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Abstract: There appears to have been natural selection for anatomical adaptations permitting efficient predation in the cheetah, which have led to corresponding behavioural adaptations away from the typical predatory sequence and killing behaviour of other Felidae. Strangulation as a means of killing prey is a maturation of an innate tendency. Stalking and chasing of prey are relatively fixed behaviour patterns but seizing and killing of the prey develops properly only with experience and is modifiable. The training given to cubs by their mother is critical for the eventual development of the entire predatory sequence from its innate components. Training probably allows the cubs to modify more effectively the predatory and killing behaviour best suited for the prey of the specific area in which they live.

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**The Predatory Sequence, with Emphasis an Killing Behavior  
and its Ontogeny, in the Cheetah (*Acinonyx jubatus* Schreber)**

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## The Predatory Sequence, with Emphasis on Killing Behavior and its Ontogeny, in the Cheetah (*Acinonyx jubatus* Schreber)

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### Introduction

There has been recent work on predatory behavior of the Felidae with emphasis on killing, in the laboratory by LEYHAUSEN (1956 a, b, 1965) and in the field, principally by SCHALLER (1967, 1968, 1969). In a field study of cheetah ecology and behavior in East Africa, I frequently observed predatory behavior in wild cheetah (*Acinonyx jubatus* Schreber). Data from these observations are presented here and comparisons are made with other large Felidae. The ecological factors responsible for the evolution of killing behavior are discussed. An attempt is made to explain why killing techniques in the larger Felidae are different from those in smaller Felidae. The roles of phylogenetically acquired (*innate*) and individually acquired or (*learned*) information in the ontogeny of cheetah killing behavior are discussed.

### Methods and Materials

Cheetah were followed in a vehicle or on foot and observed throughout their daily period of activity, from about half an hour before sunrise to half an hour after sunset. Cheetah were rarely active at night. Binoculars were used frequently. Photography was essential for recording certain behavior patterns and in identifying individual cheetah by the spots and black lines on their faces; however, individuals soon became recognizable on sight. A tape recorder was used for verbal descriptions whenever behavioral sequences occurred rapidly. Killing behavior did not vary with the proximity of the observer, and I feel that my observations represent "normal" behavior. The study was conducted chiefly in Nairobi National Park and Masai Amboseli Game Reserve, both in Kenya, from October 15, 1966, through February, 1967.

### Acknowledgements

I thank Drs. F. WALTHER, P. LEYHAUSEN, and E. KLINGHAMMER for reading and commenting on the manuscript and the University of East Africa for a grant that enabled me to carry out of the research reported here. Figures 1, 3 and 4 were taken by H. Patel of Nairobi, Kenya, who accompanied me in the field.

### The Predatory Sequence in Cheetah

The observations below are from observations of 157 hunts and 30 kills by cheetahs. Hunting, especially stalking, is much more variable; it varies with the habitat-type, prey species, size of hunting group, the cheetah's hunting experience, etc. The more strictly ecological aspects of hunting have been presented elsewhere (EATON, 1970).

The cheetah does not typically exhibit the normal predatory behavior of the other cats; however, most of the cheetah's predatory sequence is essentially homologous to "... watching, crouching, stalking, seizing, and 'angling,'" in LEYHAUSEN's (1965: 489) model.

### Watching, Crouching and Stalking

The cheetah watches prey intently, depending greatly on vision to determine at what time to stalk and attack (Fig. 1). The cheetah watches for cues such as the attentiveness of the potential prey animals (e. g. alert calls) and the direction in which they are looking. From this, it appears to be able to evaluate the general level of awareness of danger in the prey.

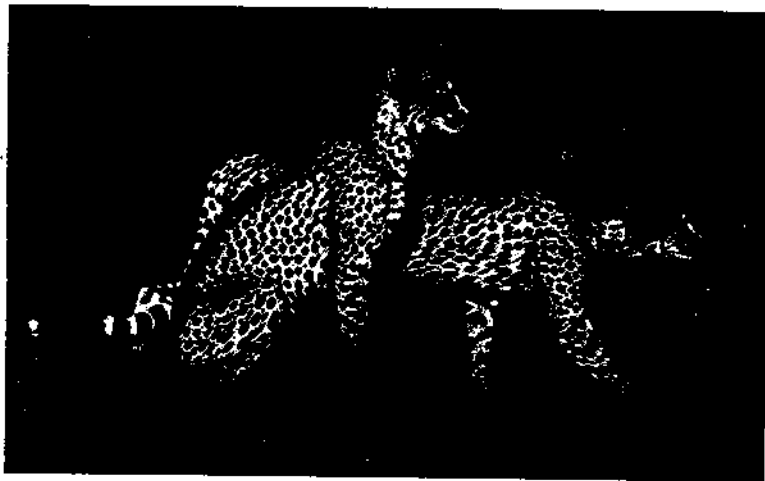


Figure 1. Two cheetahs exhibiting close visual alertness of prey with one of them beginning a stalk

The cheetah does not crouch like most cats. It walks along slowly, looking for game, lifting the head up either to get a better view or to more closely examine game already spotted. While the cheetah is closer to prey, it keeps its body low with its head held higher than the body, rarely taking its eyes away from the game. The prey often notice movement or the silhouette of the cheetah. Before being recognized and responded to as a predator, the cheetah often recognizes that it is being watched, even if by only one animal in a large herd. The ability of the cheetah to recognize the slightest awareness of any of the herd enables it to stop and remain stationary until the prey lose interest. "Staring contests" of 5-7 minutes between cheetah and small herds of prey were common at this stage of a hunt. The very instant that all of the prey appeared not alert, the cheetah, without taking its eyes away from the prey, stalked a little further, again stopping instantly if an animal looked in its direction. The "crouch" aspect of predatory behavior in the cheetah is modified to a state of alertness that requires holding the head up high and remaining sufficiently motionless to

maintain visual contact with the prey. This visually oriented behavior enables the cheetah to approach the prey as close as possible before actually attacking.

### Pouncing, Seizing and Killing

"Pouncing" in most cats is homologous to the behavior in the cheetah, involving chasing and catching the intent prey animal. Most cats attack over very short distances, and often the prey is not aware of the cat until it is very close or already upon the prey. Cheetah seldom kill in this manner, but instead must bring down the prey while both are running very fast. In order to make a kill, the cheetah must first overcome the prey and bring it down.

The cheetah knocks over the fleeing prey, the exact manner varying with the species of prey, its size and how fast it is moving when overcome by the cheetah. For large prey species such as sub-adult kongoni (*Alcelaphus buselaphus cokii* Gunther), the cheetah runs until it is along the flank of the

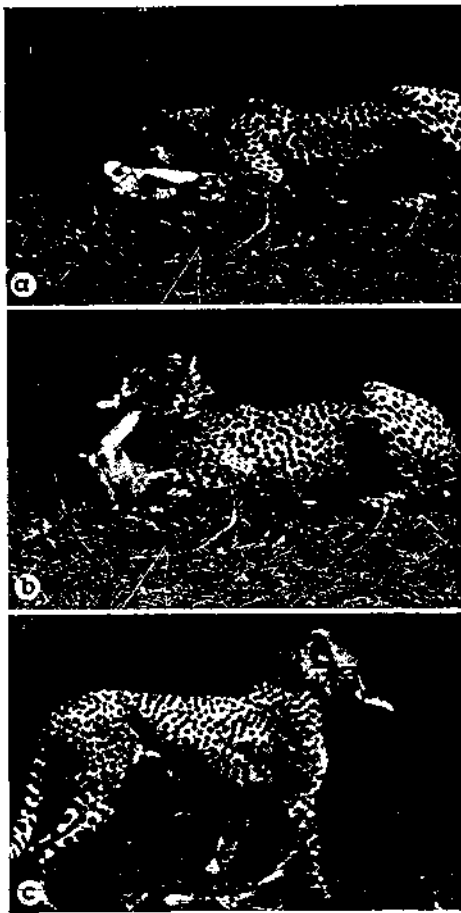


Figure 2. The cheetah captured a young impala, spent 5 minutes strangling it and was carrying it away when it began to struggle; whereupon,

- a. the cheetah dropped the impala holding it down with both forelegs, one on its head the other on the lower neck, while gripping the upper ventral neck in its mouth.
- b. The impala bleated several times over the second 5 minute period but during the third 5 minute period was still and the cheetah maintained a neck bite long after the last signs of life.
- c. The ventral neck strangle hold was used in dragging the kill away.

animal. Then it strikes with its fore-paws anteriorly above the prey's front legs or posteriorly above the hind legs. Due to vegetation and dust it was not possible to see if the cheetah ever left contact with the ground completely, but considering its speed and the use of the fore-legs, the hind legs probably leave the ground. This blow knocks the animal over, and, as it falls, the cheetah quickly jumps stiff-legged into the head, neck and shoulder area of the fallen prey. It instantly grabs the throat on the ventral side with its mouth and exerts weight on the victim's anterior end by extending the front legs over the head and neck, one fore-limb on each side of the neck-hold (Fig. 2a).

With smaller prey such as impala (*Aepyceros melampus* Lichtenstein), the cheetah knocks the prey over in the fashion described above, but in one case a cheetah reached for the animal's neck with its mouth long enough to pull the animal's neck and head downwards and cause it to topple over. The grabbing and holding down of the prey once it is toppled is comparable to the "seizing" phase of the predatory sequence in house cats (*Felis domestica*) (LEYHAUSEN 1965).

With the young of large prey and with very small game species or their young, such as warthogs (*Phascochoerus aethiopicus* Pallas) the cheetah simply lands on or hits the animal's body with one of its front legs as it runs up to and overcomes the animal from behind and above, or from the side. When the animal falls over, usually rolling, the cheetah keeps the prey down by standing on it and/or then very quickly grabs the animal by the upper back or neck and carries or drags it to nearby cover where it is then killed and eaten (Fig. 3). When the prey is dragged off, the cheetah grips it in the anterior ventral neck region (Fig. 2b+c). In open areas, such as in parts of the Serengeti, the cheetah has little cover in which it can eat prey. Presumably cover hides the prey and the cheetah from potential scavengers or



Figure 3. Where available, cheetah drag the kill immediately to cover, where it is eaten. The mother cheetah spends several minutes after dragging the prey to cover just standing alert near the cubs while they eat, apparently watching for other predators

other predators. House cats also take captured prey to a secluded place for eating; however, the prey is normally killed first (LEYHAUSEN 1956 a).

Where there are several cheetahs in a hunting party, predatory behavior is more or less the same, "division of labor" seldom occurs; however, individuals of a group sometimes cooperate in holding the prey "at bay". In the cases of group hunting that I observed, the same animal knocked over and killed the prey. The leader of a group, always a ♂ in adult groups, did most killing; he determined what, when, and how the group hunted, and appeared to select the particular prey to be pursued. The others followed him.

Cheetah spend several minutes killing prey. Five minutes is common, but 15—25 minutes was not rare, even with small impala fawns. Some prey revive from strangulation killing attempts and have to be "strangled" two to three more times before death occurred (Fig. 2).

Prey such as young warthogs have very short and thick necks. They offer relatively little space for the cheetah to grip the throat. In these cases, inflicting death appears difficult. Death sometimes comes from crushed skulls, since the bones are soft in very young prey and the brain is easily damaged. A bite directed to the dorsal side of a young warthog's neck was observed, but death resulted from a crushed skull, not from spinal damage or blood loss.

Blood was seldom seen externally on the bodies of prey during or shortly following killing. In order to determine whether or not death was, in fact, the result of strangulation, the head and the neck of prey were examined immediately after the cheetah left the carcass. The head and upper neck are normally not consumed by cheetah except in very young animals that are eaten entirely. Teeth did not puncture major vessels and no necks were broken or damaged. Slight rupture and hemorrhaging in the ventral and lateral parts of the upper neck were common but the loss of blood was not appreciable, and apparently not the cause of death. Punctures of the prey's skin were slight and not always present. The trachea or larynx were not removed for examination to determine collapse or damage. However, death is probably not the result of injury to the nervous or circulatory systems. In all probability it is the result of strangulation. Dr. F. WALTHER (verbal communication) has confirmed these observations with his own. He noted that gazelles killed by cheetah died of apparent strangulation, and SCHALLER (1968:99) says, on the basis of examining 136 carcasses believed to be cheetah kills, that "Gazelle are killed by strangulation. . . ."

### Review of Killing Behavior in Larger Felidae

In 1965, the East Africa Wild Life Society conducted an investigation aimed at presenting all known aspects of cheetah life history (GRAHAM and PARKER 1965). The answers to question 17, which asked for descriptions of cheetah kills, consisted of 40 eye-witness accounts of cheetah making kills. Information from all observers resulted in the following conclusion: "The prey is knocked over, held down and killed, the actual cause of death being unknown." DENIS (1964:39) described cheetah killing behavior as follows: "Then comes the famous lightning dash ending with a blow at the victim's hind legs, or a spring at its throat or onto its back bringing hunter and hunted to the ground. Though neither teeth nor claws are as strong as a leopard's, they do not easily relax their grip, and death usually comes from a bitten jugular vein or windpipe." The conclusion by DENIS that death of the prey results from damage to the jugular vein or windpipe is held by other observers. SHORTRIDGE (1934:107) said, "Cheetah are said invariably to kill by strangulation, and seldom to relax their first grip on the throat until the animal is dead." SHORTRIDGE, like DENIS, does not give any explicit data on how the throat is gripped, i. e. from what angle, or how it is damaged. Nor is there any detail on how the cheetah actually brings down the prey animal. WENDT (1959:57) said that cheetahs ". . . race after the prey, beat it down with their feet. . . ." ESTES (967:23) in writing about killing behavior says, "Leopards and lions, and particularly the cheetah also frequently kill large prey by gripping the throat until the animal suffocates." No exact information is given on how the animal is brought down or dispatched. LEYHAUSEN (1965: 452-3) describes killing behavior in the lion (*Felis leo* L.) as composed of various steps

including: seizing the animal from behind with both or one paw, and, while biting and scratching the hind end, attempting to pull the animal down as it tries to escape. Once the animal is down it is held down and the bite is directed to the spinal area of the upper back or neck. LEYHAUSEN concludes that death results from severing the spine. SCHALLER (1967:293) describes almost exactly the same behavioral sequence for tigers, only biting from the dorsal side of the neck in tigers is less common than gripping the throat from the ventral side. SCHALLER (1969) notes that lions kill most frequently by strangulation, and I am presently studying this experimentally in a large captive lion population.

LEYHAUSEN (1965) did not observe cheetah killing behavior, but from extensive observations of various other Felidae concludes that the death of the prey of felids is the result of damage from the teeth of the cat usually to the nervous system and that the fatal bite is at an angle from, above or dorsal to the prey's neck. SCHALLER (1967:294) describes killing in tigers (*Panthera tigris*) as consisting of 2 steps: ". . . (1) the attack, during which the animal is thrown off its feet, and (2) the actual killing, usually by biting into the throat or the back of the neck." Usually, the death of prey is the result of the tiger holding the ventral side of the neck several minutes until the animal suffocates. SCHALLER, however, did not examine tiger (or cheetah) kills to determine the area of damage from the ventrally directed killing bite. LEYHAUSEN (verbal communication) recently suggested that biting from the ventral side can also kill by damage to the central nervous system and that death in such cases may be quite prolonged.

### Ecological Factors Affecting the Evolution of Killing Behavior

There are several possible reasons why some of the larger Felidae kill by strangulation, as opposed to biting at the nape of the neck and inflicting central nervous system damage as occurs in smaller Felidae.

LEYHAUSEN (1965: 488) points out that in the cats biting is specialized for killing and the forelimbs for seizing. This certainly is the case for tigers, cheetahs, lions and perhaps for the leopard (*Panthera pardus* L.). LEYHAUSEN states further, "This evolutionary process is paralleled by the development of the canine teeth, which, by their structure, shape and position in the jaws, have become well adapted to being wedged between the vertebrae of a prey animal's neck. The vertebrae are thus disconnected and the hind brain or spinal cord is lacerated, which results in instantaneous death. Feline canine teeth are quite unsuitable for crunching hard bones or piercing large blood vessels." Lions use the teeth behind the canine for crushing bones when feeding at a kill and this supports LEYHAUSEN's view that canines are not adapted for crushing. D. SIMPSON (verbal communication) relates that Rhodesia adult ♂ lions kill two-year-old lions by crushing their skulls with the canines. Leopards may kill some of the time by using their canines to crush skulls, e.g. primates and the young of many species.

The cheetah's canines in fact have not been specialized at all for piercing the spine of prey. The cheetah is comparable in weight with the leopard, both ranging between 100—150 pounds (ROBERTS 1951). The skull measurements are vastly different from those of the leopard, which has much larger skull and teeth measurements (ROBERTS 1951: 564—5). The leopard is more typical of other cat species in skull and teeth size and body proportions. It is also more typical in the way it hunts, employing pouncing from trees or stalking and pouncing from distances very close to the prey. It is to be expected that the canines would be selected to be relatively large since killing, as opposed to stalking and pouncing, makes up a more important part of the overall predatory sequence in the leopard as compared with the cheetah.

The method of capturing prey in the leopard has probably led to selection for the larger skull and teeth, which are used to kill by severing and crushing parts of the neck and skull, as well as for strangulation. Besides longer canines, the leopard's carnassials have cusps on the inner edges which are an adaptation for crushing. The cheetah lacks these cusps.

Opposing selection forces acting on cheetah killing behavior. Selection for speed favors reduced skull and teeth size; counteracting selection pressure favors skull and teeth size large enough to dispatch prey effectively. Rapid death of captured prey is especially important to prevent disabled, but live animals, from vocalizing and attracting other predators and scavengers. GRAHAM and PARKER (1965) noted that in many cases, cheetah have been driven from their kills by lions, leopards, and hyenas (*Crocuta crocuta* Erxleben), and even jackal (*Canis mesomelas* Schreber). U. V. De PIENAR (in press) and SCHALLER (1968) also noted the frequent robbing of cheetah's kills by other predators in Krüger Park, South-Africa, and the Serengeti Area, East Africa, respectively.

Strangulation appears to be a behavioral adaptation counteracting the apparent anatomical deficiencies, which are modifications for speed. Without strangling behavior, the cheetah would be anatomically unequipped for killing most prey. LEYHAUSEN (verbal communication) noted that the lack of the diastema in the cheetah's jaw supports the conclusion that cheetah are unable to use the canine to pierce the prey's spine. The cheetah's mouth is so small that it usually must bite and strangle from the ventral side of the prey's throat; however, probably in the cheetah, and certainly other species, another factor favors biting from the ventral side—the danger to the predator from the horns or antlers of the prey. SCHALLER (1967: 296) points this out, "The throat hold confers the following additional advantages on a tiger: (1) horns and antlers cannot be used effectively by the prey; (2) the thrashing horns cannot reach the tiger as long as it remains near the head; and (3) by holding the neck of the prey to the ground, the cat can with relative ease prevent it from righting itself and gaining its feet, an important advantage when handling a gaur, which may weigh seven times as much as the tiger." The cheetah holds the prey down with both fore-legs and its mouth. It also lies at right angles to the prey and close to its head, which gets it far away from the legs and horns of the prey (Fig. 2).

There appear to be other ways for lions to avoid injury from their captured prey. ELOFF (1964) describes many cases observed in the Kalahari region, South Africa, of gemsbucks goring with their horns and killing attacking lions. ELOFF argues that lions there have adaptively modified their predatory behavior by breaking the prey's back before proceeding to kill the disabled prey with a ventral strangle-hold or dorsal neck bite. The lions attack in one of their usual ways from behind (LEYHAUSEN, above) but once the lion is on top of the haunches it grips the posterior, dorsal surface in its teeth and pulls upward, thereby breaking the back between the last lumbar and first sacral vertebra and snapping the spinal cord (kills were dissected to determine the nature of these injuries). This vertebral region is especially weak against upward, but not downward, force.

### Ontogeny of Killing Behavior in Cheetah

One litter of 4 cheetah cubs and a parent adult ♀ were observed closely from the time the cubs were about 5 1/2 months old until they were 9 1/2 months old (Fig. 4). Fewer observations were made of 2 other litters aged 6–10 and 10–14 months during the study (Fig. 3 and 5). Sexual maturity is at about 14 months (GRAHAM and PARKER 1965).

Behavior suggestive of innate predatory behavior is observed in very young cheetah. Predatory-related behavior in cubs only 2 weeks old was

observed by STEVENSON-HAMILTON (1947). He states, "... when one of them rushed at a terrier which had gotten into the cage he struck at the dog with his forepaws as he charged, just as a domestic cat often does." It is



Figure 4. A litter of 4 cubs born in May in Nairobi National Park were closely observed from November through February, shown here at 6 months of age shortly before they received their first "lesson" in hunting

possible that the cubs were exhibiting the predatory component that adults use to knock prey down. ENCKE (1960) says about captive cheetah cubs: "The typical cheetah type attack (knocking the prey down with the paws) was first noticed at about the eleventh or twelfth week." Data from the wild on cheetah prior to hunting experience support a different hypothesis. CRANDALL (1964: 396) says, "Just as wild-caught birds are preferred to hand-reared ones by the falconer, so is the cheetah with natural hunting experience esteemed by the trainer." STERNDALE (1884: 200) says, "For this



Figure 5. The mother of the 4 cubs is second from the right, her cubs are about 14 month old and have been killing for at least two months. The second cheetah from the left is a male and led the group in hunting in Nairobi Park

purpose the adult animal is always caught, it being considered by the chitacatchers that a young leopard would never turn out well for the purposes of the chase." SHORTRIDGE (1934: 108) said, "In Northern India and Persia, where they are sometimes trained to hunt blackbuck and chikara, it is said to be essential to capture adult animals for this purpose, since the cubs do not develop the required skill unless first taught by their parents." DENIS (1964: 68) said, "... it could catch Bennet's gazelles but not pull them down; it appears that the hunting leopard has to be taught by its parents. The speed but not the skill is inherited."

A ♀ with cubs gives a low pitched "ughh" that has the effect of keeping the cubs in one place while she is gone (Fig. 6). They remain still until the ♀ gives a high pitched "chirp" which brings the cubs to the kill site. When the cubs were 6 1/2 months old, the ♀ showed intense interest in an adult warthog



Figure 6. Up to 6 1/2 months the cubs did not actually hunt with their mother and even after a few hunting lessons with the female, they were often left behind while their mother made kills. An "ughh" from the mother resulted in the cubs remaining stationary while a "chirp" brought them to their mother

with 2 newly-born young and for the first time allowed the cubs to follow. The cheetah and the cubs slowly approached the warthogs, all of them exhibiting typical stalking behavior. The cubs had often watched their mother stalk but lacked stalking experience of game themselves. The warthogs were "rooting" and facing away from the cheetahs. The cheetahs approached from 100 yards at about half speed until, when about 30 yards away, the warthogs began to run. The mother cheetah instantly exhibited full speed chase, but ran beyond the young warthogs and pursued the adult. The cubs proceeded to give chase after the young warthogs, while the adult cheetah kept running back and forth between the adult warthog and the young warthogs. (When the adult warthogs stays with the young warthogs, even groups of adult cheetahs cannot prey on the young successfully unless the young can be separated from the parent.) The adult warthog finally stopped "trying" to reach her young and the adult cheetah then ran back to follow her cubs while they chased one of the young warthogs. The cubs followed close behind the warthog, within inches at times, but showed no movements indicative of an attempt to knock over or grab it. It appeared that the adult cheetah could have caught the prey at any time but instead ran closely behind the cubs. After 3 minutes of chasing, one warthog was out of sight and the one being chased ran into a hole.

In other hunts, the cubs were allowed to chase the prey before the caught it. The prey was not dispatched but appeared to be in a state of shock and remained down while the cubs bit the animal in several places (but not the anterior end).

Another litter of 4 cubs at 12 months of age could catch and kill typical prey. The actual learning of how to kill was not observed, but it can be inferred that cheetah cubs first bring down and kill prey between the ages of 9 and 12 months. The observations on the younger litter can surely be considered as an indication of lessons in hunting. The innate behavior patterns of stalking and chasing prey are manifest at a very young age in play. They apparently require little or no experience as compared with killing. The cubs may have to learn the stimuli (prey) to which they direct the "knocking over" behavior pattern, which is apparently innate. During play, cubs bite one another on the neck from the dorsal side, and this implies an innate orientation for biting that is altered by experience to the ventral bite in killing prey. However, in early morning mock-fights between adult cheetahs, biting was directed dorsally to the neck, implying that the dorsal bite is not just a phylogenetic remnant and may function in intra-specific behavior, e.g. mating or serious fighting (though it was not observed in these contexts). The cubs observe the ♀ stalking and chasing prey for several months before they hunt with her. Learning by observation may occur but in the field this was impossible to determine. The effect of experience on innate stalking behavior is pointed out by the observations of KRUGER and TURNER (1967) in the Serengeti, where adult cheetah rarely stalk, but the cubs exhibit stalking frequently. However, SCHALLER (1968) observed a ♀ with cubs in the Serengeti that stalked often.

The adult cheetah is probably a requisite for the cubs to learn to catch and kill prey. Whether observational learning occurs in the cubs or simply the opportunity to practice, develop, and improve innate behavior patterns is not known. STEVENSON-HAMILTON (1947: 199—200) said of 2 cubs raised by a ranger, "... they took to absenting themselves in the evenings for gradually prolonged period, until at last they failed to return and were seen no more." Speculation would lead to the belief that the cubs were able to catch animals, perhaps crippled or vulnerable prey, and learned to kill properly after a few attempts. They were being fed by men, otherwise they probably would have starved before the predatory sequence was perfected.

### Comparative Ontogeny of Killing

Tiger cubs "are wholly dependant on the ♀ until they are about six months old. While she is hunting, they lie quietly hidden in a thicket, a patch of high grass, or an overgrown ravine, waiting for her return. If the tigress has captured some large prey, she leaves it at or near the kill site and leads her cubs to it" (SCHALLER 1967; 265).

Perhaps the denser vegetation of the tiger's habitat is not conducive for using vocalizations over long distances such as the cheetah does with her cubs. "The behavior of the tigress when attacking the third buffalo was of note. In contrast to her usual efficient method of pulling livestock down and strangling the animals by grabbing their throats, she merely threw the buffalo off its feet and then retreated, permitting the cubs to attack on their own. She made no attempt to kill in either attack. This suggests that the tigress provided the cubs with the opportunity to practice the techniques of

killing. The cubs, although twelve month old, obviously had little or no previous experience in dispatching such a large animal. They were reasonably adept in pulling it down, but they failed to kill efficiently, largely confining their attack to biting and clawing around the rump, back, and belly rather than grasping the throat" SCHALLER (1967: 273).

Similar behavior was observed in cheetah. SCHALLER (1967: 276) points out that hunting independence is at about 18—24 months; in cheetah it is at about 14 months. Cheetah begin experiencing predatory behavior at about 6 months, while most tigers begin at 12 months. It is of further interest that SCHALLER (1967: 275) observed the development of efficient killing that began with cubs bringing down and eating prey without killing it. SCHENKEL (1966) observed this in young lions. The adult parents in these species are giving their cubs a chance to experience actual killing, by not killing the prey themselves. Since ♀♀ with cubs at the stage of predatory learning were the only adults cheetahs observed not to kill prey, this hypothesis seems plausible. This inhibition against normal killing must be innately acquired and dependent on particular stimulus conditions, e.g. the cubs' size or perhaps some latent post-partum hormonal changes.

SCHALLER (1967: 270—290) points out that domestic pigs (*Sus sus*) were killed by tiger cubs learning predatory behavior, and that full grown wild boars (*Sus scrofa*) are formidable prey in that they have been recorded to kill adult tigers. Cheetah cubs had some of their first predatory practice with young warthogs, while adult warthogs, very similar to wild boars in India, are not attacked even by adult cheetah. At 8 months of age, the cubs were once waiting for the ♀ while she hunted, when a herd of zebra passed within 30 yards; the cubs showed neither hunting nor fear responses. The zebras saw and watched the cubs, but showed no fear response to them. It is probable that young felids learn what animals are prey by hunting with adults. It is not known how distinction is made between dangerous and non-dangerous prey. The corollary question of how some prey discriminate between dangerous and non-dangerous predators, or their hunting mood, is equally baffling. I am now investigating these questions in lions and cheetahs.

### The Ontogeny of Predatory Behavior and LEYHAUSEN'S Model

LEYHAUSEN (1965: 489) states, "The way the killing bite clicks into place after only one or very few successful attempts is comparable to the imprinting process which determines the object that a duckling will subsequently follow as its 'mother'." It appears that for the tiger and the cheetah this may be the case. Either the mother makes available the possibility for the cubs to kill by refraining from killing herself, or the cubs may come upon or catch a weak or crippled animal on which to practice and experience killing. Obviously the mother cannot provide the motivation for killing behavior and there must be an innate tendency (an instinct) to elicit and/or learn the appropriate behavior patterns. With the killing instinct and just a few attempts, the proper behavior "clicks into place". The killing behavior is an "intercalation" (LORENZ 1965), it appears, of innately acquired and individually acquired components that allow for modification or plasticity. Since killing techniques and some predatory behavior patterns can best be implemented according to the particular prey species in an area, it is to be expected that some of the behavior patterns in the predatory sequence might require experience for their development and thereby be modifiable. This is

borne out, for example, in the lions in the Kalahari Gemsbok Reserve that prey chiefly on gemsbok and have modified their predatory behavior to fit this potentially dangerous prey. Observations on the ontogeny of this apparently learned behavior would prove most interesting. It is probably a cultural trait. The less-modifiable predatory behaviors such as chasing in cheetah or "bringing down the prey" in tigers, appear to be equally effective on most prey and it is to be expected that they would depend less on experience for their development.

Although laboratory study is desirable, the field data imply that the tiger and cheetah fit into the behavioral model for the ontogeny of predatory behavior set out by LEYHAUSEN (1965: 490). "After a cat has caught, killed and eaten one of several prey animals and has thus experienced the causal connection between these three activities and the provision of food, it starts experimenting with the appetitive links of the chain and gradually fits learned appetitive patterns in the place of innate ones. These learned patterns vary considerably, both between individuals of the same species... and the instinctive patterns remain independent and unaffected, and required patterns are stored in addition." The predatory sequence that LEYHAUSEN (1965: 489) presents, "... watching, crouching, stalking, pouncing, seizing and 'angling'," is easily modified to fit the cheetah as follows: watching, stalking, crouching (not always), chasing, knocking over (or pulling down as in tigers or lions), and seizing. "Angling" as described by LEYHAUSEN for Felidae was not observed in cheetahs.

Young cheetah cubs, like lion cubs observed by SCHENKEL (1966), were observed prior to their hunting lessons to drag sticks much like adults drag instinctive behaviors in the predatory sequence, as may be the preference for thick cover where prey are taken and eaten.

### Summary

There appears to have been natural selection for anatomical adaptations permitting efficient predation in the cheetah, which have led to corresponding behavioral adaptations away from the typical predatory sequence and killing behavior of other Felidae. Strangulation as a means of killing prey is a necessity in cheetah. The orientation of the strangle bite appears to require maturation of an innate tendency. Stalking and chasing of prey are relatively fixed behavior patterns but "seizing" and killing of the prey develops properly only with experience and is modifiable. The training given to cubs by their mother is critical for the eventual development of the entire predatory sequence from its innate components. Training probably allows the cubs to modify more effectively the predatory and killing behavior best suited for the prey of the specific area in which they live.

### Zusammenfassung

Der Gepard scheint in Körperbau und Verhalten auf eine besondere Art des Beuteerwerbs spezialisiert, durch die er sich von anderen Großkatzen unterscheidet. Geparden müssen ihre Beute erwürgen. Die Orientierung des Würgebisses nach der Kehle scheint als Folge der Reifung einer angeborenen Tendenz aufzutreten. Anschleichen und Jagen der Beute bestehen aus ziemlich starren Erbkoordinationen, Festhalten (seizing) und Tötungsbiß entwickeln sich nur unter Erfahrung vollständig und können modifiziert werden. Die Unterweisungen durch die Mutter ist wesentlich für die spätere Entwicklung der



gesamten Folge von Beutefangverhaltensweisen, die aus angeborenen Komponenten besteht. Die Belehrung durch die Mutter ermöglichen den Jungtieren, ihr Beutefang- und Tötungsverhalten an die im betreffenden Gebiet lebenden Beutearten anzupassen.

#### Literature cited

- CRANDALL, L. S. (1964): Management of wild animals in captivity. Univ. Chicago Press • DENIS, A. (1964): Cats of the world. Houghton Mifflin Co. Boston • EATON, R. L. (1970): Hunting behavior of the cheetah. *J. Wildl. Mgmt.* • EATON, R. L. (1969): Group interaction, spacing and territoriality in cheetahs. *Z. Tierpsychol.* 26, . . . • EATON, R. L. (1969): Cooperative hunting behavior between cheetah and jackal and a theory of domestication of the dog. *Mammalia* 33, 87-92 • ELOFF, F. C. (1964): On the predatory habits of lions and hyaenas. *Koedoe* 7, 105-112 • ENCKE, W. (1960): Birth and rearing of cheetahs at Krefeld Zoo. *Int. Zoo Year Book*, 85-86 • ESTES, R. (1967): Predators and scavengers. *Natural History*, 21-29 and 38-47 • GRAHAM, A. D. and I. S. C. PARKER (1965): East African wild life society cheetah survey. Report by Wildlife Services. East African Wild Life Society. Nairobi • KRUIK, H. and M. TURNER (1967): Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti Area, East Africa. *Mammalia* 31, 1-27 • LEYHAUSEN, P. (1956a): Verhaltensstudien an Katzen, Verlag Paul Parey, Berlin und Hamburg • LEYHAUSEN, P. (1956b): Das Verhalten der Katzen (Felidae). *Handb. Zool.* 8 (10), 1-34 • LEYHAUSEN, P. (1965): Über die Funktion der relativen Stimmungshierarchie. *Z. Tierpsychol.* 22, 422-494 • LORENZ, K. (1965): Evolution and modification of behavior. Phoenix Science Series. Chicago • DE PIENAAR, U. V. (in press). Predator-prey relationships amongst the larger mammals of the Krüger National Park. *Koedoe* 12 • ROBERTS, A. (1951): The mammals of South Africa. South Africa • SCHALLER, G. B. (1967): The deer and the tiger: a study of wild life in India. Univ. Chicago Press. Chicago • SCHALLER, G. B. (1968): Hunting behavior of the cheetah in the Serengeti National Park, Tanzania. *E. Afr. Wildl. J.* 6, 95-100 • SCHALLER, G. B. (1969): Life with the king of beasts. *Nat. Geogr.* 135 (4), 494-519 • SCHENKEL, R. (1966): Play, exploration and territoriality in the wild lion. *Symp. Zool. Soc. London* 18, 11-22 • SHORTRIDGE, G. C. (1934): The mammals of South West Africa. Vo. I. Heinemann. London • STERNDALE, R. A. (1884): Natural history of the mammalia of India and Ceylon. Thacker, Spink and Co. Calcutta • STEVENSON-HAMILTON, J. (1947): Wild life in South Africa. Cassel and Co. London • WENDT, H. (1959): Out of Noah's ark. Houghton and Mifflin Co. Boston.

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