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References:

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13. Cheetah Ecology and Behaviour - George W. Frame

Abstract:

The status of cheetahs in the Serengeti ecosystem is considered good, with an estimated population of at least 500. The secrecy of most cheetahs accounts for the apparent scarcity. In the dry season cheetahs concentrate along the woodland edge, and around Seronera, where the density becomes one cheetah per 3 sq.km. - the highest known density of wild cheetahs anywhere in Africa. Optimum habitat is lightly wooded or bushed grassland. Cover is very important for hunting, protection, and shade. Cheetahs prey on whatever is abundant, small, and easily caught; at Seronera this is mainly Thomson's gazelles. Various aspects of behaviour are being studied; these are grouping, spacing, courtship, and the development of cub play. Aspects of tourist viewing and management are discussed.

Introduction:

Cheetah numbers throughout Africa are declining by about half every decade (Myers 1975). It is therefore becoming more important to understand the ecological requirements of cheetahs, so that they can be conserved. The Serengeti ecosystem, because of its size and protection, is potentially one of the world's most important areas for cheetah conservation.

Fieldwork began in 1974, and will continue through 1978. During the period 1969 through 1973, Brian Bertram compiled some data on cheetahs in the Seronera area, incidental to his lion research. The present cheetah study is being done concurrently with a study of wild dogs (see separate report). Three main purposes of the cheetah research are to evaluate the status of this species in the Serengeti ecosystem, to identify optimum ecological conditions for cheetah conservation, and to contribute to an increased understanding of cheetah behavior.

Methods:

Two main approaches are being used for the collection of cheetah data: One method is periodically to search extensive areas by vehicle in order to identify as many cheetahs as possible. This provides good demographic data as well as incidental information on seasonal movements, behavior, hunting and habitat. The second approach is to follow

selected individuals day and night for about a week. This provides good quantitative data on hunting success, food consumption, water and habitat requirements, and daily movements, as well as incidental information on interactions with other cheetahs and other predators. During these week-long watches, mother-cub relations and the development of cub behavior are being measured with 15-minute focal animal samples.

Social Organization:

Cheetahs are mainly solitary. Adult females nearly always are alone, except during courtship or when they have cubs. Adult males are somewhat more sociable, with about 40 percent of their sightings consisting of male groups. Cheetah associations are summarized in Table 1. In this study the largest group seen was nine cheetahs, which consisted of two adult females each with a litter of cubs. In the Loliondo area, northeast of the park, a group of 12 cheetahs was reported hunting together (Balson 1970), and it is most likely that this group, too, consisted of 2 adult females with their litters.

Cubs stay with their mother until they are 14 to 18 months old. Gradually the litter separates from their mother, but they stay together as a sibling group for several more months. Then the young adult females leave, one by one, presumably as they come into estrus. Brothers usually stay together for a longer time.

Spacing and Movements:

Spacing is accomplished mainly by avoidance when one cheetah sees another. Eaton (1970) reported that cheetahs also avoid meeting by moving away from trails that are freshly scent-marked by other cheetahs, but our data do not support this. Adult female cheetahs urine mark, and sometimes their independent cubs of previous litters follow their scent trail. Scent marking by females becomes more frequent when they are in estrus, and we witnessed a male finding an estrus female by following her scent trail; courtship and mating followed.

Breeding males scent mark frequently. These olfactory signposts may serve to warn other males of their presence. We speculate that the scent marks of a breeding male might also be of important communicative value to females by habituating the females to the male's presence. This might possibly facilitate the female's acceptance of the male during courtship and mating. It is even possible, although unproven, that the male's scent marks may be one of the factors inducing estrus in the female.

Table 1 : Cheetah Associations (487 Sightings):

Association	Number of Sightings	Percent
Adult female with cubs	269	55.2
Lone adult female	93	19.1
Group of grown littermates, separated from their mother	47	9.7
Lone adult male	29	6.0
Group of adult males, relationship unknown	20	4.1
Lone adult female, with one or more adult males:		
(a) males known to be not sons or littermates of the female	12	2.5
(b) relationship unknown	4	0.8
Adult female with cubs and with one or more adult males:		
(a) males known to be not sons or littermates of the female	3	0.6
(b) relationship unknown	8	1.6
Lone adult male with a group of grown littermates who were separated from their mother	1	0.2
Two adult females, each with a litter of cubs	1	0.2

Young adult female cheetahs, after leaving their mother, continue residing in their mother's home range. Initially, at least, they sometimes approach within 20 meters of each other, but avoid actual meeting. We are continuing the monitoring of movements to see if eventually a partitioning of ranges occurs.

Young adult male cheetahs emigrate from their mother's home range, and we have resighted them in new areas. We suspect that the resident breeding males chase away the young adult males. This is futher supported by two reports of male cheetahs fighting, and in each case one male died (Stevenson-Hamilton 1947).

Mother cheetahs with newborn cubs are restricted in their movements. One example is a mother cheetah who gave birth to a litter at Maasai Kopjes in September. During their first month of life the cubs were occasionally moved to new lairs, all within a range of one square kilometer. In the same period, because gazelles were present in moderate density, the mother cheetah hunted over an area of about 10 sq.km.

The Seronera area seasonally has the highest density of cheetahs known anywhere in Africa. During the dry season, when cheetahs are concentrated around Seronera and the rest of the woodland edge, the density reaches one adult cheetah per 6 sq.km., or, including cubs, one cheetah per 3 sq.km. In the wet season (November through May), when migratory prey move onto the plains, most of the cheetahs follow and disperse to a lower density. During one annual cycle, a typical adult cheetah ranges over an area of about 1,000 sq.km.

Population Analysis:

Births occur thoughout the year, but there appear to be two peaks (Fig.1). It is not known if these peaks truly represent months of increased births, or if they reflect a differential mortality of cheetah litters. One speculation is that increased mating activity occurs in January and May, with resulting birth peaks in April and August. January and May could be considered the two best months for Serengeti Plains cheetahs, because in January there is an extensive movement of prey and cheetahs onto the plains, and May is the month with perhaps the greatest density of prey and cheetahs on the plains. But there is no explanation of why the peaks are not distributed over the entire rainy period January to May. A similar pattern of increased conceptions in the months of greatest food availability was reported for lions in Nairobi National Park (Rudnai 1973).

Litters as large as 8 cubs have been born in zoos (Thompson and Vestal 1974). However, litters this large are rarely seen in the wild. In the Serengeti, the mean litter size of cubs less than a month old is 4.2, but already much mortality has occurred by that age. At three months old the litter size decreases to a mean of 2.6. The range of litter sizes in each age class are shown in Table 2

Table 2 : Range of litter sizes and mean litter size for each age class. (Includes Brian Bertram's data from 1969-73, and data from the present study for 1973-76. Sample size is 54 litters with repeated sightings in subsequent age classes).

Age Class of Cubs	Number of litters of each size						Mean litter Size
	One	Two	Three	Four	Five	Six	
0 to 31 days	0	0	4	3	4	1	4.2
5 to 8 weeks	2	4	5	3	2	1	3.1
3 months	3	6	4	2	0	1	2.6
4 months	3	8	2	1	2	0	2.4
5 to 7 months	3	8	3	1	2	0	2.4
8 to 10 months	4	10	9	4	1	0	2.6
11 to 13 months	3	6	4	2	1	0	2.5
14 to 18 months	1	7	4	2	2	0	2.8

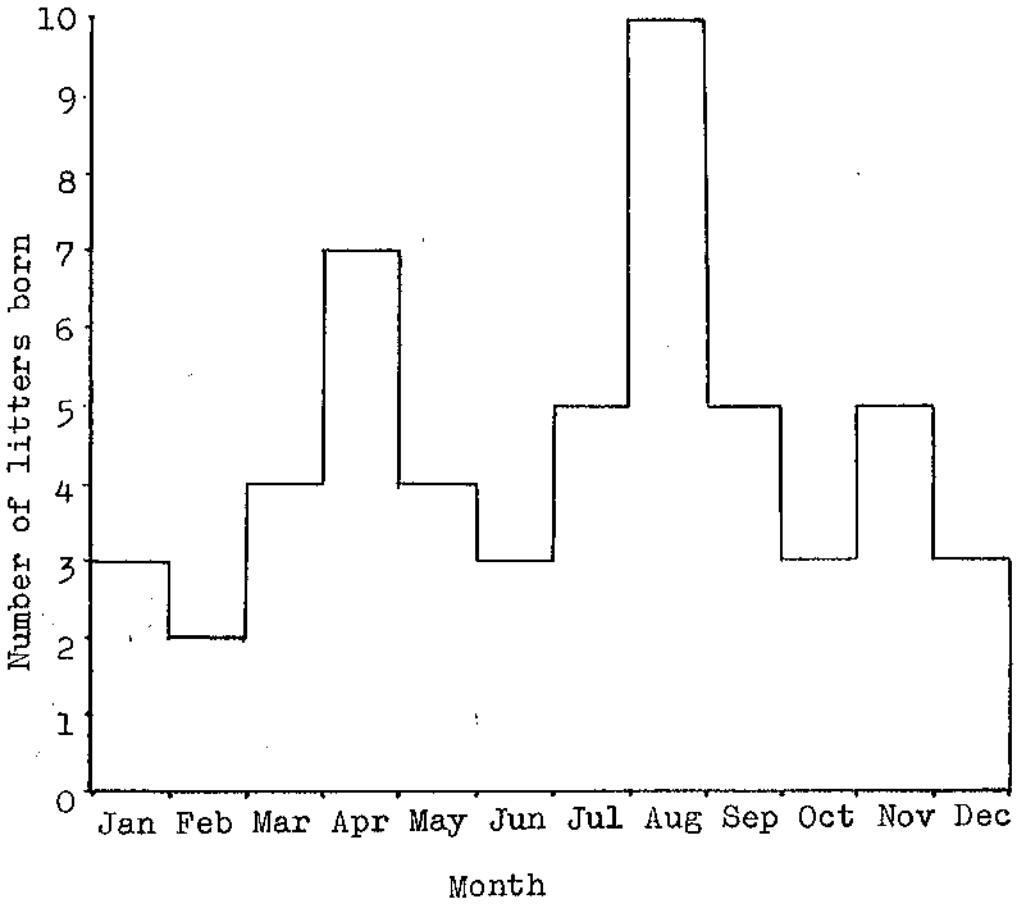


Fig. 1. Month of birth of 54 cheetah litters. (Includes 19 records from Brian Bertram for the period 1969-73, and 35 records from the present study for the period 1973-76.)

The sex ratio among all the cheetah litters in which it was possible to sex the cubs was 28 males to 29 females (49 percent males to 51 percent females), which is essentially equal. However, among all the adult cheetahs that are recorded in our photographic recognition file, 36 percent are males and 64 percent are females. In other words, there are twice as many known adult females as there are males.

There are three probable reasons for this differential sex ratio in adults. First, young adult males emigrate from their mother's home range, and presumably are subject to a higher mortality in their wandering. Second, the tame adult males in our study area seem to be more secretive than adult females, thereby causing us to see them less often. Third, the tame young-adult males emigrate out of our study area. However, young-adult males who are emigrating from more distant areas, and who are passing through the study area, are generally so shy that it is impossible to identify them or to recognize their sex.

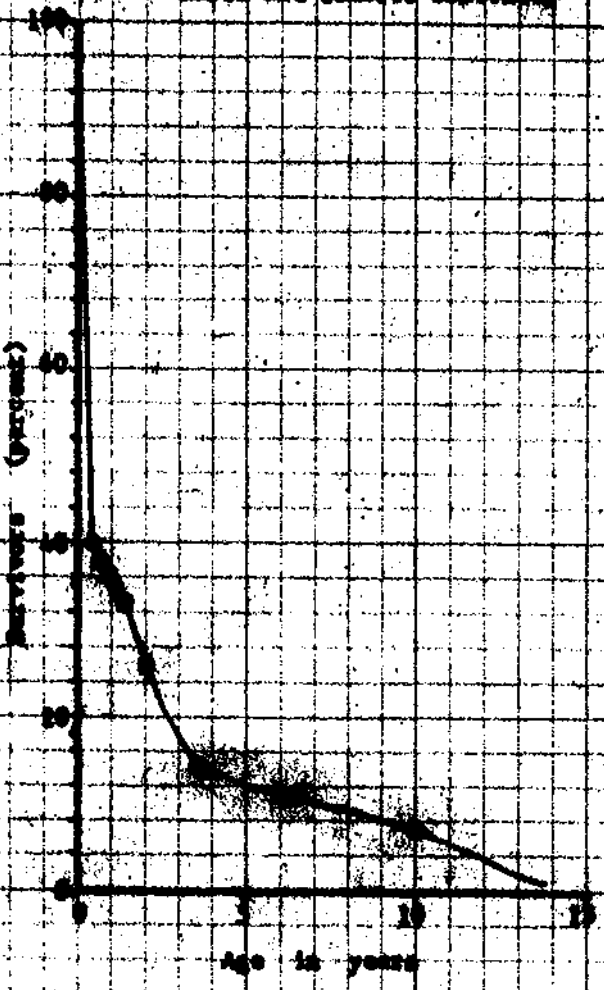
A crude life table (Table 3) and a survivorship curve (Fig.2) were constructed from data on 155 cheetahs, based on the assumption that the population is stationary. Ages of these cheetahs were either actually known from their birth date, or estimated from the criteria we have outlined (Frame and Frame 1975).*

The age class 0 to 3 months is the most difficult to deal with, because of the impossibility of making accurate field observations during this brief and secretive time of life. It is generally agreed (Schaller 1972, McLaughlin 1970, Eaton 1974, B. Bertram, pers.comm.) that mortality is very high during this period, mainly from predation, exposure, abandonment, and grass fires. From several tame adult female cheetahs we were able to estimate the numberof litters lost in their entirety, plus the number of cubs lost in surviving litters. The cub mortality in the first three months of life was estimated at 60 percent, and this was assumed to be representative of the population. Both the life table and the survivorship curve use this estimate for their first age class, but all the other age classes are based on the observed structure of the population. They are subject to further revision, but we believe they present ~~a reasonably accurate~~ an approximate picture of the population.

The structure of the cheetah population, with nearly a quarter of the individuals between the ages of 3 months to 18 months old, is indicative of an expanding population, or else a stable population with heavy mortality of adults. Spotted hyenas are not a serious threat to adult cheetahs (Kruuk 1972:294), but leopards are known to prey on adult cheetahs (M. Turner In Schaller 1972:301-302). It appears that only about 4 percent of the cheetahs born in the Serengeti reach the age of 12 years old.

Both the life table and the survivorship curve are time-specific,

Figure 2. Survivorship curve for cheetahs, male and female combined.



Note: The survivorship curve and the life table (Table 3) were prepared at different times and with different amounts of data, so there are some minor discrepancies.

Table 3 : Preliminary Life Table of Cheetahs, Males and Females Combined : August 1976:

x	l_x	d_x	q_x *
0 to 3 months (black cubs)	387[a]	232	0.60
3 to 7 months (1/3 to 2/3 grown)	155[b]	10	0.07
7 to 13 months (attaining adult size) 76%	145	29	0.20[c]
13 to 18 months (adult size but not yet independent)	116	4	0.03
18 to 36 months 11%	112	37	0.33
3 to 5 years	75	34	0.45
5 to 8 years 13%	41	24	0.59
8 years or older	17	17	1.00

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* = Mortality rates assuming a stationary population.

a = Note that this datum has not been converted to an arbitrary rounded figure.

b = This is the known-age population and starting point for the calculations; the first l_x figure is calculated from the survivorship curve (Fig.2), which assumes approximately 60 percent mortality

c = This unexpectedly high figure is probably an artifact of the small sample size; our observations do not support the inference of high mortality in this age class. Even when adjusted for the varying lengths of the age classes, this figure still is very hi

Habitat:

Cheetahs are not well-adapted for living and hunting in short grasslands. However, most of the Serengeti Plains are suitable for cheetahs because of the cover of medium-height grasses (Themeda triandra and Pennisetum mezianum) and herbs (Indigofera basiflora and Hypoestes sp.). Also important for cover are drainages, erosion terraces and kopjes. Cheetahs seldom stray far from these features because of the need for cover while hunting and eating, for protection from other predators, and for shade during the heat of the afternoon.

The Seronera area and much of the western corridor, wherever there is a mosaic of woodland and grassland, can be considered prime cheetah habitat. The plains are marginal habitat, except during the rainy reason. Most of Oldupai Gorge is good cheetah habitat throughout the year because of some resident prey, but the availability of water may be a limiting factor.

Cheetahs in the Seronera area drink water once every four days, usually. If they encounter water more frequently, they generally ignore it. However, by the fourth day cheetahs travel 5 to 10 kilometers, if necessary, to drink. In the Kalahari desert cheetahs are reported able to go 10 days or more without drinking, but sometimes they eat melons, presumably for their water (Wrogemann 1975:65).

Hunting:

Cheetah hunting is being studied for the purpose of evaluating success rate in various ecological conditions. One parameter being considered is the availability of different prey species and their abundance. After trying several approaches, we decided to follow George Schaller's and Brian Bertram's method of a density rating of 0 through 4 for each species. Notes are also made of the habitat type in which each cheetah is found, the habitat in which it hunts, its use of cover and competition with other predators and scavengers.

Descriptions were recorded for 209 hunts, in which 106 prey were caught. Only 129 hunts were observed in their entirety, but from these details a pattern of cheetah hunting technique has emerged. Basically, every cheetah hunt consists of one or more of the following five components: Unconcealed approach, stalking, rushing, chasing and capture. Their frequencies of occurrence are shown in Table 4. For a different approach to describing cheetah hunting, see McLaughlin (1970).

The unconcealed approach occurs roughly a third of the time. It consists of simply walking closer to the prey to minimize hunting time and effort. Either stalking or rushing follow next, but seldom both.

Stalking is the concealed approach to a prey individual, and it depends upon the cover of vegetation, ditches, erosion, rocks, or sometimes just the unalertness of the prey. Wind direction is ignored. The stalking cheetah uses any combination of the following: walking semi-crouched with head lowered to shoulder height, trotting, freezing, flopping to the ground, lying crouched, or sitting. Stalking must enable the cheetah to approach within 10 to 50 meters of the prey, if the chase is to be successful. Many stalks end in failure (Table 5).

One report (Kruuk and Turner 1967) concluded that cheetahs do not stalk their prey. This conclusion is in disagreement with all subsequent reports, and is probably a consequence of the casual nature of their cheetah observations. Also, most of their sightings may have been in short grassland, where cheetahs less often stalk and more often rush their prey.

The selected prey individual is usually alone, or else in a small group, which presumably reduces the chance of the stalking cheetah being seen. The same preference for isolated prey was reported from Nairobi National Park (Eaton 1974:58). Apparently the prey are seldom selected with regard to physical conditions. Stalking is important for enabling the cheetah to reduce the distance to its prey, so that an exhausting long chase will be avoided. Cheetahs store body heat while running (Taylor and Rowntree 1973), and this may be the primary factor limiting the distance that a cheetah can chase its prey (actual chases are rarely more than 300 meters).

Table 4 : Composition and Success of Cheetah Hunts: (Sample of 129 hunts recorded in their entirety)

	Number of hunts	Components of the Hunts					Percent hunting success: (divide No. of captures by No. of hunts)
		Number of unconcealed approaches	Number of stalks	Number of rushes	Number of chases	Number of captures	
Thomsons gazelle	91	36	66	14	35	21	21.9
Hare	12	0	0	0	12	11	91.7
Grants gazelle	12	5	11	1	1	1	8.3
Reedbuck	3	0	1	0	3	1	33.3
Wildebeest	1	1	0	1	0	0	0
Kongoni	1	1	0	1	0	0	0
Topi	1	0	1	0	0	0	0
Dikdik	1	0	1	0	1	0	0
Warthog	1	0	0	0	1	0	0
Banded mongoose	1	0	1	0	1	0	0
Helmeted guinea fowl	2	0	2	1	1	0	0
Crowned crane	1	0	1	0	0	0	0
Black-bellied bustard	1	0	1	0	0	0	0
Kori bustard	1	0	0	0	1	0	0

Table 5 : Reasons Why Cheetahs Failed in Stalking Prey: (Sample of 129 hunts recorded in their entirety, during which there were 85 stalks).

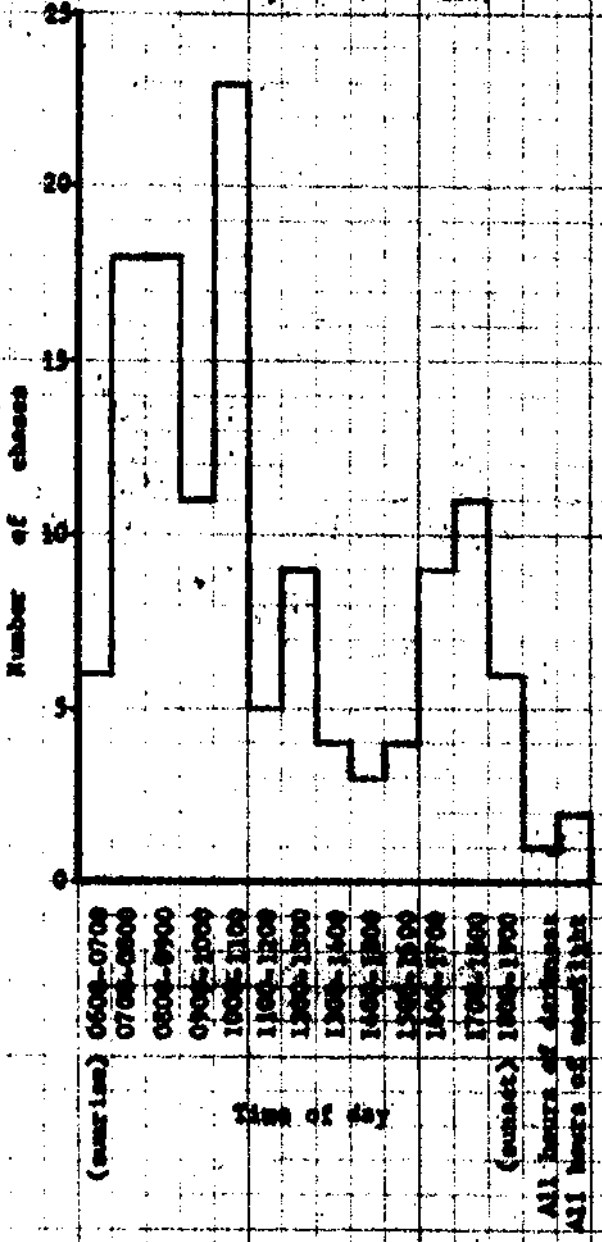
Reason the Stalk Failed	Number of stalks failed
Prey saw the stalking cheetah and fled	14
Prey saw the stalking cheetah, so the cheetah terminated stalk	14
Prey wandered further away, unaware of the cheetah, so the cheetah terminated stalk	5
Cheetah cubs alerted the prey, so the cheetah terminated its stalk	5
Inadequate cover, so the cheetah terminated stalk before being seen by the prey	3
Tourist vehicles alerted prey to the presence of the stalking cheetah	2
Hyena alerted prey to the presence of the stalking cheetah	1
The stalking cheetah switched to a different prey	1
Became dark, so the cheetah terminated stalk	1
Total Number of Failed Stalks	46

Rushing is the least-often used component of the hunt. It is unconcealed trotting, walking, or slow running toward an alert prey group. The cheetah resorts to this technique when the prey are in a large herd and alert to the cheetah's presence. The function of the rush is to enable the cheetah to reduce the distance to the prey while simultaneously causing the prey to move. In this way prey individuals who are less alert, unfit, or very young are exposed.

Less than half of the cheetah hunts that are begun, progress to the chasing stage. Most hunts stop when the prey flees, or when the cheetah terminates the stalk or rush. Cheetahs are diurnal hunters with decreased hunting activity during the heat of early afternoon (Fig. 3). Rarely, brief chases occur in moonlight and even darkness.

The capture occurs when the pursuing cheetah bowls over the fleeing prey with a swat of its forepaw. The prey is then grasped by the underside of the throat until it suffocates. If cover is available within 20 or 30 meters, the cheetah usually carries the carcass to it. Trees, bushes, and even clumps of tall grass provide adequate cover, both for shade and secrecy.

Figure 3. Time of day of chestnut chases.
(Sample size = 130)



A cheetah requires about one hour to consume fully an adult Thomson's gazelle, and during that time there is danger of losing the meal to other predators and scavengers (Table 6). Of the 106 prey killed, 10 (9.4 percent) were lost. Four of these were appropriated by spotted hyenas before the cheetah began eating. One prey was abandoned uneaten by a group of shy cheetahs, because of the combined reasons of a large number of aggressive vultures surrounding the kill and the presence of a vehicle 300 meters away. The other 5 carcasses were stolen after the cheetahs had eaten the major portion of the meat--one was lost to a hyena, three to lions and one to people who approached too closely.

Table 6 : Number of kills on which Scavengers arrived while the Cheetah was still eating: (Sample of 58 successful hunts with complete scavenger data)

	Number of Kills on Which Scavengers were present		
	Thomson's gazelle (41 kills)	Hares (9 kills)	Other ungulates (8 kills)
Vultures	22	1	5
Eagles	5	1	0
Marabou storks	1	0	1
Black-backed jackals	11	1	2
Golden jackals	5	1	0
Spotted hyenas	9	0	1
Lions	3	0	0
Total number of kills in which scavengers were present	27	2	6
Percent of kills in which scavengers were present	66	22	75

Prey Selection:

Prey selection, as represented by the animals killed by the cheetahs, shows that Thomson's gazelles are by far the most important species for cheetahs in the study areas (Table 7). During the present study, 62 percent of the kills were Thomson's gazelles, whereas Schaller (1972:314) reported 91 percent. Seventy percent of the Thomson's gazelles killed by cheetahs were adults, and twice as many adult males were killed as were adult females. This contrasts to Walther (1969), who reported that adult female Thomson's gazelles, and subadults of both sexes, were the most frequent prey. Age criteria for Grant's and Thomson's gazelles are based on Walther (1972 and no date).

Table 7 : Prey Killed by Cheetahs on the Serengeti Plains and Woodland edge:

	Number of Prey Killed	Percent
Thomson's gazelle	66	62
Hares	13	12
Wildebeest	9	8
Grants gazelle	6	6
Impala	6	6
Reedbuck	2	2
Topi	1	1
Kongoni	1	1
Waterbuck	1	1
Dikdik	1	1
Total	106	100

Hares were the second most frequently killed prey. Although the hares are small in size, they are an extremely important food resource because they serve as a buffer food supply in times when the migratory ungulates are absent from an area. Incidental to our cheetah fieldwork, we are censusing hares on the plains.

Other prey killed were wildebeest, Grant's gazelles and impala, which were fairly well represented in all sex and age classes. Topi, Kongoni and waterbuck were selected only as half-grown or younger.

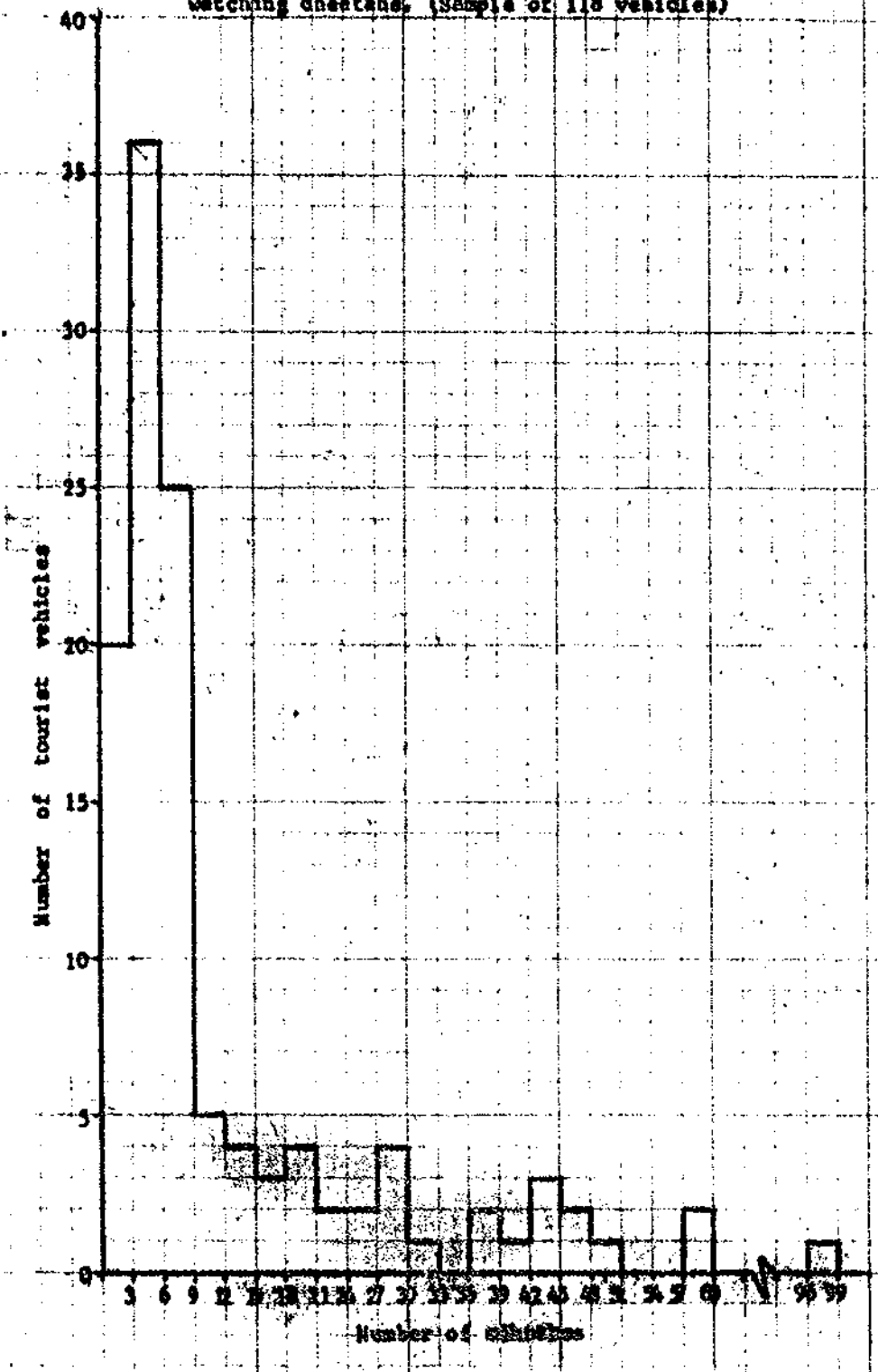
The importance of various prey species certainly must vary with the locality. In the Serengeti woodlands, impala undoubtedly are a more important prey species than is indicated by the data in Table 7.

Cheetahs almost always ate all of the animal they killed. The only portions which they consistently left in a sample of 106 kills, were the skeleton, the skull (except for very young prey), some skin, and usually the rumen and intestines. One exception was a young adult female cheetah who ate only the hindquarters of an adult male Thomson's gazelle, and then left the remains in order to go to the river to drink. It appears that most reports of cheetahs eating only the hind leg of a prey, and then abandoning it, are really examples of cheetahs being frightened away by the presence of scavengers and/or the human observers.

Tourism and Management:

About 69 percent of the tourist vehicles sampled spent less than nine minutes watching cheetahs (Fig.4). This differs slightly from Amboseli National Park, where only 52 percent of the visitors

Figure 4. Number of minutes each vehicle of tourists spent watching cheetahs. (Sample of 118 vehicles)



stayed less than nine minutes (Henry 1976). Tourist vehicles closely approaching cheetahs sometimes interfere with hunting. Taking the Serengeti Plains as a whole, tourist vehicles disrupted few cheetah hunts (Table 5), although this slight interference was greater than that caused by spotted hyenas. Around the Seronera area, however, where the vehicle density is high, tourists probably have a much greater influence on the hunting success of some cheetahs. Quantitative data on this aspect will be presented in a future report. Possible interference with cheetah hunting is aggravated by the fact that most of the tourist drives are in the mid-morning and late afternoon, the hours when most cheetah hunting occurs (Fig.3). The network of roads around Seronera is extensive, so restricting vehicles to the roads is a good management policy.

Data are being recorded separately to see if there is a differential tourist interest in cheetahs shown by package-tours in minibuses, by tourists who rent their own vehicle, by luxury safaris, and by East African residents. Also, the time spent observing cheetahs is being recorded with regard to whether or not the vehicle has a parks guide and to whether or not it is driving off the road.

Under the present ecological conditions the Serengeti cheetah population appears to be doing well. Considering movements, spacing and available habitat, the Serengeti population is estimated at 500 cheetahs. The best insurance for conserving cheetahs in the Serengeti ecosystem is to maintain diversity in the environment. The mosaic of woodlands, bushlands, and grasslands, and the availability of waterholes, help to ensure a fairly even distribution of cheetah prey throughout the year. On parts of the plains where all ungulates are locally absent for brief periods, hares are especially important as prey. Hares seem to be absent above ground in the daytime, in areas of sparse vegetative cover. But wherever there are herbs or clumps of taller grass, hares are available for the diurnal-hunting cheetahs.

Some cheetahs are now resident throughout the dry season in the drainages of the Serengeti Plains. A few years ago when the dry seasons were drier and there were fewer gazelles on the plains during the dry season, much of the plains may have been without resident cheetahs. If prey populations decline in the future, or if the dry seasons become harsher, there probably will be some cheetah mortality from starvation and from increased predation by other predators.

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14. Wild Dog Ecology and Behaviour - Lory Herbison Frame

Abstract:

A four-year study of the population dynamics and ecology of African wild dogs (Lycaon pictus Temminck) was undertaken to determine the status of this predator in the Serengeti National Park, Tanzania. Study of hunting methods, prey selection and ecological requirements indicate that the Serengeti plains are not ideal habitat for wild dogs. Therefore, high densities of wild dogs should not be expected to occur there. The long-range population regulating factor, at least on the Serengeti Plains, is probably food supply. In areas of higher annual rainfall larger packs have been recorded, and it is possible that overall dog density there is greater than on the plains. A decline in numbers of adults living on the plains has occurred since 1975, but it is not yet known if this is a normal fluctuation in the population. Competition with spotted hyenas, and the occurrence of disease, may have serious immediate effects on the wild dog population, but data are not conclusive. A program of artificial immunization of wild dogs against distemper is not considered feasible, and may actually be dangerous to the population. However, a cautious conservation measure would be to eliminate all domestic dogs and domestic cats from the Serengeti National Park. Within the Ngorongoro Conservation Area all domestic cats should be eliminated, and the number of domestic dogs severely restricted.