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Abstract: Detailed description of hunting and killing behavior. Cheetahs seldom crouches like most cats. It walks along slowly, looking for game. The "crouch" aspect of predatory behavior in the cheetah is modified to a state of alertness that requires holding the head high and remaining motionless enough to maintain visual contact with the prey. The cheetah knocks over the fleeing prey. The ontogeny of killing behavior was observed with a litter of four cubs and the mother.

# **Z** *Predatory and Killing Behavior*

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 the question 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, for example 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 (1967:23) 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 (1965:452-453) describes killing behavior in the lion as composed of various steps including: seizing the animal from behind with both paws 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.

Leyhausen (1965) did not observe cheetah killing behavior but from extensive observations of various other *Felidae* concludes that the death of the prey 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 as consisting of two 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." Most of the time the death of prey is the result of the tiger holding the ventral side of the neck for 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 (pers. comm.) 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.

This recent work on predatory behavior in the cat family with emphasis on killing behavior in the laboratory by Leyhausen (1956, 1965) and in the field, principally by Schaller (1968, 1969) can be verified here. I frequently observed predatory behavior in wild cheetahs. 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,'" as Leyhausen describes for many cats.

The cheetah watches prey intently, depending greatly on vision to determine at what time to stalk and attack. The cheetah watches for cues such as the attentiveness of the potential prey animals, for example alert ears and in which direction they are looking, and from this appears to be

able to evaluate the general level of alertness or sense of danger in the prey.

The cheetah seldom crouches like most cats. Though Schaller (1972) interprets their stationary posture during hunting as crouching, I am using "crouching" as a descriptive not a functional term. It walks along slowly, looking for game, lifting the head up either to get a better view or to examine more closely game that has been spotted already. While the cheetah is close to prey it keeps its body low with its head 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 in turn 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 five to seven minutes between cheetah and small herds of prey are common at this stage of a hunt. The very instant that all of the prey appear not alert, the cheetah, without taking its eyes away from the prey, stalks a little further, again stopping instantly if an animal looks 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 motionless enough 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" in most cats is homologous to the behavior in the cheetah that involves chasing and catching the intended 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 make kills 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 of which varies with the species of prey, its size, and how fast it is moving when overcome by the cheetah. For large prey species such as subadult kongoni I observed that the cheetah ran until it was along the flank of the animal. Then it struck with its forepaws 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. This blow knocked the animal over, and, as it fell, the cheetah quickly grabbed the throat on the ventral side with its mouth and exerted weight on the victim's anterior end by extending the front legs over the head and neck, one forelimb on each side of the neck hold. Schaller (1972) observed broken legs in gazelles which resulted from their being knocked down by cheetahs.

With smaller prey such as impala the cheetah knocked the prey over in the fashion described above. 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 (Leyhausen, 1965).

With the young of large prey and very small game species or their young, such as warthogs, the cheetah simply lands on or hits the animal's body with one or both 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. When the prey is dragged off, the cheetah grips it in the throat region. 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 other predators. House cats also take captured prey to a secluded place where it is eaten; however, the prey is normally killed first (Leyhausen, 1956).

Cheetah spend several minutes killing prey. Five minutes is common but for some cheetahs 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 occurs.

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 appeared difficult. Death sometimes came 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 death is the result of strangulation. Dr. Fritz Walther (pers. comm.) 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. . . ."

## ONTOGENY OF KILLING BEHAVIOR

One litter of four cheetah cubs and a parent adult female were observed closely from the time the cubs were about 5½ months old until they were 9½ months old. Fewer observations were made of two other litters aged 6–10 and 10–14 months during the field study.

Behavior suggestive of predatory instincts is observed in very young cheetah. Predatory related behavior in cubs only two 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 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 on cheetah from the wild 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 purpose the adult animal is always caught, it being considered by the chita-catchers 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 kill is inherited."

One female with cubs gave a low pitched "ughh" that had the effect of keeping the cubs in one place while she was gone. They remained still until she gave a high-pitched "chirp" which brought the cubs to kill site. When the cubs were about six months old the mother showed intense interest in an adult warthog with two 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 experience with 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 warthog stays with the young warthogs even groups of adult cheetahs cannot prey upon 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 closely 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 three minutes of chasing, one warthog was out of sight and the one being chased ran into a hole.

In several similar hunts the cubs were allowed to chase the prey but the female 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). Similar observations were made by Schaller (1972) and others in the Serengeti.

Another litter of four cubs at about 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 for cheetah cubs to bring down and kill prey, experience between the ages of 9 and 12 months is necessary, though Schaller (1972) states that cubs may capture prey by themselves by the age of about 8-12 months. The observations of the younger litter can surely be considered lessons in hunting. The instinctive behavior 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 apparently is 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 in adult cheetahs, biting was directed dorsally to the neck implying that the dorsal bite is not just a phylogenetic remnant and may function in intraspecific behavior, for example in mating or serious fighting, and it was observed in mating at Lion Country Safari. The cubs observe the female stalking and chasing prey for several months before they hunt with her. Learning by observations may be going on but in the field this was not possible to determine. The effect of experience on innate stalking behavior is pointed out by the observations of Kruuk and Turner (1967) in the Serengeti, where adult cheetah rarely stalk, but the cubs exhibit stalking frequently. However,

Schaller (1968) observed a female 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 two cubs raised by a ranger, ". . . they took to absenting themselves in the evenings for gradually prolonged periods, 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.

#### FURTHER STUDIES

My field study provided details of the hunting behavior (Eaton, 1970a) and predatory sequence (Eaton, 1970b) of the cheetah in the wild. Since these findings were reported I have been able to study experimentally and observe repeatedly predatory and feeding behavior under improved observational conditions in seminatural conditions. I have discovered much additional information and even changed some earlier conclusions derived from study in the wild.

The cheetahs I observed were kept adjacent to an ungulate area which included gazelles, zebra, waterbuck, lechwe, sitatunga, rhinoceros, giraffe, addax, elephant, and hippopotamus. Only a fence separated the ungulates from the cheetahs, which had a clear view of the ungulates and vice-versa.

Even when fed to the point of fully distended stomachs and with much fresh meat still available, cheetahs responded to dead, whole chickens, white in color. They exhibited a form of predatory play behavior which consisted of raising the front end up off the ground then coming down with both forefeet striking the chicken, much as coyotes and foxes do when catching mice. When fed the larger, whole carcasses of horse, gazelle, moufflon sheep, etc., these responses were not seen.

The striking with both or one foreleg is not seen elsewhere in predatory behavior though I earlier believed that the dew paw was employed in striking the fleeing prey and that this physical blow knocked the prey over; however, this is not the case. The use of one or both dew paws is restricted to play with prey and conspecifics and to fighting.

On several occasions an abundance of cut-up horsemeat was fed until the cheetahs stopped feeding. After reaching what was considered satiation, a whole carcass of a horse or other ungulate was introduced.

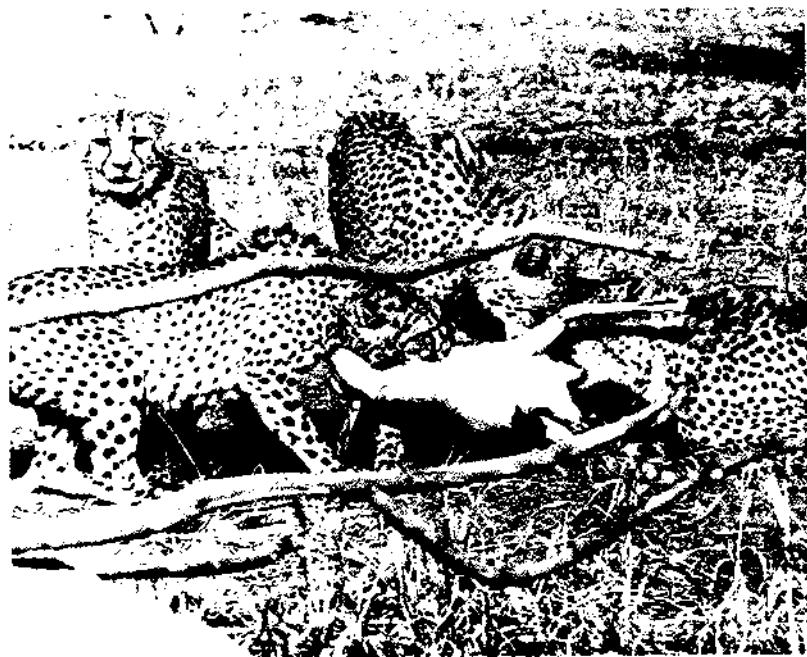


Figure 7-1 Captive cheetahs, satiated on prepared meat, feed ravenously when a whole carcass is presented. (Photo: R. L. Eaton.)

Immediately the cheetahs fed ravenously, and did not stop until all was consumed, except for the skin, larger bones, skull, stomach, and intestines (Fig. 7-1).

In some carcass feedings, there were cheetahs that delivered the killing bite to the upper, ventral throat of the carcass, exactly as is seen in the wild and by these same cheetahs to live prey.

Carcasses were dragged behind a vehicle into the cheetah area. The cheetahs immediately ran to and chased the carcass, some of them digging the dew claw into the carcass and pulling backwards as it moved forward.

Models in the form of mounted specimens were brought into the cheetah area to test the responses of the cheetahs. A mounted specimen of a gazelle was placed on the ground 50 yards from the closest cheetahs, all of which were lying down. The first cheetahs to approach walked slowly to the model. Olfactory inspection continued for several minutes, primarily at the anterior and posterior ends of the model. Other cheetahs that eventually saw the cheetahs inspecting the model ran to the model. Those that ran from a direction that brought them directly in front of and

facing the model's head stopped abruptly and threatened the model's head before walking around to the side and then olfactorily inspecting the model (Figs. 7-2 and 7-3).

After about ten minutes, one female attacked the model by raising up in the front, her weight shifted posteriorly as she reached both forelegs out and over the back of the model, bringing both forepaws down on the model, digging the dew claws into the model and pulling it towards her.

These experiments were repeated several times and after the first trial, with one of two gazelle models, the model became surrounded by as many cheetahs that could lie around it side by side, usually about six. One or two of the same females always "killed" the gazelle by biting it on the ventral throat and holding this, the suffocation bite. The other cheetahs tried to eat the model, biting into it and trying to tear the hide, until they were driven away.

The cheetahs employed the interspecific threat behavior when we approached and took the model away. These threats, reserved for the interspecific realm, are seen in the wild when cheetahs are approached by competing predators. They are never followed by a physical attack, neither are they ever seen in intraspecific threat or fighting.



Figure 7-2 Cheetahs investigating a mounted gazelle specimen. (Photo: R. L. Eaton.)

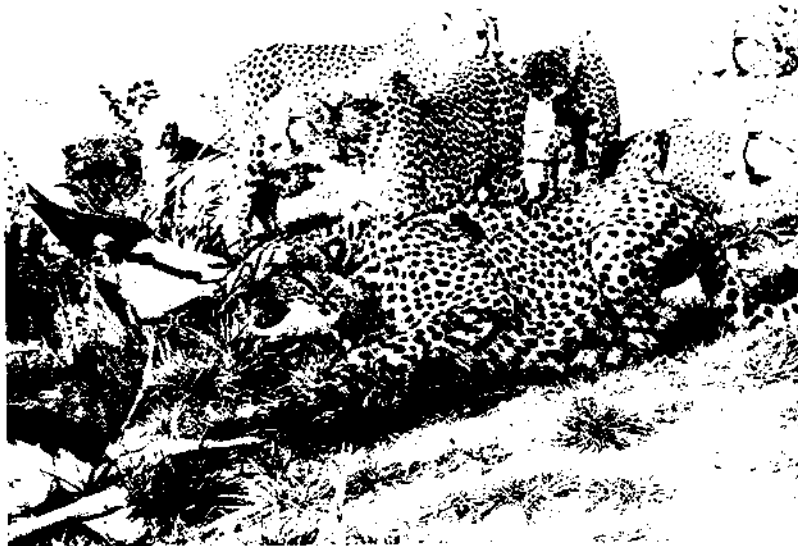


Figure 7-3 Cheetah exhibits some fear and inhibition while facing gazelle specimen. (Photo: R. L. Eaton.)

Prior to any experiments in which live prey were released into the cheetah's area, observations of the response of cheetah to live prey in the adjacent area were made. Would formerly wild-living cheetahs, kept well fed, go on "hunting" prey that was visually accessible, and at times only inches away separated only by a fence?

Indeed, the cheetahs' response to live prey that they could not catch, kill, or eat (that is, their behavior was not reinforced) maintained a high level of expression over one year's period, beginning six months after they had been removed from the wild and any contact with live prey. The onset of live feeding during this period did not alter the level of their hunting behavior of the inaccessible prey.

The cheetahs stalked and observed prey in a number of postures typical of wild, hunting cheetahs. They often lay close to the fence separating them from distant prey and also sought higher-elevation areas from which they intently watched far distant prey and wild native deer and livestock, outside the reserve confines, as distant as 1000 yards or more. Prey that was closer or approached the cheetah area were actively hunted. In several cases, typical prey species walked right to and along the separation fence. The cheetahs then attacked the prey at the fence, sometimes starting the

prey to running along the fence in which case the cheetahs ran alongside the running prey. Many times a prey at the fence or up to 200 yards distant turned and ran away. This immediately released a chasing attack in most of the cheetahs. There was no doubt that, as found in the wild, running away releases predatory attack.

Of special interest was the cheetah's response when standing and facing prey inches away on the other side of the fence (equally noteworthy is the fact that some captive-born prey species hunted by cheetahs in the wild showed little or no fear when charged by cheetahs). The cheetahs responded variously, including threatening the prey, swatting the fence, and, most curious, running away a few yards, turning around and charging the prey. It was as if the cheetahs were trying to make the prey run away (as though this would enhance success of an obviously impossible hunt). It also resulted in frequent short fight encounters between those cheetahs closest to the prey at the fence, when they looked around and saw other cheetahs close by and apparently staring at them, a threat.

It should be mentioned that the cheetahs that showed least interest in prey were the few subadults. They had been captured in the wild at ages of five to seven months of age, just as their "education" in hunting and prey-killing would have begun. Apparently the lack of hunting education and experience affected their motivation to "hunt" the visually but not physically available prey. Experiments with a naive cheetah, imported into the United States at five months of age, showed that typical killing was elicited by live prey after three trials in which an experienced cheetah killed as the naive cheetah observed and then fed. Such a complex behavior could not be learned by imitation, but rather seemed to be evoked by excitation from observation and feeding.

Hunting of the inaccessible prey was not less intense following normal feeding, but was decidedly less so after feeding from carcasses, when greatly more food is consumed. Hunting activity was highest, regardless of proximity of prey, in the early and late daylight hours as well as on bright moonlight evenings. This has been well established for wild cheetahs.

Only a few adults killed live chickens, though nearly all cheetahs chased and caught them. The chickens were white, unlike any likely prey encountered in South West Africa. I am told by Bill York that when he fed black chickens to captive, wild-caught cheetahs in Africa, they always killed and ate them, as they do the more darkly colored guinea fowl in Africa.

Chickens that "froze" were softly pawed repeatedly. Those that ran were chased. Two cheetahs killed all of the two dozen chickens, and they did so with bites to the upper neck and head which they held for up to several minutes, typical of the suffocating bite used on mammalian prey.

A few of the cheetahs plucked and ate the chickens while most of them

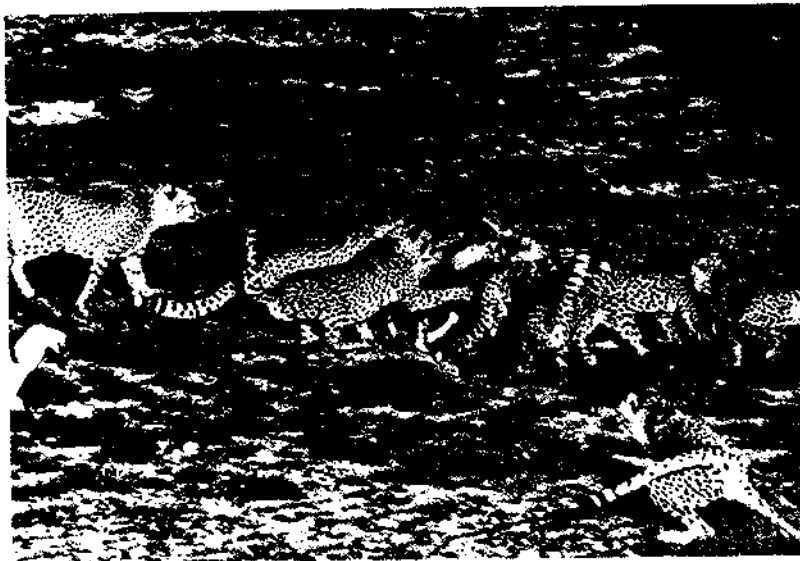


Figure 7-4 Cheetahs chase, bring down and kill fleeing goats. Note the rudder-like use of the tail as cheetah changes directions (lower right). (Photo: R. L. Eaton.)

ignored the chickens once they were dead. Fowl is not a significant prey item in the wild, and excluding color, possibly as an imprinted stimulus, there is a very good chance that most of these cheetahs never killed or ate fowl of any kind previously. However, all the cheetahs did feed on an adult ostrich carcass, which is far larger, has been recorded more often as prey than smaller fowl, and which is sparsely covered with feathers.

A number of live prey, moufflon sheep and goats—mammals of the same size as typical cheetah prey—were introduced into the cheetah area. All of the cheetahs attacked and chased these prey; however, it was the adults that always killed them with the suffocation bite. Surprisingly enough, as many as 12 cheetahs sometimes had difficulty in bringing down one sheep or goat. This was the result of the fact that the prey were so close. When they ran the prey were moving so slowly that they could not easily be knocked off balance. Also, the cheetahs' speed was slow, preventing them for using the movements normally effective at greater speeds.

When the prey was released further away and/or ran faster away from the cheetahs, there was no difficulty in bringing the fleeing prey down and quickly dispatching it (Fig. 7-4).

In filming these interactions with live prey, which I was unable to do in the wild, I discovered additional aspects of predatory behavior which

went unnoticed and undescribed in my earlier field work. As it turns out, finer analysis proves that the cheetah's predatory sequence fits more closely the behavior of other felids than previously believed.

For example, as Fig. 7-4 depicts, the fleeing prey is not knocked over with a blow from the cheetah's forepaw(s). In fact, the dew claw is most critical in the component functionally labeled "bringing prey down." The claw is inserted in the prey's hide and the cheetah's weight is shifted posteriorly (Fig. 7-4) thus exerting a posterior force on one side of the forward moving prey. This causes the prey to lose balance; its rear legs fold under and it falls to its side.

Also worth emphasizing is the use of the tail in making fast changes of direction, as shown in Fig. 7-4.

It is even more remarkable that at great speeds, accurately measured to be as high as 71 miles per hour, the cheetah is able in one motor sequence, to momentarily shift its weight posteriorly while extending the forepaw to bring down the prey (Fig. 7-4).

With slower-running prey cheetahs grab ahold with both dew claws on the fleeing prey's hind end, shift their weight backwards, and pull back with the forepaws, thus weighting and bringing the prey down.

These observations also established that the orientation of the killing bite is elicited in a more elaborate manner. Once the prey is fallen the cheetah approaches the head from the dorsal side of the lying prey. The head and upper neck are rotated towards the cheetah by digging one dew claw into the head or upper neck and pulling, while holding the prey down with the other foreleg placed over the lying prey's shoulders and lower neck, which prevents the entire body from rolling as the head and neck are rotated (Fig. 7-5).

During these movements the cheetah lowers its head so that the mouth faces posteriorly. The upper ventral neck of the prey is gripped in the mouth. Once the neck grip is achieved, the cheetah uses this grip to rotate the neck (and head) towards itself, thus twisting the neck. When the ventral neck is rotated laterally the cheetah holds the bite and suffocates the prey.

This complex of orientations and movements accomplishes at least two things. It prevents the cheetah from being exposed to the hooves of the fallen prey, and by rotating the neck and head upwards, the horns are moved further away. Perhaps the twisting of the neck also makes the trachea more vulnerable to collapse from the throat bite. Examination of three gazelle carcasses, killed by cheetah from South West Africa, showed two with collapse of the trachea and one whose spine was crushed.

At greater distances the twisting technique was not observed in East African cheetahs, but was observed in cheetahs from South West Africa. Perhaps, as Eloff (1973) has found in the Kalahari lion, a specialized killing





Figure 7-5 Experienced in the wild, this captive cheetah quickly kills a sheep. The head is rotated while the throat is gripped thus suffocating the prey.

technique is culturally evolving in the cheetahs of South West Africa. This hypothesis is unlikely since cheetah cubs could learn only from their own mother, and it is adult groups of males that show the highest specializations in predatory behavior.

There are several possible reasons why some of the larger cats kill by strangulation as opposed to biting at the nape of the neck and inflicting central nervous system damage as occurs in smaller cats. Leyhausen (1965:488) points out that biting is specialized in the cats for killing and the forelimbs for seizing. This certainly is the case for tigers, cheetahs, lions, and perhaps for the leopard. 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 (pers. comm.) relates that adult male 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, for example of 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 about 100 and 150 pounds. The skull measurements are vastly different than in the leopard, which has much larger skull and teeth measurements (Roberts, 1951:564-565). The leopard is more typical of other cat species in skull and tooth size and 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 make 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.

Acting on cheetah killing behavior are opposing selection forces: selection for speed which favors reduced skull and teeth size, and counteracting selection pressure on skull and tooth 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, and even jackals. Pienaar (1969) and Schaller (1968) also noted the frequent robbing of cheetahs' kills by other predators in Kruger Park, South Africa, and the Serengeti Area, respectively.

Strangulation appears to be a behavioral adaptation that counteracts the would-be anatomical deficiencies that are modifications for speed. Without strangling behavior the cheetah would be anatomically unequipped for killing many prey. Leyhausen (pers. comm.) noted that the lack of the diastema (the space between the canine and the molars) in the cheetah's jaw supports the conclusion that cheetah are unable to use the canine to pierce the prey's spine (however, this does occur with small antelope).

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 in other species, another factor favors such an orientation—the danger to the predator from the horns or antlers of the prey. The cheetah holds the prey down with both forelegs and its mouth. Twisting the head so that the horns point to the ground, 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.

There appear to be other ways for lions to avoid injury from their captured prey. Eloff (1964, 1973) describes cases in the Kalahari region, South Africa, of gemsbucks goring with their horns and killing attacking lions. Eloff suggests that the Kalahari lions 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, 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 to upward but not downward force.

#### PREDATION COMPARED TO AGGRESSION

How is aggression related to predation? Is the motivation in fighting the same as the drive to kill a prey animal? It is widely accepted that aggression in large predators is inhibited so as to prevent death and injury to members of the species. If lions fought each other in the same way they effectively kill buffalo, they would soon kill themselves off. I studied the expressions and behavior of cheetah in hunting and killing prey to see how these compared to their threat and fight behavior between themselves.

When cheetahs stalk, attack, and chase prey they show no overt signs of aggression. The mouth is usually closed, the eyes are fixed on the prey, and there is no growling or vocalization of any kind. The prey is not swatted. Instead it is knocked off balance with the backward pull resulting from the dew claw dug into the flanks of the prey. Without the single dew claw on the forepaw, a cheetah could not bring down the majority of its prey. The teeth are used only to kill the prey.

The cheetah only rarely employs its teeth in fighting. There is a ritualized or inhibited bite directed to the cheek, but it is short in duration and not damaging. It acts more as a threat that communicates: "Go away or I might do you real harm." In the most severe fights there are bites delivered to the forelegs primarily, but never to the throat. In summary it can be concluded

that the use of the prey-killing tools—teeth and claws—does not resemble the use of these same tools in fighting.

One of the most surprising results of predator—prey behavioral interactions is that cheetahs do threaten prey. This occurs only rarely, in the unusual circumstance of the prey that does not take flight. Cheetahs are so specialized for catching swift prey on the run that they are helpless when an ungulate stands its ground. To kill the prey it must first be brought down to the ground, and this is possible only when the prey runs away. It is the forward movement of the prey coupled with the opposing pull of the cheetah's forepaw that causes the prey to fall.

Cheetahs respond to a prey that stands and faces them by exhibiting the complex of interspecific threats. They lunge and foot stamp, growl and show their teeth. Sometimes this response puts the prey to flight and it is then overcome and killed. Other times the prey is successful in avoiding death by refusing to flee or by even making short charges at the cheetahs and driving them away.

The cheetah is no exception to other predators that have so far been studied, in that actual physical aggression is limited and rarely damaging. Also, like other predators, the cheetah exhibits aggressive behavior that is different from its predatory behavior. Unlike many other predators, the cheetah is often a prey animal, due to its many adaptations for speed. Because it is anatomically ill-equipped to defend its kills, a compensating set of interspecific threat gestures has evolved, which mimic the threats of the cheetah's competitors. The precise way in which the forepaws are used in fighting is different from other cats due, again, to an anatomy in this case, the feet and claws, that is modified for speed.