Eaton RL. 1974. The cheetah. In: The Cheetah - The biology, ecology, and behavior of an endangered species. New York: Van Nostrand Reinhold Company; p 16-40.

Keywords: 1Afr/1KE/1TZ/Acinonyx jubatus/cheetah/condition/cub/demography/distribution/East Africa/evolution/habitat/habitat selection/habitat use/litter size/map/morphology/mortality/Nairobi National Park/population/predation/reproduction/Serengeti/taxonomy

Abstract: A detailed description on taxonomy, distribution, morphology and appearance, habitat use and demography is presented, including a map with cheetah sightings throughout East Africa made during 1955-1964, and a distribution map for Kenya. The cheetah population of Nairobi National Park was estimated at 15 resident animals, 20 different individuals were observed. In the Amboseli Game Reserve 8 cheetahs were counted. In 1965, the total estimate for East Africa was 1932-1950 different animals. This figure might be too low.
Inter birth intervals were 17-19 months, so females came into estrus when their cubs were 12-14 months old. Gestation period was 90-95 days. The litter size was at least four cubs. The primary birth season was from March to June. In the Serengeti, births were observed from January to August. Seasons of birth may vary with different ecological conditions. Data on six litters indicate that predation is an important mortality factor of cheetah cubs.

2 The Cheetah

EVOLUTION

The earliest known fossil records of cheetah are from the Olduvai 1 bed, which includes many lower Pleistocene fauna fossils (Hopwood, 1951). The "Larousse Encyclopedia of Animal Life" (1967) says that since there are no fossil remains of cheetah in Africa, this negative evidence points to an Asian origin. The cheetah has evolved independently from the other big African cats, the *Panthera* group. The lion and leopard and the tiger in Asia evolved more recently in response to the increase in size and kinds of larger prey animals. The *Panthera* cats are distinguished by a difference in the hyoid bone apparatus which permits roaring. The cheetah, unlike these other big cats, does not roar; however the cheetah purrs similar to the *Felis* cats, for example the housecat and cougar.

TAXONOMY

Acinonyx jubatus was used as the cheetah's scientific name by Schreber in 1776; *Felis jubata* was used by Exrleben in 1777 (Shortridge, 1963:104). The taxonomy of the cat family has been in a state of flux. From up-to-date classifications by many authors, Denis (1964:133–136) produced a checklist

of the family Felidae. This classification shows that of 36 distinct species, excluding varieties and subspecies, 30 are in the genus *Felis,* 5 in *Panthera,* and 1 in *Acinonyx.* Although some authors used *Felis* for the cheetah as late as 1884 (Sterndale, 1884:200), in general *Acinonyx* is in widest usage (Shortridge, 1934:104; Burton, 1962:187; Roberts, 1951:181; and others). A few authors have used generic names other than *Felis* or *Acinonyx.* Roberts (1951:181) lists the following: *Cynofelis* by Lesson, 1842; *Guepardus* by Duvernoy, 1834; *Geuparda* by Layard, 1861; and *Cynailurus* by Elliot, 1883. Flower and Lydekker (1891:523) also used *Cynailurus.*

There have been many species, subspecies, and races described for the cheetah. Denis (1964:136) states that there are two races, in Africa and Iran, but does not say what their differences are. Several subspecies have been described: a South African cheetah, *A. jubatus jubatus* (Schreber); three East African cheetahs, *A. jubatus ngorongorensis* (Hilzheimer), *A. j. velox* (Heller), and *A. j. rainey* (Heller); a Sudan subspecies, *A. j. soemmeringii* (Fitzinger); a Senegal or North African subspecies, *A. j. hecki* (Hilzheimer); an Indian subspecies,*A. j. venaticus;* and *A. j. raddei* (Hilzheimer), a Turkestan subspecies.

Only a second African species, the King or Cooper's cheetah, *A. rex* Pocock, is listed by Harper (1945:286). There can be little doubt that much of the subspeciation, as the three in East Africa, is artificial classification. Isolated populations, such as those formerly found in India, have been geographically isolated long enough to obtain distinct physical characteristics. The King (Rex) cheetah or *A. rex* appears to be a population in which all phenotypic features, according to Roberts (1951:182), are the same as *A. jubatus* except for coloration and pattern of the fur (Fig. 2–1). All other cheetah populations show only slight variation in markings. Sightings and specimens of Rex have come from a small local region of Southern Rhodesia, northwest of Salisbury. This type has probably arisen via a single mutation, and the population probably should not be given species status unless it can be demonstrated that there has been genetic isolation from the nonmutant form. The Rex cheetah may now be extinct, since none have been seen for several years.

The name cheetah is derived apparently from the Hindi language in India that uses the word "chita," which means spotted one. Early writers in India use "chita" and "cheeta" (Flower and Lydekker, 1891:523). "Hunting leopard" is also in common usage today (Burton, 1962:187; Sterndale, 1884:200; Flower and Lydekker, 1891:523; Denis, 1964:136; Shortridge, 1934:104; Crandall, 1964:396; and others). Additional names in various continental languages are *guepard,* French; *Gepard,* German; *gheparde,* Italian, and *onza,* Spanish. Roberts (1951:181) and Shortridge (1934:104) list numerous native words for the cheetah. In Swahili, which was used often in my field study to question natives about cheetah whereabouts,

Figure 2–1 King cheetah from the Siki Reserve in Rhodesia. Mounted specimen in the Natal Museum.

"enduma" is the name. The Masai call the cheetah "nginyarasho." The Kikamba use the name "munyongoro," and there probably are many more local usages.

DISTRIBUTION

In the writings of Marco Polo (Wendt, 1959:56–57) cheetah were described and apparently numbered in the hundreds as hunting pets of the Mongol rulers. It can not be certain that cheetah were native in the Far East, since they may have been imported by the Mongols from areas further west. Crandall (1964:396) includes much of Africa, Arabia, Persia, and India as original cheetah range. Others include the arid and semiarid regions of South, East, and North Africa as well as less arid areas in India, Russian Turkestan, Syria, Palestine, and Arabia. In 1891, Flower and Lydekker (523) gave its distribution as throughout Africa and southwestern parts of Asia as far as southern India. Sterndale (1884:200) gave central and southern India, and in the northwest from Kandeish to the Punjab as its Indian range, and wide distribution through Syria, Arabia, Asia Minor, and all of Africa.

Its Asian range is greatly reduced and the same pattern seems to be

developing in Africa. MacDonald (1966:70) says, ". . . but now they have almost disappeared from those lands [India and Near Eastern countries] and are plentiful only in Africa." The cheetah is extinct in India and is reported to be very rare in Pakistan, Afghanistan, and Russia.

The history of the cheetah in Asia is one of decline and no recovery. The most recent sighting in India was 1951. Iraq, 1928 was the last sighting and until recently remnant populations persisted in Saudi Arabia, Oman, and perhaps Asian Russia. However, the cheetah is increasing now in northwest Iran, a tribute to the excellent game department there (Firouz, 1971; F. Harrington, pers. comm.).

In South West Africa the cheetah had a widely scattered range throughout the eastern sand-veld regions and apparently were increasing in Buchuanaland in 1934 (Shortridge, 1934:105). In southern Africa the cheetah has disappeared from the Cape Province, the Orange Free State, Natal, and the southern Transvaal. Thirty years ago they were rare throughout Southern Rhodesia, sparse in Northern Rhodesia (Zambia today), and rare in Nyasaland (Shortridge, 1934:105–106; Roberts, 1951:182). Cheetah occur throughout East Africa, north through Somalia, Ethiopia, and Arabia west to Nigeria (Petrides, 1965), but the only areas of real abundance outside of East Africa were probably Somalia and Ethiopia and the Somalia population has declined very recently due to no protection there. The East African countries Uganda, Kenya, and Tanzania until recent times had sizable populations (Fig. 2–2) (Graham and Parker, 1965). For Kenya, Stewart and Stewart (1963:6) give the present range of the cheetah based on sightings from many sources (Fig. 2–3).

A recent study (N. Myers, pers. comm.) indicates that the largest cheetah population in the world is in South West Africa, and that the population in East Africa is second largest.

DESCRIPTION

Meinertzhagen (1938) gives the weights of four freshly killed males in Kenya as from 127 to 143 pounds and that of a single female as 139 pounds. Shortridge (1939:109) lists two specimens weighing 136.5 pounds and 90 pounds, sex of the animals not given. Roberts (1951:181–182) gives weights of specimens from near Kruger National Park, males weighing 130, 110, and 108 pounds and a female weighing 127 pounds. Bourliere (1963) gives an estimate of 120–140 pounds for cheetah.

Letting Meinertzhagen's four male weights average 135 pounds, the average of 11 cheetah is 125.5 pounds. All known males average about 127 pounds, known females average 133 pounds in weight. This sample is entirely too small to generalize on male-female weight comparisons, but it

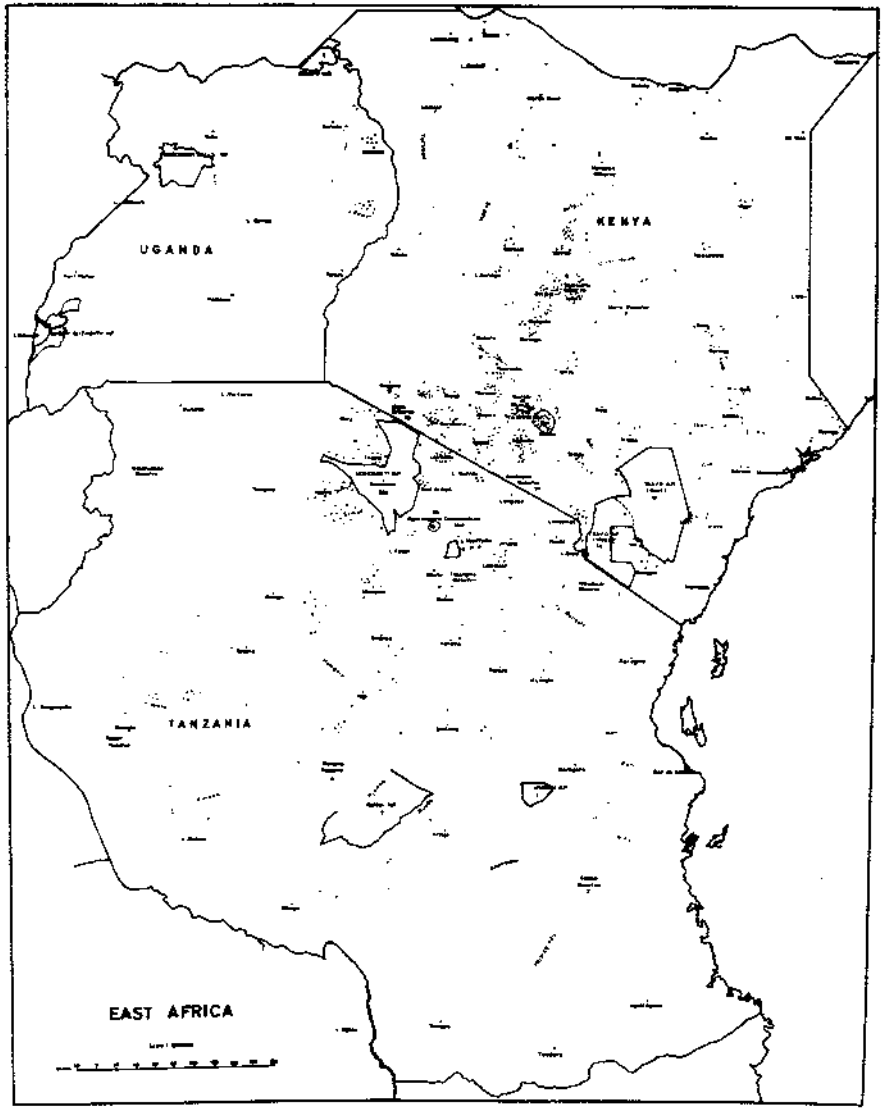

Figure 2–2 The sightings of cheetahs in East Africa between 1955 and 1964. Each dot represents one sighting; the numbers are cheetahs observed in respective reserves. (From Graham and Parker, 1965. Reproduced with permission.)

does give some idea of average adult weight. The Lion Country Safari and the San Pasqual Wild Animal Park's 34 cheetahs were all taken from the wild in South West Africa. Weights range from about 80 pounds for the smallest female at two years age, to 110 pounds for the largest males. Average adult weight was about 100 pounds.

Shoulder heights are recorded by Shortridge (1934:104) as 2 ft 11 in. for a large specimen; 2 ft 6 in. to 3 ft for several cheetah (exact number not given); and 2 ft 5 in. to 2 ft 7 in. as the range by Lydekker. Stevenson-Hamilton (1947:348) gives 2 ft 6 in., 2 ft 7 in., and 2 ft 8 in. for three males.

Total length measurements (nose to tip of tail) are given below. Shortridge (1934:109–110) lists the total length of the three largest specimens recorded by Rowland Ward Safari Company; the fourth one is from a female, and the last two are unidentified as to sex:

1. 7 ft 9 in., Kenya
2. 7 ft 3 ¼ in., North West Rhodesia
3. 7 ft 2 ½ in., North West Rhodesia
4. 6 ft 3 in., Kenya
5. 6 ft 8 in., Eastern Transvaal
6. 7 ft 7 in., Eastern Transvaal

Stevenson-Hamilton (1947:348) gives 6 ft 11 in., 6 ft 8 in., and 6 ft 4 in. for the total length of three males in South Africa. Roberts (1951:181–182) gives as total lengths of unsexed cheetahs 6 ft 7 in. (straight) and 6 ft 10 in. (on curves).

These total length measurements may not be meaningful. It is not known if they were measured properly. One specimen recorded by Roberts showed there is quite a difference in measuring straight or along body curvations.

Stevenson-Hamilton (1947:348) lists body and tail measurements (along with total length) and they are respectively: 52 in., 31 in., 51 in., 30 in.; and 47 in., 29 in. Roberts (1951:182) treats *A. rex* separately, and gives body and tail measurements for it from dry skins: 50 in., 30 in.; and 53 in., 30 in. Although these measurements correspond with Roberts' measurements of *A. jubatus* from whole carcasses, dry skin measurements are meaningless.

Skull measurements provided by Roberts (1947:564) indicate that cheetah in South Africa have the same measurements as those in East Africa. This indicates taxonomic similarity of widely separated populations and supports a "clumping" view of cheetah taxonomy. However, captive cheetahs from East Africa are decidedly less rangy than cheetahs from South West Africa. Also discernible is the darker pelage of South West African cheetahs.

The dentition of the cheetah differs from other *Felidae* by the inner

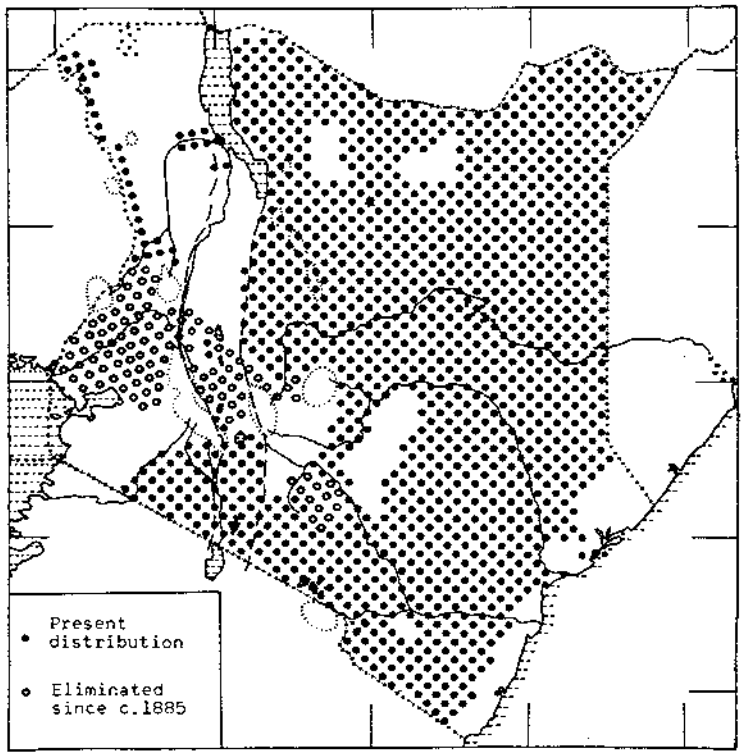

Figure 2–3 The distribution of the cheetah in Kenya. (From Stewart and Stewart, 1963.)

tubercle of the upper carnassial, although supported by a distinct root, it has no salient cusp (Flower and Lydekker, 1891:523).

GENERAL APPEARANCE

The cheetah's exaggerated cursorial proportions are well known and apparent to any observer (Fig. 2–4). General color would have to be considered yellow or tan but individuals vary as to the degree of color, some being light and others dark. They are covered everywhere with round black spots about half an inch in diameter. The neck and shoulders have longer thin hair that forms a short mane. The face, too, is covered with small spots and a long black line from the inside of the eye to the mouth. The ear is small and round with a black patch on the back side, which is apparently an adaptation similar to that found in many animals

that serves as a pair of "fake" or mimic eyes. It has not been tested, but hypothetically a predator approaching from the rear of the cheetah might perceive the cheetah as being aware, and therefore should not attack.

The tail is long, and in adults, white on the tip. Ewer (1971) believes that the tip of the tail helps cubs follow the mother through high grass. The eyes are extremely large with golden or brown irises. The cheetah's feet are unusual for *Felidae*, being very dog-like with partially nonretractile claws (Fig. 2–5 and 2–6). The claws, according to Shortridge (1891:523) are less retractile because of feebler development of the elastic ligaments. Adamson (1969) noted that even newborn cubs could not retract claws. The head is small and round.

Besides a skeletal framework that is, like the greyhound's, highly adapted for speed, the cheetah has relatively large nasal passages for heavy breathing, large bronchi and lungs, relatively large heart and adrenals, and highly muscular arteries. The long tail functions to maintain balance at high speeds, and the nonretractile claws, which become blunt and short with wear, serve for good traction and quick turns.

Estimates of maximum speed in the cheetah vary from 60 miles per hour to nearly 80 miles per hour. The slower speeds have been made in artificial situations, for example on a dog racing track with a hare as bait.

Figure 2–4 The cheetah's anatomy is highly specialized for speed. (Photo: H. Patel.)

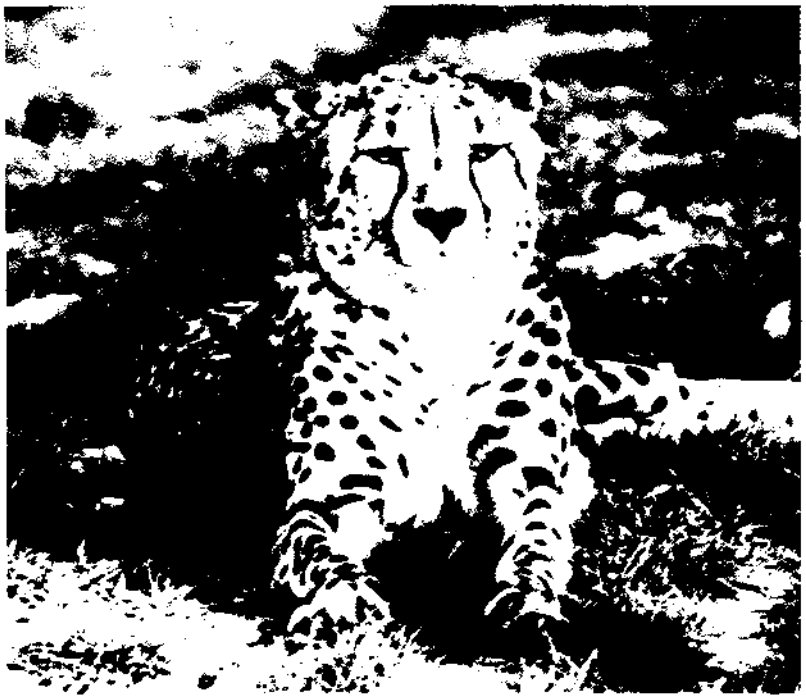

Figure 2–5 Relaxed cheetah exhibits its partially nonretractile claws. (Photo: R. L. Eaton.)

Observations in the wild that employed stop watches and measurements of distances covered should more accurately assess top speeds. One such record [illegible] a cheetah covered more than 700 yards in 20 seconds, which is a little more than 71 miles per hour (Bourliere, 1954:6.7). My own observations do not corroborate Bourliere's. A cheetah seldom runs at top speed for more than 200–300 yards. Moreover, in Florida a captive cheetah [illegible] 71 miles per hour top speed (K. Sevrin, pers. comm.).

Professor Hildebrand of the University of California, Davis, has intensively studied the functional anatomy of the cheetah. His researches have disclosed the interesting hypothesis that, if the legs were discounted entirely, the movements of the body would propel the cheetah forward at a speed of five miles per hour. By using slow motion films, Hildebrand has been able to stop, analyze, and diagram the locomotory movements, showing the progression of each foot during high-speed running.

HABITAT PREFERENCE

There is some question as to what is the habitat preference of the cheetah. It is too often assumed by popular writers that the cheetah is found only in the open grassland. I think this stems from the fact that photographers and hunters have most often seen cheetah only in the very open grasslands, especially in northwestern Tanzania and southeastern Kenya. Burton (1962:187) gives "open grassland or scrub" as cheetah habitat. Denis (1964:40) says they are adapted to savanna or open grassland. In India, cheetahs were recorded in very dense forest regions. In South Africa, Stevenson-Hamilton (1947:196) describes cheetah as found in open or lightly forested grass country and adds his opinion that thick bush is detrimental to its method of securing prey. Shortridge (1934:106) met cheetah in South West Africa on stony ridges as well as in the sand veld and less often in country clothed with dense bush or thick dry forest montane moorland or swamp. The species would appear to occupy a wide range of habitat from near desert through open grassland to thick bush.

The Cheetah Survey (Graham and Parker, 1965:11) did not disclose many sightings in the extensive tracts of brachystegia or miombo woodland that make up large areas of Tanzania and much of Africa. In addition, the survey showed no sightings in the extensive "long grass" areas of Uganda. Lamprey (1963:65) divides the habitat in the Tarangire Game Reserve into three types: grass, open woodland, and dense woodland. He shows the cheetah (Fig. 2–7) as preferring mostly grassland with some use of open woodland. My observations show that cheetah frequent open woodland

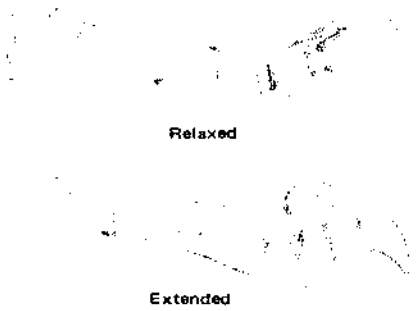

Figure 2–6 Cat claws. When not in use, the claw-bearing joint of each toe is folded back over the preceding joint and held in place by a ligament. In this position it is encased in a sheath of skin for further protection. When the animal extends its paw to strike, a tendon attached to each toe pulls the joint forward and bares the claws for instant use. The cheetah differs from other cats in the absence of claw sheaths; the blunt claws always remain exposed and extended.

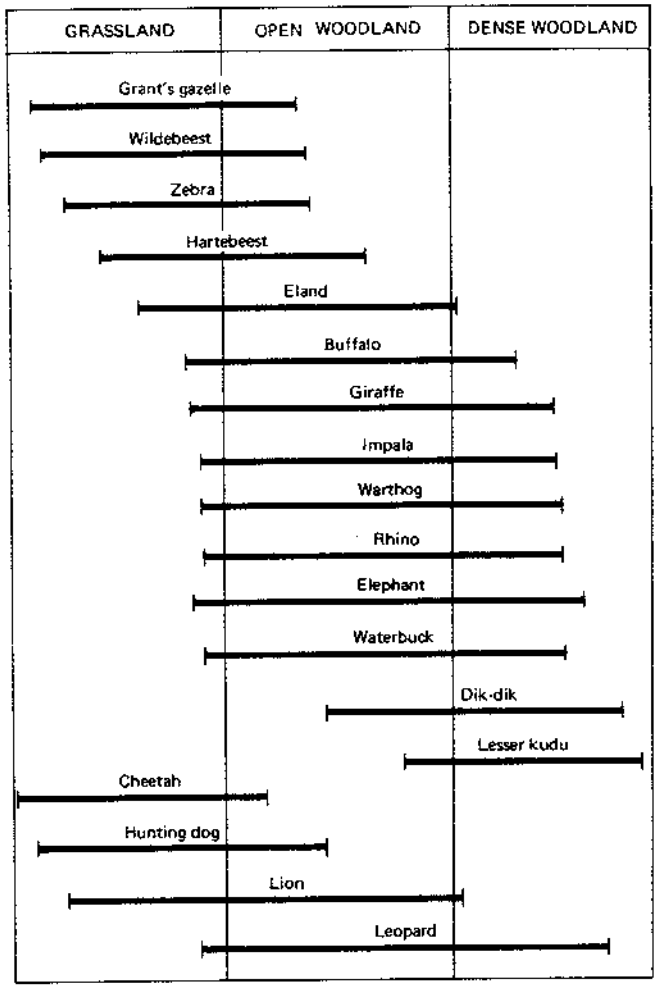

Figure 2–7 The ecological separation of mammals shown by Lamprey (1963:65) for Tarangire Game Reserve, Tanganyika. (Reproduced with permission.)

more often than shown by Lamprey, in fact they occasionally use dense woodland in hunting (Fig. 2–8). Warren Garst (pers. comm.) filmed cheetahs in Rhodesia in *miombo* woodland [illegible] open space.

Only observations from following animals continually would reveal the total habitat visitation of the species. Cheetah in open or dense woodland

are naturally less visible and this factor, I think, has biased earlier interpretations of their habitat. Of course, my observations do not represent the habitat visitation of all cheetah everywhere and in fact they may be biased due to special habitat preferences of the local populations I observed. Still, the fact that any local population, as in Nairobi National Park, frequents open woodland and savanna and even uses dense woodland expands the habitat preference for the species as a whole and may indicate that other populations behave similarly.

Adamson (1969) noted the frequent use of trees as lookouts in her tame, wild-living cheetahs in Kenya. She deduced that man had driven the cheetah out of the open plains into wooded areas thus indirectly leading to use of trees and climbing. While mortality from man is probably higher in open areas, I am confident that cheetahs have always occupied the less open, wooded areas. Cheetahs climb and seek out high lookouts in open areas as well.

ABUNDANCE

The only area in the cheetah's distribution for which information is available concerning density and abundance is East Africa. Graham and Parker (1965) and Graham (1966) analyzed data from the East African Cheetah Survey. The density was estimated at 1 animal per 18 square miles for the Narok District in Kenya and surrounding areas, based on 12 animals in the Mara triangle of 216 square miles. For the Tarangire Game Reserve, Tanzania, and surrounding country the estimate of density was 1 animal to 170 square miles; however, this is based on transect counts of two square miles of Tarangire between 1958 and 1961, a crude approximation to say the least!

The only area for which estimates of density were more than crude approximations is Nairobi National Park and the Serengeti Area. The

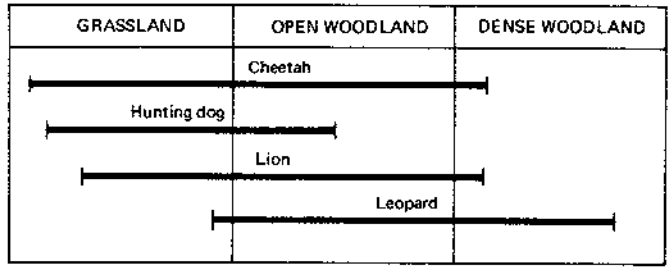

Figure 2–8 In Nairobi National Park the "niche" is wider for the cheetah than shown by censuses in the Tarangire Game Reserve by Lamprey (1963).

Cheetah Survey (Graham and Parker 1965:9–10) gives an estimate based on numerous reliable observations by Dr. R. Schenkel, Zoologist, and D. Kierney, Chief Game Warden, Nairobi National Park. These two competent observers agreed on the presence of 12–14 animals consisting of 2–4 single adults, 4 male adults, and 1 adult with 5 young. The density for the park based on the 1963–64 period of observations by Schenkel and Kierney was 12–14 animals in 44 square miles or 1 animal to 3–4 square miles.

In all fairness, it should be stated that these men probably had good knowledge of some groups of cheetah in the park, but from my own experience I can say that Kierney was not aware of some of the resident cheetah while I was working there. Of course some of the occasional sightings not recognized by Schenkel and Kierney could have been nonresident cheetah that came in from outside the park for a short time only. Still, there were recorded a group of 2, a group of 3, and a group of 2 adults with 3 young. If these cheetah were also residents of the park, then the maximum number of cheetah in the park would have been almost twice as large—22–24 animals or a density of 1 animal to about every 2 square miles. The inclusion of these animals in the original estimate gives a revised estimate very much like the density and abundance of cheetah present during my study.

I observed a total of 20 different cheetah in Nairobi National Park. Of these 20 animals, I considered 15 to be residents (Table 2–1), that is, cheetahs whose home range included some or all of the park. One group, a female adult with three young and a single adult were observed in the park only twice and once respectively, and were considered nonresidents.

That the seldom observed cheetah were nonresidents of the park is supported by the fact that they showed greater fear of vehicles and were "jittery" in general. Assuming that there were at least 15 resident cheetahs, my data show a density in the park of 1 animal to nearly 3 square miles. Since I observed more resident cheetah but fewer single adults than Schenkel and Kierney, and since they had no means of identifying animals other than by group size, they may have been observing fewer single

TABLE 2-1 SIZE, AGE, AND SEX OF FOUR RESIDENT CHEETAH GROUPS OBSERVED IN NAIROBI NATIONAL PARK

	Adult		*Juvenile*			
Group	*Male*	*Female*	*Male*	*Female*	*?*	*Total*
#1	—	1	2	1	1	5*
#2	3	2	—	—	—	5
#3	2	—	—	—	—	2
#4	2	1	—	—	—	3
Totals	7	4	2	1	1	15

* Two of the four cubs were lost on December 15, presumably by lion predation.

adults than they realized. After I left Nairobi Park, a second researcher, McLaughlin, studied cheetahs. He found about 20 cheetahs that resided in the park.

In the Masai Amboseli Game Reserve, which is thought to be a good cheetah sanctuary, I observed a total of 8 cheetahs. The reserve is 1300 square miles and I was not able to locate and record individuals throughout the entire area. It is difficult for a researcher to determine where in the reserve he is. There are no signs, permanent roads, or fences partly due to its management for the government by the Masai people. What is more, the area is fast losing any value as a reserve due to extreme competition between Masai cattle and game for food and water. Schaller (1970) earlier estimated that the average density of cheetah in the Serengeti was 1 per 100 square miles. He felt population was declining there for unknown reasons, but more recently (1972) has stated that the population appears to be holding its own. Schaller (1972) guesses that there are about 200–250 cheetah in the Serengeti ecological unit, a density of less than one cheetah per 40 square miles.

The total estimate for East Africa based on 1225 sightings of 2785 cheetah was 1932–1950 different animals in 1965. The accuracy of cheetah estimates will vary with the number of observers in the area, the terrain, and vegetation, and the experience of the observers. If about 2000 different animals were actually seen, then there probably were many more in highly unvisited areas such as in Northern Kenya. For example, no cheetah were observed in Rodgers Valley in the North Frontier District of Kenya according to the Cheetah Survey's map (Fig. 2–2). Yet, reliable observers recorded 15 different cheetah in Rodgers Valley in one trip. The North Frontier District (N.F.D.) has yielded very high numbers of observations in its few inhabited areas. These facts imply that the estimate given by the Cheetah Survey probably falls very short of the actual numbers of cheetah in some areas, and for the whole of East Africa was probably too low in 1965.

Earlier visitors, for example Bill York, frequently saw from a dozen to 20 or more cheetahs in a small area of southern Sudan near the Illemi triangle. In recent times reports have indicated fewer or no cheetahs there. We shall await the results of Norman Myers' current study of cheetahs to reevaluate its status in several countries.

REPRODUCTIVE BIOLOGY

With any threatened species, such as the cheetah, it is important to have information on reproductive biology as an aid in breeding them in captivity so that individuals will not be removed from existing popula-

tions. Further, population trends can be evaluated from analysis of reproductive organs as well as composition of a population by sex and age classes. Captive animals as opposed to individuals from wild populations can be used to restock areas formerly occupied, and this is now being tried in South Africa. Table 2–2 includes measurements and estimates of gestation periods in cheetahs. There are few data on wild cheetahs, but most observations indicate a 90–95 day gestation period.

TABLE 2–2 ESTIMATES AND MEASUREMENTS OF GESTATION IN CHEETAHS

Source	*Wild or Zoo Cheetahs*	*Gestation, Days (No. Litters)*
Asdell (1964)	zoo	95
Ulmer (1957)	zoo	92
Wilhelm, in Shortridge (1934)	wild	90
Kenneth (1943) in Asdell (1964)	zoo	95
Adamson (1969)	semi-wild	90 (3)
Herdman (1972)	semi-captive	92-95 (2)
Florio and Spinelli (1968)	zoo	86–90

Crandall (1964:397) describes a female in captivity that gave birth on March 24, 1956, and again on April 25, 1957. Assuming that gestation was about 90 days, this female was impregnated 10 months following parturition, an anestrous period of 13 months. Graham and Parker (1965:18) describe an adult female and a three-fourths grown male that were approached by an adult male. The adult male kept driving off the young male and kept very close to the female. In Nairobi Park, J. B. Foster (pers. comm.) observed a group of adult male cheetahs approach and mate with a female that was accompanied by cubs estimated to be one-half to three-fourths grown. Since females raise their young in isolation from other adults until the cubs reach sexual maturity at 14–16 months, the three-fourths grown male was probably the female's cub, apparently about 10 months old. The cubs observed by Foster were also roughly 10 months old. In both cases anestrus was about 13 months. Sterndale (1884:203) observed a female with two older cubs accompanied by an adult male. The female was probably in estrus, but from Sterndale's description it is not possible to determine the age of the cubs. Spinelli and Spinelli (1968) describe a captive female that came into heat four months after birth of a litter.

In Nairobi Park I observed one female with cubs from the time the cubs were 5½–10 months old. During this period adult males did not approach the family group. Foster and McLaughlin (1968) observed this same female after I left Africa. Her cubs left her when they were 15 months of age and

in another 3–4 months she gave birth again, a period of 15–16 months between birth and conception. Adamson's (1969) semiwild cheetah, Pippa, gave birth to her first litter which was lost at six weeks of age. The female mated again within two weeks and about three months later gave birth to four cubs. Pippa mated again when these cubs were 15 months old; however, the third litter was lost after two weeks and Pippa mated within one week, giving birth about three months later. Adamson noted that a cheetah in Nairobi Park had a second litter shortly after being attended by her first, from which she sneaked away to give birth. McLaughlin (1970) in Nairobi Park recorded intervals between births of 17, 18, and 19 months. Schaller (1972) reports an 18-month period between birth and conception for a Serengeti female.

Visual encounters between adult groups of both sexes or all males and the family group in Nairobi Park occurred but no further associations were observed. Schaller (1972) observed two family groups momentarily meet and then separate. Scent markings are critical for spacing of cheetah groups but they also communicate estrus condition and serve to enable males to locate females. I observed a second female in Nairobi Park that had an older litter of cubs. The female exhibited estrus when her cubs were 12–14 months old. Data on birth-to-birth and birth-to-estrus periods when cubs are not lost or removed are summarized in Table 2–3.

TABLE 2–3 BIRTH-TO-BIRTH AND BIRTH-TO-ESTRUS PERIODS WHEN LITTERS WERE NOT LOST OR REMOVED

Captive or Wild Cheetahs	*Birth-to-Birth Periods (Mos.)*	*Birth-to-Estrus Periods (Mos.)*
Captive	13	10
Captive	11	3.5
Wild (Kenya)	—	10
Wild (Kenya)	—	10
Wild (Kenya)	—	12–14
Wild (Kenya)	18	15
Wild (Kenya)	18	15
Wild (Kenya)	17	—
Wild (Kenya)	18	—
Wild (Kenya)	19	—
Wild (Tanzania)	—	18

The first recorded birth of cheetahs in captivity was in 1956 at the Philadelphia Zoo. The female gave birth to two males and one female (2:1) cub. The female killed one instantly; the two surviving cubs were removed but lived only a few days. Thirteen months later the same female gave

birth to two cubs (1:1). The mother raised the cubs until they died of distemper at an age of three months.

The Krefield Zoo, Germany, had four cubs born in 1960. None of the cubs survived (Encke, 1960).

A cheetah at the Oklahoma City Zoo gave birth to two litters, three and two cubs respectively, in 1962. None survived (Thomas, 1965).

It was not until 1966 that a female in a private Roman zoo gave birth to a cub that was raised by its mother (however, with human assistance). The cub was a male. The same cheetah gave birth late in the same year to three male cubs (Florio and Spinelli, 1968).

In 1967, a cheetah at the Whipsnade Zoo gave birth to 1:2 cubs. Only one cub died but the female raised the other two (Manton, 1970). The same cheetah had a litter (1:1) in 1970, which she also raised successfully. I have been informed that one of the captive born cubs has matured and since given birth at Whipsnade. This is the first case of a second generation captive birth.

In France at the Montepellier Zoo, a litter of three cubs was born in 1968, and raised by their mother (Vallat, 1971).

At the San Diego Wild Animal Park, a cheetah from South West Africa gave birth in 1970 to three cubs, two of which were killed by a male. The surviving cub was removed and hand-raised but later died. This male cub had lived longer than any cheetah born in the U.S. (Herdman, 1973). The same female gave birth again in 1972 to three cubs, all of which survived and are being raised by their mother (Herdman, 1972).

Table 2–4 summarizes data on captive cheetah births (Thompson, in press).

In the wild, Denis (1964:40) found a litter of four cubs and refers to another of three; both litters estimated to be seven to eight weeks old. Shortridge (1934:108) tells of Wilhelm finding a litter of two cubs in South West Africa that were apparently four to six weeks old. Foster and McLaughlin (1968) report a litter of five cubs born in Nairobi Park. McLaughlin (1970) reported on six litters, from three to six cubs each, averaging 4.3. Pienaar (1963) records a litter of five cubs in Kruger Park. Adamson's (1969) cheetah had four litters under wild conditions that numbered three, four, four, and four cubs. Sex ratios in two litters were three females to one male and three males to one female. Even litters of seven to eight weeks in age may not accurately reflect birth litter size since many probably die in early life. This is indicated especially by Adamson's observations: out of eleven cubs born only three lived to adulthood and all but one of those lost died very young. Of 15 wild litters estimated less than one month old by Graham and Parker (1965:4), six had four cubs; the average size was 3.7. The largest litters ever sighted, one young and the other two older, had eight cubs. Sightings in the Cheetah Survey (Graham and Parker, 1965:4) show that in older age classes litters are progressively smaller.

TABLE 2–4 A SUMMARY OF CHEETAH BIRTHS IN CAPTIVITY (FROM THOMPSON, IN PRESS)

Zoo	*Date*	*No. Born*	*Remarks*
Philadelphia, USA	24 March 1956	2, 1	
Philadelphia	25 April 1957	1, 1	
Krefeld, Germany	24 April 1960	1, 1	
Krefeld	?	?	No details
Oklahoma City, USA	7 April 1962	2, 1	
Oklahoma City	14 November 1962	2	
Arnhem, Netherlands	?	?	No details
Spinelli, Italy	13 January 1966	1	Tame pet
Spinelli	14 December 1966	3	
Whipsnade, England	15 September 1967	1, 2	
Whipsnade	22 July 1968	1, 2	
Whipsnade	6 February 1970	1, 1	
Whipsnade	7 March 1971	3	
Whipsnade	24 October 1972	?	Marvin Jones
Montpellier, France	1 December 1968	2, 1	
Montpellier	May 1970	3, 1	
San Diego, USA	22 November 1970	3	
San Diego	28 April 1972	3	
Toledo, USA	26 December 1971	1, 3	

From these observations of young litters in the wild plus data from five litters averaging five known cubs after birth, it can be said that the average cheetah litter in the wild is at least four cubs. This assumes that some cub mortality occurs in the first six weeks. There is an obvious disparity between captive and wild litter sizes at birth. Smaller litters in captivity may be the result of physiological stress due to captive conditions or poor nutrition.

The dates of cheetah births are summarized in Table 2–5. Hamilton (1912 in Asdell, 1964:493) and Stevenson-Hamilton (1947:200) do not provide numbers of litters for their estimates of birth seasons in the latter half of the year in the Transvaal. Smithers (1966) and Ansell (1960) both record cheetah births in Zambia in November through March. All other birth dates are based on specific litters and are estimated within one to two specific months. The birth dates in East Africa and captivity indicate a primary birth season from March through June; however, Schaller's (1972) sample of 14 litters in the Serengeti indicated an even distribution of births from January to August. He observed no births between September and December. Using aging criteria of size, length of pelage, condition of teeth, and level of play behavior, Lion Country Safari received cheetahs that were apparently born in South West Africa in November, December,

TABLE 2-5 LOCATIONS AND BIRTHS IN WILD CHEETAHS

Source	*Location and/or Origin*	*No. Litters*	*Wild or Captive*	*Birth Months*
Hamilton (1912) in Asdell (1964:493)	Transvaal	—	Wild	July–December
Stevenson-Hamilton (1947:200)	Eastern Transvaal	—	Wild	June–December
Stevenson-Hamilton (1947:200)	Eastern Transvaal	—	Wild	August–December
Shortridge (1934:108)	South West Africa	1	Wild	December or January
Ansell (1960)	Northern Rhodesia	2	Wild	March or April and March
Graham and Parker (1965:8)	Nairobi National Park	2[a]	Wild	May
Graham and Parker (1965:8)	Nairobi National Park	1	Wild	August, late
Eaton	Nairobi National Park	1	Wild	May, early
Eaton	Nairobi National Park	1	Wild	April–June
Eaton	Nairobi National Park	1	Wild	November
Eaton	Masai Amboseli Game Preserve	1	Wild	April–June
Foster and McLaughlin (1968)	Nairobi National Park	1	Wild	November
Adamson (1969)	N.F.D., Kenya	2	Wild	March
		1	Wild	August
		1	Wild	July

[a] One litter of three young was estimated at about eight months old when observed in January.

and January. These same cheetahs exhibited highest mating activity in July, August, and September, implying that they would have given birth in the latter half of the year. San Diego Zoo's cheetahs, also from South West Africa, showed a similar mating season, and one of their five females gave birth in November and in April. Herdman (1972) found highest mating activity in South West African cheetahs at San Diego Wild Animal Park to be July–August and December–January. World Wildlife Safari cheetahs also from South West Africa have shown breeding in June–July and October–November.

Births appear to occur seasonally and at different times of the year in East as opposed to South Africa: 14 of the 21 more exact estimates of captive and wild litter births to cheetahs from both regions are from March through June. Peak rains for Masailand, which includes Nairobi Park and Masai Amboseli Game Reserve, are in March and April (Talbot

and Talbot, 1963:16). Game is widely scattered over the plains once the rains come and large game concentrations are rare. When most litters are six to ten months old, October to February, a second but less intense and often irregular rainy season occurs. The female raising cubs goes through stages in rearing the young that vary in their demands: (1) feeding the cubs from birth to six months, by herself; (2) teaching the cubs, age 6–12 months, to hunt while still providing most of the food; and (3) hunting with the cubs, which are effective hunters, from age 12 months on. When these periods are plotted against the rainy seasons and game concentrations, which are inversely related, it is seen that the first step parallels lower game concentrations, the second phase parallels higher game concentrations, and the third stage parallels lower game concentrations again.

Factors affecting hunting success that are related to seasonal changes, other than game concentrations, are vegetation growth and color. The height of vegetation appears to change little, and may not affect cheetah activities. The color of vegetation does change distinctly. Whether or not prey species possess color vision, contrast of cheetahs to cover is probably less detectable in the dry season. In the rainy seasons, in lush green grass, cheetahs should be more visible. The second phase of cub rearing parallels not only higher game concentrations but lower visibility of cheetahs by prey. The second phase is the most difficult period for the female in rearing young for several reasons. The cubs are growing fast and demand ever-increasing diets. This food must be provided by the female until the cubs can hunt effectively by themselves. During this period the female is also teaching the young how to hunt. This requires much time and is highly unproductive; the cubs contribute very little to the family's food supply, they "scare" game away frequently, and the female's time is cut short for hunting. As the cubs approach the ability to make kills they are increasingly active in learning how to hunt, which would require increased energy expenditures. It is to be expected that natural selection would favor females that bear young at a time when they can best meet the energy requirements of the cubs. This contention is made in general by Lack (1954:64). There would be a differential reproductive success of females that give birth when the dry season does not parallel the most precarious period in rearing young. Robinette et al. (1961:210) have demonstrated that reproduction in the mountain lion (*Felis concolor*) is timed so that the small cubs are born not in the colder months but in the summer. Similar results were found by Eaton et al. (1973) in a large, captive population of mountain lion. Birth season appears to be an adaptation to prevent young from freezing while the female goes on hunts.

Seasons of birth may vary in regions with different ecological conditions. Since relatively few data on wild cheetah are available from other

than East African areas, it is difficult to speculate on birth seasons elsewhere.

It is to be expected that factors such as abundance of susceptible young prey might be related to birth seasons in cheetahs. In East Africa most ungulates drop their young either throughout the year or at the onset of the rainy season. Since cheetah cubs are frequently preyed upon by other predator species and the cubs remain sedentary until they are about eight weeks old when they accompany the female, the ease of preying upon ungulates born at the onset of the rainy season could be an advantage to the female with very young cubs. Similar ecological correlation should be expected in South West African cheetahs.

MORTALITY

With the effect of hunting and economic exploitation of cheetah perhaps it is impossible to weigh the importance of various natural mortality factors on cheetah numbers. Although the natural conditions which existed before the entrance of European man into Africa are impossible to determine, present conditions in protected areas should bring basic relationships into sight.

In the field work I collected cheetah feces from at least 15 animals of four different groups, and in all 29 "scats," tape and intestinal roundworms were present. These parasites appeared plentiful but no further work was carried out with respect to internal or external parasites. No sick or dead cheetahs were acccessible for autopsy. Upon worming, Adamson's cheetah, Pippa, excreted a large tapeworm; unfortunately, it was unidentified. She did identify dog tick fever (*Babesia canis*) in young cheetah cubs. Her cheetahs were frequently covered with ticks and camel flies (hippoboscids).

The important information that has come from the intimate contacts between species of wild animals and their keepers can not be overemphasized. It is often the habit of hard-nosed experimentalists to scorn the works of naturalists or animal lovers; however, the frequent reference throughout this book to the observations of Mrs. Adamson should be testimony to the great value of her approach in uncovering hard to unravel facts. Although I could not both keep cheetahs and study them in the field in Africa, I feel that I came to know the animal much better by being able to observe them so closely at Lion Country Safari and World Wildlife Safari. It is a desirable procedure for ethologists carrying out naturalistic field studies or experimental investigations to also keep some subjects as pets just so additional insights into the species' nature will be discovered. A modern classical case is the work of Fritz Walther (1965) in which he

assumed the role of mother to several young antelope. Only by acting as a member of the species could Walther unravel the processes of imprinting and how the young animal comes to know its own mother.

Disease is common in young captive cheetahs. Crandall (1964:397) points out that in many zoos felids, panleucopenia (feline distemper) is a common deadly disease in young animals including cheetahs. In fact it is panleucopenia that has largely prevented the breeding in captivity of cheetahs since they are exceptionally susceptible. Of the 11 cubs born in captivity between 1956 and 1960, eight died of panleucopenia, one was killed by the mother when she was excited, and only two lived a short while. Immunization is available but it involves a series of injections during which the cubs can contract the disease. It is not known if this disease is an important mortality factor to cheetahs in the wild, but since most mortality in the wild is explainable by factors other than disease, it is unlikely that the disease is nearly so important in natural populations. Since cheetahs are so vulnerable to panleucopenia, it is probable that they have not lived with it in the wild, or that some larger molecules (antibodies) incapable of passing through the placental barrier are transferred directly to cubs via nursing, in the mother's milk. In captivity the cubs are usually removed just after birth, thus, perhaps, prevented from acquiring immunity to panleucopenia and other communicable diseases.

Rickets is a common disease in captive cheetahs (Mercier, 1961; Young, 1967). Adamson (1969) reported rickets in free-living cubs; however, much of the cubs' food was being provided by her and since rickets is usually due to a vitamin deficiency or mineral imbalance, the occurrence of the disease in purely wild animals can not necessarily be inferred. Cheetahs, as cubs, do appear to be more susceptible to rickets than any of the other cats (Young, 1967). Gastroenteritis is brought on in cheetah cubs in several ways: changes of diet, inadequate diets, old milk, and infection from internal parasites, bacteria, and viruses (Young, 1967). Pienaar (1969) found anthrax as a cause of death, and malnourished or vitamin-deficient cubs in Kruger Park.

Post-mortem examinations on four cheetahs that died in captivity showed that two adult males both showed toxic dystrophy of the liver (Gandras and Encke, 1966). Two young females both had Laennec's cirrhosis of the liver. While in the Miami area I spoke with people who had had cheetahs that died, and the diagnosis was in each case some kind of liver ailment. This has been the most common cause of poor health in captive cheetahs. It is plausible that lack of activity could be responsible for liver disease. Few animals must rely on as specialized a liver as the cheetah, in mobilizing energy for "the fastest chase on earth."

Two cubs that died in Nairobi National Park were examined by Murray

et al. (1964). They took blood smears and found severe anemia. Histological analysis turned up *Spirocera lupi* worms in the aortic media. The worms had damaged the endothelial lining of the aorta which resulted in thrombosis. In 1967 Murray found bacillary particles indicating *Eperythrozoon felis*, a cause of hemolytic anemia in house cats.

A summary of cause of death in 123 captive cheetahs is provided in Table 2–6 (derived from Van de Weaken, 1968, in Thompson, in press).

TABLE 2–6 AUTOPSY FINDINGS ON 123 CAPTIVE CHEETAHS (DATA FROM VAN DE WEAKEN (1968), IN THOMPSON, IN PRESS)

Post-Mortem Findings	*Percentage*	*Average Longevity*
Tuberculosis	24	2 years, 1 month
Cirrhosis of liver	11	4 years, 8 months
Other liver diseases	16	3 years, 4 months
Feline distemper	25	1 year
Pneumonia and other bronchial diseases	12	1 year, 4 months

Stevenson-Hamilton (1947:198) writes of several cases of cannibalism. In one instance a ranger saw two cheetahs fighting in a clearing of the bush and in the morning found a dead male cheetah lying where he had seen the fight. A reedbuck (*Redunca redunca*) ram lay nearby but had not been eaten, but the dead cheetah had a portion of its neck and shoulder eaten away. Stevenson-Hamilton (1947:198) records another instance in which a Major Fraser observed two large males fight until one was dead. Whether or not cannibalism exists is not nearly so important as the fact that cheetahs do exhibit actual physical aggression toward each other. Aggression is rare in that it has been recorded in the literature in only one other instance, when a male showed slight but unharmful aggression to a curious cub of a female that was apparently in estrus. I observed slight physical aggression in the wild only once, between a mother and her adult sons when they attempted to mount her. Actual aggression is sometimes a mortality factor in some species, and often it plays a function in population regulation. Hundreds of fights that I observed between wild cheetahs at Lion Country Safari resulted in not one serious injury.

The threat of aggression has replaced physical aggression for the most part. Aggression leading to physical combat resulting in death is surely not a means of population control. The threat of aggression plays a different role from combative, injurious aggression; it does not eliminate individuals but rather acts as a spacing mechanism between groups and maintains social order within groups. Aggressive behavior is described in detail below.

The effect of injuries on an animal so completely dependent on its highly specialized anatomy for survival are bound to be important. Graham and Parker (1965:18) give data on seven cheetahs with limps and another cheetah with an injured back. Adamson's (1969) cheetahs, both adult and cubs, suffered many leg injuries, some of which were analyzed as fractures, to the long bones. Starvation as a result of injury is to be expected and would have to be considered indirectly as accidental death. Several cheetahs at Lion Country Safari had old leg and foot injuries, and some became injured in captivity. Steel traps used to capture cheetahs alive probably account for the damaged feet and legs in Lion Country Safari cheetahs.

Actual starvation from lack of food directly and not as an indirect effect of disease or injury would be almost impossible to determine unless carcasses were closely examined. Three adult cheetahs have been found dead, cause unknown, and one adult with three cubs was recorded as very thin and weak (Graham and Parker, 1965:18). D. O. Thompson (pers. comm.) came upon a starving cheetah in Kenya. In descriptions of this type it is impossible to tell what caused weakness or death.

Predation on cheetahs by other predators appears to be important as a mortality factor. Graham and Parker (1965:18) recorded the following: three cases of lions feeding on cheetahs and one of leopard; two cases in the Serengeti of hyena chasing very young cheetahs with no intervention by the adults; and two animals with parts of their tails missing. Lions have attempted to catch young cheetahs in Nairobi Park. Schaller (1972) recorded a cheetah killed by a leopard, and an emaciated female killed by lions.

Data on six litters, five in Nairobi Park and one in Masai Amboseli Game Reserve, indicate that predation is an important mortality factor of cheetah cubs, or indirectly, when parent cheetahs are killed. In Masai Amboseli Game Reserve, where hyena are very common, two cubs of a litter of five were killed by hyena according to one of the native rangers. In Nairobi Park, two cubs of a litter of four were lost during one night. A litter of five newly born cubs and an adult female suddenly disappeared in Nairobi Park according to park records. A litter of five cubs lost one cub according to park records and another litter of six cubs was lost entirely.

Also, I observed a female with three cubs in which the female did not return from a hunt. The possibility of poaching or accidental death is highly unlikely in the central part of the park where she left her cubs and was last seen. Hunts away from the cubs seldom last more than a couple of hours. The female did not return that day and the cubs began running wildly; they did not eat or hunt. It is probable that they died of starvation if not from predators. It is possible that the female fell prey to the park's

central pride of lions which had their main territory near where the female separated from the cubs.

The litter in Nairobi Park that lost two cubs (Fig. 7) during the evening of December 15, 1966, were quite healthy on that day and I left them when they were bedded down at 7:00 P.M. Previously they could always be found in the morning where they had been left the prior evening, but early on the morning of December 16, I discovered them gone from the bed site and spotted them later about half a mile away. There were only two of the four cubs with the female. The three of them behaved quite unusually. They were extremely wary and were not nearly as approachable as before. The mother walked with her ears back and was more observant of the immediate terrain than usual. She and the two cubs darted and ran at the slightest sounds or upon my approach to normally unheeded distances. The only conclusion that I can come to is that the cubs probably were killed by other predators. Since Nairobi Park is almost never frequented by hyena or hunting dog and since it is believed that leopards are solitary and hunt alone and could not probably kill two half-grown cubs at the same time, lions seem the most likely cause of death of the two cubs. Also, since lions hunt in groups, it would be easier for them to kill more than one cub once the group was startled. There are no data from the wild which indicate that other cheetahs also prey on cubs; however, it should be expected, and has been observed in semicaptive cheetahs (Herdman, 1973).

Adamson (1969) is convinced that a hyena killed Pippa's four newly born cheetah cubs. Predation accounts for at least half the losses to her cheetah's four litters. These data of 36 cubs include only two direct observations of actual predation. Still I think that predation is the obvious explanation for most cub losses. All of the cubs were less than ten months old. This agrees with Graham (1966b), who points out that between one and ten months, litters decrease by about one half in number of cubs, from 3.7 to 2.0 cubs per litter. Mackintosh (1970) reported 43% mortality in Nairobi Park cubs, thus corroborating my earlier study there, and both our studies agree with Pienaar (1969), who recorded about 50% mortality in Kruger Park.

The hypothesis that predation on cheetah cubs is the most important natural limiting factor on cheetahs is supported further by the inverse relationships between cheetah group size (and abundance) in an area with the abundance of other predators. More field work is required to test this hypothesis.