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Abstract: Courtship behaviour has rarely been seen in the wild. Increasingly successful breeding programs in wildlife parks allow to learn more about courtship and mating requirements. Observations on social behaviour of cheetahs mainly from Lion Country Safari are presented, from grooming to courtship and mating are presented.

5 *Courtship and Mating Behavior*

Courtship behavior has rarely been seen in the wild, and has never been completely described or photographed. One of the values of the new environmental zoos such as San Diego Wild Animal Park, is their ability to more successfully breed rare and endangered species. Breeding programs in wildlife parks have already succeeded, not only in producing cheetahs but also in learning more about courtship and mating requirements.

At Lion Country Safari cheetahs frequently groomed each other by licking, particularly in the face, lateral neck, and shoulders (Fig. 5-1). Groups of cheetahs (up to five), male, female, and mixed, laid or sat in a star formation, all licking one another's faces simultaneously. There are certain older males to whom the young females seem attracted for grooming sessions. These males are similar in that they tend to lie-up alone. The young females were members of the same social group while the older males from whom they so often solicited grooming were not. When one young female was released from isolation in the enclosure after five days, she went from cheetah to cheetah and licked each of their faces briefly. She made her way across the entire section stopping at nearly every cheetah. It is believed that mutual grooming is socially reinforcing in the wild groups, and appears to obtain at higher levels in members of social groups still together in captivity at Lion Country Safari and World Wildlife Safari. Short grooming sessions after prolonged lack of interaction

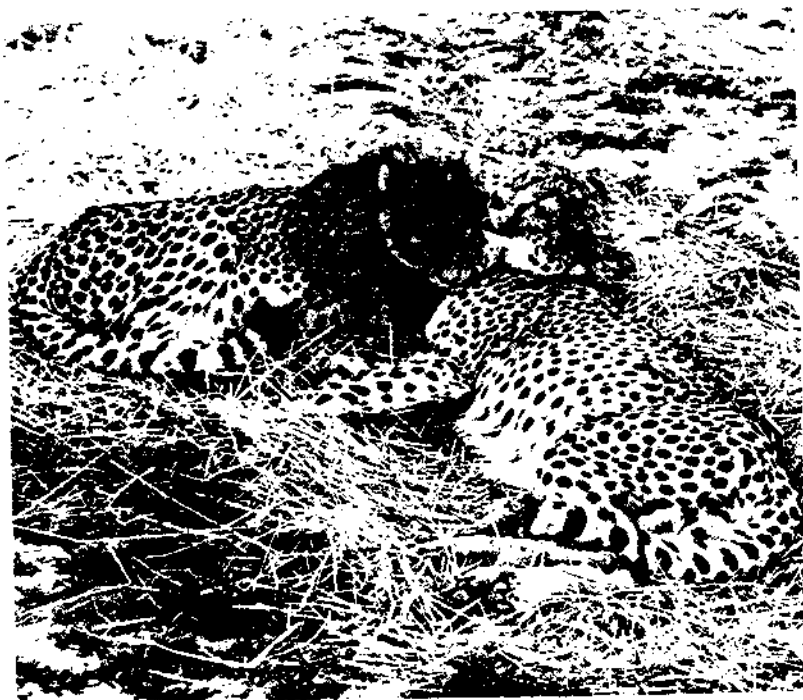


Figure 5-1 Socially familiar and courting cheetahs frequently groom one another (Photo: R. L. Eaton.)

may constitute a form of inspection and identification of other cheetahs since the *Flehmen* response often follows. There does not appear to be any significant reflection of dominance or status in who grooms whom except that females often initiated grooming with older, larger males.

Grooming of other cheetahs by females in behavioral estrus was similar in motor pattern to the social grooming described above but it differed in several significant ways (the use of the tongue is the same in both cases and usually both animals have their eyes closed). First, the female in estrus elicited the behavior much more frequently, going from male to male. Males either reciprocated by licking the female or they simply did not respond. Secondly, unlike social grooming which lasts anywhere from 5 to 30 minutes, the courtship grooming was shorter with any single male. The female either moved on to another male or more advanced stages of courtship then took place.

In the summer months, courtship grooming and all phases of courtship

occurred throughout the day while social grooming was seen later in the day or following feeding. However, as winter approached and the cheetahs were more active, social grooming occurred throughout the day (S. J. Craig, pers. comm.).

Typically, it is the male that marks in the wild, and at Lion Country and World Wildlife Safari this was also the case. The usual posture is a tail-up while standing and facing 180° away from the marked object—tree, rock, stump, etc. The hind legs are raised and lowered alternately four or five times during the emission of from two to six urine jets. This treading movement (sometimes referred to as “skating”) appears to have been derived from scraping behavior associated commonly with marking in other felids. Scraping movements of the hind legs were observed in wild cheetahs only rarely, and then only in males. It was observed at Lion Country only in the two oldest males.

The tail touches the marked object and the tip of the tail is moved backward and forward and laterally touching both sides of the object prior to the squirting of urine. It appears that tactile information from the tail allows proper orientation in effectively directing the urine. The cheetah does not orient visually to the marked object once its rear is turned toward the object. The same is true of lions but they do not tread extensively; instead, the scraping movement of the hind feet alternately is exhibited more commonly.

In the wild only two, older male cheetahs were observed marking in the rear-end down posture or squat. At Lion Country several males urinated in the rear-end down posture. It was seen when males ran toward an estrus female that had given the “yelp” call. The males, running from 100 yards or more away, stopped abruptly, lowered their rear ends, urinated, and scraped with their hind feet. In these cases the fluid was passed not in jets but in a steady stream. Scraping during urination (a steady flow of urine) was also exhibited by the two older males in situations unrelated to mating.

The tail-up posture markings were frequently made by cheetahs on the same objects, inspected by smelling and marked over by other cheetahs. In no cases observed did cheetahs smell at or mark over the urine passed in the rear-end down posture by a male.

Urine markings are smelled and often *Flehmen* follows. *Flehmen* in wild cheetahs was not described in my field study, I simply did not recognize it as such. After smelling a urine mark or some novel object, the cheetah raises its head to the horizontal plane, the mouth is opened 3 in. and held open for only two to three seconds. Occasionally the tongue is slowly extended and touches the odoriferous object, or, repeated, relatively slow lapping of the tongue is elicited prior to *Flehmen*. There is no raising of the lips or wrinkles in the face during *Flehmen*. Lions raise the head above

the horizontal usually. In both species, smelling and *Flehmen* are often repeated and marking of the marked object may follow. My olfactory inspection of fresh markings or frequently marked objects resulted in a strong sensation. The odor is decidedly "musky."

In periods preceding or between courtship chases involving one male and one female, both sexes lick the posterior and inside, lateral surface of the upper rear legs of the other (Fig. 5-2). This is often associated with licking of the genitals and surrounding area. Licking of the hair on the hind legs is often accompanied by small biting movements with the incisors and pulling of the hair as the head is drawn backwards. *Flehmen* may follow both the hind leg licking and nipping.

Males smell the genital area of other males and of females by approaching from behind while both are walking. The male places his nose between the rear legs and below the abdomen of the cheetah walking ahead. Then the dorsal surface of the nose is raised upwards in short quick movements against the genitalia. A male following a male or female, with his head extended forward and nearly touching the rear-end of the cheetah ahead, at times exhibits an erect penis.

A male and an estrus female often stand side by side, facing opposite directions, and orient their heads laterally to each other's genitalia (Fig.

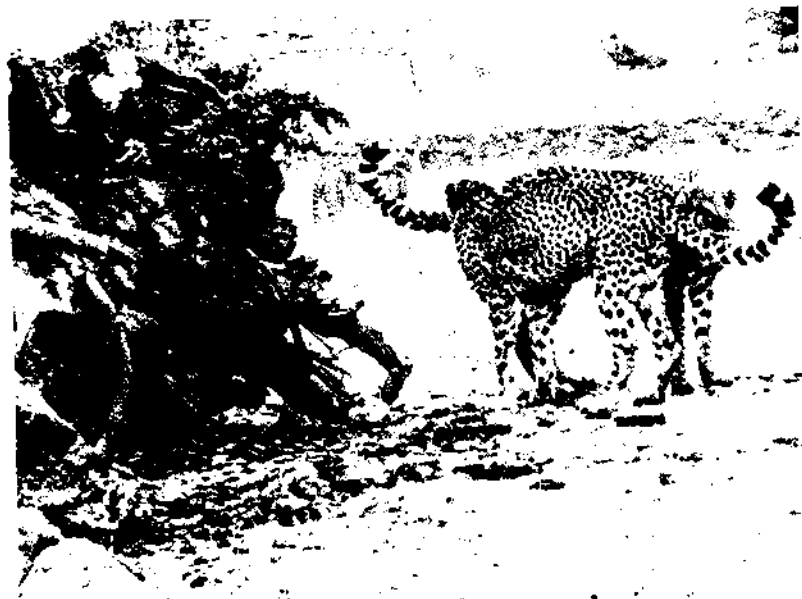


Figure 5-2 A male and female inspecting ano-genital areas. (Photo: R. L. Eaton.)

5-2). This posture is often maintained as the pair walks in a circle. Orientation by the male in smelling is to the female's mid-back dorsally, and then her genital area prior to mounting.

COURTSHIP

Courtship was highly variable in temporal patterning, and with respect to numbers of males pursuing an estrus female. The male group courtship behavior was relatively restricted to early mornings and late afternoons, and after sundown on moonlight nights. The single male and female courtships were seen at the above times but also later in the mornings and earlier in the afternoons. At World Wildlife Safari and San Diego Wild Animal Park, male group courtship did not occur. In these captive cheetahs, one male was decidedly dominant over other males, and was the primary courting male.

Associated with the courtship chases were frequent play or mock fights between the estrus female and male(s), and between the estrus female and other females. In fact, in several cases a female joined males in chasing an estrus female and also took part in the mock fights with the estrus female. The mock fights associated with play chases in courtship are typified by raising up on the hind legs and coming down with the forelegs on the "opponent." These brief encounters are often followed by chases.

In the one male-one female courtship, there is, along with the chases and as a part of the mock fights, frequent pawing and biting oriented to the scruffy, short mane on the dorsal neck. Both sexes exhibit the behavior, and estrus females direct the neck bite to other females prior to mounting and thrusting them.

During the end of a courtship chase, and prior to mounting, the male may place his open jaws over the laterodorsal neck while slowly running, walking, or standing alongside the female. The bite does not appear to be full strength, but rather highly ritualized and inhibited, as compared, for example, with the neck bite of copulation. The bite has the effect of slowing the female down and inhibits her behavior generally. Here, the female frequently responds by "flopping" or falling onto her side, which is seen in fighting contexts as a submissive gesture (Fig. 5-1).

When the female bites the male in the same way, or places one forepaw on his dorsal neck or shoulders, he too often exhibits the "flop" response. It is common at this stage for either the male or female to place one foreleg over the other's back, and around the midsection, suggestive of foreleg claspings in mounting.

The male chases the female who runs with her tail in the "tail-up"

posture or the "curled over" posture. Chases are frequent and for distances of usually 50–150 yards. They end when the chased animal either actively elicits the flop response in submission, or the pursuer overtakes the pursued and places a forepaw or ritualized bite on the pursued's dorsal neck, shoulders, or midback.

At Lion Country Safari the same group of five males took part in courtship of estrus females, and though other single males not members of the group had courted and mated females, no other males than these five exhibited group courtship. The group pursuit of a female was initiated in either of two ways: (1) a single male courting or copulating a female attracted the group of males; (2) the estrus female running with the tail-curved over or tail-up posture in sight of the group. A description of the first case follows from my notes: "A male and female play-fight in a wrestle-type posture. Both are lying side by side on the ground, their stomachs facing each other. There is mutual pawing with the forelegs against the other's lateral neck and head, and occasional soft kicking with the hind legs. The male stands over the female, she is now on her back facing upwards at him. She paws his lateral neck and head with both forepaws. The female rolls over onto her stomach. The male mounts, holds the scruff of the female's neck. The female stands up quickly and runs with the tail straight up. The male chases her." The chase ends when either the female flops or simply stops and stands still. In the latter case the female turns towards the approaching males, faces them and swats them on the head. Often then the female walks slowly away with her tail up and the males follow, smelling at her rear and showing penile erection.

The female normally initiates another or several chases, followed by a flop. When she did not dart away, the five males formed a circle around the female and lay down. In a short time one male (other females may join in the chase and lie in the circle) was up and approached the estrus female, and soon another and possibly a third. A fight broke out between one of the males and the female, the female fought defensively on her back, swatting with her forelegs and kicking with her hindlegs. Soon the males were fighting amongst themselves, and the female lay nearby watching. These courtship fights were unique in that they involved so many individuals at one time (Fig. 5–3). Hundreds of fights observed and filmed in other contexts, for the most part feeding competition on a single "kill," showed not one case of more than two cheetahs involved in the same fight even when many were at close quarters.

The most intense fight, that is, with the most biting and longest duration, was observed between two males in competition for an estrus female (S. Craig, pers. comm.). In intense aggression, males exhibit the tail-under posture, similar to that of submission in canines. It is also seen during threatening of an approaching human and precedes flight. Feeding



Figure 5–3 Male cheetahs competing for mating rights of female in heat. Fights between males during courtship at Lion Country Safari, California, were the most intense expression of aggression. The great number of males present may explain the lack of a clearly established dominance rank among males, which occurred at the San Diego Wild Animal Park. (Photo: R. L. Eaton)

fights seldom involved biting while courtship fights did. Bites in food competition are highly ritualized and directed to the lateral face. Biting in courtship fights was more intense and directed to several areas. Rising up on the hindlegs and sparring with the forelegs was common in courtship, only seldom in feeding.

The female remained lying down throughout the courtship fight between males, and the other females in the "mating circle" also remained lying down. Once the fight was over, the female got up and walked away. The males smelled the ground where the female was last lying, then followed the female. It was impossible to determine which male "won" in the courtship fights, if indeed one did. It has not been apparent to date whether or not fights in group courtship affect which male actually mates the female. At the San Pasqual Wild Animal Park of the San Diego Zoo, ten cheetahs were kept in two five-acre paddocks. In one, with a group of three males and two females, one male was decidedly dominant. He was most active in courtship and was aggressive to the other males when they approach the estrus female (R. Herdman, 1973.) At Lion Country Safari no

instances of such long-term absolute dominance have emerged; however, the World Wildlife Safari cheetahs behaved similarly to those at San Diego. At San Diego and World Wildlife Safari fewer cheetahs are kept in larger areas than at Lion Country Safari. The exceptionally high density of cheetahs at Lion Country is probably responsible for these differences.

Although it is generally the rule that females are submissive in courtship, or that they are aggressive only insofar as they swat pursuing males, it should be noted that in the one male-one female courtships, a female sometimes becomes quite aggressive, to the point of eliciting submissive postures in the male.

COPULATION

Copulation is the same in both the one-male and male-group courtship. In the latter, while one male copulates the female the other males of the original courting group stand or sit nearby, as close as four feet. The nonmating males show no fight or threat behavior during copulation. After copulation, no courtship was observed by the same female for about an hour, and usually not until the following early morning when a copulation occurred in the preceding evening.

The female is approached by the male. The male places his teeth on the scruff of her neck. The female, whether standing, sitting, or lying down, moves into the receptive posture—hind-end elevated by posterior placement of the hind feet under the rear end. The tail is moved laterally, the posture resembles that of the female house cat. The male places his forelegs around the female's body just behind her shoulders and grips the skin of her dorsal neck very tightly in his teeth. The male intromits and thrusts rapidly about 20-30 times in succession. The female remains motionless throughout copulation. After thrusting, the male relaxes his grip on her neck, dismounts and walks away.

As the male dismounts, the female rolls over onto her back and swats the dismounting male on the side of the head. The female then exhibits an after-response, she rolls over from side to side and remains lying down for several seconds before standing up. The other males remain around her, and she dashes away with the males chasing her. The chase is short and the female lies down, unresponsive to the males.

In testing response to mounted specimens of cheetahs, one male mounted the dummy and clasped it in the typical manner, then thrust it with an erection (fig. 5-4). The same male behaved similarly with a dummy leopard but after "mating" the cheetah, the male exhibited an extensive after-response, just like the female's, only exhibiting an erection. This was the only after-response seen in a male cheetah.



Figure 5-4 Cheetahs inspecting a mounted cheetah specimen. (Photo: R. L. Eaton.)

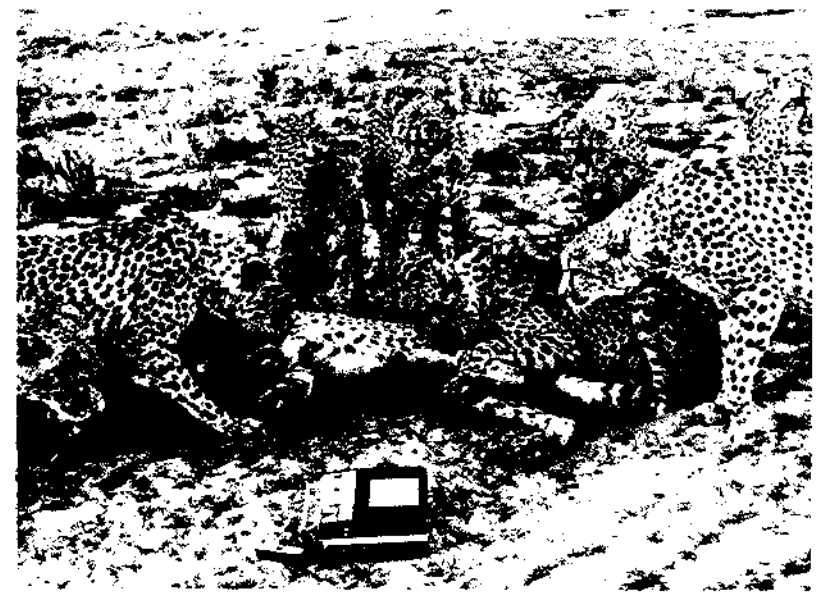


Figure 5-5 Cheetah calls being recorded to later observe their effects on behavior. (Photo: R. L. Eaton.)

COMPETITION FOR MATE

Females did not compete in any direct way for males when more than one was in estrus. Only two females of the six at Lion Country Safari ever came into season, the other four were either too young, or in the case of one, injured and removed and kept isolated in the enclosure. In the dummy experiments, both males and females threatened the cheetah dummy but not the leopard except by approaching it at a distance. Males and females inspected both leopard and cheetah dummies by smelling and nipping at the head and neck and at the genital area and upper, posterior hind legs—the same locations inspected on live cheetahs. After inspecting the cheetah dummy females attacked with intraspecific aggressive behavior, but the males did not. With the leopard, the females, after inspection, treated it as prey—pulling it over and immediately directing the strangle bite to the ventral throat. The males responded to the leopard as prey only after the females “killed” it, at which time the males circled around the fallen “prey” and began to lick and attempt to eat it. What is interesting is that the female cheetahs apparently recognized the dummy cheetah as a conspecific and were aggressive to it, perhaps a reflection of their less sociable nature.

At Lion Country Safari males competed directly for a female on several occasions besides the ceremonial and highly ritualized fights in the “mating circle.” A single male following an estrus female attacked and fought with three or four approaching males. More frequently than actual combat was a single male staying close to a female and simply turning towards an approaching male, threatening with the open mouth, and staring directly at the male. This was sufficient to deter the potential competitor’s approach.

A female lying down with a male was often approached by a second male that first smelled at her mid-dorsal back, then progressively backwards to her genital area. The male already with the female got up and faced the second male, and the second male submitted by turning his head away, then walking away. In one instance a male had been mating with and following a female all morning. The pair was lying down together away from any other cheetahs when four adult males approached them and laid down close by. The mating male threatened the four males, and immediately one of the males mounted another male. Being threatened and at the same time sexually motivated and attracted to the threatening male’s mate resulted in redirected sexual behavior to another male.

The above case was one of the three instances in which homosexual behavior was observed in males. It is reported in zoos as quite frequent, which to me indicates that something is amiss at the zoos. Often the homosexual behavior correlates with loud noises or unusual disturbances,

all the more reason to believe it is an abnormal response or is indicative of frustration. A female displayed the full range of male copulatory behavior to another female when the former was in heat. She mounted and clasped with the forelegs, gripped the neck and thrust several times. The mounted female did not exhibit an after-response.

An estrus female often got up, walked away to higher ground, and gave the “chirp” or whistle call (it resembles the cheep of a chick). Immediately, all the cheetahs in sight lifted their heads and faced the female. Usually only one or two males approached a chirping female, and once there attempted to mount her without success. The chirp is heard in many contexts unrelated to mating and is made by males and females alike. When given by an estrus female it sometimes but not always attracts males. It is the same call that brings cubs to their mother in the wild. It was elicited from day of birth by a cheetah cub born at the San Pasqual Wild Animal Park, where it was removed from the mother the day it was born (R. Herdman, 1973).

The stutter call is surely derived from purring, but is also quite distinctive. It is the pitch of the purr, and consists of four to six short notes given in rapid succession, resembling the cooing of a pigeon. It is heard as cheetahs approach water or food. In mating it is heard from the female after a male attempts to mount but the female is aggressive to him. It was heard from an estrus female that was surrounded by three males. The call resulted in additional males running towards the female. When given by a male, other males pull the head away and close the eyes suggesting that the call is a warning. We played recordings of the stutter call back to the cheetahs and it elicited immediate attention and approach by all males and females (Fig. 5-5). Furthermore, it induced males to smell the genital areas of females and other males when this behavior had not been seen for several weeks.

A third call associated with courtship is the “yelp.” It is high-pitched but lower than the chirp. Phonetically the yelp is “eeow,” starting at a higher pitch and ending at a lower pitch, about one-half second in duration. A female made the call and three males ran from 100 yards to where the female had been sitting and then smelled the ground and marked nearby trees without pursuing the female. Most frequently it is associated with submission.

In evenings when courtship and mating behavior were frequent, males and females both displayed behavior reminiscent of that seen in house cats with catnip, and resembling the after-response. Individually, they pushed the sides of the head, neck, and shoulders against short, two to three foot high shrubs. This resulted in lying on their sides and pawing the shrubs in that position. Rolling onto the back and moving the dorsal head laterally, rubbing it against the ground and the bent-over shrub was

frequent. Several cheetahs chewed at leaves between sessions of cheek-rubbing the plants. Some of these plants were known to have been marked in the past but none were marked just before, during, or after the catnip response.

Unlike lions, cheetahs are not polyestrous. At Lion Country Safari mating activity was much more frequent during July, August, and September. It tapered off and from December through March was not observed at all. Our cheetahs at World Wildlife Safari were also imported from South West Africa and they showed first signs of courtship in mid-June, which continued through July. Then a more intense season occurred from mid-October thru mid-November, in general the same as San Diego's cheetahs (Herdman, 1972).