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ECOLOGY OF THE CHEETAH

by

Randall L. Eaton[1/]

In an attempt to round-out this section, I have analyzed several aspects of cheetah ecology which have not been reviewed to date by myself or others. References to my own field data are derived from a study in Kenya, 1966-67. Hunting behavior, predator-prey ecology, and social organization are covered in detail elsewhere (Eaton, 1970a; 1970b; 1970c; Schaller, 1968). This paper points out our still limited knowledge of cheetah life history, and raises many questions that should be answered through further ecological field study.

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Distribution

In the writings of Marco Polo (Wendt, 1959) 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) includes much of Africa, Arabia, Persia and India as original cheetah range. Harper (1945) includes 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 gave its distribution as throughout Africa and South-western parts of Asia as far as Southern India. Sterndale (1884) gave central and southern India, and in the north-west from Kandeish to the Punjab as its Indian range and says it is found widely 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. McDonald (1966) 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, Afghanastan and Russia.

The history of the cheetah in Asia is one of decline and no recovery. The most recent sighting in India was 1951. In Iraq 1928, was the last sighting and until recently a remnant populations persisted in Saudi Arabia, Oman and perhaps Asian Russia. However the cheetah is increasing now in northwest Iran, a tribute to their excellent Game Department.

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). 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 (Zamiba today), and rare in Nyasaland (Shortridge, 1934; Roberts, 1951). Cheetah occur throughout East Africa, north through Somalia, Ethiopia and Arabia west to Nigeria (Petrides, 1961)

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 (Graham and Parker, 1965). For Kenya, Stewart and Stewart (1963) provide the present range of the cheetah based on sightings from many sources. Current field surveys (N. Myers, pers. comm.) indicate that cheetahs have disappeared from many areas of East Africa where they were fairly common six years ago.

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) gives ". . . open grassland or scrub . . ." as cheetah habitat. Denis (1946) says they are adapted to savanna or open grassland. In India, Hicks (1911) recorded cheetah in very dense forest region. In South Africa, Stevenson-Hamilton (1947) 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) met cheetah in South West Africa on stony ridges as well as in the sand yeild and less often in country clothed with dense bush or thick dry forest montane moorland or swamp. They also say that the species occupies a wide range of habitat from near desert through open grassland to thick bush.

The Cheetah Survey (Graham and Parker, 1965) 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) divides the habitat in the Tarangire Game Reserve into three types: grass; open woodland; and dense woodland. He shows the cheetah (Fig. 5) as preferring mostly grassland with some use of open woodland. My observations show that cheetah frequent open woodland more often than shown by Lamprey, in fact they occasionally use dense woodland in hunting (Fig. 6). 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, prefers open woodland and savanna and even uses dense woodland expands the habitat preference for the species as a shole and may indicate that other populations behave similarly (Fig. 7).

Mrs. Adamson (1969) noted the frequent use of trees as look-outs 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 look outs in open areas as well.

Abundance

The only area in the cheetah's distribution for which information is available concerning density and abundance in 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.

The only area for which estimates of density are more than crude approximations is Nairobi National Park and the Serengeti Area. The Cheetah Survey (Graham and Parker, 1965) gives as 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 to 4 single adults, 4 adult males, 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.

I observed a total of 20 different cheetah in Nairobi National Park. Of these 20 animals, I considered 15 to be residents (Tab. 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 non-residents. After I left Nairobi Park, a second graduate student, Mr. McLaughin, studied cheetahs. He found about 20 cheetahs that resided in the Park.

Tab.1 >

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. Besides, it is difficult for a researcher to determine where he is in the reserve. 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) estimates that the average density of cheetah in the Serengeti is one per 100 square miles, and the population appears to be declining there for unknown reasons.

The total estimate for East Africa based on 1225 sightings of 2785 cheetah, was 1932 to 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 ther 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. Yet, reliable observers recorded 15 different cheetah in Rogers Valley in one trip. The North Frontier District (N.F.D.) has yielded very high numbers of observations

Table 1. Size, age and sex of four resident cheetah groups observed in Nairobi National Park.

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

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

in its few inhabited areas. These facts imply that the estimate given by the cheetah in some areas and for the whole of East Africa was probably too low in 1965.

Earlier visitors, for example Bill York (verb. comm.), frequently saw from a dozen to twenty or more cheetahs in a small area of southern Sudan near the Ilemi triangle. In recent times reports have indicated fewer or no cheetahs there.

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 faeces from at least 15 animals of four different groups and in all 29 "scats", tape and intestinal round worms 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 accessible for autopsy. Upon worming, Joy Adamson's cheetah, Pippa, excreted a large tape worm, 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).

Disease is common in young captive cheetahs. Crandall (1964) points out that in many zoo felidae, panleucopenia 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 know 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 the cheetah is so vulnerable to panleucopenia, it is probable that they have not lived with it in the wild, or that some larger molecules 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 acquired immunity to panleucopenia and other diseases.

Rickets is a common disease in captive cheetahs (Mercer, 1961; Young, 1967). Joy 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 disbalance, 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). Gastro-enteritis 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).

Post moretem examinations on four cheetahs that died in captivity are reported by Gandras and Enke (1960). Two adult males both shwed toxic dystrophy of the liver. 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 diagnoses were in each case some kind of liver ailment. This has been the most common cause of poor health in captive cheetahs.

Two cubs that died in Nairobi National Park were examined by Murray et al. (1964). They took blood smears and found sever 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.

Stevenson-Hamilton (1947) 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) 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 towards each other. Aggression is rare in that it has been recorded in the literature in only one 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. The threat of aggression has replaced physical aggression for the most part. Aggression leading to physical combat resulting in deat is not a means of population control. The threat of aggression plays a different rôle than combative, injurious aggression, it does not eliminate individuals but rather acts as a spacing mechanism between groups and maintains social order within groups.

The effects of injuries on an animal so completely dependent on its highly specialized anatomy for survival are bound to be important. Graham and Parker (1965) 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.

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 of death unknown, and one adult with three cubs was recorded as very thin and weak (Graham and Parker, 1965). 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) 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 tail missing. Lions have attempted to catch young cheetahs in Nairobi Park (Anonymous, 1966).

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 a litter of four cubs lost two of them 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. 9) during the evening of December 15, 1966, were quite healthy on that day and I left them when they were bedded down at 7:00P.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 one-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, then 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 one the group was startled.

Fig. 2 >

Joy 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 cheetha's four litters. These data of 36 cubs include only two 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 (1966) 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.

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. Territoriality appears unimportant in regulation of cheetah populations. Their spacing system merely prevents interference of one group's hunting efforts by another group (Eaton, 1970).

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 way 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) 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-grey fine hair, while the sides, tail, belly and legs are covered with dark, solid spots. At three months cubs begin losing the long grey hair and dark spots become apparent all over the body. Morris (1965) says that the mane, which Stevenson-Hamilton (1947) described as being lost in the third month, disappears after the 10th 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 grey fur (Shortridge, 1934; Sterndale, 1884). These observations were confirmed by Adamson (pers. comm.) and her observations on maturation are summarized below (Tab. 5).

2

Tab. 2 >

Table 5. 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, stalking
14 days	climb well, cling to roof of cage (Stevenson-Hamilton, 1947)
21 days	walk steadily, "chirp" call attracts mother
28 days	teeth irrupting
190 days	permanent molars
240 days	canines, last of first set of teeth, lost
245 days	lower incisors irrupt

The stages following the loss of the grey 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) are aged by relative size comparisons. 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 of illustrations could then be used in the field to age animals without having to capture them. This work can now be facilitated with the use of carefully established dosages of several drugs to immobilize cheetahs (see York's chapter).

There is very little data on sex and age ratios. Graham (1966) 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. In addition to the Cheetah Survey (Graham and Parker, 1965) 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 (verb. comm.) said the sex ratio in the Serengeti was 1:3 while Eloff reports (verb. comm.) a 3:1 in Kruger Park. We have no idea why such diverging sex ratios obtain in different areas.

Graham and Parker (1965) 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 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 to observers~~ and more likely was off hunting. Although Graham and Parker (1965) 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 of these can be assumed to be female mothers and 79 as adults in groups comprising roughly 64 males and 15 females in which the males of the groups were pursuing mothers in "heat".

In Nairobi Park I found seven males and four females among resident adults and an adult male and one female among non-resident 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. Observers see adult groups more readily than litters (Graham and Parker, 1965). Less frequent sightings of litters means fewer sightings of adult females and the total sex ratio is biased in the male direction.

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) 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. 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. Burton (1962) 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, seven months, in captivity. He also says that cheetahs seldom live more than six years in captivity but Crandall (1964) says it is even less. Graham and Parker (1965) 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, but adults are killed by other predators. Their attempts to defend kills against hyena, leopard, lion, wild dog and even jackals at times are usually futile. A 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 big cats, implying that length of reproductive life may be relatively short, or litter mortality high, or be

Robinette et al. (1961) and Hornocker (1970) point out that in mountain lions, like 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 asbsence 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 they seldom are 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.

The only wild individuals on which I have dates for determing 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 (Fig. 3) were mature in July, 1964. Putting the four brother's ages at a minimum of 16 months in July, 1964, their ages (only two of them

were present in February, 1967) at the termination of the field study were 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.

Fig-3 >

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 gave birth the first time at about 18 months. The only other recording of 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. Cheetah females apparently mature sexually at an earlier age than mountain lions (Robinette et al. 1961) or lions (Asdell, 1946) in which 2 1/2 to 3 years is usual.

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) sets forth.

To really understand a population's trends and to be able to predict its future one mush have data over several years. With the cheetah it is desirable to evaluate the annual cyclic environmental changes and how theyeeffect productivity. The age makeup of a population at any point in time should be present in the data of 2785 cheetah observed in East Africia. The age composition of these cheetah is 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 fifficult to observe the younger they are. As they mature they are much more active and are larger, both of which should increase observability. Beyond about six months 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) present data on the age groups of the immatures observed. Litter size increased with progressive age until the 4-7 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 300:100 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 post-reproductive 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 post reproductive age mortality probably is 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 everytime, it is believed that mortality to members of all-adult groups is relatively low. Adult groups are predominantly 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 ~~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, but not in lions, also has a high sex ratio. The Serengeti, where other larger predators are most dense there appears to be a sex ratio in favor of females.

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 and the loss of energy in excretions. 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 were recorded in N.N.P. an altitude of nearly a mile high, all near mid-day with partial cloud over (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 spped 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 adult, a female, exhibited 136 and 140 respirations per minute, 2 and 6 minutes, respectively, after and 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.

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

Biomass Transfer

The possiblity 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 44 square miles gives a density of about .6 cheetah per square mile. Again, for maximum predation, we will 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. Each day the cheetah eats a maximum of 1.5 pounds per 10 pounds of body weight. This means that the maximum consumption is 18 pounds/day/cheetah or 450 pounds/day/25 cheetah which is 160,200 pounds per year. This figure is equivalent to 10.8 pounds per day/cheetah or 3,845 pounds/cheetah each year. The average total prey weight/sq. mi. 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 uneaten entrails. The 3,845 pounds of meat consumed by cheetahs converts to 5,768 lbs. of the 71,294 supported annually

or less than 9% of the biomass available. This figure is maximal for Nairboi Park, which harbors the highest density of cheetahs. Surely the biomass transfer is only a fraction of the N.N.P. 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. Losses can be counter balanced by tourist income from photography of cheetahs in the game ranch.

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 Bourliere (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, i.e., 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 (1968) 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 (Tab. 13).

Tab. 3 ?

Bourliere (1963) explained this high level of competition by pointing out 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 of the same populations of ungulate prey or are they extracting different classes (age, 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 coats 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:

I. The effectiveness of the method of hunting
II. The habitat visitation of prey to the predator's area
III. The make-up of the prey animals in relation to their herds.

Table 13. The index of overlap (Horn, 1968) as applied to Wright's data from Nairobi National Park, 1957.

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

$$\text{Overlap} = \frac{\sum_{i=1}^{s} XiYi}{\sum_{i=1}^{s} Xi^2 + \sum_{i=1}^{s} Yi^2} = .20$$

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

overlap = .75

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

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 bio-economics 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 or cheetah's hunting area would be compared with the attempted and actual kills of each

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