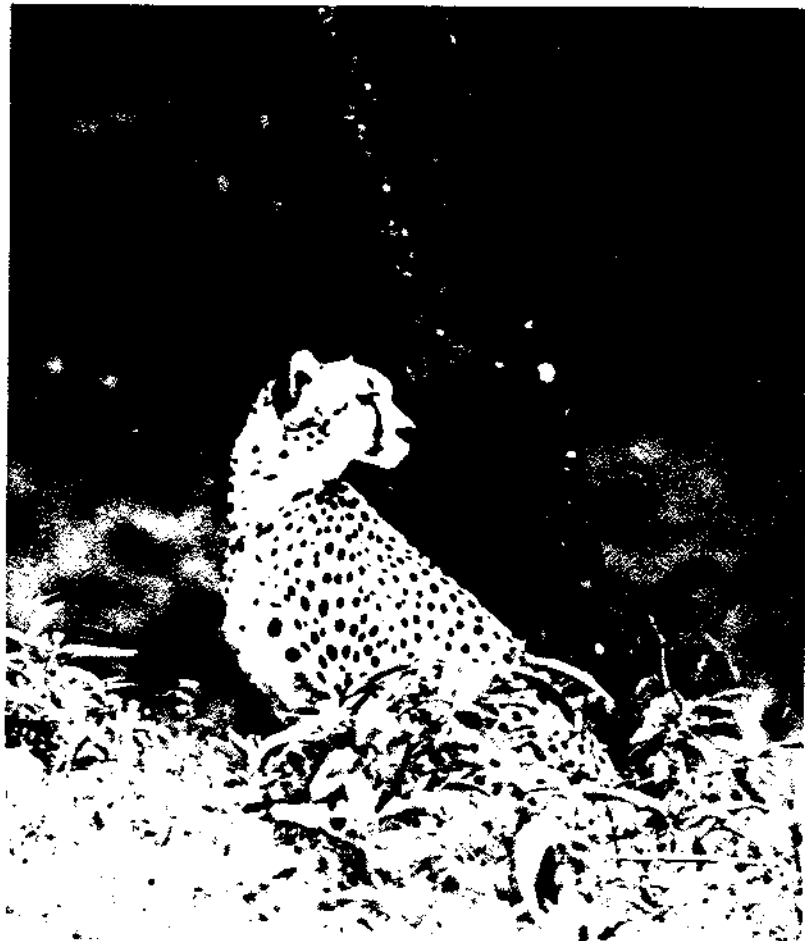


Figure 3-6 One female that had four cubs (group 1) was highly successful at hunting impala which frequent the heavier bush. Most hunts by cheetahs are in more open areas, but this individual hunted in habitat that is typical of the leopard's. (Photo: R. L. Eaton.)

3-6). Her kills were impala, which frequent the woody, more dense areas more than other important prey. An observation by R. Casebeer (pers. comm.) and mine of the adult female of group 1 killing a reedbuck constitute the only two kills of the rarest, in occurrence, cheetah prey species in the park. The preference quotient for reedbuck is 18 for all cheetahs' kills but even higher for group 1.

Both reedbuck kills and seven more hunts were around the edges of the

same small marsh. Marshes constitute less than 1% of the park's total area. No other cheetahs were observed hunting in marshes.

Group 2 with five adults often moved into savanna but did their hunting in the open plains along the Athi River bush area where their principal prey—waterbuck—were concentrated, though not abundant.

The two males of Group 3, formerly of the four male group, hunted in both *Acacia* savanna and in the open plains where kongoni were found. Park records showed this group in only these two cover types. The original group and the two remaining individuals hunted and killed the largest species known to be cheetah prey.

Group 4 with three adults hunted in the same habitat as group 3; however, they never hunted or killed the four larger species that group 3 did. Impala and Grant's gazelle were the largest species they hunted.

For all observed kills, if hunting success is related to the prey's responses before attacked then the hunt/kill is 12.7:1 when prey are aware as opposed to 2.0:1.0 for unaware prey (Table 3-9).

TABLE 3-9 HUNT/KILL RATIOS RELATED TO PREY RESPONSE BEFORE ATTACKED

Group	Aware	Unaware
1	85:1 (N = 85)	30:16 (N = 30)
2	4.2:1 (N = 17)	2.3:1 (N = 7)
3	2.5:1 (N = 5)	1:1 (N = 1)
4	5:1 (N = 5)	3.5:1 (N = 7)
Total	14.9:1 (N = 107)	2:1 (N = 45)

The success of the group 1 cheetah depended almost entirely on the prey being unaware prior to attack. The prey were much less vulnerable when they were aware. This cheetah typically underwent extensive stalks sometimes involving several hours in which only a few yards were traversed. Where open spaces separated the cheetah from a herd the cheetah often hid in cover. If the herd grazed closer the cheetah waited until they were close enough to attack (Fig. 3-7). In cases where the prey saw the cheetah, snorting alerted all prey species in the vicinity which often led to "mobbing" of the cheetah. Prey animals often searched out and followed the cheetah as it moved off, snorting as they went and alerting other potential prey along the way. This procedure often continued until the cheetah had moved completely out of range of any prey.

Group 2 showed a higher hunting success when prey were unaware but were more successful with aware prey than was group 1. The cover type of open plains by necessity made stalking less important than overt attacks. This group hunted in the same way as described for cheetahs in the open

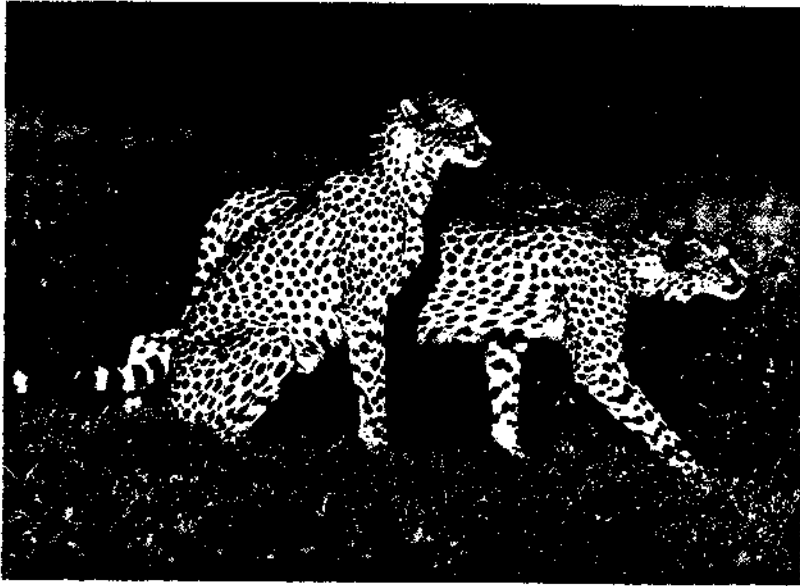


Figure 3-7 Starting out on a hunt employing sparse ground cover in open plains. (Photo: H. Patel.)

plains of the Serengeti (Kruuk and Turner, 1967) where prey are usually aware of cheetah prior to an attack.

Hunts by groups 3 and 4 were not frequently observed; however, the two males of group 3 depended on kongoni being aware. It is the antipredator attack by yearling males that enabled them to kill kongoni so readily.

Using only those hunts including an attack, hunting success is related to the prey's response during the attack (Table 3-10).

The prey's responses are divided into five classes: (1) prey (2 or more) ran together at the same time; (2) not together; (3) not at the same time; (4) not together and not at the same time; and (5) antipredator attack by the prey. The hunt/kill is 4.3:1.0 or less for all categories of prey response except for response 1 which is 9.5:1.0.

Group 1's hunter, the mother, had a low hunt/kill ratio (higher success) when prey did not run together or at the same time. More total kills were made when they responded to the attack by not running together simultaneously. When this cheetah attacked juvenile kongonis, yearling males responded by charging, and the cheetah turned and fled.

Group 2 had no success when the prey responded to attack by running as a herd at the same time. Whenever one or more of a herd ran before the

TABLE 3-10 HUNTING SUCCESS RELATED TO PREY RESPONSES DURING ATTACK
HUNTS WITH NO ATTACK ARE EXCLUDED

Preys' (Two or More) Response	Group				Total
	1	2	3	4	
1 Ran together at same time	9:1 (N = 53)	8:0 (N = 8)	—	6:1 (N = 6)	9.5:1 (N = 67)
2 Not together	7:1 (21:3)	1:1 (N = 2)	—	3:1 (N = 3)	4.3:1 (N = 26)
3 Not at same time	6:1 (N = 17)	1:1 (N = 3)	—	2:1 (N = 2)	3:1 (N = 22)
4 Both 2 and 3	—	—	1:1 (N = 1)	—	1:1 (N = 1)
5 Antipredator attack	4:0 (N = 4)	2:0 (N = 2)	1:1 (N = 2)	—	3.5:1 (N = 7)

rest of the herd, or when the herd separated, then a kill was made. Antipredator attacks by kongoni deterred this group's attacks.

The only kill by group 3 of other than kongoni was observed when one of the two males killed a newly born warthog. In this case the cheetah was 30 yards from an adult warthog and two young before the warthogs were alerted. The two young ran one way, the adult ran the other. The cheetah pursued the young and in the meantime the adult turned around and pursued the cheetah. When one young warthog was caught the adult circled twice around the cheetah within five feet before running off after its surviving young.

Group 4 showed a lower hunt/kill when the herd escape response was not a cohesive one. Whenever a warthog with young was aware of the cheetah before they were close, or if the warthogs had a good head start, the adult female turned to face the cheetah with her young standing directly under her stomach. Individuals of the cheetah group surrounded the warthogs, charging in turn at them but were not successful in separating adult from young unless the warthogs turned and fled.

Hunting success was related to cheetah-prey distances when prey ran as opposed to cheetah-prey distance when cheetah ran (Table 3-11). These data exclude hunts consisting of a stalk only. In unsuccessful hunts the distance between predator and prey when the prey ran averaged 157.2 yards, the distance when the cheetah ran averaged 217 yards. In successful hunts the average distance for all observations when the prey ran was 50.4 yards and for cheetah it was 58 yards.

Group 1 killed when it was on the average 56 yards from the prey when it attacked and then it ran 20 yards before the prey ran.

In unsuccessful hunts the female also attacked before the prey fled but not always.

Group 2 usually did not attack until the prey had already run. In many

cases the cheetahs simply walked toward a herd until an animal ran and they pursued it. These five cheetah were on the average 81 yards from the prey when their pursuit ended in a kill.

On unsuccessful hunts they often began running toward prey at distances up to 400 yards. In these hunts the prey were alerted before the cheetahs were close enough to pose a real threat and they escaped easily. Although four of the five cheetah were nearly mature they were less experienced than their mother. The hunts involving attacks of great length were always led by the younger cheetah.

The males of group 3 had very small distances between them and the prey when they attacked. This is partly due to the fact that in two of the three kills they simply loped toward kongoni when, at about 60 yards, a kongoni attacked the cheetah. When the kongoni had come about 25 yards closer, the two males attacked and killed it.

TABLE 3-11 HUNTING SUCCESS RELATED TO CHEETAH-PREY DISTANCES*

	Group 1		Group 2		Group 3		Group 4	
	Unsucc. N = 66	Succ. 17	Unsucc. 5	Succ. 7	Unsucc. —	Succ. 3	Unsucc. 8	Succ. 3
Distances (yards) when prey ran	80.4	36.2	234	65	—	50	120	65
Distances when cheetah ran	96	56	338	81	—	37 ^b	100	80
Averages	88.2	46.1	286	73	—	43.5	110	72.5

* Includes only those hunts where distances could be measured or estimated with relative accuracy.

^b Two of the three kills involved antipredator attack by kongoni.

Group 4 attacked the prey on the average just before it ran. For the hunts that were successful the group averaged a distance of 58 yards between it and the prey when the cheetah attacked.

The importance of continuous field observations in arriving at an accurate assessment of predatory behavior and ecology is obvious. The accumulation of kill data by chance observations, as for example from park personnel or visitors, cannot be considered random. Nairobi Park's visitors' records indicate an entirely different species, age, and sex composition of cheetah prey from mine. By following a cheetah, a family, or an adult group it is possible to establish the similarities and differences between hunting units.

Pienaar's (1968) data on cheetah predation in Kruger Park is based on carcass location and not direct observation; he speculates that many smaller species of birds and mammals and the young of smaller antelope species probably are quite important as prey. In Nairobi Park no hunts or kills of birds other than ostrich have been observed or recorded. The point

is that in any one area, behavioral data should supplement carcass data as a means of properly assessing a predator's ecological role in the community.

PREY SELECTION

It was shown that the largest prey were killed by groups but there is not a constant relationship between group size and size of prey, for example some groups killed the same size prey as single hunting cheetah. In the same local area, groups presumably equal in killing effectiveness show quite different kill data.

Graham and Parker (1965) conclude that "there is no tendency to select juvenile animals as 79 percent of all kills are of adult animals." Their data show a two to one sex ratio of adult males to adult females; however, 92 of 130 adult kills were not sexed. Estes (1967:201-202) states that cheetah select adult gazelles when hunting. Wright (1960:8) shows that of those kills aged and sexed, all were males and five of seven were adult. Kruuk and Turner's (1967:14-15) data give adult Thomson's gazelles as the most important diet item—52%. Of seven Thomson's gazelles sexed, six were females. F. Walther (pers. comm., 1969) in the Serengeti observed cheetah kill Thomson's gazelles. His observations show a remarkable nonrandom selection of females from predominantly male adult herds and subadult males from bachelor herds.

Pienaar (1969) shows for Kruger Park a nonrandom selection of juveniles, and among adults, a 2:1 ratio of females to males. Schaller (1968:96) shows that a cheetah pursued a small fawn whenever it was available, and had 100% hunting success with that age group.

In order to establish the importance of selection of prey by predator, it must be demonstrated that the kills comprise other than a random sample of the prey populations. Walther's and Schaller's data specifically support the view that cheetahs discriminate age and sex differences in prey and that (either innately or learned or both) cheetah hunt and kill the more vulnerable prey. Walther's data on flight distances in the different sex and age groups correspond directly with cheetah prey selection. It is to be expected that selection would favor greater flight distances to predators in the prey classes most vulnerable to predation.

It is interesting that in many prey species the territorial male is under the influence of conflicting pressures of natural selection. On the one hand is the selection for differential reproductive success, higher as a result of an individual's territoriality, while on the other hand is the greater vulnerability to dangers, such as predators, against which the herd is supposedly the best defense. If territorial Thomson's gazelles are most susceptible to predation, kill data and flight distances should indicate it.

Flight distances are shortest for territorial males and Walther (1969) noted that they were preyed upon proportionately less than bachelor herd males or females. Thomson's gazelles in the Serengeti defend territories for the most part in flat, open plains that offer good vision, while bachelor males are found where open plains and bush meet, the area of greatest ease for predators to make kills. It is to be expected that predation of "thommies" in areas of homogeneous habitats would probably show that flight distances of territorial males is closer to that of bachelor males and females and that kills are more evenly distributed between these classes.

In the group of two males, learning, probably quite by accident, determined selection of kongoni as their principal prey. The group of five preyed heavily on waterbuck which abound only in the locality in which the four cubs were reared by the female. The killing of waterbuck by the mother may have been a necessity, but the selection of waterbuck by the grown cubs is now traditional, undoubtedly the result of learning and possibly a kind of imprinting.

Specialization on different prey by cheetah in the same area certainly occurs, and regional differences, though often reflecting prey abundance, may be partially the result of specialization.

The impala is the most abundant prey species in Kruger Park but ranks only fifth in terms of preference; two species—reedbuck and waterbuck—that occur also in Nairobi National Park are preferred by cheetahs in both areas.

In Kruger Park (Pienaar, 1969, and pers. comm.) reedbuck have the highest preference of all cheetah prey. In fact, the cheetah is the most important predator of reedbuck there, responsible for 21.76% of all predator mortality. What is peculiar is that in Kafue National Park, Zambia, reedbuck are more abundant than in Kruger and yet are not an important cheetah prey according to Mitchell et al. (1965).

The "habit image" offered to explain the preference by lions for wildebeeste in Nairobi Park (Foster and Kearney, 1967) indicated a common specialization for prey by different prides. This implies less inter-group variation in prey selection by lions than exists for cheetah in Nairobi Park.

Newly born warthogs are common prey for cheetah, but adult warthogs are avoided altogether. The same is reported for Kruger Park (Pienaar, 1968). That cheetah of different groups show this common avoidance implies an ability to recognize particular qualities of particular species. It is conceivable that cubs learn to hunt only what their mother hunts and that once learned, only particular prey stimuli release the predatory sequence of behavior. How discrimination between young and adult warthogs is made is not known unless it is by trial and error in which cases a cub would likely be injured or killed. Lions (*Panthera leo*) are killed by

warthogs (Watt, 1968:135) and tigers (*Panthera tigris*) by wild boar (*Sus scrofa*) (Schaller, 1967). Several studies (Estes, 1967; Wright, 1960; Kruuk and Turner, 1967) disagree on which classes of prey are differentially selected by cheetah. Walther's (1969) data and Schaller's (1968:97) continuous observations of one cheetah's hunts show a selection of females over males in adult herds and of juveniles over adults. Recognition and selection of juveniles from adults could be based on size; however, female adults in typical cheetah species are barely smaller than males. In impala, recognition could be by presence or absence of horns but both sexes of the gazelle species are horned. This explanation is confounded by flight distances of prey. Females with greater flight distances may, by running first from a herd, cause visual fixation by the cheetah on them, and release the cheetah's attack.

Driver and Humphries (1967) pointed out experimentally that in order for a predator to respond effectively to fleeing prey, response time must be cut down by fixating on one of many prey stimuli. In the Serengeti, differential flight distance may lead to differential predation but in Nairobi Park cheetah often attack *before* prey take flight and still differential selection of prey is apparent. Kruuk and Turner (1967) observed a cheetah that was not able to kill an adult Grant's gazelle. Such experiences could enable cheetah to learn to discriminate males from females; if so, one-trial learning would be adaptive since such encounters could be injurious.

In the case of group 3's predation on subadult male kongoni, the apparent selection of male prey is only an artifact of the kongoni's antipredator behavior.

PREFERENCE AND VULNERABILITY OF PREY

Wright (1960:10) says, "Seven predators preyed upon impala, although it is comparatively few in numbers." Wright (1960:11) assigns relative vulnerability to prey species according to the number of predators that kill them. This scale takes no account of prey species' abundance, or availability to the predator. Schaller (pers. comm. in Foster and Kearney, 1967:118) notes that lions choose larger over smaller prey when both appear equally available. Foster and Kearney (1967:118) propose that lions form an "habitual prey image" of abundant species and this results in differential predation of these prey species even when their populations have declined to levels lower than other prey apparently of the same "preyability." Guggisberg (1961) applies the term "habit killers" to lions to describe their ability to specialize on certain prey species. Bourliere (1963) compares the relative frequency of the different ungulate species as prey of the lion with the abundance of these prey in three parks. Bourliere does

not give any kind of value that demonstrates the presence or absence of preference for certain prey by lions. It is obvious that abundance alone is not the only factor determining prey selection. Bourliere postulates palatability as possibly influencing prey selection.

I have applied the preference quotient to cheetah kill data from the Serengeti (Table 3-12), using one million as the approximate Serengeti ungulate population from various estimates. Kruuk and Turner's 23 recorded cheetah kills show that the most important prey, Thomson's gazelle, are not killed any more than they occur. Kruuk and Turner's data show that kongoni are the most vulnerable prey, while wildebeeste (juveniles), the second most important prey in diet, are taken less than they abound.

Schaller (1968:95-96) shows quite different species selection in the Serengeti. Schaller's data on 136 kills (40 hunts were observed) show Thomson's gazelles occurring as prey 88% of the time, far greater than they

TABLE 3-12 THE PREFERENCE-VULNERABILITY QUOTIENT APPLIED TO PREY CENSUSES OF THE SERENGETI AND KRUK AND TURNER'S (1967) CHEETAH KILL DATA

Prey Species	Relative Frequency of Abundance	Relative Frequency of Diet	Preference-Vulnerability Index
Wildebeest	.33	.26	0.78
Kongoni	.0013	.087	66.0
Zebra	.16	.043	.27
Thomson's gazelle	.50	.56	1.12
Hare*	—	.087	—

* No estimates of abundance.

occur. Schaller pointed out that actual availability of Thomson's gazelles is greater in the cheetah's preferred hunting habitat, since during the dry season they are highly concentrated in the plains and practically the only prey species available.

In Kruger Park impala-made up 47 of 65 (73%) cheetah kills while impala comprise 83% of the ungulate population there (Bourliere, 1964). It appears that impala are not especially vulnerable or preferred there.

If a prey species occurs in the diet at a higher level than its relative abundance, it could be either more vulnerable or preferred or both. Wright's scale of relative vulnerability of prey is based on occurrence in the diet of several predators. Vulnerability scales should be related to abundance of prey and more specifically to relative availability. The prey's visitation to the predator's area should give an even more accurate picture of prey vulnerability.

The application of the index of preference shows that relative availabil-

ity or abundance is not the only factor determining prey selection. Here it is assumed that in general preference for a prey represents the prey's vulnerability; however, biochemical deterrents affecting palatability certainly are possible. That vulnerability may not be a direct measure of preference is shown by group 1 in which the female hunted several species equally but killed chiefly only one. Although this cheetah's kills give the impression that it specializes on and therefore "prefers" impala, its hunts show that impala are vulnerable but not necessarily preferred. This hypothesis is not borne out in predation of reedbuck by cheetah in which reedbuck are rare but are highly vulnerable; or by wildebeest in Nairobi Park that have shown a continued high vulnerability to lions in spite of a vastly decreasing population. Since the reedbuck habitat in Nairobi Park consists of small isolated marshes, heavy predation pressure is to be expected. The marshes are scarce enough to allow ease of predation but limit population growth.

The data from four descriptions by Kruuk and Turner (1967) show that cheetah attacks averaged 183.3 yards and that the cheetah-prey distance when cheetah attacked averaged 95 yards. Cheetah began their attack before the prey ran and overcame the prey after it fled for 88.3 yards. All these kills were in the open plains of the Serengeti, none of which involved a stalk. In all cases the prey were aware of the cheetah prior to the attack.

Walther (1969), working on gazelles, observed 88 hunts by single cheetah, of which seven were successful, a hunt/kill ratio of 12.5:1. In the successful hunts cheetah attacked from 150-200 yards. The average flight distance from cheetah was 200-300 yards, rarely less than 100 or more than 600 yards, varying with the prey species and age or sex classes. Contrary to Kruuk and Turner's observations the cheetah often did not attack until the prey had taken flight.

Schaller (1968:98-99) describes hunting in one cheetah, the behavior of which corresponds closely to the female with cubs in Nairobi Park (group 1). He does not quantify the cheetah's behavior, so it is difficult to make comparisons. Schaller describes a "typical hunt"; however, in Nairobi Park hunting was typical only within a group. It would be helpful to have accurate descriptions of several cheetahs, single and in groups, in the Serengeti, so the factors related to regional differences—cover types, prey species, etc.—could be assessed. Nairobi Park data imply that hunting is in large part a product of a particular cheetah's or group's hunting experience.

The lower hunt/kill ratio for Nairobi Park cheetahs as compared to Serengeti cheetah may indicate that the best cheetah habitat is other than strictly open plains; however, kills are made no more frequently in Nairobi Park. The open plains of the Serengeti demand an open pursuit hunt

which is by its nature less economical in number of hunts but more economical in that it is less time consuming than the stalk-attack hunt common in Nairobi Park.

Group comparisons in Nairobi Park show that the single hunter requires more hunts per kill than a group but groups vary. The most efficient group had two cheetahs and this group also showed the highest prey specialization, which for them was more efficient in terms of reward for energy expended.

Hunting success was higher in herds of 30 or less. Larger herds presumably offer a greater predator alarm system; however, the threshold for "alert" may be lower in smaller herds which may result in each individual being more alert than if in a larger herd. Although difficult to quantify, the individuals in very small herds appeared to spend more time being alert and watching for predators than did animals in larger herds. The "fear" of predators often resulted in flight in small impala herds without the alarm calls and intense watching associated with the predator alarm system of the larger herds. Although it has not been studied, flight distances may be found to vary as a function of herd size.

The predator-reaction system in the prey is probably a compromise of two selection factors. On the one hand there is selective advantage to individuals that are wary and alert for predators, while on the other hand, any herbivore must spend a large part of its time and energy eating. The final product of selection forces is a behavioral repertoire that includes, for most individuals, the optimal balance of energy expenditure for predator alertness and eating. Individuals that deviate from this optimal and delicate energy budget are probably selected against by either being nutritionally less fit or the obvious disadvantage of being killed by predators. The regularity of five to seven minutes for "staring contests" between slightly alerted prey in smaller herds and the cheetah reflects this principle, that is, this time span, afforded for a low level of arousal, is optimal for determining potential danger without taking too much time away from eating which is also of great survival value to herbivores.

Condition may have been an important factor in selection of prey by cheetah but in only one case was poor condition of prey apparent. Schaller (1968) noted that none of the kills he saw appeared to be of prey in poor condition. This study should have employed techniques to determine prey condition, for example bone marrow analysis.

Hunting success was higher when prey were not aware before attacked. The hunt/kill ratio when prey were aware prior to attack in Nairobi Park is almost identical to that for the Serengeti, where prey are almost always aware before attacked.

The hunt/kill ratios for prey response during attack indicates that flight of the prey as a tightly knit herd reduces predation.

The failure of an individual of a herd to respond in the same way as the others increases its chances of being singled out and killed. The abnormal flight responses of a particular animal may indicate a higher vulnerability and this may explain the release of the cheetah's attack when one or more animals take flight before the rest of the herd.

It appears that cheetah seldom make kills when they attack at greater than 200 yards and hunting success increases the shorter the distance is between cheetah and prey. Perhaps the cheetah depends on its ability to assess the weakening of prey while chasing it, for in many cases the cheetah would stop pursuit even though it appeared to be closing the gap between it and the prey.

DETAILED DESCRIPTIONS OF SPECIFIC HUNTS

As was stated above, it is not possible to describe a typical hunt for the cheetah since so many variables affect any particular hunt. But in order to provide specific accounts in detail I have selected a day's hunts for each of three groups in Nairobi Park (Tables 3-13, 3-14, and 3-15). Some hunts are graphically depicted in Figs. 3-8-3-11.

ENERGY BUDGETS

The number of possible hunts involving a chase is limited by the time spent in finding, stalking, and pursuing prey. The limitations set by the output of time and energy in hunting must be balanced by the input into the system which is the energy derived from eating captured prey. Data on the actual energy expended in hunting could only be measured by knowing oxygen consumption during all activities, calories and materials used to maintain bodily functions, the loss of energy in excretions, etc. These data cannot be gathered under field conditions.

The only measure of expenditure of energy in hunting was breathing rates. Breathing rates were recorded on several occasions. The data presented (Table 3-16) were recorded in Nairobi Park at an altitude of nearly a mile, all near mid-day with partial cloud cover (field estimates 15-20%) and similar temperatures, close to 80°F on each day cited.

The few data indicate that the cheetah's adaptations for speed include a capacity for large changes in respiratory rate. Rates ranged from 16 for one adult male lying in shade to 156 for a second adult male following a chase and prolonged kill by strangulation. The latter male's respiratory rate may have been unusually high due to the inhibition of respiratory recovery involved in the maintenance of the strangle hold on the prey. Another

TABLE 3-13 HUNTING DAY OF GROUP 1, DECEMBER 17, 1966

Species Hunted	Sex	Age	Cond.	Cover	Herd Makeup	Response Before Attack	Response During Attack	Distance Stalked	Distance Chased	Kill
Grant's Gazelle	m	ad.	good	grass, open	30 Grant's & Thommies	Aware, 2 m Grant's ran from herd, cheetah pursued	2 Grant's ran, kept 200 yards from cheetah	0	300 yards	No
Impala	m f	ad.	good	Acacia, high grass	2 f & 1 m impala	Ran just before attack	Ran together, directly away from cheetah	25 yards	25 yards	No
Grant's Gazelle	f	ad.	good	Acacia, high grass	4 f Grant's	Ran when downwind without seeing cheetah	No attack	30 yards	0	No
Reedbuck	—	ad.	good	heavy marsh	1	Ran from marsh, not seen by cheetah	No attack	40 yards	0	No
Kongoni	m f	2 ad. 1 juv.	good	grass, open, cheetah in gully	3	Unaware, walking single file right angle to cheetah	m kongoni attacked cheetah, then f, juv. ran, f pursued cheetah	30	50	No
Warthog	f	1 ad. 2 juv.	good	Acacia-savanna	3	Unaware	Cheetah separated f from juvs., 1 juv. into hole, other escaped	30	150	No
Thomson's Gazelle	—	ad.	good	Acacia-savanna	20	Aware, ran	1 lagged behind herd, was chased	20	100	No
Grant's Gazelle	f	ad.	good	Acacia-savanna	4	Aware, ran	No attack	20	0	No
Impala	m f	ad. juv.	good	shrub, heavy	30 f 10 juv. 1 m	Staring contests	Herd split up, ran in different directions	60	50	Yes, juv. m

TABLE 3-14 HUNTING DAY OF GROUP 2, JANUARY 22, 1967

Species Hunted	Sex	Age	Cond.	Herd Makeup	Response Before Attack	Response During Attack	Dist. Stalk	Dist. Chase	Kill	Comments
Impala	f	ad.	good	1	Aware, standing watching cheetahs	Ran	200	300	0	Leader cub led chase, followed by mother only
Kongoni	m f	ad.	good	30	3 m ads. closest to cheetahs watching & alarm calls, rest of herd—f & juv. ran off 100 yards watching cheetahs, ad. f cheetah stalked, cubs not move,	No attack, f called cubs to her	150	0	0	f cheetah continued stalk but all prey alert and watching her
Waterbuck	1 m 2 f	ad.	good	3	Aware, watching cheetahs	Ran cohesively	200	0	0	Leader cub kept breaking from stalk and running at prey As running toward impalas cheetahs alerted waterbuck chased earlier which alerted impalas
Impala	4 f 1 m 2 juv.	5 ad. 2 juv.	good	7	Unaware	Ran cohesively	0	300	0	Lead cub only chased impala (See Fig. 3-11.)
Impala	m	ad.	good	20 kongoni 1 zebra 1 giraffe 1 waterbuck 1 impala	Aware, 1 m kongoni approaches the cheetahs while stalking, impala broke and ran first then herd ran in different direction	Ran, not with herd	200	300	0	

TABLE 3-14 (continued)

Species Hunted	Sex	Age	Cond.	Herd Makeup	Response Before Attack	Response During Attack	Dist. Stalk	Dist. Chase	Kill	Comments
Impala	f	ad.	good	1	Unaware of cheetah but staring contest with stalking lion	No attack	100	0	0	Lead cub saw lioness when 200 yards away from impala & lion. Stopped hunt. Kongoni alarm to cheetah alerted impala which ran, lion not follow
Waterbuck	f	2 ad. 1 juv.	good	3	Unaware	1 ad. into bush, others into open	250	140	x	Lead m cub chased ad. & juv., they saw other cheetahs & split, lead cub killed juv.

TABLE 3-15 HUNTING DAY OF GROUP 3, DECEMBER 28, 1966 (ONE OF TWO MALES HUNTING)

Species Hunted	Sex	Age	Cond.	Cover	Herd Makeup	Response Before Attack	Response During Attack	Dist. Stalk	Dist. Chase	Kill	Comments
Warthog	f	1 ad. 2 juv.	good	Acacia, grassland dense	3	Unaware, feeding	Juvs. ran one way, f ran other	10	110	x	See Fig. 3-8.
HUNTING DAY OF GROUP 3, JANUARY 17, 1967 (BOTH MALES HUNTING)											
Kongoni	m	ads. & juvs.	good	Acacia, grassland open	30	Unaware	Subadult m attacked cheetahs	70	50	x	See Fig. 3-10.
HUNTING DAY OF FEMALE AND TWO CUBS, MASAI AMBOSELI GAME RESERVE, JANUARY 4, 1967											
Thommie	m	ads.	good	grassland flat, open	15 Thommies	Unaware	All but 2 ran one direction, cheetah chased these 2	250	140	x	Cheetah stalked over barren ground

adult, a female, exhibited 136 and 140 respirations per minute, 2 and 6 minutes, respectively, after an extensive chase. It appears that lying down is less efficient for recovery following a chase, presumably as a result of a decrease in expansion of the rib cage in the prone position.

TABLE 3-16

Date, Time	Activities	Respiration/Minute
11/18/66, 10:35 A.M.	Adult female chases prey	
11:00	Female sitting on haunches, proceeded by slow walking	60
2:18 P.M.	Same female and its six month old cubs chase prey	
2:20	All cheetahs lying down in partial shade:	
	female	136
	cubs	176
2:24	Female	140
	Cubs	168
2:27	Cheetahs walk slowly to and lie down in full shade	
2:38	Female	60
	Cubs	
11/20/66, 10:30 A.M.	Three adult cheetahs walking slowly	
11:00	Cheetahs walk to shade, lie down	
11:30	One male, lying down	16
12/28/66, 11:30 A.M.	Adult male chases, catches, and carries live juvenile warthog (<i>Phacochoerus aethiopicus</i> Pallas) to shade, lies down holding warthog in mouth	
11:45	Warthog dies from strangle hold, cheetah remains lying down	156
11:48	Cheetah sitting on haunches	112
11:49	Cheetah lying down	126
11:55	Cheetah, still lying, licks blood from carcass	120
12:00	Cheetah feeds on rear quarters	115
12:05 P.M.	Still feeding, intermittently sits up, looks around	

That recovery ratio limits the number of full-intensity chases relative to time was indicated by an observation of an adult cheetah which had just chased prey unsuccessfully and came upon a steinbuck (*Raphicerus campestris* Thunberg) that ran from the cheetah at a distance of a few feet, but was pursued only momentarily. The cheetah's respiratory rate appeared very high just before encountering the steinbuck and probably precluded a second chase immediately following the first. It is also typical for cheetahs to seek and lie down in shade following an unsuccessful chase for one-half hour before resuming hunting. It appears reasonable to

assume that the movement to shade facilitates respiratory recovery; however, this same movement with prey would be adaptive in preventing localization by other predators or scavengers.

BIOMASS TRANSFER

The possibility of using the wild ungulates of Africa as a protein source for the African makes it necessary to evaluate the effects of the predators on the wild populations. Maximum figures for the effects of the cheetah on its prey are used in calculating how much live weight is taken by them. Nairobi National Park has the highest density of cheetah known.

Using 25 adult cheetah as the park's maximum population in an area of

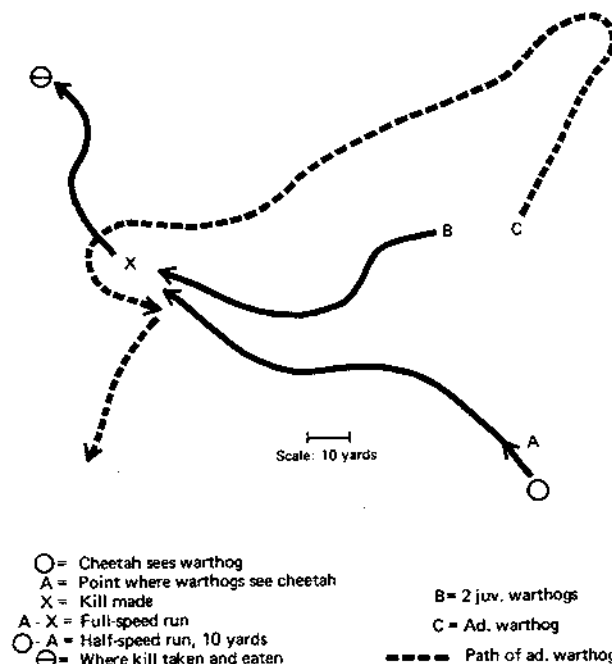


Figure 3-8 The single male cheetah saw the warthog family at B and C, the two piglets grazing away from their mother. The cheetah started running slowly towards the piglets at location B but was quickly seen by them. They ran away from their mother who then took flight in a different direction. The cheetah intercepted the young and caught one of them before the mother warthog circled back to defend her young. As the cheetah held its prey the mother charged nearby and then ran off after the other piglet. If the three warthogs had escaped together in the same direction, there probably would have been no kill.

44 square miles gives a density of about .6 cheetah per square mile. Again, for maximum predation, we shall assign body weights of 120 pounds to each of the 25 cheetah. The park's game herds must support 3000 pounds of cheetah or 72 cheetah-pounds/square mile. (See Fig. 3-12.) Each day the cheetah eats a maximum of 1.0 pounds/10 pounds of body weight. This means that the maximum consumption is 12 pounds/day/cheetah or 400 pounds/day for all the 25 cheetah, which is 146,000 pounds per year. The average total prey weight per square mile in Nairobi Park is 71,294 pounds for the year. For each pound of meat consumed by cheetah there is a maximum of another one-half pound wasted in skin bones and

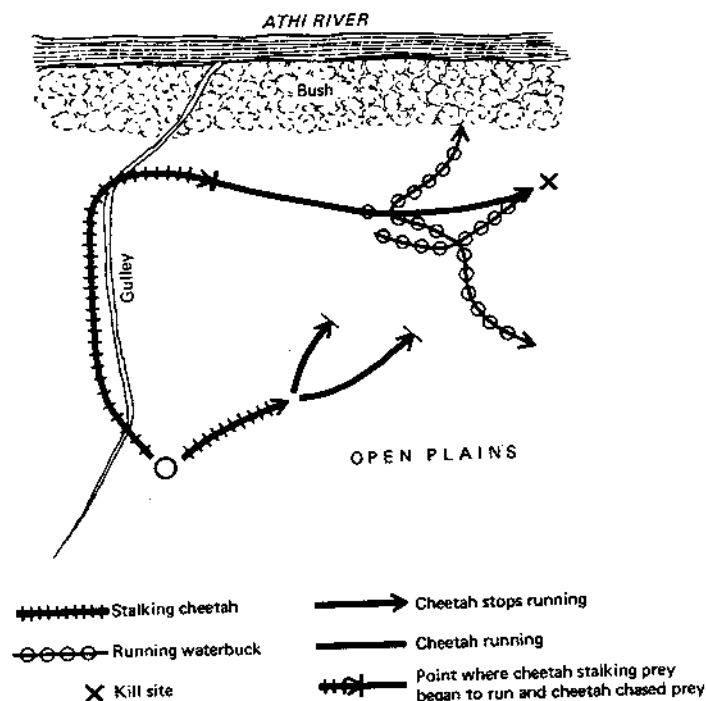


Figure 3-9 A female cheetah and her four nearly adult cubs sighted a band of three waterbuck. The mother separated from her litter and made an indirect stalk utilizing a gully and its cover. The younger cheetahs stalked slowly towards the waterbuck. As the adult cheetah stalked away from the gully she was in less cover and was seen by the waterbuck. The escape pattern of the three prey was disorganized. One adult ran towards the heavy cover by the river. The two juvenile waterbuck ran in the same direction momentarily but then saw the younger cheetahs, now attacking. One of the waterbuck cut back towards the river and the adult cheetah and was killed.

uneaten entrails. The 146,000 pounds actually consumed by cheetahs converts to 219,000 pounds of total prey killed.

The maximum predation for each square mile is 4,977 pounds of the 71,294 supported annually or about 9% of the biomass. The figure for Nairobi Park is maximal, since it harbors the highest density of cheetahs. Surely the biomass transfer is only a fraction of the park estimates in most areas of the cheetah's range. This plus the selection of infirm, old, and young prey should discourage killing of cheetahs in game ranching. Economic losses from predation can be counterbalanced by tourist income from photography of cheetahs in the game ranch.

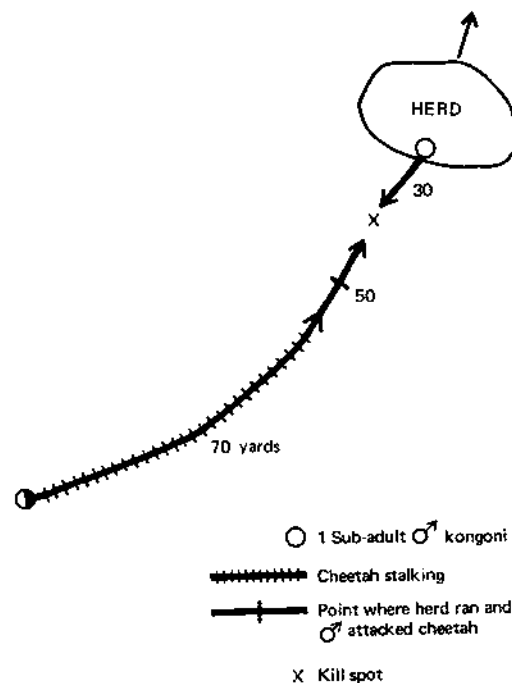


Figure 3-10 Two adult males stalked a herd of kongoni. The cheetahs were sighted and the kongonis took flight except one close kongoni, a sub-adult male, which charged the cheetahs and was killed.

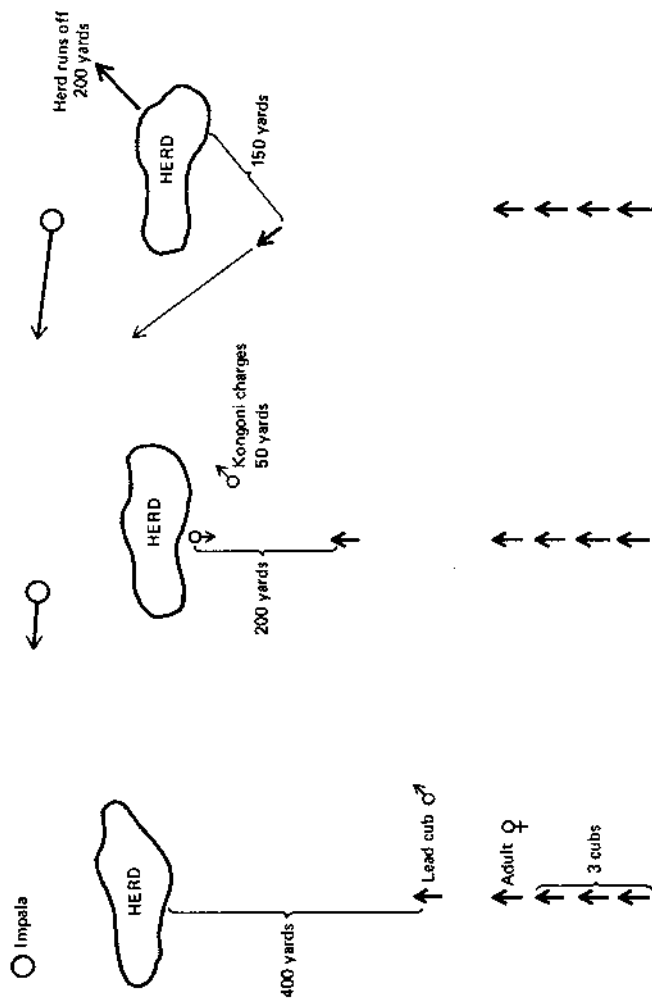


Figure 3-11 The entire cheetah family stalked a distant herd of mixed antelope. The lead cub, a nearly adult male, ran ahead of the other cheetahs, straight at the herd. As he got closer a male kongoni charged and a lone impala behind the herd took flight. As the mixed herd ran off the cheetah changed its direction of attack and pursued the impala but could not overtake it. The other cheetahs remained stationary during the attack.

COMPETITION WITH OTHER PREDATORS

To date there has been little intensive analysis of possible competitive interactions among the primary carnivores. There are data on the food habits of these top predators and Bourlieve (1963) has asked the question, how do the carnivores "... avoid coming into competition with one another and how can the closely related species ... remain ecologically isolated though geographically living side by side?" It could be stated that competition does occur between coexisting species, the degree of which is measured by the impact one species has on another, that is, what would happen to the population of species A if species B were removed from the same area?

Actually very little field work has been done with competition and coexistence in natural communities. Nor do we have any real notions of how different is different enough. To evaluate the competition between predators it is important to know the segregation into habitats, age, and condition of their respective prey diets. A basis for an initial indication of competition is a test of overlap between species for their requirements. Horn (1966) has developed a useful index of overlap for ecologists. I have applied this index to available data on the prey animals taken by the lion, leopard, and cheetah in East Africa (Table 3-17).

Bourliere (1963) explained this high level of competition by pointing out

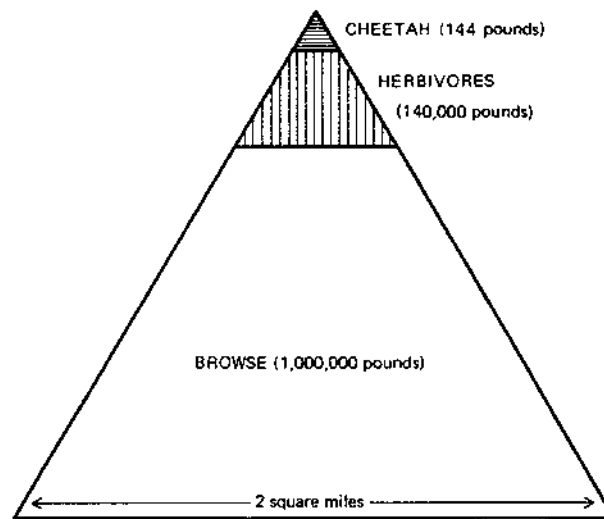


Figure 3-12 Pyramid of biomass in Nairobi National Park based on maximum estimates of cheetah density.

that the cheetah hunts in the open plains and the leopard in the riverine bush, and in different ways, the cheetah by running its prey down and the leopard by waiting and usually pouncing from a tree onto its prey. This explanation does not solve the problem. The question that now needs to be answered is, how do these two ways of living as a predator allow coexistence if there is competition for the same limited natural resources? More specifically do the cheetah and leopard really live off the same populations of ungulate prey or are they extracting different classes (age,

TABLE 3-17 THE INDEX OF OVERLAP (HORN, 1966)
AS APPLIED TO WRIGHT'S DATA FROM
NAIROBI NATIONAL PARK, 1960

Food	Lion	Leopard
Thomson's gazelle	.10	.50
Wildebeest	.49	.14
Impala	.03	.14
Zebra	.15	.07
Baboon	.00	.07
Wild dog	.00	.07
Giraffe	.04	.00
Grant's gazelle	.00	.00
Buffalo	.05	.00
Kongoni	.02	.00
(Others)	.12	.00
	1.00	1.00

$$\text{Overlap} = \frac{\sum_{i=1}^s X_i Y_i}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2} = .20$$

The results of the lion-leopard overlap test is what is normally expected with predators in the same trophic level. However, note the leopard-cheetah overlap:

Food	Leopard	Cheetah
Thomson's gazelle	.50	.58
Wildebeest	.14	.09
Impala	.14	.25
Zebra	.07	.00
Baboon	.07	.00
Wild dog	.07	.00
Reed buck	.00	.00
Grant's gazelle	.00	.09
	1.00	1.00

$$\text{Overlap} = .75$$

From 407 Observations (407) by Brynard and Pienaar, Kruger National Park during 1958-59 (Bourriere, 1963).

sex, condition, etc.) of individuals of the same species? Perhaps with the impala, for example, the cheetah visually locates a slower or less wary animal to attack while the leopard from the tree above picks out prey only on the basis of what happens to pass close enough for a kill.

To investigate this problem one has to determine the energy budgets or the energy gains and energy costs that make these two systems workable. Such a study would have to compare the cheetah system with the leopard system by evaluating each predator with respect to the following:

1. The effectiveness of the method of hunting.
2. The habitat visitation of prey to the predator's area.
3. The makeup of the prey animals in relation to their herds.

For each predator, observations of the hunting success tallied against attempted kills and the relationship of this ratio to the density of prey species have to be made. Also comparisons of biomass killed and utilized provide the data necessary for measuring competitive impact.

In comparing the ways of living found in the cheetah and leopard, for example the bioeconomics of each predator is not complete with a compilation of data from kills. Just as important in attempting to evaluate the interactions between the leopard and cheetah is the measure of visitation of suitable prey animals to each predator's domain. There are two questions inherent in this problem: (1) What constitutes a suitable prey animal, and (2) How available are prey animals to each predator in its respective habitat? Some information on the first problem is obtained by examining prey once it is attacked and killed by the predator. The second question can be answered by measuring whether or not certain animals spend more time than others in each of the predator's areas. The habitat segregation of prey animals in a leopard's or cheetah's hunting area would be compared with the attempted and actual kills of each. A longer-term study of several predators in one area, such as Schaller's (1972) study, will bring us closer to an understanding of 1 and 2; however, no field investigation has yet adequately evaluated 3 relative to concomitant predation by several predators.

INTERACTIONS OF CHEETAH WITH OTHER SPECIES

The alerting by prey of other prey was mentioned above, as was the "mobbing" response of prey. Several species, typically not prey, were responsible for such alerts, including giraffe (*Giraffa camelopardalis*), crowned cranes and species of bobos. The giraffe simply fixated on the cheetah visually and the prey species in the area responded by looking for

a predator. Crowned cranes, when seeing a cheetah, honked and hovered overhead, sometimes swooping down and even lighting nearby. These activities brought the prey's attention to the cheetah.

Lions, when hunting the same prey as cheetah, caused the cheetah to stop and move away. The mere presence or even sound of lions often resulted in cheetah changing their activities and moving away from the lions.

The normal interaction between two predators occurred when the jackals hunted in the late afternoon and came onto a group of cheetahs. The jackals, often four or five, were normally spread out over several hundred yards and maintained contact by barking as they moved. When cheetahs were encountered by one of the jackals, it barked to the others and they all came to the cheetahs, sniffing the air as they approached, apparently looking for a kill. If the cheetahs were not on a kill, the jackals searched the immediate area looking for a carcass that might have just been left by the cheetahs. If nothing was found, they remained near the cheetahs for some time, following them as they moved; and when a kill was made the jackals fed on the leftover carcass. If the cheetahs had already fed and were inactive and if a carcass was not found nearby, the jackals moved on.

In November, 1966, one area of the park was often frequented by a female cheetah with four cubs (group 1) and was also the territory of a pair of jackals with three pups. The jackal young remained at the den while the adults hunted either singly or together. Upon encountering the cheetah family, the jackals approached to about 20 yards and barked but were ignored except for an occasional chase by the cubs. The jackals ran back and forth barking between the cheetahs and a herd of Grant's gazelles feeding nearby. The two jackals had gone on to hunt and were almost out of sight by the time the adult cheetah attacked two male Grant's gazelles that had grazed away from the herd. The hunt was not successful. The jackals took notice of the chase and returned to look for a kill; it appeared that they associated food with the presence of the cheetahs and perhaps with the chase.

One month later, while observing the same cheetah family, I noticed that the entire jackal family was hunting as a group. The cheetah and her cubs were about 300 yards from a herd of mixed species. This same herd had earlier spotted the cheetahs and given alarm calls. The adult cheetah was too far away for an attack, there was little or no stalking cover, and the herd was aware of her presence. The cheetahs had been lying in the shade for about half an hour since the herd spotted them when the jackals arrived. Upon discovering the cheetahs lying under an *Acacia* tree, one of the adult jackals barked until the others were congregated around the cheetah family. The jackal that had found the cheetahs crawled to within

ten feet of the adult cheetah which did not respond. The jackal then stood up and made a very pneumatic sound by forcing air out of the lungs in short staccato bursts. This same jackal turned toward the game herd, ran to it and, upon reaching it, ran back and forth barking. The individuals of the herd watched the jackal intently. The cheetah sat up and watched the herd as soon as it became preoccupied with the activity of the jackal. Then the cheetah quickly got up and ran at half-speed toward the herd, getting to within 100 yards before being seen by the herd. The prey animals then took flight while the cheetah pursued an impala at full speed.

Upon catching the impala and making the kill, the cheetah called to its cubs to come and eat. After the cheetahs had eaten their fill and moved away from the carcass, the waiting jackals fed on the remains.

In six other hunts a jackal from this same family was observed facilitating the stalk of the adult cheetah and one kill was made. Of 108 hunts alone the cheetah was successful 15 times giving a hunt-to-kill ratio of about 7:1; while, with the aid of jackals, the cheetah was successful 2 times during the 7 hunts giving a ratio of 3.5:1.

In most areas, other than Nairobi Park, where cheetahs and jackals are both found, the jackals do not wait for a predator to leave their kill but rather attempt to take what they can before the predator abandons the carcass. In fact, the competition between predators and scavengers is often keen (Estes, 1967). In Nairobi Park hyena (*Crocuta crocuta*) are rare and wild dog (*Lycaon pictus*) are not seen. Apparently this is the reason the jackals lack competition for the cheetahs' kills.

There seems to be no other explanation for the behavior of the jackals and cheetahs except that it is a case of interspecific cooperation in which both benefit. It is doubtful that this phenomenon is widespread between these two species; it appears to be a learned behavior characteristic of a few individuals.

It is conceivable that these two families learned to cooperate during the month interceding my first and second observations of interaction between them. It is tenable that on some occasion while the adult cheetah was near a herd, and probably hunting, one or several of the jackals were moving through the same herd and barking, as they frequently do. Consequently, the jackals distracted the herd and enabled the cheetah to attack and probably make a kill.

The fate of this learned trait probably depends on the survival of the jackals. The behavior is not likely to spread since the competition between scavengers in most areas is too keen to allow it. It is also unlikely that the cheetahs could perpetuate the behavior to other jackals since it was the scavenging habits of the jackal that made possible the interaction in the first place.

The importance of the dog (*Canis familiaris*) in the evolution of modern

man and in the survival of many living cultures has long been recognized. Speculation based on fossils of dogs in stone age middens have placed the domestication of the dog at least 10,000 years ago. One common view held by many anthropologists is that when man settled down to an agrarian way of life, wild canids, long dependent on scavenging from the refuse of nomadic hunters, caught up with man, figuratively speaking, and were domesticated (Downs, 1948). The usual reasons that are offered for domestication of the dog are: for an alarm system, to rid of refuse and pests, for warmth and as a pet (Downs, 1948; Montagu, 1942).

It has been proposed that man and dog, both of which have great social affinities (Woolpy and Ginsburg, 1967), learned to cooperate in hunting (Zeuner, 1954). Just how this cooperation developed is only speculative, but evidence from hunting symbiosis in primitive peoples with their canids and between predator species is enlightening.

Several living primitive cultures that are not agrarian strongly depend for survival on their association with dogs. Aboriginies apparently brought the dingo with them to Australia and use them for hunting larger game as well as for warmth and to give warnings (Meggit, 1961). To the bushmen of the Kalahari in South Africa their bushdogs are invaluable for hunting (Dart, 1965). The Ituri pygmies live closely with a dog species, the basenji, which shows little relationship with modern dog breeds domesticated from the wolf (*Canis lupus*) (Scott and Fuller, 1965). The basenji is avocal and cooperates in hunting in the forest. It is possible, at least in the case of the pygmies, that these cultures have domesticated canids quite independently of domestication in the Northern Hemisphere, which is considered by many to be the origin of domestication. The hunting symbioses in these three cultures is mutualistic in that in return for tracking, running, and holding the game at bay, the dogs get the offal when the prey is killed by the men with their weapons. In a sense these cases are opportunistic exploitations of dogs by man, but it is equally probable that the percent of kills made cooperatively by the two species is higher than would be possible by either species hunting alone (Downs, 1948).

If cheetah and jackal can learn to hunt mutually then it is to be expected that man's presence for hundreds of thousands of years in areas with scavenging canines would have led to cooperative hunting between the two. In fact, it is hard to believe otherwise. It is equally possible that it was man who scavenged the canid and thereby established a symbiosis. Perhaps this symbiosis facilitated the learning of effective social hunting by hominids. Selection may have favored just such an interspecific cooperation.

Agriculture probably ended the importance of hunting as the binding force between man and dog and sponsored the more intensive artificial selection of breeds for various uses. It is possible that until this period men

lived closely with canids that in fossil form are indistinguishable from wild stock (Zeuner, 1954).

Domestication may have occurred through both hunting symbiosis and agricultural life; however, a hunting relationship probably led to the first domestication. Fossil evidence may eventually reconstruct behavioral associations between early man and canids. Such evidence may further delineate the evolutionary line of the predatory *Australopithecus pithecus* from *Australopithecus robustus*.