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HUNTING BEHAVIOR OF THE CHEETAH[1,2]

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Abstract: The predator-prey aspects of four cheetah (*Acinonyx jubatus*) groups were studied in Nairobi National Park, Kenya, from October, 1966, through February, 1967. Hunt:kill ratios were applied to direct observation data of 157 hunts and 30 kills. Hunting success apparently varied with habitat-type, prey species, sex and age-classes of prey, herd size, cheetah group size, and the cheetah's or group's hunting experience. Cheetah kills appeared to be other than a random sample of prey populations. There was differential selection in prey of females and juveniles.

Recent studies have contributed to our knowledge of the predator-prey ecology and behavior of the larger Felidae (Bourliere 1963; Eaton 1969 *a*, *b*, *c*, in press *a*, *b*; Foster and Kearney 1967; Graham 1966; Kruuk and Turner 1967; Pienaar, in press; Schaller 1967, 1968, 1969; Wright 1960).

To describe the "input" into a predator's energy budget, it is not sufficient to give the percentage of occurrence of each prey species in the predator's diet. Wright (1960, and personal communication), for example, lost much valuable information because he located carcasses usually long after the animal had been killed and largely consumed by predators and scavengers. Foster and Kearney (1967:118) pointed out a similar limitation: "The smaller species are probably always under-represented due to the rapidity with which they are eaten." Young prey with soft, edible bones are either more quickly or completely eaten, and both cases lead to biases in data which are gathered by examination of prey remains.

This paper reports the predator-prey behavioral interactions of cheetah and their prey. It is an attempt to determine the factors related to successful predation by cheetah and to examine regional differences and similarities in food habits, prey selection, and hunting techniques.

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[2] A condensed version of this paper was presented December 11, 1968, at the 30th Annual Midwest Fish and Wildlife Conference, Columbus, Ohio.

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B. Wright, Northeastern Wildlife Station, New Brunswick, and U. de V. Pienaar, Kruger National Park, South Africa, supplied unpublished information from their field studies. F. Walther, Department of Zoology, University of Missouri, was quite helpful in allowing me to examine his unpublished manuscripts on gazelle behavior. Mary Ross gave advice on statistical analysis of the data.

METHODS

Initially, photography was an important aid in determining the identity of individual cheetah. The spots on the left side of the face were used as a means of identifying each cheetah. Within a short time, however, cheetah became recognizable upon sight. A portable tape recorder was used for verbal descriptions whenever behavior sequences followed each other too rapidly for written descriptions.

Duplicate maps were used in the field to record daily movements and locations of various activities. A surveyor's field tape was used in measuring distances and for checking estimates for accuracy.

Interviews with Nairobi National Park (NNP) personnel, wildlife photographers, and park visitors, as well as access to the Park's recordings of cheetah sightings and kills, contributed important data. Field work began October 15, 1966, and continued through February, 1967.

Table 1. The cheetah groups in Nairobi National Park (NNP) and their hunt:kill ratios.

Group	Adult		Juvenile			Total	Hunt:kill Ratio[b]
	Male	Female	Male	Female	?		
1		1	2	1	1	5[a]	115:17
2	3	2				5	24:7
3	2					2	6:3
4	2	1				3	12:3
Total	7	4	2	1	1	15	157:30

[a] Two cubs lost on December 15, presumably by lion predation.
[b] Chi-square = 3.47, $P = 0.94$.

Study Area

Data were collected in study areas of widely divergent habitat types: (1) rolling *Themeda triandra* grassland—*Acacia* savanna in NNP; and (2) flat, drier *Acacia*-savanna in Masai Amboseli Game Reserve, both in Kenya. Most of the data presented here came from NNP. The park is an area of about 44 square miles, closed in on three sides by tall fence and open on the south to the Athi-Kapiti Plains. It has a year-round supply of water from artificial dams. A dense forest lies in the extreme western border, and the park is sectioned north to south by strips of riverine bush along water runoff areas. Most of the park is short grass plains interspersed predominantly with short (4–7 ft) *Acacia drepanalobrium*.

RESULTS

The Hunting Units

Fifteen cheetahs comprising four groups in NNP offered a variety of sex and age compositions for comparison of hunting success (Table 1). Because of the cohesive-

Table 2. Index of preference of cheetah prey species in NNP.[a]

Species	Relative Frequency of Abundance	Relative Frequency of Diet[b]	Diet/Abundance = Index of Preference
Kongoni	0.26	0.10	0.38
Impala	0.16	0.433	2.7
Grant's Gazelle	0.13	0.166	1.2
Thomson's Gazelle	0.092	0.033	0.35
Waterbuck	0.024	0.133	5.5
Wildebeeste	0.067	0.00	—
Reedbuck[c]	0.0018	0.033	18.0
Warthog	0.041	0.10	2.4
Zebra	0.126	0.00	—
Ostrich	0.025	0.00	—

[a] Relative frequency of abundance computed from Foster and Kearney (1967).
[b] Uses only Eaton's data (Table 3).
[c] Specie not listed in Foster and Kearney but NNP censuses in October and November, 1966, average = 7.

ness of adult or family groups (Eaton in press *a*), each group was considered functionally as a separate, distinct, hunting unit.

Analysis of Hunting Techniques

A hunt can arbitrarily be divided into a stalk and an attack. This division is artificial in that a hunt may consist of a stalk or an attack but not both. For instance, if prey stumbled onto resting or hiding cheetah, an overt attack occurred without a prior stalk. Also, cheetahs, in spite of a careful stalk, were often discovered by the intended prey and an attack was not made. In this discussion, a hunt is either a stalk, an attack, or both; a kill is a successful hunt. Factors possibly related to hunting success are many, and a hunt:kill ratio is applied to each in an attempt to evaluate its importance. The differences in hunt:kill ratios are not significant nor are they correlated with group size.

Food Habits and Prey Selection

The kill weights of Groups 1, 2, and 4 were similar, with nearly identical ranges, and mean weights which were not very different. Group 3 killed significantly larger prey, with kill weights up to 600 lbs. The weights of eight impalas (*Aepyceros melampus*) killed by the lone hunter of group 1 ranged from 40–120 lbs and averaged 70 lbs.

In NNP, impala, Grant's gazelle (*Gazella granti*), kongoni (*Alcelaphus buselaphus*), and waterbuck (*Kobus ellipsiprymnus*) occurred most frequently in the cheetah's diet.

A preference quotient, relative frequency in diet/relative frequency of abundance, showed a value of 1.0 or higher for impala, Grant's gazelle, and waterbuck but less than 1.0 for kongoni (Table 2). Reedbuck (*Redunca redunca*) showed the high value of 18 due to a single kill of that prey species.

Ten observers (Verbal communications) in NNP reported a total of 23 kills during the study (Table 3). These data and mine cannot be lumped when the following is seen:

	Adults	*Juveniles*
Eaton	12	18
Others	13	1.

Of 16 species in the park known to be cheetah prey in East Africa (Graham and Parker 1965), ten were hunted and seven were killed. Park records, visitors' observations, and photographs add three species to the prey list, including zebra (*Equus burchelli*) and wildebeeste (*Connachaetes gnou*). Steinbuck (*Raphicerus campestris*) were not recorded as kills, but were hunted.

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

Table 3. Compiled kill data from ten observers (Verbal communications) in NNP during the period of the study. Eaton's observations are in parentheses.

	ADULT			JUVENILE				
	Male	Female	?	Male	Female	?	?	TOTAL
Impala	1(1)	2(7)	–	–(2)	–(3)	–	3	6(13)
Grant's Gazelle	2	1(2)	–	–(2)	–	–(1)	1	4(5)
Thomson's Gazelle	3	–(1)	–	–	–	–	1	4(1)
Kongoni	–	–	–	–(2)	–	–(1)	2	2(3)
Waterbuck	–	–	–	–(2)	–(1)	–(1)	1	1(4)
Others	–(1)	2	2	–	–	1(3)	1	6(4)
Totals	6(2)	5(10)	2	–(8)	–(4)	1(6)	9	23(30)

The adult female's eight impala kills included four adults; the only male was weak and apparently quite old. Other observers recorded adult females and juveniles for six of seven additional kills.

Group 2 hunted five and killed two prey species. They were especially effective with waterbuck; the preference quotient shows waterbuck highly vulnerable to this group. All the waterbucks killed were subadults and the impalas were adult females.

Group 3 hunted four species, killing kongoni and warthog (*Phacochoerus acthiopicus*). The group originally consisted of four males, thought to be siblings, and are known (NNP records and verbal communications) to have killed adult zebra, wildebeeste, waterbuck, ostrich (*Struthio camelus*), and Grant's gazelle. The NNP records and two of my observations showed kongoni as most important in this group's diet. All their kills in park records are listed as adults, sex unknown. The warthog was newly born and was killed by one of the cheetah while hunting alone. Both kongoni kills, from which I collected skulls, and additional kills aged by M. Gosling (Verbal communication) were sub-adult males about 14 months old.

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

Size of Prey Herds

There are no data available for frequency of herd size of the species in NNP, only monthly censuses (Foster and Kearney 1967).

When hunted herds are arbitrarily divided into sizes (Table 4) for comparison, 136 of 157 hunts were of herds numbering 30 or less. One to five was the most commonly hunted herd size: groups number-

Table 4. Group hunt:kill ratios related to prey herd sizes.

	CHEETAH GROUP				
HERD SIZE	1(*N*)*	2(*N*)	3(*N*)	4(*N*)	TOTAL
1–5	7:1(28)	4:1(16)	4:1(4)	2.5:1(5)	4.8:1(53)
6–10	5.1:1(26)	2:1(4)	—	2:0(2)	4.6:1(32)
11–20	8.7:1(26)	2:1(2)	—	3:1(3)	6.1:1(31)
21–30	5:1(15)	2:0(2)	1:1(1)	2:0(2)	5:1(20)
30+	9:1(18)	—	1:1(1)	—	6.3:1(19)
Total hunt:kill	115:17	24:7	6:3	12:3	5.2:1(157)

* Number of hunts observed in parentheses.

Table 5. Hunt:kill ratios for groups 1 and 2 in the habitat types of NNP.

Group	*Acacia*-Grassland Savanna (*N*)[a]	Open Grassland Plains (*N*)	Heavy Bush (*N*)	Marsh (*N*)	Total
1	7.7:1(70)	7.7:1(23)	3:1(12)	10:1(10)	115:17
2	—	3.4:1(24)	—	—	24:7
Totals	7.7:1(70)	4.7:1(47)	3:1(12)	10:1(10)	139:24

[a] Number of hunts observed in parentheses.

ing 1–5, 6–10, 11–20, 21–30 had an average hunt:kill ratio (5.1:1) about equal to the ratio for all herd sizes (5.2:1). The single hunting female of Group 1 hunted herds of 1–30 individuals 70 percent of the time. She hunted Grant's gazelle, Thomson's gazelle, impala, and kongoni 60 percent of the time. These species frequently appeared in herds of 1–30 animals.

Seventy-five percent of Group 2's hunts and 57 percent of its kills were of herds numbering 1–5. Waterbuck, this group's principal prey, were seen most frequently in small bands.

Group 3 hunted 1–5 animals four times; its kongoni kills were from herds of 21–30 and 41–50. Several kongoni kills (M. Gosling, personal communication) were from hunts of large herds.

Cover Type

On the study unit *Acacia*-grassland savanna was about equal in total area to open grassland plains. All cheetah groups' home ranges overlapped (Eaton in press *a*).

For all four cover-types (Table 5) there were, for all cheetah groups, 83 hunts and 13 kills in *Acacia*-grassland savanna, 52 hunts and 12 kills in open grassland, 12 hunts and 4 kills in heavy bush, and 10 hunts with one kill in marshy habitat.

Group 1 hunted mostly in *Acacia*-grassland savanna, where it made nine of its 17 kills. This group was the only one to hunt in either heavy bush or marsh. Hunts were particularly successful just inside heavy bush areas adjacent to savanna or plains. These kills were impala, which frequented the woody, more dense areas more than other important prey. An observation by R. Casebeer (Verbal communication) and my observation of the adult female of Group 1 killing a reedbuck constituted the only two kills of the rarest, in occurrence, cheetah prey species in the park. The preference quotient for reedbuck was 18 for all cheetahs' kills but even higher for Group 1.

Both reedbuck kills and seven more hunts occurred around the edges of the same small marsh. Marshes constitute less than 1 percent of the park's total area. No other cheetahs were observed hunting in marshes.

Group 2, with five adults, often moved into savanna but did its hunting in the open plains along the Athi River bush area where its principal prey, waterbuck, were concentrated.

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

Group 4, with three adults, hunted in the same habitat as Group 3, but did not hunt or kill the four largest species as did Group 3. Impala and Grant's gazelle were the largest species Group 4 hunted.

Prey Responses

The criteria for awareness of prey were any or all of the following: visual orientation in the direction of the cheetah(s); "snorts" or alarm calls; flight; or mobbing responses. For all observed kills, if hunting success is related to prey responses before being attacked, the hunt:kill ratio = 14.0:1.0 (when prey are aware), as opposed to 2.0:1.0 for unaware prey (Table 6).

The success of the Group 1 cheetah depended almost entirely on the unawareness of prey prior to attack. The female of Group 1 typically stalked extensively, sometimes for several hours, but traversing only a few yards. Where open spaces separated the cheetah from a herd, the cheetah often hid in cover. If the herd grazed closer, the cheetah waited until it was close enough to attack. In cases where the prey saw the cheetah, snorting alerted all prey species in the vicinity, which often led to "mobbing" of the cheetah. Prey animals searched out and followed the cheetah as it moved off, snorting and alerting other potential prey along the way. This procedure continued until the cheetah had moved completely out of range of any prey.

Group 2 showed a higher hunting success when prey were unaware but was more successful with aware prey than was Group 1. Hunting in open plains, by necessity, made stalking less important than overt attacks. This group hunted in the same way as described for cheetahs in the open plains of the Serengeti (Kruuk and Turner 1967) where prey are usually aware of a cheetah prior to its attack.

Hunts by Groups 3 and 4 were less frequently observed; however, the two males of Group 3 depended on kongoni being aware. It was the anti-predator attack by yearling male kongoni that made them vulnerable.

Using only those hunts including an attack, hunting success is related to the prey's response during the attack. The prey's responses are divided into five classes: (1) prey (two or more) ran together at the same time; (2) not together; (3) not at the same time; (4) not together and not at the same time; and (5) anti-predator attack by the prey.

Table 6. Hunt:kill ratios related to prey response before Groups 1 and 2 attacked.

GROUP	AWARE (*N*)[a]	UNAWARE (*N*)
1	85:1(85)	1.87:1(30)
2	4.2:1(17)	2.3:1(7)
Totals	17.0:1(102)	1.94:1(37)

[a] Number of hunts observed in parentheses.

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

Group 2 had no success when the prey responded to attack by running as a herd at the same time. Kills were only made when one or more of a herd ran before the rest of the herd, or when the herd separated. Anti-predator attacks by kongoni deterred this group's attacks.

The only kill by Group 3 other than kongoni was a newly-born warthog. In this case, one of the two males was 30 yards from an adult warthog and two young before the warthogs were alerted. The two young ran one way, the adult ran another. The cheetah pursued the young and, in the meantime, the adult turned around and pursued the cheetah. When one young warthog was caught, the adult circled twice around the cheetah within 5 ft before running off after its surviving young.

Group 4 had more success when the herd escape response was not a cohesive one.

For example, a warthog with young was aware of the cheetahs before they were close; it turned to face the cheetahs with her young standing directly under her stomach. Individuals of the cheetah group surrounded the warthogs, charging in turn at them, but were not successful in separating adult from young.

Cheetah-Prey Distances

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

Group 1 killed when it averaged 56 yards from the prey when it attacked, and it ran 20 yards before the prey ran. In unsuccessful hunts the female also (although not always) attacked before the prey fled.

Group 2, on the average, did not attack until the prey had already run. In many cases the cheetahs simply walked towards a herd until an animal ran; then they pursued it. These five cheetahs were, on the average, 81 yards from the prey when their pursuit ended in a kill.

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

There were very small distances between the males of Group 3 and the prey when they attacked. In two of the three kills, these males simply loped toward kongoni and when, at about 60 yards, a kongoni attacked and came about 25 yards closer, the two cheetahs attacked and killed it.

Group 4 usually attacked the prey just before it ran. For the successful hunts the group averaged a distance of 58 yards between it and the prey when attacked.

DISCUSSION

The importance of continuous field observations in arriving at an accurate assessment of predatory behavior and ecology is obvious. The accumulation of kill data by chance observations, for example, from park personnel or visitors, cannot be considered random. NNP's visitors' records indicate an entirely different species, age and sex composition of cheetah prey than mine (Table 3). By following individual cheetahs, families, or adult groups, it is possible to establish the similarities and differences between hunting units in an area, and from these data to make regional comparisons.

U. de V. Pienaar's (in press) data on cheetah predation in Kruger Park are based on carcass location and not direct observation; he speculates that many smaller species of birds and mammals and the young of smaller antelope species probably are quite important as prey. In NNP no hunts or kills of birds other than ostrich have been observed or recorded. The point is that in any one area, behavioral data should supplement carcass data as a means of properly assessing a predator's ecological role in the community.

Food Habits

A total of 25 species has been recorded as cheetah kills in East Africa (Graham and Parker 1965:15). U. de V. Pienaar (in press) listed 24 species for Kruger National Park.

This variety of prey ranges from hares (*Lepus capensis*) and newly born warthogs to adult wildebeestes and zebra—a weight range of less than 5–600 lbs (weights after Bourliere 1963). Impala, Grant's gazelle, and Thomson's gazelle, which as adults average 120–160, 130–155, and 40–50 lbs, respectively, comprise about two-thirds of all recorded kills in East Africa (Graham and Parker 1965:13).

Hunting Behavior

The hunting technique in the Serengeti, as compared with NNP, is probably more often open pursuit. Cheetahs hunting in habitats that offer cover, such as most of NNP, stalk the prey; but in open short-grass plains, for example, in part of NNP and much of the Serengeti area, open pursuit is employed. In the open, flat plains of the Masai Amboseli Game Reserve, where ground cover is scarce, a cheetah with cubs stalked by crawling on the ground before attacking. Since cheetah cubs stalk in the Serengeti but adults seldom do, then stalking, as a portion of the innate predatory sequence, must "drop-out" with hunting experience (Leyhausen 1965, Eaton, in press *b*).

In areas conducive to only open-pursuit hunting, where prey are also usually aware of the predator, it is to be expected that the cheetah's role is more that of a natural culler of less fit individuals from prey populations. In such areas, cheetahs appear to prey more selectively by making a greater number of hunts/unit time and kill, and thereby sample prey herds more effectively.

Prey Selection: Sex and Age-Classes

Graham and Parker (1965:14) conclude that, "There is no tendency to select juvenile animals, as 79 percent of all kills are of adult animals." Their data showed a 2:1 sex ratio of adult males to adult females; however, 92 of 130 adult kills were not sexed. Estes (1967:201–202) stated that cheetah selected adult gazelles when hunting. Wright (1960:8) showed that of those kills aged and sexed, all were males and five of seven were adults. Kruuk and Turner's (1967:14–15) data gave adult Thomson's gazelle as the most important diet item—52 percent. Of seven Thomson's gazelles sexed, six were females. F. Walther (Personal communication) observed cheetah kill Thomson's gazelles in the Serengeti. His observations showed a remarkable non-random selection of females from predominantly all male adult herds and sub-adult males from bachelor herds.

Pienaar (in press) showed for Kruger Park a non-random selection of juveniles, and, among adults, a 2:1 ratio of females to males. Schaller (1968:96) stated that a cheetah pursued small fawns whenever they were available, and had complete hunting success with that age group.

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

Flight distances are shortest for territorial males, and Walther (in press) noted that they were preyed upon proportionately less than bachelor herd males or females. Thomson's gazelles in the Serengeti defend territories for the most part in flat, open plains

that offer good vision, while bachelor males are found where open plains and bush meet, the area where predators most easily make kills. Predation of Thomson's gazelles in areas of homogeneous habitats would probably show that flight distances of territorial males are closer to that of bachelor males and females and that kills are more evenly distributed between these classes.

In the group of two cheetah males, learning, probably quite by accident, determined selection of kongoni as their principal prey, as indicated by NNP records, M. Gosling (Verbal communication), and my observations of two kills. The group of five preyed heavily on waterbuck which were abundant only in the locality in which the four cubs were reared. The killing of waterbuck by the mother may have been a necessity, but the selection of waterbuck by the grown cubs became traditional, undoubtedly the result of learning and possibly a kind of imprinting.

Specialization on different prey by cheetah in the same area certainly occurred, and regional differences, though often reflecting prey abundance, may be partially the result of specialization. Since groups or individuals may specialize on different prey in the same local area, it is especially important that field studies of predators include close observation of several individuals and/or groups.

The impala was the most abundant prey species in Kruger Park but ranked only fifth in preference; two species—reedbuck and waterbuck—found also in NNP, were preferred by cheetahs in both areas.

In Kruger Park (Pienaar, in press), reedbuck had the highest preference of all cheetah prey. In fact, the cheetah was the most important predator of reedbuck there, responsible for 21.76 percent of all predator mortality. It is peculiar, however, in Kafue National Park, Zambia, where reedbuck were more abundant than in Kruger they were not an important cheetah prey (Mitchell et al. 1965).

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

Newly born warthogs were common prey for cheetahs, but adult warthogs were avoided altogether. The same selection is reported for Kruger Park (Pienaar, in press). That cheetah of different groups showed this common avoidance implied an ability to recognize particular qualities of particular species. It is conceivable that cubs learned to hunt only what their mother hunted and that once learned, only particular prey stimuli released the predatory sequence of behavior. How discrimination between young and adult warthogs is made is not known, unless it is by trial and error, in which case a cub would probably be injured or killed. Lions are killed by adult warthogs (Watt 1968:135) and tigers (*Panthera tigris*) by adult wild boar (*Sus scrofa*) (Schaller 1967:290).

Several studies (Estes 1967, Wright 1960, Kruuk and Turner 1967) disagreed on which classes of prey are differentially selected by cheetah. Walther's (In press and verbal communications) data and Schaller's (1968:97) continuous observations of one cheetah's hunts showed a selection of females over males in adult herds, and of juveniles over adults. Recognition and selection of juveniles from adults could be based on size; however, female adults in typical cheetah prey species are barely smaller than males. In impala, recognition could be by presence or absence of horns, but both sexes of the gazelle species are

horned. This explanation is confounded by flight distances of prey. Females with greater flight distances may, by running first from a herd, cause the cheetah to fix on them visually, and release the cheetah's attack.

Driver and Humphries (1967:1768) demonstrated experimentally that in order for a predator to respond effectively to fleeing prey, response time must be cut down by fixating on one of many prey stimuli. In the Serengeti, differential flight distance may lead to differential predation, but in Nairobi Park, cheetah often attacked *before* prey took flight and differential selection of prey was less apparent. Kruuk and Turner (1967:13) observed a cheetah that was not able to kill an adult Grant's gazelle. Such experiences could enable cheetah to learn to discriminate males from females; if so, one-trial learning would be adaptive since such encounters could be injurious.

In the case of Group 3's predation on sub-adult male kongoni, the apparent selection of male prey was only the result of the kongoni's anti-predator behavior.

Prey Preference and Vulnerability

I have applied the preference quotient to cheetah-kill data from the Serengeti, using 1 million as the approximate Serengeti ungulate population from various estimates (based on Talbot and Talbot 1963: 19; Kruuk and Turner 1967:3; Schaller 1968:96). Kruuk and Turner's 23 recorded cheetah kills showed that the most important prey, Thomson's gazelle, were not killed any more than they occurred. Kruuk and Turner's data showed that kongoni were the most vulnerable prey, while wildebeeste (juveniles), second most important prey in diet, were taken less than they occurred in abundance.

Schaller (1968:95–96) showed differences in species selection by cheetahs in the Serengeti. His carcass data on 136 kills (only 40 hunts were observed) showed Thomson's gazelles occurred as prey 88 percent of the time, far greater than their abundance. Schaller pointed out that actual availability of Thomson's gazelle is greater in the cheetah's preferred hunting habitat, since during the dry season they were highly concentrated in the plains and practically the only prey species available.

In Kruger Park, impala made up 47 of 65 (73 percent) cheetah kills, while impala comprised 83 percent of the ungulate population there (Bourliere 1963). It appeared that impala were not especially vulnerable or preferred there.

If a prey species occurs in the diet at a higher level than its relative abundance, it could be either more vulnerable or preferred or both. Wright's (1960:11) scale of relative vulnerability of prey is based on occurrence in the diet of several predators. Vulnerability scales should be related to abundance of prey and more specifically to relative availability. The prey's visitation to the predator's area should give an even more accurate picture of prey vulnerability.

The application of the index of preference shows that relative availability or abundance are not the only factors determining prey selection. It is often assumed that, in general, preference for a prey represents the prey's vulnerability; however, biochemical deterrents affecting palatability certainly are possible. That vulnerability may not be a direct measure of preference is shown by Group 1, in which the female hunted several species equally but killed chiefly one. Although this cheetah's kills gave the impression that it specialized on and therefore "preferred" impala, its hunts showed that impala were vulnerable but not necessarily preferred. This hypothesis was not borne out in predation of reedbuck by cheetah in which reedbuck were rare

but highly vulnerable; or by wildebeeste in Nairobi Park that have shown a continued high vulnerability to lions in spite of a vastly decreasing population. Since the reedbuck habitat in Nairobi Park consisted of small isolated marshes, heavy predation pressure is to be expected. The marshes are scarce enough to allow ease of predation but limit reedbuck population growth.

Factors Affecting Hunting Success

It would be helpful to have accurate descriptions of several cheetahs, individuals and groups, in the Serengeti, so that the factors related to regional differences—cover types, prey species, etc.—could be assessed. NNP data imply that hunting was, in large part, a product of a particular cheetah's or group's hunting experience.

The lower hunt:kill ratio for NNP cheetahs as compared to Serengeti cheetah may indicate that the best cheetah habitat is other than strictly open plains; however, kills are made no more frequently in NNP. The open plains of the Serengeti demand an open pursuit hunt which is by its nature less economical in number of hunts but more economical because it is less time-consuming than the stalk-attack hunt common in NNP.

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

Hunting success was higher in prey herds of 30 or less. Larger herds presumably offered a more efficient predator alarm system; however, the threshold for "alert" may be lower in smaller herds which causes each individual to be more alert than if in a larger herd. Although difficult to quantify, the individuals in very small herds appeared to spend more time being alert and watching for predators than did animals in larger herds. The differences in hunting success between herd sizes of 1–10 and larger support this. The "fear" of predators often resulted in the flight of small impala herds without the alarm calls and intense watching associated with the predator alarm system of the larger herds. Although the possibility has not been studied, flight distances may be found to vary as a function of herd size.

Condition may have been an important factor in selection of prey by cheetah but, although not studied specifically, in only one case was prey in poor condition apparent. Schaller (1968:97) noted that only two of the 136 kills he examined were in poor condition.

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

The hunt:kill ratios for prey response during attack indicated that the flight of the prey as a tightly-knit herd reduced predation. The failure of an individual of a herd to respond in the same way as the others increased its chances of being singled out and killed. The abnormal flight responses of a particular animal may indicate a higher vulnerability, and this may explain the release of the cheetah's attack when one or more animals take flight before the rest of the herd.

It appeared that cheetah seldom made kills when they attacked at greater than 200 yards and hunting success increased the shorter the distance was between cheetah and prey. Perhaps the cheetah depends

upon its ability to assess the weakening of prey while chasing it, for in many cases the cheetah would stop pursuit even though it appeared to be closing the gap between it and the prey.

Undoubtedly people in cars affected the hunting behavior of cheetahs and the effects varied with the area and the visitors' interests in a group. The female with four cubs, Group 1, spent much time in a highly visited area of the park and on Sundays or holidays the group's movements were greatly hampered. On other days I was often the only observer, and movements and hunting success did not appear to be greatly affected by my presence.

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