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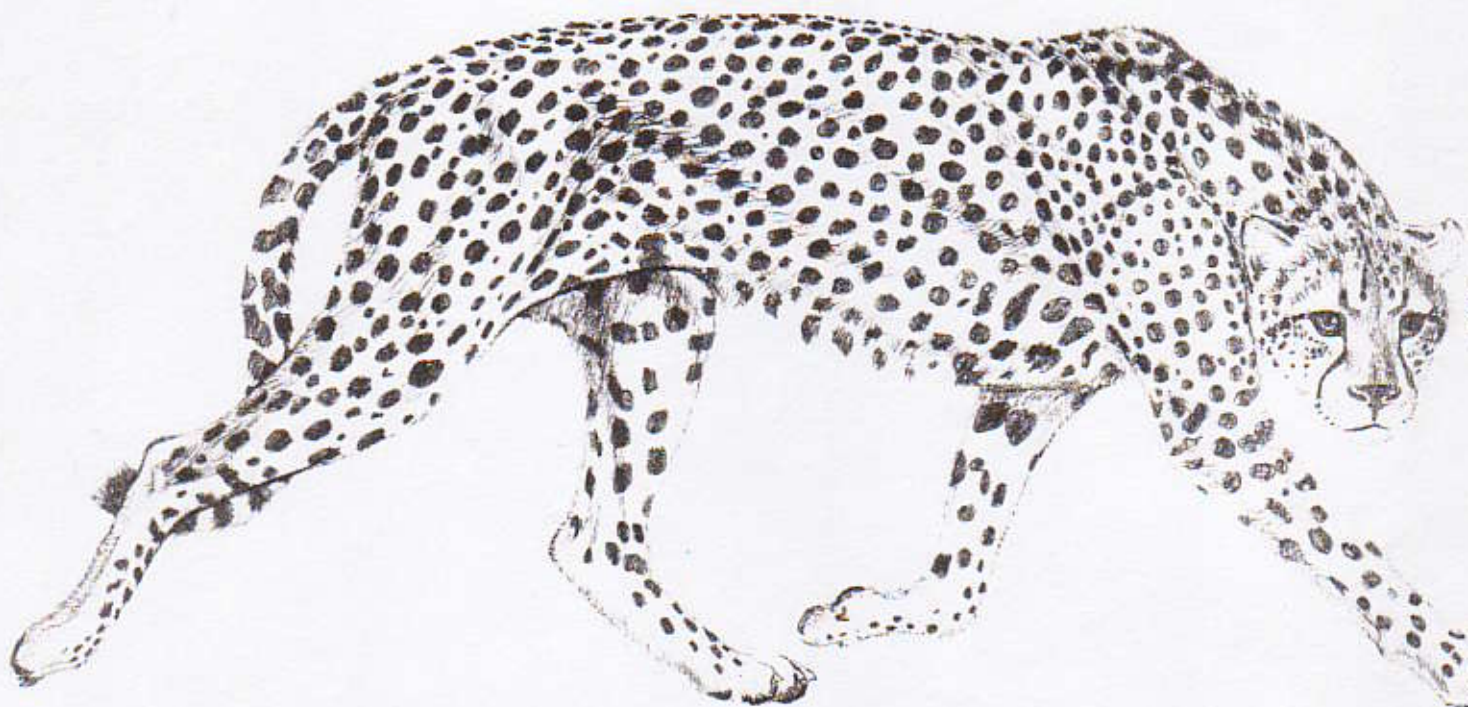
Abstract: Very ancient association between humans and cheetahs are dated 2300 B.C. This association began, because cheetahs are timid and extraordinarily effective and frequent killers. Adult females are the least tolerant of all cheetah classes and are very seldom seen together. Males or male coalitions occasionally attack other males.

The stripes in the face seem to serve to emphasize expression.

The usual number in a litter is three or four. The heaviest mortality occurs when the young start to follow the mother.

Limiting factor on cheetah populations are very poorly understood. Interest in conservation has highlighted the poor breeding record of cheetahs in most zoos.

In any event, the elusive cheetah remains a challenge to the naturalist.



Cheetah
(*Acinonyx*
jubatus)

Family
Order
Local names

Duma (Kiswahili), Rumu litutu
(Kichagga), Liteeli (Luhya), Kibau
(Kikuyu), Ngaku (Kikamba), Liwindi
(Lwo), Sumelil (Kalenjin), Arara (Ateso),
Andarafes (Kiliangulu), Harmaad
(Somali)

Felidae
Carnivora

Measurements
head and body

130 (112—150) cm

height

78 (70—90) cm

tail

75 (60—80) cm

weight

50 (35—65) kg

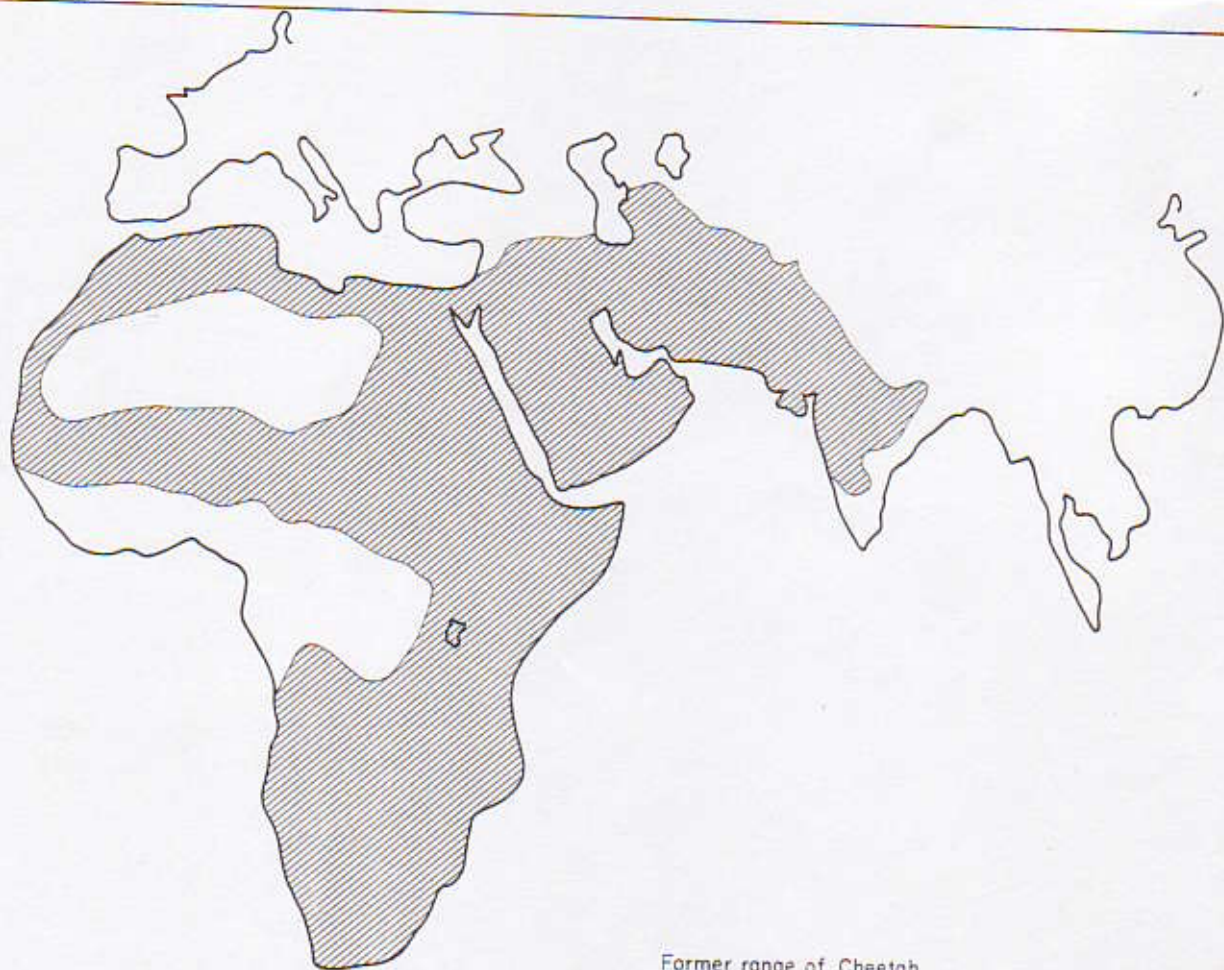
(Males weight
approximately 10 kg
more than females)

no races

Cheetah

(*Acinonyx jubatus*)

The cheetah's name derives from an Indian word meaning "the spotted one" and it is in India and the plains of southern Asia that early civilizations first came into intimate contact with this animal: a silver vase found at Maikop in the Caucasus is decorated with the representation of a cheetah wearing a collar; the burial mound in which this vase was found has been dated 2300 B.C., which points to a very ancient association between humans and cheetahs.



Former range of Cheetah

One can only guess at how such an association began, but cheetahs are perhaps more frequently robbed of their kills than other predators so need to compensate by being extraordinarily effective and frequent killers. Long before the Maikop culture early hunters were likely to have joined other scavenging carnivores in robbing cheetahs of their kills. People living in this way would not have tamed cheetahs, but in favourable localities one can imagine that the dividends of fresh meat would have sharpened human

awareness of the cheetah's habits and behaviour. The relative timidity of cheetahs and their diurnal habits would have been especially appreciated by human scavengers as would their use of relatively open country. Wherever both predators exploited concentrated populations of gazelles and other small ungulates one can be reasonably certain that our hunting scavenging ancestors were well acquainted with the cheetah and its habits. Wherever there have been prey populations to support them, scavenging societies have managed to persist side by side with a variety of post-neolithic cultures. The techniques of the hunters have been readily borrowed or adapted by aristocrats in search of recreation so that the early management of cheetahs that is implied by the Maikop vase might have been founded upon an already ancient familiarity between men and cheetahs.

The Scythians and Assyrians as well as the Ancient Egyptians and Indian civilisations have all left evidence of the taming of cheetahs. In Italy, cheetahs were coursed during the fifth century as well as the early Renaissance. The presence of 1,000 cheetahs in the stables of Akbar the Great (Ali, 1927) illustrates how widespread and abundant cheetahs (and their prey populations) must have been in the subcontinent during the sixteenth century.

Cheetahs were hardly ever bred or even hand-reared and wild populations evidently yielded considerable numbers of weaned or adult animals into captivity. Until very recently cheetahs were captured and trained according to ancient techniques that exploited some of the animals' peculiar characteristics.

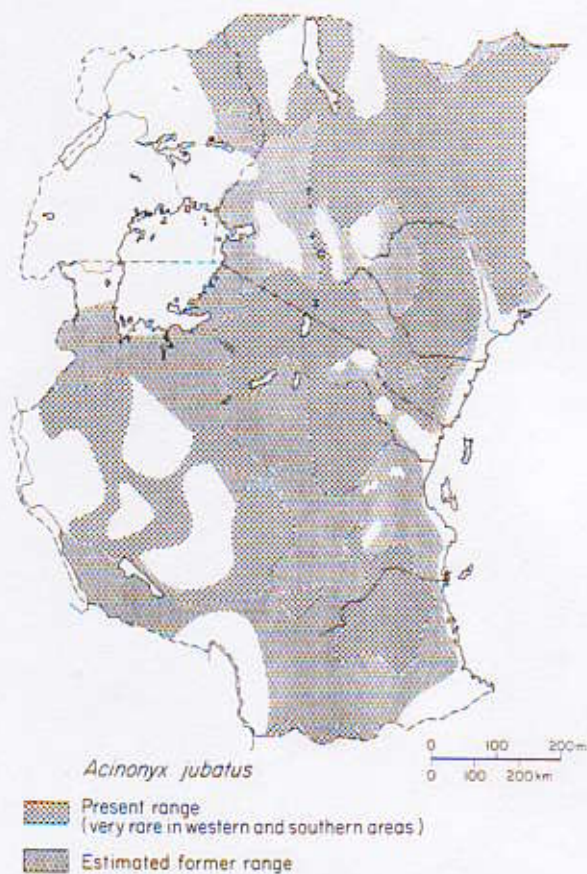
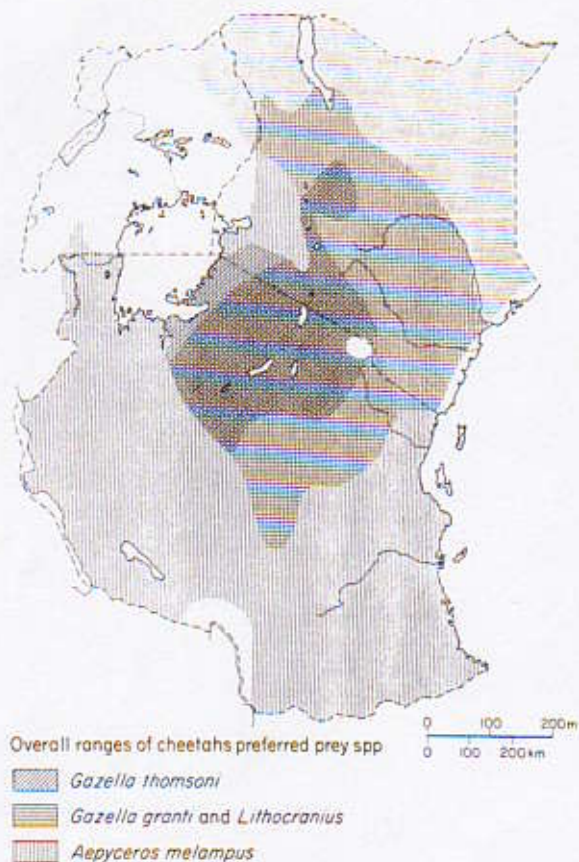
Cheetahs can run up to 112 km per hour (Bourlière, 1964) but are exhausted after a few hundred metres. Mounted riders could therefore tire and capture cheetahs very quickly. Once caught the first act was to slip a hood over the animal's eyes. The use of this simple device (which is shown in a famous painting of a cheetah by George Stubbs) represents the trainer's recognition of the primacy of vision in a cheetah's life, which orients its escape, defence and hunting by means of this sense. Hand-feeding returned the hooded animal to a dependence on its human keeper that simulated that of cubhood and was heightened by sightlessness and exposure to strange smells and sounds. Thereafter the cheetah graduated from darkened rooms to controlled hunts.

Like the other spotted cats this species throws up the occasional mutant with peculiar colouring or markings; light brown unspotted individuals, melanistic and white with bluish spots and blotched individuals have all been recorded. Several examples of the latter originating from Rhodesia and Botswana were once described as a separate species, *Acinonyx rex*. It is doubtful whether this species can be meaningfully subdivided even into races despite its far-flung and increasingly fragmented range. Once found all over the more open parts of Africa and from Syria and Arabia to the Kazak steppes and the Indian plains, it has retreated as gazelle populations have declined. Pastures suited to gazelles can often support sheep, and the principal reason for the cheetah's decline has been the steady expansion of sheep herding because, as their natural prey had been supplanted, cheetahs started to kill the sheep precipitating a confrontation that has been won by the shepherds.



Cheetah mutant with marbled spots

Any large population of small or medium-small ungulates is likely to



support cheetahs if their habitat is not too broken and the vegetation not too dense. In fact, patchy cover helps cheetahs to approach their prey close enough to rush it, whereas completely open plains often allow the quarry too much of a head start. On the other hand, if the ground is too uneven and heavily bushed, the cheetah's rush is impeded. I have seen, for instance, a cheetah come over a hillock on the heels of a fleeing impala and skid on to its back as it tried to avoid an obstacle, betraying that its powers of manoeuvre were inferior to those of the impala.

In East Africa, the cheetah's overall distribution coincides with that of the gazelles and to the south with some of the denser populations of impala. Thus Schaller (1972b) records Thomson's gazelles comprising 91% of cheetah kills recorded on Serengeti, while Pienaar (1969) recorded 68% impala out of 1,092 kills in the Kruger Park. However, they also take a variety of other species; oribi, reedbuck, dik-dik, duiker, young warthogs and the young of various larger antelopes are commonly eaten, while jackals, porcupines, *Orycteropus* and even various large ungulates, including young giraffes and buffaloes have also been recorded. Large prey is only tackled by several cheetah hunting together: the solitary hunter seldom tackles any animal weighing more than about 60 kg.

Cheetahs often appear to choose an individual prey animal before embarking on a chase and they can sometimes be seen on a termite mound or other eminence watching a herd attentively before beginning a stalk. Occasionally they will wait in ambush for a herd moving in their direction and

will then rush from very close quarters. Some species of plains ungulates can be approached openly and in these circumstances cheetahs may trot to within 50 metres before launching their high speed attack. In heavily grassed country, cheetahs are particularly helpless while the grass is long, yet even when there have been severe fires, the cheetah's approach may still be difficult because the ungulates appear to have a greater fleeing distance than those habitually living in the open and this may be in excess of the cheetah's striking range. These factors might help to discourage cheetahs from occupying long grass areas. If a herd happens to remain in tight formation when a cheetah rushes it, a kill is unlikely because of the difficulty of selecting an individual victim. The scarcity of zebras in cheetahs' kills may be a result of this. It is also important that the prey should flee. Schaller (1972b) remarked that stationary territorial gazelles may be passed by a hunting cheetah and any antelope or pig standing its ground is also unlikely to be molested. The cheetah painted by Stubbs was presented to George III and was ceremoniously released after a red deer in Woodstock Park to display its hunting prowess to the assembled nobility. However, the stag did not behave as it should and turning on its attacker tossed it high into the air, after which the cheetah absolutely refused to hunt.

In captivity, cheetahs will often charge the fence and stampede ungulates in the neighbouring pens; at Entebbe Zoo the cheetahs persisted in this behaviour long after the zebras, ostriches and antelopes had become habituated and no longer fled when charged. Causing a panic, scattering or stampede would seem to be an integral part of the cheetah's hunting technique as a fleeing animal's balance is very easily upset and the cheetah can quickly attain a stranglehold during the few seconds in which the animal is lying on its back or side. The cheetah pins its prey down at the base of the neck, after twisting the head round so that it can clamp the throat between its jaws while its own body lies facing the prey's back, thus avoiding the flailing



Cheetah strangling prey (from photograph)

legs of the suffocating beast. Because the cheetah's canines are rather short, they only just pierce the skin and the prey is killed by pressure closing off its air supply rather than through wounding. When the prey is very young or weak the cheetah may simply hold the muzzle in its mouth and suffocate it that way. The initial unbalancing of the animal may be achieved in several different ways. When the chase is really fast it is probably easiest for the cheetah to trip the animal up by hooking one of its legs from under it, and this technique has actually been filmed. If the prey is moving more slowly or standing, the cheetah has to rear up, hook into a flank or on the back and yank backwards, the asymmetric pull causing the animal to fall on its side. As the cheetah's toe claws are only moderately curved and are not flexible, the cheetah depends upon its specialized dew claws to hook its prey off balance. This reliance was well understood by Indian huntsmen that coursed cheetahs after gazelles.

"Cheetahs with blunted dew claws were not able to control full-sized black buck as effectively as those that possessed sharp undamaged ones. We have found therefore that the dew claw is very important to the cheetah and he can also inflict a severe wound with it. Sometimes it is solely by means of the dew claws that the black buck is secured in the chase." (Burton, 1952)

Because females have to rear families, they are probably the most frequent and well practised killers and it has been noticed that within small groups of cheetahs, particular adult females frequently take the lead in catching and killing. After the prey has been suffocated the killer often continues to rest for a while but cheetahs appear to feed rather more rapidly than other cats, a trait that may have been adapted to avoid losing the prey to other predators. Gnawing with the carnassial teeth, the cheetah cuts open the skin on the abdomen; the larger muscle masses on the limbs, back and neck are generally eaten first. An individual cheetah can consume 14 kg at a go and groups of four have been seen to finish an impala carcass in just over fifteen minutes. Bones and skin are usually rejected and sometimes the intestines also. When the latter are eaten, the contents may be squeezed out by the teeth as the gut is sucked into the mouth and throat. A mother making a kill on her own has been known to scratch earth or grass over the partially eaten or untouched carcass and return later with her cubs, but this behaviour is evidently much rarer than in other cats and many observers have asserted flatly that cheetahs never return to their kills.

The degree of success enjoyed by cheetahs is evidently very variable. In the Nairobi Park, McLaughlin (1970) found that 37% of all chases were successful but where the prey were juveniles the chance of being caught rose to 76% and in fact juvenile ungulates accounted for over half the cheetahs' prey in this park, in spite of representing only about 20% of the ungulate population. Nairobi cheetahs kill impala most frequently, followed by Grant's and then Thomson's gazelles. McLaughlin reckoned an average of one kill a day but solitary animals, particularly males, may kill only once in two to five days. Schaller (1972) estimated that a mother with cubs killed an average of 300 animals a year and solitary animals half this amount; 60% of the Serengeti records were of gazelles and about two-thirds of these

were fawns. On the basis of these figures he calculated a biomass representing 8.8 kg a day, of which an average of 4—5.3 kg of meat were eaten.

Hunting is generally conducted in the two or three hours after dawn or before dusk and both the heat of the day and the night are generally spent in concealment or resting. While resting, the narrow deep body lies on its side and only the head is raised from time to time, eyes cresting the surface of the grass. This posture and the conformation of the head with its raised eyes and lowered ears are well adapted to make the cheetah very difficult to see.

McLaughlin noted that males were most mobile, travelling on average about twice the distance travelled by a female and her family, the latter living within a restricted home range and covering about 3.7 km a day to the males' 7.1 The latter are also more willing to continue moving after dark, although several observers have noted cheetahs becoming nervous if darkness found them still feeding or in an exposed situation. Most sightings of cheetahs are in the morning or evening when they are on the move hunting, and even the sharpest-eyed observer is likely to miss seeing cheetahs if they are deliberately evading detection by lying in grass clumps or thickets. This evasiveness and the regular changing of lying-up spots and hunting grounds have probably contributed to the belief that cheetahs are very rare, yet this cryptic behaviour is an important strategy in their survival amidst numerous competing predators, particularly hyaenas, lions, dogs, humans and, in some areas, leopards, all of which have been recorded killing cheetahs. Records of lions killing cheetahs are especially numerous and the roar of a lion nearby is often sufficient to make a cheetah flee, take cover and freeze, change course, or even abandon a meal and the sight of one always precipitates instant flight.

The ability to "disappear" in the open grassy country and the animal's timidity are allied to physical defencelessness. The cheetah's hunting and killing techniques are so dependent on the fleeing response of its prey that they cannot be adapted to defence. As a result cheetahs escape confrontations by hiding or else they may attempt a bluff threat, which appears to be a somewhat more extreme form of intraspecific threat. The teeth are exposed in a wide-mouthed snarl and the body is bunched while the eyes glare upwards from the lowered head. Sudden forward leaps or even short charges are accompanied by a hard synchronized thump with the forepaws, similar to the striking action used against small prey like rodents or game birds: but threats have not been seen to develop into a serious attack, although a fleeing jackal has been reported to have been killed. Nonetheless, these threats are certainly effective as two cheetahs have been seen to repulse eight hyaenas. The fact that this kill had been made in the early morning might have influenced its outcome, for the reverse situation, hyaenas chasing a cheetah, was seen at night on Serengeti. Threats are accompanied by moaning or, at higher intensities, by hissing and very occasionally by a growl. If the animal lunges it may make a short yap as it snaps its teeth.

Cheetahs have an extensive repertoire of sounds. The most striking call is an explosive yelp, in which the animal's chest and head jerk with the effort. This call has a great carrying power and McLaughlin (1970) could hear it from a distance of 2 km. It is essentially a contact call and is most commonly uttered by a separated mother, juveniles or sibling companions but adult males also yelp. Its timbre can be likened to the spurfowl's croak and at a

lower volume to a passerine's chirrup, but the call appears to have a wide range of intensity and be subject to considerable variation, in which the individual's "signature" may play a not inconsiderable part. Juveniles at a kill make a whirring sound which may be equivalent to the warning growl of other felids, which can subside into a high-pitched rasp or rise to a ferocious squeal which generally signifies active fighting. Chirping accompanies any excited meeting between cheetahs that know one another, at a kill, around an oestrous female or at a scenting post and it is frequently interspersed with a rather metallic purring.

Purring accompanies play and various friendly encounters in which cheeks are rubbed together and much mutual sniffing and face-licking may take place but no body-leaning or side rubbing as is commonly seen in other cats. Purring is quite distinct from a curious humming noise which is occasionally heard from captives anticipating food. Adamson (1972) heard a cub make this noise as it began to stalk. She also describes a "nyam, nyam, nyam" associated with eating. Several calls have only been heard in the context of a mother and her young. Eaton (1970b) described cubs grouping and keeping still in response to a short low-pitched sound from the mother; cubs will even stay and watch the mother feeding until she releases them from their immobility by calling them: releasing calls are the loud yelp (from a distance) or a call Adamson (1969) describes as "ihn, ihn, ihn", which is used to call up hidden or lost young, or else a sharp "prrrrr", which is specifically associated with movement and elicits close following of the mother. Very young cubs in a hiding place may respond to disturbance or to the arrival of the mother with a sound like the breaking of a stick. Although moaning is heard in threat a rather bleat-like moan denotes distress and is made by a pursued or lost animal.

The most lasting and conspicuous social bonds are between a mother and her cubs and between siblings. Also there have been repeated observations of several adult males together but of unknown relationship (see Foster and Kearney, 1967) and the latter grouping often results in the hunting and killing of prey that is larger than average.

The most thorough study of the cheetah's social life and behaviour to date is that of McLaughlin (1970) in the Nairobi National Park. Here he was able to follow three distinct and independent groups numbering eleven animals altogether. He encountered 21 other cheetahs in the park, all of which were transient. The total range of one family group was estimated at 82 sq km and another at 76 sq km. These figures are probably a fair average for a locality with reasonably abundant prey but it is obvious that food resources are an important determinant of the extent of the cheetah's range. Schaller (1972b) noted a mother and her cubs remaining within ten sq km for about one-and-a-half months and Adamson's partly hand-fed but free-ranging female lived within a range of about 56 sq km. The large proportion of transients recorded by McLaughlin illustrate how mobile most cheetahs are even in areas with abundant prey. The large-scale movements of gazelle populations on Serengeti are followed by cheetahs and might result in different seasonal ranges, but even Adamson's cheetahs, with every inducement to remain in a small locality, chose to change their lying-up spots and hunting grounds every few days or even daily. Very young cubs slow down this con-

tinuous circulation but even so the mother changes her shelter regularly if only for a few hundred metres or so. Both McLaughlin and Adamson noted extensive overlaps of home range among adults in spite of this. A individual's or family's favourite area was very seldom intruded into for very long, even by adult offspring of a former litter.

The favourite area always contains a number of elevated points which are regularly marked by the resident cheetahs with excreta. These marked trees, stumps, termitaries, hillocks, rocks or banks are focal points for any cheetah. Those living within the area revisit them regularly, males and females depositing dung and the former also squirting urine. Transients also tend to go from one vantage point to another and often add their deposits after sniffing at what was already there. It looks as if viewpoints also provide natural foci for all types of indirect social contact, for urine and dung can presumably carry the signature of a known individual as well as indicate a stranger's sex and condition. These places are certainly social landmarks for cheetahs but they have been variously described as meeting points or rendezvous, territorial marking posts and latrines. The Indian huntsmen knew these places well and used to trap cheetahs when they revisited such landmarks (Sterndale in Hanström, 1949). A cheetah's reaction to the message contained in a urine-sprayed tussock or dung on a termitary must obviously vary according to its own sex and status, but evasion is by no means the only reaction as some authors have asserted.

McLaughlin stressed that a scent mark may excite curiosity in the first place rather than avoidance and Adamson described her family of cheetahs often choosing to play around these places. She also noticed that previously attractive viewpoints were abandoned after the group dispersed. Deliberate chasing away of female members of the former litter was seen and there was a readjustment of home range; with the arrival of a new litter there was a quite different choice of trees and termitaries from those that had been frequented with the previous one. This suggests that the female's deposits are one manifestation of a particular family's link with its environment (the tendency to play at such spots implies a heightened sense of security) and the link dissolves with the dispersal of that family and requires to be built up anew with another litter. The fact that female members of an older litter are no longer tolerated can only reinforce the obsolescence of the landmarks associated with them.

Adult females are the least tolerant of all cheetah classes and are very seldom seen together. Furthermore, the mother of a litter is the most sedentary of all classes and her marking of the favourite viewpoints in her range probably repels other females. Adamson (1969) knew and followed four related females over a period of several years and they were effectively territorial in that none of them seemed to intrude into one another's hunting grounds, while males, on the other hand, appeared to roam around at random. Mrs Adamson was frequently threatened by a particularly aggressive subadult female when on the cheetah's home ground, but this animal lost all trace of aggression if she accompanied her hand-reared mother on visits to Mrs Adamson's camp. This and other young females exhibited an altogether more defensive disposition than male cubs, a trait that was apparent at an early age. An example of female intolerance was provided by this mother's bolting, together with

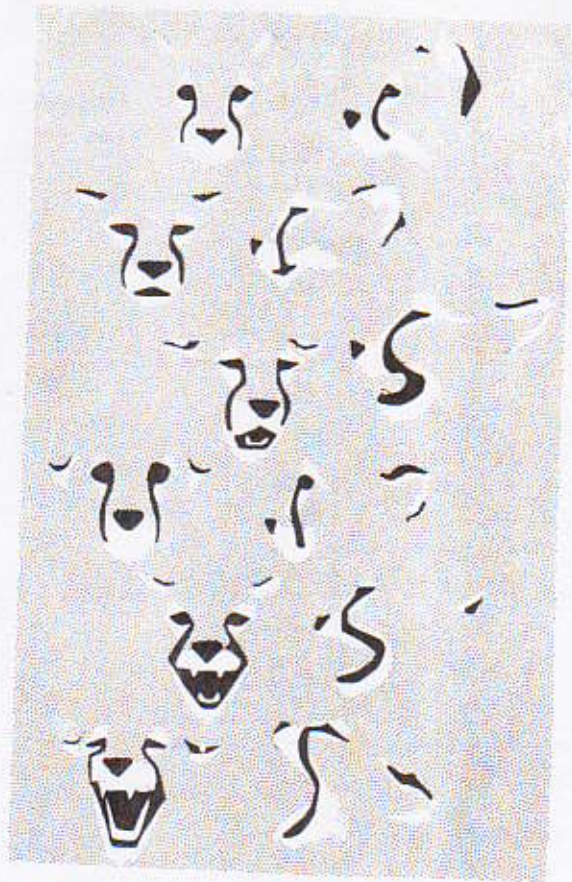
her cubs, at the sight of an adult daughter. However, having hidden her young the mother made an aggressive come-back.

McLaughlin often saw males together but never all-female groups; he thought mixed groups represented recently independent litter-mates and Moss (1976) recorded that one young male in the Nairobi Park joined up with two others when he left his mother. In a captive colony in America, Eaton (1972) introduced a stuffed cheetah dummy. Males did not attack this, whereas females gave every sign of trying to kill the intruder.

The results of a questionnaire survey covering nearly 1,000 sightings were reported by Graham and Parker (1965) (in Graham, 1966). Nearly half these were of single adults and 31.6% were of two and 11.8% of three; only 3.1% were of groups containing over five adults. Again, these authors remarked on the absence of female groups and noted that females do not even travel very often with males. McLaughlin frequently saw males make attacks on family groups, but given the extended and aggressive nature of courtship it is likely that these attacks were a manifestation of sexual behaviour (see below).

Males occasionally attack other males and Alan Root has filmed an occasion where two males killed a third. On two other occasions a fatal fight has been seen to break out over a kill. However, Stevenson-Hamilton (1954b) reported a male killed in a fight over a female and captive males often fight fiercely over an oestrous female. Eaton (1973) regarded the fights he observed in a zoo pen as highly ritualized in nature. An interesting interaction between two males in Kidepo National Park was seen by Ross (personal communication). A solitary adult male lying near a small hillock was approached by a second male, which announced its arrival with yaps interspersed with purring. The first male flattened itself as though to hide but the second cheetah could nonetheless see him. However, he continued to move in an agitated manner, still yapping over the top of the hillock, where he was out of sight of the first cheetah, which then moved over and sheltered under a bush. Some hours later the situation appeared not to have changed; the second cheetah was still near the top of the hillock, trotting around there, yapping and he was twice seen to smell and spray a tree trunk. Suddenly he started to run and Ross thought he was after some nearby gazelle but he broke right, charged the first cheetah and struck him with his forepaw. He then moved off into the dusk, still yapping and purring. Although the cuff was the only sign of direct confrontation, it is tempting to believe that the second cheetah displaced the first and that the calling, posturing and urine spraying on the hill top represented a dominance display. Although too little is known about cheetah behaviour in general and the nature of inter-male relationships in particular, to be able to interpret such incidents with any certainty, there are close resemblances with sexual behaviour which will be discussed shortly.

While families tend to be the most restricted in range there is also some evidence that some males or even male groups may be more resident than others (McLaughlin, 1970; Schaller, 1972b). Cheetahs may resemble the other cats in that young and inexperienced males tend to be forced into a more nomadic existence by the intolerance of older cats. As they wander over a large area males probably meet many other individuals. Although these encounters may be sporadic it is possible that loose hierarchies emerge between individuals and groups as well as within groups. Adamson (1972) saw



clear evidence of a hierarchy between members of both sexes within litters but she also saw changes in status.

Like other cats, cheetahs signify submission by falling on their backs and presenting their white underparts to the aggressor. They moan at the same time and this seems to inhibit attack. At greater distances a threatening advance may be deflected by the submissive animal sitting down sharply on its haunches and looking away with its mouth closed and somewhat pursed. This response has even been seen when large or aggressive animals, instead of running away, turned to face a charging cheetah. The facial expression of a submissive cheetah is peculiarly pinched because the black margins of the mouth are hidden. In confident or aggressive expressions the black tear stripe and lips are joined together in an emphatic geometric figure. Eaton (1970b) suggested that the stripe might be an anti-glare device but a more plausible explanation is that it serves to emphasize expression. Expressions are primarily directed at other cheetahs but snarls and snaps are part of the animal's bluff in defence of its prey and so a spectacular snarl might also be advantageous against a competitor.

There is no ruff to enlarge the face mask as there is on many other cats, on the contrary, the overall pattern of spots continues past the ears so that at a distance the head becomes almost as difficult to see as the body. Camouflage is useful to the cheetah both as a hunter and as the first line of defence for a persecuted subordinate of more aggressive carnivores and scavengers. It is



only at very close quarters that the mouth, muzzle and eyes emerge from the spotted matrix, and the black markings that surround and link these organs of expression certainly serve to bring them into great prominence once the animal is close enough to be actively responding to the presence of another animal. Although the back of the ears are also boldly patterned, these markings only show up well from behind or when the head is lowered in intra-specific threat. The visual role of the black stripe and lip margins is best illustrated by comparing drawings of the animal's expressions with identical outlines in which the black margins have been removed.

In an environment of grass and scattered scrub the cheetah is a very inconspicuous animal and it is only on their elevated viewpoints that cheetahs allow themselves to become conspicuous and assume what might be called display stances; cheetahs rely mainly on sound, however, to communicate with one another over a distance.

Amongst the litters watched by Mrs Adamson there was one containing a female and two male cubs; when the males matured at fifteen months they engaged in much homosexual mounting as well as attempting to copulate with their sister, and copulations were interspersed with metallic purring, urine squirting around a fallen tree, circular chasing and spanking at one another's legs. There are numerous observations of several males copulating with a female in turn. On average the female's oestrus lasts about two weeks and is preceded and succeeded by periods of increasing and diminishing receptivity, during which time the scent of her vaginal discharge and frequent urine squirts may be responsible for the males' convergence. Akbar, The Mogul Emperor, recorded trapping six male cheetahs which were apparently in pursuit of a female in season (Ali, 1927).

The males in a captive group watched by Herdman (1972) fought one another in order to remain closest to the female, and a dominant male emerged. As a female came into oestrus Herdman noticed a marked increase in the frequency with which males sprayed urine on to prominent landmarks or tussocks. Urine is also directed on to debris piled together by scratching by the hindlegs. Clawing, which is important in most felid species, seems to be mainly associated with courtship in cheetahs and Schaller (1972b) saw a female raking her front claws past the face of an advancing suitor. She would roll in front of him and then dash away only to approach again. Although males are larger and more powerfully built, females are usually the more aggressive sex and exhibit submissive behaviour only during oestrus. Males are frequently aggressive towards an oestrous female, knocking her over and slapping at her, even biting at her flanks or hindquarters. The female often attempts to hide under thorn bushes, but impulses appear to alternate and she emerges only to be subjugated again. Mutual mouth to mouth licking and grooming of the chin is common in siblings and also occurs between adults during resting periods in between bouts of harassment or copulation, but interest in one another wanes as oestrus declines and the males eventually desert the female completely.

The gestation period lasts 90—95 days and, although there is a record of eight cubs in one litter (Graham, 1966), the usual number is three or four. They are born and hidden in a well-concealed retreat under a bush.

(Mrs Adamson's Pippa always chose the wait-a-bit thorn, *Acacia mellifera*, to hide her young.)

There seems to be an extended birth season in tropical East Africa between January and August with the majority of births between March and June. Late litters are occasionally burnt to death in the grass fires that start in June or July. Indeed, the timing of births may have been influenced by this hazard. There is no evidence to suggest that females are unable to feed themselves or their young at any time of the year, but Cade (1966) describes three well-grown cubs that had lost their mother wandering into a Kenya township in the last stages of starvation, illustrating how vulnerable and helpless young or inexperienced juveniles are. However, it seems very unlikely that the vicissitudes of large cubs and subadults could influence the timing of a birth season as has been suggested by some authors.



At birth the young are unco-ordinated and blind but they can turn their heads towards a disturbance and spit explosively. They weigh about 150—300 g and appear to be dirty white above and black below; before long the spots begin to assert themselves as the underparts lighten but the long mantle of greyish fawn fur covering the cubs' back, nape and crown disappears more slowly. Although a cub is tawny and spotted almost all over by the time it is three months old, the last traces of a crest are still present when a cub becomes independent at the age of about fifteen months. Various suggestions have been made about the meaning of this pale woolly mantle: that it acts as a thermostatic umbrella against rain and the radiation of the



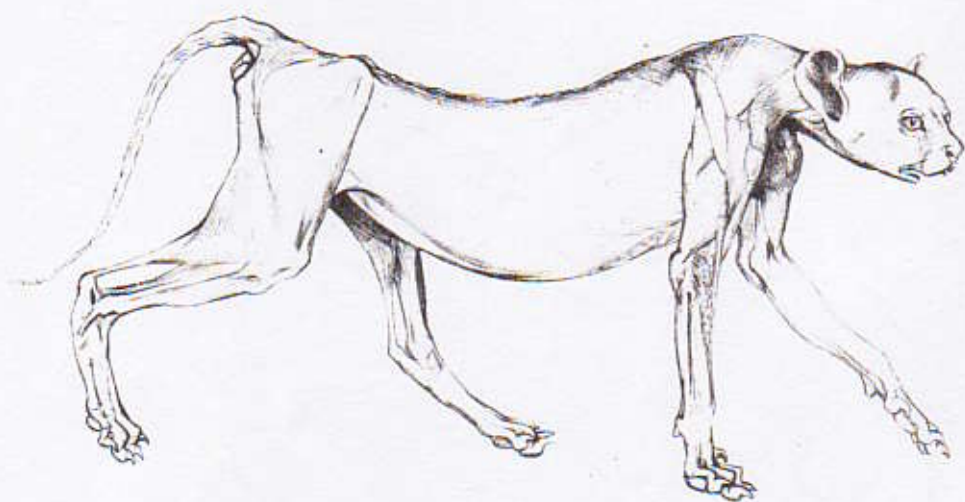
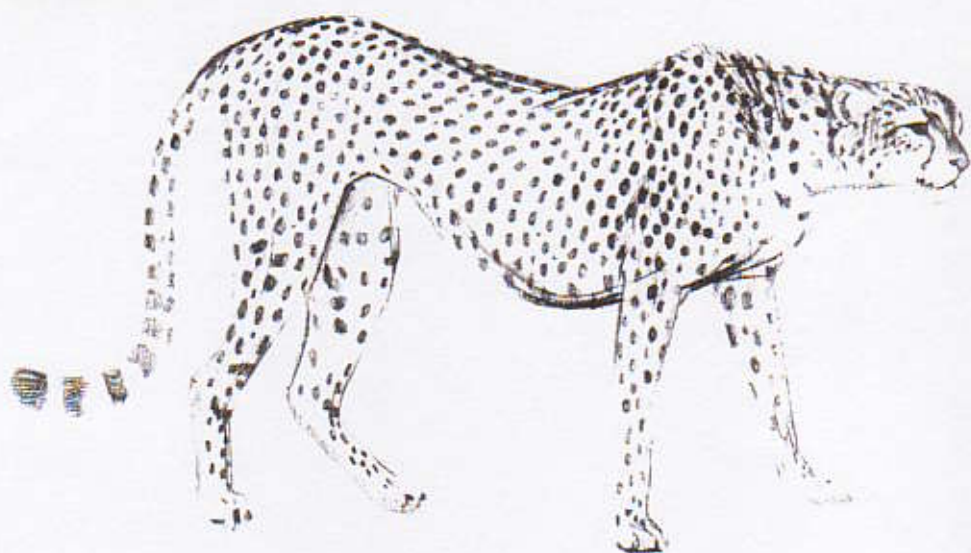
sun and that it is a camouflage imitating the dry dead grass. While it is likely that both these functions are served, there is also a third possibility. Intra-specific appeasement behaviour, exposing the belly, starts rather late among cheetahs, when they are fully mobile and with semi-adult colouring. Very young cubs respond to an alarm by freezing and this immobile position leaves the young's back exposed. Males have occasionally been recorded killing cubs, but such a response could perhaps be inhibited by a reversal of colouring. If it could be shown that aggression was inhibited by the sight of white fluffy fur in adult conflicts, the light fur on the baby cheetah's back might

then be shown to have a survival value. It has already been mentioned how a mother fled and hid her young cubs from her adult daughter. This mother would decoy anyone attempting to follow her to her recently-born litter by going in the opposite direction and then doubling back. Her evasion technique was to sit quite still until she could slip away unnoticed. All observers have stressed how cautious and patient females are when visiting their hidden young. This makes Mrs Adamson's report on the mother's lack of concern for elephants all the more astonishing (Adamson, 1972). She suggested that the mother deliberately kept her young close to a herd of elephants for the security they engendered and she describes the cubs being enveloped in dust churned up by an elephant's feet while it fed on the branches of the bush beneath which the cubs were sheltering. Shelters are sometimes moved daily and Adamson recorded twenty-one moves in six weeks and a maximum stay in one spot of twelve days.

The young open their eyes at four to eleven days and teeth break through the gums at about three weeks. Florio and Spinelli (1967) record a captive mother regurgitating meat in front of the cubs when they were eighteen days old, but such behaviour has not been seen in the wild. The cubs can generally walk well at three weeks but do not accompany the mother until they are about six weeks old, keeping very close to her and responding quickly to her calls; from this time onwards they are normally inseparable from the mother and during the first three months the young are an obstacle to successful hunting. The mother, however, appears to be able to inhibit following by a short low-pitched noise and their immobility is released by another call. At other times Mrs Adamson's mother cheetah was seen to induce playing cubs to follow her by dashing round them in circles, whereupon they chased her and she then led them off. The same animal appeared to solicit her human companion for a walk by deliberate jerking of the head.

The mother plays with her young but the most intensive and continuous play is amongst siblings. Elements of hunting behaviour are unmistakable with chasing, batting with forepaws, leaping into the air and spinning round and round an injured prey animal. Perhaps the readiness of captives to retrieve balls and their trembling with excitement in anticipation of the next throw is part of this early practice of hunting skills. Play very often takes place on a favourite tree or other elevated landmark and may involve mock fighting and chasing as well as invitations to tugging contests and attempts to dislodge one another. Much mutual mouth licking is characteristic of resting spells in between bouts of activity and before the young leave their mother elements of sexual behaviour also appear. Hierarchies are apparent in play but these first appear as infants struggle at the mother's nipples and, according to Adamson, the status of a sibling may change.

The time of weaning varies as the female may cease to lactate between fourteen and twenty-four weeks but growth is very rapid. They are half adult size at six months and at eight months lose the last of their deciduous teeth, the canines. At about this time the cubs are allowed to make their first clumsy attempts at stalking and catching and if fawns are around these efforts may be successful. Prior to this the mother catches all the food, although she may carry living young animals to the cubs, which attempt to strangle dead



or dying prey from an early age. Between twelve and fourteen months the young start making successful kills on their own.

The heaviest mortality occurs when the young start to follow the mother and McLaughlin estimated that a litter average of 4.2 cubs at birth was down to 2.5 by the time the young are independent. A female can conceive at 21—22 months and thereafter the average interval between giving birth and conceiving is about eighteen months (Schaller, 1972b), although Spinelli and Spinelli (1968) noted a captive female coming into oestrus four months after giving birth and Adamson's female mated a few weeks after a new litter.

Schaller (1972b) points out that the population turnover is higher than that of lions or leopards and he remarks that unknown factors keep the Serengeti population depressed and seemingly stable at a very low level, his estimate of density standing at about one cheetah per 260 sq km, whereas McLaughlin's estimate for the Nairobi Park was about one per 5 sq km. Such disparities make any attempt at estimating total populations virtually

impossible, but popular interest in the cheetah has encouraged some conservationists to guess figures. Meyers (1975) suggested 15,000 for the whole continent while Eaton (1971) published a figure of 2,000. The latter is lower than a realistic estimate for Kenya alone, where cheetahs range at variable and unknown densities.

Limiting factors on cheetah populations are very poorly understood. The roles of competition, of the physical environment, of fires and of prey populations have been mentioned earlier. Diseases known to affect cheetahs are anthrax, (Pienaar, 1969), tick fever, Babesia felis, feline enteritis (Murray, 1967) and a variety of parasites may accumulate in a malnourished animal. Loveridge (1933) records a sick animal being infested with *Ctenocephalus* fleas, ticks, hippoboscids and the larvae of *Sphargnum*, which he thought might have been collected through eating frogs or fish. Experiments have failed to induce tse-tse flies to feed on cheetahs and they have not been recorded to suffer from trypanosomiasis, and their scarcity in the miombo woodlands is probably due to a shortage of suitable prey. The longest life record for captivity is fifteen years and seven months but the average life of captives is five years and two months. (Van der Werken, 1968.)

Interest in conservation has highlighted the poor breeding record of cheetahs in most zoos. This reluctance to breed has been recognized and discussed for many years; as wild males only approach a female when she is in season, the zoo habit of keeping a pair in permanent close confinement may inhibit mating. Whipsnade Park in England has had the greatest success to date. Eaton (1973, 1974) has discussed the problems of breeding in captivity. In this connexion it is interesting that the seventeenth century Moghul Emperor Jehangir Khan had this to say:

"It is an established fact that cheetahs in unaccustomed places do not pair off with a female and my revered father (Akbar) once collected together 1,000 cheetahs. He was very desirous that they should pair, but this in no way came off. At this time a male cheetah, having slipped its collar, went to a female and paired with it and after two and a half months three young ones were born and grew up. This has been recorded because it appears strange." (Ali, 1927)

Ghenghis Khan, Akbar and Jehangir were all avid coursers of the cheetah as was Charlemagne. For these royal patrons the cheetah was perhaps the vehicle for projections of grace, speed and superiority as well as the provider of thrills of the chase (now widely satisfied by greyhounds and mechanical contrivances). The Ancient Egyptians endowed the cheetah with the spirit of courage, while a contemporary projection is of the elusive grace of a declining wilderness.

Is it the persistence of extraneous human projections or is it the animal's intrinsic elusiveness that has been responsible for the paucity of scientific information on an animal that we have good reason to believe has been handled by men for well over 4,000 years? In any event, the elusive cheetah remains a challenge to the naturalist.