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Abstract: Experienced cheetah continue to hunt inaccessible prey at a near constant level, i.e. hunting motivation does not become habituated due to continuous visual exposure to prey. Mammalian carcasses elicit feeding, even if the animals were satiated to cut-up meat. Running away of the prey is unquestionably a releaser for attack. Cheetahs employ inter-specific threatening behavior against competing humans and prey that does not run, in the latter context threatening is effective in inducing the prey's flight. The cheetah does not knock the prey off its feet as earlier believed, but rather employs pulling with the dew claw to cause the prey to lose balance and fall down. The tail is unquestionably important as a rudder to change direction while coursing prey. The killing bite is released by the stimulus of a carcass.

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An Experimental Study of Predatory and Feeding Behavior in the Cheetah (*Acinonyx jubatus*)

By Randall L. Eaton

With 9 figures

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Introduction

Previous studies have detailed the hunting behavior (Eaton 1970 a) and predatory sequence (Eaton 1970 b) of the cheetah in the wild. Since these findings were reported I have been able to experimentally study and repeatedly observe predatory behavior under improved observational conditions in semi-captivity. I have discovered much additional information and even changed some earlier conclusions derived from study in the wild.

Results

For three months in 1970 and six months in 1971, I carried out a study of a large population of cheetahs caught in the wild as adults or sub-adults from South West Africa. These cheetahs were studied in a large (four acre) compound in an African wildlife park. They were left in the compound, free-roaming night and day. Except for my experimental manipulations, they were fed only whole chickens and butchered horse or cow meat.

The cheetahs 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 clear view of the ungulates and vice-versa.

Response to Carcasses

Even when fed to the point of fully distended stomachs and 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 (below). The use of one or both dew paws is restricted to play with prey and conspecifics and to fighting (Fig. 1).

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Fig. 1: The cheetah has a functional, slightly curved dew claw on the inside of each foot just above the pads (not shown here), and there is a highly modified dew paw, which is highly cornified, hard and pointed. The dew claw is used differently in both fighting and predatory behavior; the dew paw is used primarily in 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. Immediately the cheetahs fed ravenously, and did not stop until all was consumed, except for the skin, larger bones, skull, stomach and intestines.

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 (EATON 1970b) and by these same cheetahs to live-prey.

Carcasses were dragged behind a vehicle into the cheetah section. 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.

Experiments with Models

Models in the form of mounted specimens were brought into the cheetah area to test the responses of the cheetahs.

Gazelle Model

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 in the posture illustrated in Fig. 2. Olfactory inspection continued for several minutes, primarily at the anterior and posterior ends of the model. Cheetahs that eventually saw others inspecting the model, ran to it. Those that ran from a direction that brought them directly in front

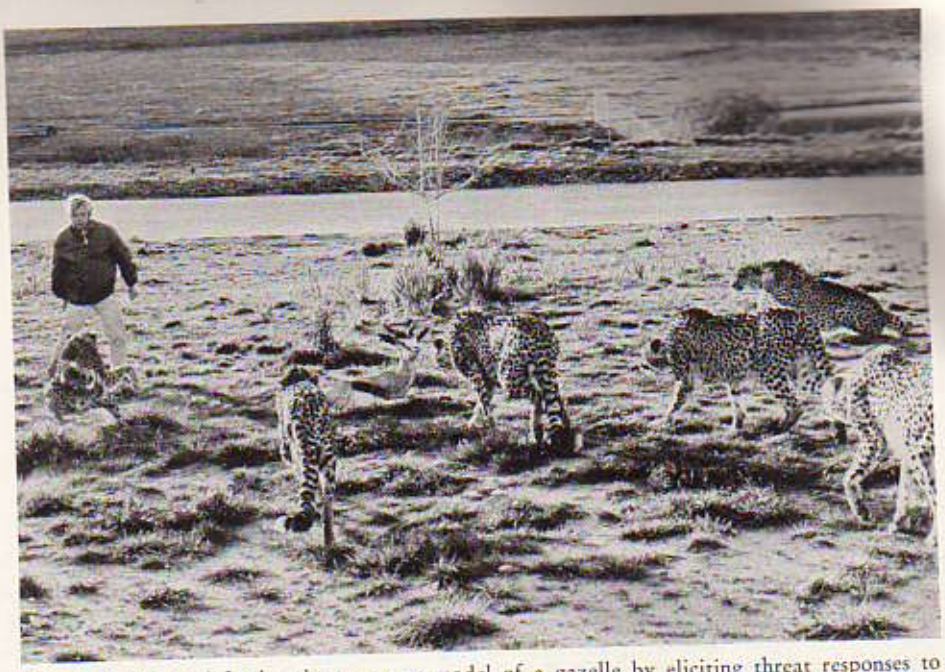

Fig. 2: Cheetahs defend a dummy prey model of a gazelle by eliciting threat responses to human intruders, just as they do to competing predators at a kill site in the wild. Some cheetahs approach the dummy in a "cautious" posture — body and head lowered. When approaching a dummy prey from head-on, cheetahs show signs of fear. Much of their olfactory inspection of the model is oriented toward the head and rear-end

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.

After about 10 minutes, one ♀ attacked the model by rising 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 as could lie around it side-by-side, usually about six. One or two of the same ♀♀ always "killed" the gazelle by biting it in 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 inter-specific threat behavior when we approached and took the model away. These threats, reserved for the inter-specific realm, are seen in the wild when cheetahs are approached by competing predators. They are never followed by a physical attack, nor are they ever seen in intra-specific threat or fighting (EATON in prep.) (Fig. 3 and 4).

Cheetah, Leopard and Tiger Models

To test recognition of conspecifics and to validify the response to models of prey, mounted specimens of cheetah, tiger and leopard were introduced.

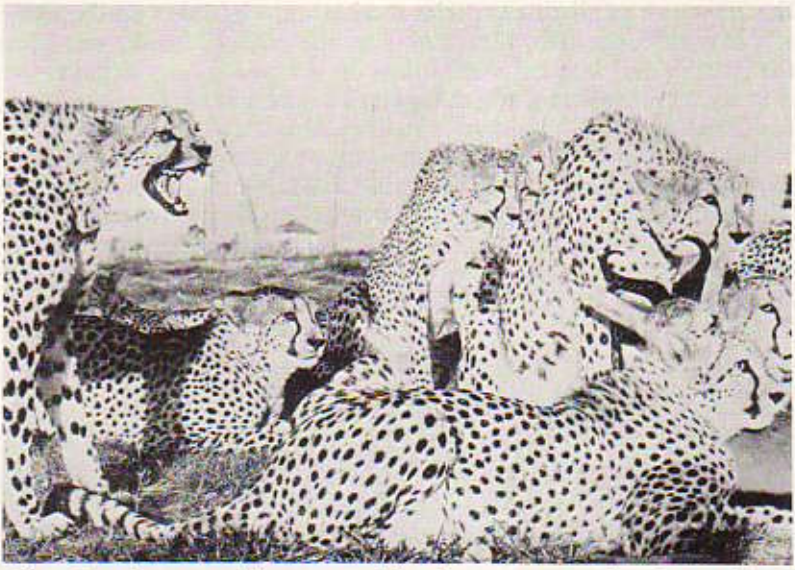

Fig. 3: Cheetahs gather around the prey models and attempt to eat them just as they do with a carcass. When approached by humans the cheetahs employ inter-specific threats, e. g. the ♂ on the left. The mouth is not opened this wide in intra-specific threatening

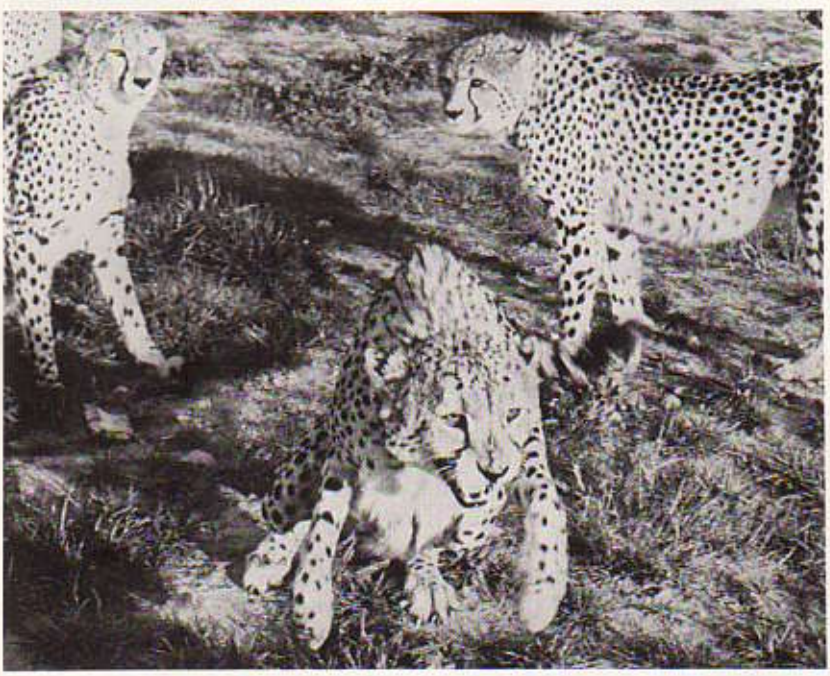

Fig. 4: A unique inter-specific threat in the "foot-stamp", shown here. The animal lunges forward while quickly raising both forelegs and then stamping them on the ground

The responses to all three species models were initially similar, consisting of the "cautious" approach, threatening at the models' heads, etc. However, both the cheetah and leopard were licked on the posterior end (EATON 1971), related to sexual recognition, and the cheetah model was mounted and copulated by a ♂. The cheetah model but not the leopard model was physically attacked and "killed" only by ♀♀. The ♂♂ showed no physical attack of a fighting or predatory nature against any of the models. Since a ♂ had behaved sexually to the cheetah model, it might be supposed that the ♀♀'s attack was a competitive one; however, ♀♀ do not compete for ♂♂ during courtship or mating (EATON 1971).

The tiger model was inspected but not licked (Fig. 5).

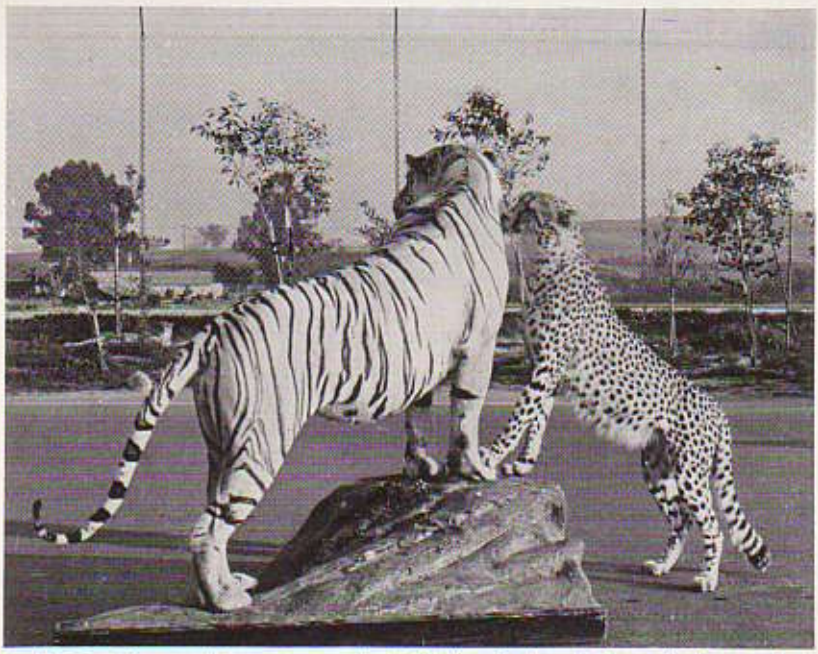

Fig. 5: A tiger model was approached with "caution" and olfactorily inspected. No signs of aggression or predation were observed

Response to Live-Prey

Live-Prey Separated by Fence

Prior to any experiments in which live-prey were released into the cheetah's area, observations of the response of cheetahs' 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, i. e. their behavior was not reinforced, maintained a high level of expression over a one year 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 (Eaton 1970b). 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 prey. Many times 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 cheetahs' 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, of 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 an obviously impossible successful hunt!). This 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 closeby and apparently staring at them, a threat.

It should be mentioned that the cheetahs that showed least interest in prey were the few sub-adults. 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 (Eaton 1970b; Ewer 1969, 1971). Apparently the lack of hunting education and experience affected their motivation to "hunt" the visually but not physically available prey.

Hunting of the inaccessible prey was not less intense following normal feeding, but was decidedly less 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 moon-light evenings. This has been well established for wild cheetahs.

Introduction of Live-Prey

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

Chickens that "froze" were softly and repeatedly pawed. Those that ran were chased. Two cheetahs killed all of the two dozen chickens, and they did so with bites in 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 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, 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 a sheep or goat. This was the result of the fact that the prey were so close. When they ran the prey was moving so slow that they could not easily be knocked off balance. Also, the cheetahs' speed was slow, preventing them from using the movements normally effective at greater speeds.

When the prey was released further away and/or ran away from the cheetahs faster, there was no difficulty in bringing the fleeing prey down and quickly dispatching it (Fig. 6).

Fig. 6: Live-feedings of typical-sized prey were carried out. The pursuing cheetahs' facial expressions have no signs of intra- or interspecific aggression

Some prey either did not run or stopped and faced the attacking cheetahs. When this happened the cheetahs stood back facing the prey. They would not strike or bite it, but instead elicited inter-specific forefeet stomping movements and facially and vocally threatened as they faced the prey. This behavior was effective in putting the prey to flight which resulted in its being caught and killed.

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 earlier (EATON 1970 b). As it turns out, finer analysis

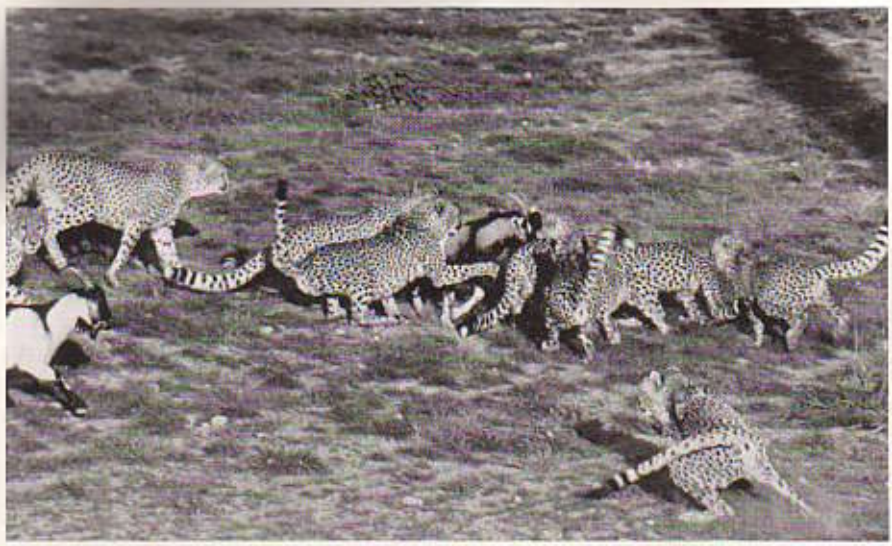

Fig. 7: The tail is invaluable in making quick changes of direction. The dew claw is used to exert a backward force on the prey and to bring it to the ground

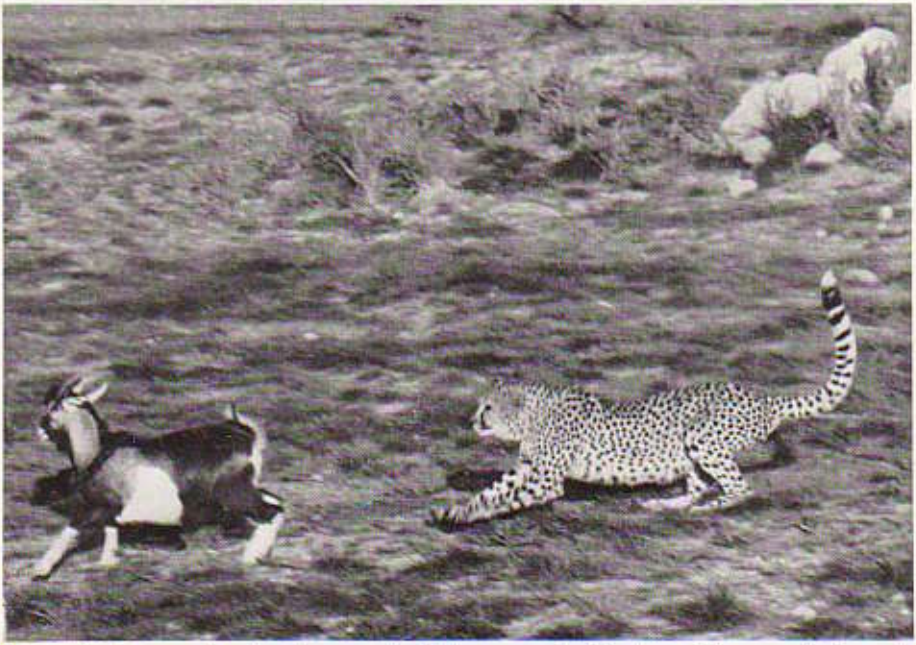

Fig. 8: As the pursuing cheetah nears the fleeing prey, it shifts its weight posteriorly as the foreleg is extended and used with the dew claw to pull the prey off balance so that it falls

proves that the cheetahs' predatory sequence fits the behavior of other felids more closely than previously believed.

For example, as Fig. 7 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 labelled "bringing prey down". The claw is inserted in the prey's hide and the cheetahs' weight is shifted posteriorly (Fig. 8) 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 on its side.

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

It is even more remarkable that at great speeds, accurately measured to be as high as 70 m.p.h., the cheetah is ables, in one motor sequence, to momentarily shift its weight posteriorly while extending the forepaw to bring down the prey.

With slower running prey cheetahs grab hold with both dew claws of the fleeing prey's hind-end, shift their weight backwards and pull back with the forepaws, thus weighting the prey and bringing it down (Fig. 9).

These observations also established that the orientation of the killing bite is elicited in another way than formerly described (EATON 1970b). Once the prey has 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

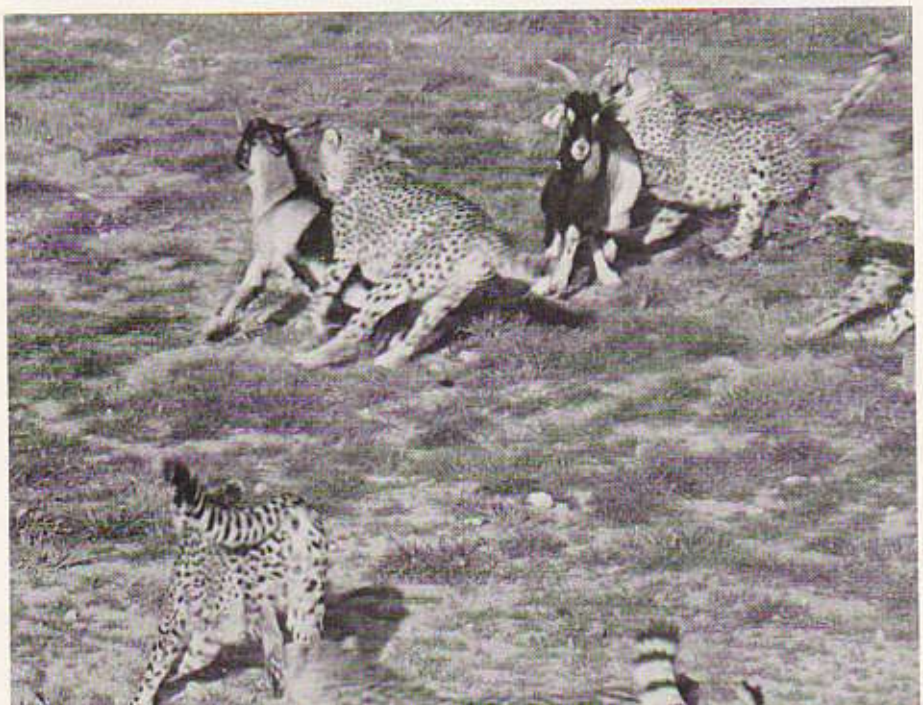

Fig. 9: In slower moving prey the use of the dew claw and backwards pull is sometimes insufficient to cause the prey to fall. In this case the prey may be weighted down by the cheetah climbing onto its hind-end

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.

During these movements the cheetah turns its head down and backwards. The upper ventral neck 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. In more recent experiments post-mortem examination of the prey has revealed occasional fractures of the spine in smaller 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.

I did not observe this technique in East African cheetahs, and it was observed in several of the cheetahs from South West Africa. Perhaps, as ELOFF (1972) has found in the Kalahari lion, a specialized killing technique has culturally evolved 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 ♂♂ that show the highest specializations in predatory behavior. Since writing this paper, similar experiments with an adult naive cheetah revealed that the killing bite was not in tact the first trail with live-prey. After feeding from carcasses killed by other, formally wild and experienced cheetahs, the naive cheetah killed on its third trial.

Conclusions and Summary

The following conclusions can be made from this study:

1. Experienced cheetahs deprived of hunting prey exhibit hunting even though they are not rewarded by the "kill";
2. Experienced cheetahs continue to hunt inaccessible prey at a near constant level, i. e. hunting motivation does not become habituated due to continuous visual exposure to prey;
3. Mammalian carcasses elicit feeding, even if the animals were satiated to cut-up meat;
4. Running away of the prey is unquestionably a releaser for attack;
5. Cheetahs employ inter-specific threatening behavior against competing humans and prey that does not run, in the latter context threatening is effective in inducing the prey's flight;
6. The cheetah does not knock the prey off its feet as earlier believed (EATON 1970b), but rather employs pulling with the dew claw to cause the prey to lose balance and fall down;
7. The tail is unquestionably important as a rudder to change directions while coursing prey;
8. The killing bite is released by the stimulus of a carcass;
9. Early experience would appear to be the best hypothetical explanation for the different response of experienced adults and sub-adults to live-prey; and

10. Field studies, by their prohibitive effect on repeated, close observation, should be duplicated, if possible, by captive studies under more controlled conditions which, for example, permit filming and more thorough analysis.

Zusammenfassung

Erfahrene Geparden jagen mit gleichbleibender Häufigkeit nach Beute, die sie sehen, aber nie erlangen. Tote Säuger regen das Fressen an, auch wenn die Geparden vorher mit geschnittenem Fleisch sattgefüttert waren.

Flucht der Beute löst den Beutefang aus. Geparden drohen den störenden Menschen und eine unbewegte Beute ebenso wie einen Artgenossen an; eine Beute flieht daraufhin.

Geparden werfen ihre Beute nicht um, sondern bringen sie mit der zuschlagenden Pranke aus dem Gleichgewicht. Der Gepardenschwanz dient in schnellem Lauf als Steuer.

Auch tote Beute löst den Tötungsbiß aus.

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