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Abstract: The majority of the data on social organization are observations of 15 cheetah of four special groups in Nairobi National Park. Members of one cheetah group did not socialize with individuals of other groups except for mating. Details on scent marking and defecation and individual's response to it are presented.

## 4 Social Organization and Spacing

The female cheetah and her four nearly adult cubs were lying on a rock outcropping near the Athi River. The family group was one of four groups that reside in Nairobi National Park, an area of only 44 square miles. The male cub that had taken over leadership of the entire family approached his mother and smelled the ground where she was sitting. The male started to mount his mother but she swatted him on the head. He turned his head away, chirped like a bird, and walked back to where he was lying.

The adult female was in heat but it was eight months later that she gave birth to a second litter. The first litter gradually separated from her as she became reluctant to follow over the succeeding three months. The female had succeeded in isolating herself.

This family group and the other adult groups, composed mostly of males, frequently used the same areas of the park for hunting. However, they never came into close contact. Their paths often crossed but not less than one day apart. I came to learn that the scent markings left by frequent urination act as warnings. As one group moves along it stops at trees and rocks, marks the objects with a small amount of urine and scent, then moves on. Another group that comes along the same path smells the first group's scent and responds by going in a different direction.

Members of one group do not socialize with individuals of other groups except for mating. The female drops scent when she comes into heat and

male groups follow the scent trail, mating with the female when they find her. Within one group or between groups I observed aggression only once—the mother swatting the male cub that tried to mate with her. Cheetahs do not compete at a kill site. All of them feed in peace, quite unlike lions, which squabble and fight incessantly over food.

It perplexed me that cheetahs were so peaceable compared with other members of the cat family. Their spacing behavior would imply that they actively avoided each other, but were the scent warnings backed up with the threat of actual physical aggression? Should scent markings be considered warnings?

The majority of the data on social organization are observations of the 15 cheetah of four social groups in Nairobi Park.

These cheetah were all seen in the northwest section of the park, an area of about eight square miles, within 48-hour periods on several occasions. Paths of one group often crossed the paths of other groups. Groups occasionally came into sight of one another, but actual intergroup association was not observed.

Extensive observations of groups 2, 3, and 4 showed that one male led each group. This individual determined the direction of movement, when the group hunted, and what was hunted, and was also more wary of humans, lions, and suspected danger. The leadership of group 2 was by the adult mother of the other four in November, when the cubs were three-quarters grown, at about 12 months of age. In December one of the three male cubs shared leadership with the mother, and in January, at 14 months of age and apparent sexual maturity, was the sole leader of the group. This male was more active and aggressive in play before, during, and after he became the leader. No overt physical fight was observed in his assuming leadership. In February, however, the mother came into estrus and she did exhibit aggression by hissing and slapping with her front paws at the young male when he attempted to mount her, the only aggression I observed in the wild. Early-morning and late-evening play-fights and chases were common in all groups.

Individuals seldom joined or left groups 1, 2, 3, and 4. Only group 3, the two males, separated temporarily but rejoined. Nairobi Park records and several individuals' photographs show that these two males originally hunted with two others for at least two years prior to the study, and they, too, broke up several times and rejoined.

Male cheetah are capable of directional urination as observed for tigers and lions (Schaller, 1967:251–253). The penis can be directed with accuracy at objects above or below the body (Fig. 4-1). Males in adult groups or singly pass small quantities of urine throughout the day on many objects, while females appear to urinate heavily only occasionally as a purely excretory function. Female tigers and lions (Schaller, 1967:252) emit wide

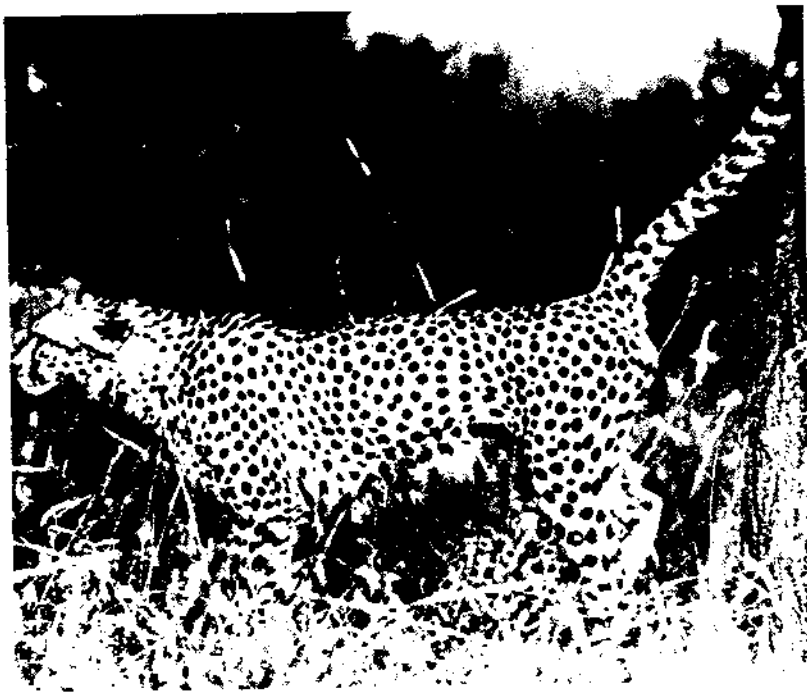


Figure 4-1 Adult male cheetah depositing scented urine on tree trunk. (Photo: H. Patel.)

sprays quite frequently. Both sexes in a cheetah group took great interest in the urination previously made by males of other groups (Fig. 4-2). Where one group marked, another group inspected and then marked the same place. The female with cubs took great interest in the markings of all other groups, and so did the cubs. Male cubs of group 1, ages 4-8 months over the study, were not observed to mark. The young males of group 2 marked at 14 months.

Places that were marked were usually objects that stood out from the immediate environment such as large trees and shrubs, dirt mounds, or concrete road embankments. In very open areas markings were made on plants that stood out against a homogeneous background of more common plants. For example thorn-tree (*Acacia drepanolobium*) makes up at least 80% of the small trees on the plains of Nairobi Park, yet *Balanites glabra*, which is much less common but usually fuller and larger, is the most commonly marked. If the *A. drepanolobium* is large or the only plant nearby, it is marked. In one area in the south end of the park three 20 ft

high *Acacia mellifera* are surrounded on all sides by many *A. drepanolobium* but only the *A. mellifera* are marked when cheetah pass through that vicinity. Even a nonwoody plant that is different in shape or foliage from surrounding plants is a preferred marking place. Walker (1964:1282) considered these trees scratching posts; however, this is doubtful since scratching was rarely observed and may have been just stretching. Only group 3 exhibited the behavior described in tigers by Schaller (1967:254), in which the two males, after smelling and marking a frequently marked tree, scraped the grass and earth alternately with their hind legs. When the ground was bare they defecated only a small amount and/or urinated onto the scrape.

Hunting success of cheetah apparently depends mainly on vision, and little, if any, on smell, yet much time is expended smelling for, locating, and marking other markings (Table 4-1). Some objects in the home range are recognized by cheetah to be habitual marking sites. These marking locations are well known and each group orients its movements to these locations wherever it is traveling, often following a zig-zagged path between certain trees. When in one area, a group's path often followed,

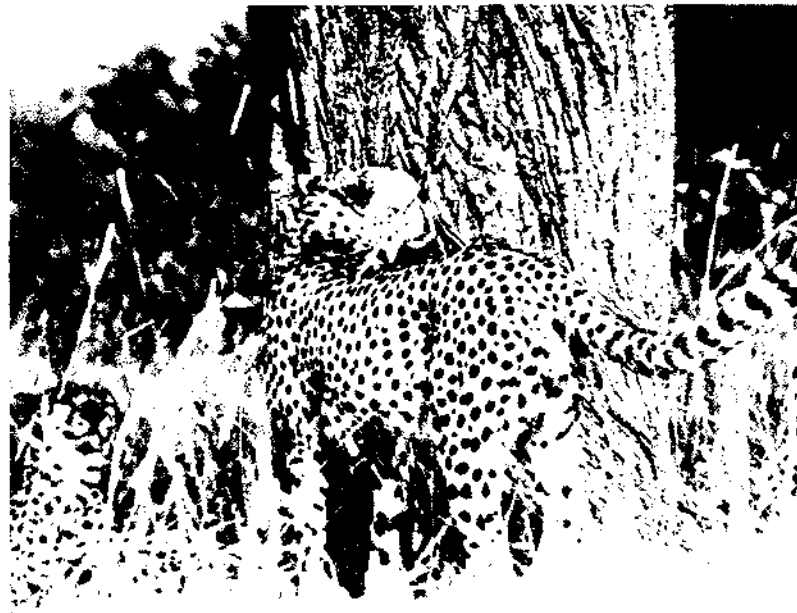


Figure 4-2 Cheetah inspecting tree for olfactory markings. (Photo: H. Patel.)

TABLE 4-1 BEHAVIOR OF ADULT GROUP OF TWO MALES, NOVEMBER 30, 1966, NAIROBI NATIONAL PARK

Time (A.M.)	Behavior
6:00	Moving east to west from evening bed
6:02	Smell then urine-mark large rock
6:05	Smell then urine-mark <i>Acacia</i>
6:07	Smell then urine-mark <i>Acacia</i>
6:10	Observe impala
6:15	Smell urine-mark large <i>Acacia</i>
6:20	Mutual face licking
6:30	Change directions, south to north (wind blowing to southwest)
6:32	Change directions towards lone female Grant's gazelle; she sees them, cheetahs stop stalking
6:33	Stop, look about for game
6:34	Stop, look about for game
6:35	Stop on small hill, look for game
6:36	Smell urine-mark 10 ft high <i>Balanites</i> , defecate on ground, scrape ground with hind legs
6:40	Female Grant's gazelle gives warning call, "snorts," at 5 sec intervals
6:41	Change directions, due east toward 15 ft high <i>Balanites</i>
6:42	Smell urine-mark <i>Balanites</i>
6:50-7:00	Watch adult male kongoni 350 yards away, stalk via vegetation at right angle to kongoni
7:01	Now 200 yards from kongoni, are discovered, lose interest, move on
7:04	Walk toward large <i>Acacia drepanolobium</i> , urine-mark it
7:06	Cross road, walking toward 20 ft high dirt mound near new dam
7:11-7:15	On mound smell top and side areas extensively, kneeling while smelling other group's markings made yesterday
7:20	Sit on mound, observe nearby herds
7:47	Male #2 defecates on mound
7:50	Move north off mound toward herds, same direction as family group moved yesterday
7:52	Mark 8 ft high <i>Balanites</i>
7:53	Male urine-marks <i>Balanites</i>
7:55	Both urine-mark concrete embankment
7:56	Drink
8:00	#2 male only urine-marks <i>Balanites</i>
8:02	On hill overlooking herds of kongoni, Grant's gazelle, and wildebeest
8:04	Both urine-mark <i>Balanites</i> after smelling it
8:05	Intent on 5 young kongoni straying from herd, no cover between cheetah and kongoni

TABLE 4-1 (continued)

Time (A.M.)	Behavior
8:09	Move off hill away from herds, west, #2 male urine-marks <i>Balanites</i>
8:15	Lie down in high grass, occasionally look at herds
9:35	Move to shade of <i>Balanites</i>
9:55	Still in shade, inactive

more or less, the same route of marking spots used before by it and other groups (Fig. 4-3).

Cheetah groups did not follow a route taken by another group on the same day; however, one group often followed in the same direction a path taken by another group on the day before (Fig. 4-3). On 14 occasions, a second group moved along another group's marking path from the day before. The distance between markings varies with the density of the woody plants, averaging about 30-50 yards in dense cover and about 50-100 yards or more in the more open plains. Of these 14 occasions, the second group followed at least 6 markings of the first group and as many as 21 with an average of 11. In no cases did the second group overtake or come into sight of the first group.

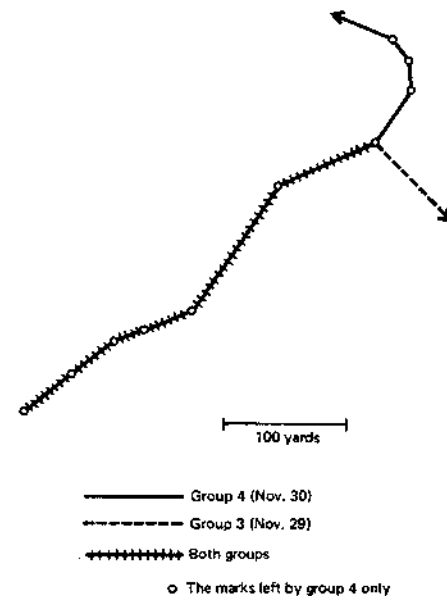


Figure 4-3 Paths and markings of two cheetah groups on two consecutive days.

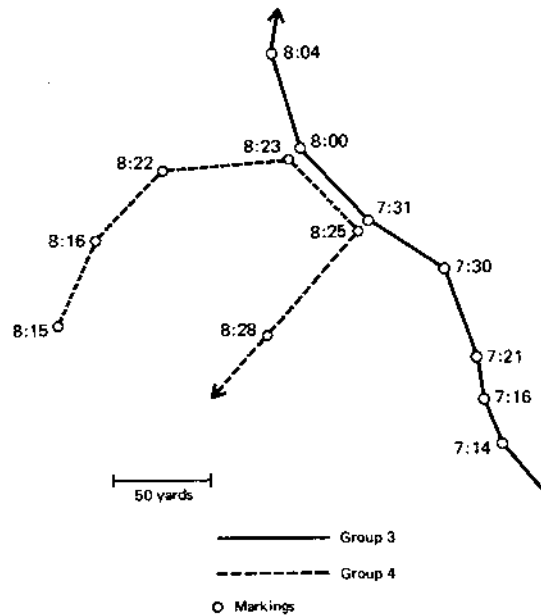


Figure 4-4 Paths of two groups on the same day.

On nine occasions a second group came upon another group's markings made on the same day. The second group was deliberate in locating and smelling other nearby markings before going on in a different direction from the first group (Fig. 4-4). The second group would spread out from where the first fresh marking was found until a second one had been located. The first animal to find another marking would kneel down and smell the scent carefully. Upon seeing one cheetah kneeling the others of the group came to where he was and behaved similarly (Fig. 4-5). After all group members took great notice of the second-found marking, the group, while marking, moved off slowly and warily in a direction different from the first group.

On five occasions two all-adult groups noticed each other while passing in opposite directions at 100-300 yards apart. Twice two groups passed within 200 yards of each other, but the vegetation prevented them from seeing each other. It should be noted here that once group 1 walked in front of a male lion only 20 yards away, and the lion watched the cheetah but the cheetah were not aware of him. The expressions that cheetah



Figure 4-5 Two male cheetahs, brothers, inspecting for the urine markings of other cheetahs on a hill in Nairobi National Park. (Photo: R. L. Eaton.)

make as group passes group fit closely the threatening behavior of other felines. In the cheetah the ears are drawn back, the head is held low and the mouth is open. In the observation of two male cheetah approaching each other on opposite ridges about 100 yards apart, yelping and marking (J. B. Foster, pers. comm.) were frequent. The two males did not meet and nothing came of the confrontation. Dogs mark in sight of each other when neither is motivated to fight (Lorenz, 1966). Group 1 when bedded down for the evening saw group 4 moving into high grass and bedding down for the night about 250 yards off. The female got up immediately and moved in the opposite direction from the three adult cheetah. She constantly turned around and looked in the direction of the other group before settling down again a mile away from the first bed site.

The absence of movement between cheetah groups indicates that members make up families. New groups are probably established as females leave a group to give birth and raise young. It is not known if females whose cubs are lost in some way reenter their old groups or simply live alone until in estrus again, but Schaller (1972) believes they remain solitary. The first possibility is supported by the fact that in a few groups, individuals left and rejoined after as long as two months. The second suggestion is supported by the fact that in some areas, cheetah are

predominantly seen singly or in twos. If there were an affinity for groups to admit foreign individuals or for single animals to join, then most cheetah sightings in these areas would be of groups, but they are not. That markings may serve to get broken-up groups back together is ostensible; however, markings do not appear to serve as a means of enabling a foreign cheetah to locate and become a member in an established group.

Predation on cheetah cubs may act as a regulatory mechanism that consequently keeps populations too low to allow natural selection for a spacing mechanism that is limiting. Apparently population control in wolves results from cub mortality (Rausch, 1967) and social castration (Woolpy, 1968). That predation may be more important in controlling numbers than territoriality is shown, for example, in muskrats (*Ondatra zibethicus*). Errington (1963:71) holds predation as relatively unimportant, but the fact that muskrat territories become compressed as density increases implies that territory cannot be acting as the only factor in regulating muskrat populations. Lions, unlike cheetah, are well known for their aggressive behavior to outsiders. The evolution of "baby-sitting" (Schaller, 1972) has decreased the problem of predation to lion cubs and of course has reproductive value (Slobodkin, 1961:51). Since predation is not an appreciable factor in lions, it is likely that a spacing system dependent on marking and other mechanisms is more important in limiting populations of lions than of cheetah. Aggression is also more important in the lion—nonpride members or territorial intruders may be killed (Schenkel, 1966, 1967, Eaton 1973).

It is worthy of speculation that aggression within the pride and toward outsiders might vary over long-term cycles of game abundance depending on the pride's size. The optimum pride size is bound to depend on game abundance levels, and levels of aggression are probably built in to compensate for reaching this optimal pride size, for example in a period of game abundance a small pride would increase in size due to a lowered level of aggression within the pride and toward strangers, a large pride would probably not alter its aggression level. Conversely, with game scarcity the small pride, being nearer an optimal size, would be at an advantage to drive off or kill strange lions that attempted to enter the group, and a large pride could be reduced toward the "best" pride size by increased levels of aggression. Also, since lions probably have a relatively long reproductive life, cubs could be kept away from kills and starved to death in order for the pride to survive through the low part of a game cycle (which is related to the approximate five year rainfall cycle in East Africa [Talbot and Talbot, 1963]).

Since members of lion prides often separate for periods while hunting (Schaller, 1972), marking could be functional in getting members together, for example to share a kill or for cooperative hunting efforts. Cheetah

groups, on the other hand, seldom have members leaving with the probable exception of females for breeding activities. The functions of marking in cheetah probably do not include a means for an individual to locate the group or vice-versa although this possibility appears likely for certain canids and possibly the tiger. Many animals use markings to communicate estrus condition (Bourliere, 1954). The cheetah female when in estrus does pass scent that is of interest to males wherever she sits or urinates; however, except during estrus, urination appears to occupy chiefly an excretory function. For lions, tigers, and house cats vocalizations may act as important mating cues. Cheetahs also appear to vocalize to attract mates.

The facial expressions of cheetah when two groups pass are typical threatening gestures. When threat behaviors are well established it is to be expected that aggression between social groups is relatively rare. Only two observed cases of overt aggression in wild cheetah (Stevenson-Hamilton, 1947) indicate that the cheetah has a system that reduces the number of aggressive encounters. It is efficient in that strangers rarely meet.

The attention that cheetah give to markings indicates that there is information transfer between cheetahs. Since cheetah groups do not associate but do notice one another's markings, then at least part of the message must be a warning.

Female tigers and lions do mark (Schaller, 1967), but female cheetahs apparently do not. Social evolution in the tiger has probably led to a need for the female to mark; however, that the degree of specialization has been limited by the female's anatomy is shown by the female's less efficient wide spray as opposed to the finer emission of males.

The male provides the chemical warnings just as in many species of birds and mammals defense of territories is only by the males. A female with cubs does not associate with adult males and therefore may lack a chemical warning system. Perhaps females with young are not spaced. According to Lorenz (1966:43), "Where only one sex cares for the brood, only that sex is really aggressive toward members of the species." It is possible that females with cubs, as in dogs, receive a "higher respect" from other adults. Regardless, the female does heed other groups' markings and moves away from another group when they are sighted, thus remaining spaced.

The cheetah groups in the study area avoided contact with each other, in spite of the relative crowding in one small area. When another group was seen, contact was not made and threat behaviors appear to function in this regard. If chemical warnings were for a fixed-area territorial scheme then they were not effective, for the groups crossed marking paths constantly. The frequent marking of a route taken by cheetah probably serves as a means to prevent other groups from stumbling onto them and

interfering with their hunting, and the possibility of aggression from the encounter. The marking must be a chemical message capable, no doubt, of losing its information content over time by dissipation. In this way, the warning is good only when needed. The markings are noticed a day after they are made, and later, but they are not respected. They probably have lost their warning intensity level.

The minimum time observed in the field after which one group would follow in the same direction on the same path as another group was 24 hours. Since cheetah are diurnal and normally active only from 5:30 A.M. to 7:00 P.M., the earliest marking made on one day would still be in effect up to the same time on the following day. This system may be facilitated by the fact that cheetah are constantly moving, and when so doing, they mark. Often these moves are just short distances, at the longest every few hours, such as at mid-day, but it apparently serves to guarantee that a group's last marking will still be in effect.

In thinking about spacing systems in cheetah it is helpful to ask why a fixed-area territory is not found. Brown (1964) uses this approach with birds but the ideas in general are applicable. To maintain an exclusive territory is often advantageous, but for such a system to evolve, territories must be biologically economical. The organism must be able to exclude intruders at a time and energy expense that is practical. If the costs of defense are too great then the advantages are not sufficient to counterbalance them.

With the cheetah it can be asked, "Could the cheetah conceivably defend an exclusive territory?" The answer is probably no. The space or area needed by a group is too large for constant patrolling without complete disruption of the group's hunting. Therefore, however advantageous it might be for a group to have an exclusive hunting area there is probably no way of maintaining such an area. If the presence of one group tends to cause another group to move elsewhere, then natural selection would favor any behavioral patterns that would more clearly indicate the presence of the group. Thus marking behavior can be expected to evolve, and this may come to have significant impact on the distribution of groups. Within groups, marking may have significance as an act of dominance.

I prefer to conceptualize this spacing mechanism as a moving territory that is maintained by markings that constitute temporary boundaries.

All of the following observations indicate that an intraspecific spacing mechanism which is territorial in nature is acting in the cheetah: (1) cheetah are highly specialized anatomically for marking, which they do frequently; (2) cheetah examine closely the markings made by other cheetah; (3) 15 cheetah belonging to four social groups were frequently seen in the same area at nearly the same time without meeting or

associating even when in sight of one another; and (4) cheetah alter their direction of movement when they encounter fresh markings of other cheetah, but do not if the other group's markings are a day old.

A similar spacing system is described for the house cat by Leyhausen and Wolff (1959). Many cats use the same set of paths in their overlapping home ranges, but isolation is accomplished by frequent urine-marking as each cat moves along a trail. Any other cat that encounters a mark will stop, look ahead and possibly wait, or will head down a different, unoccupied route.

## RESPONSE TO MARKS: CAPTIVE STUDIES

At Lion Country Safari and World Wildlife Safari I was able to learn more about marking behavior and its probable role in spacing, and to compare cheetahs to lions. A comparison of lion and cheetah in their response to marks of urine and feces is provided in Table 4-2.

TABLE 4-2 COMPARISON OF MARKING BEHAVIOR AND RESPONSES TO MARKS IN CHEETAH AND LION

	Cheetah		Lion	
	Male	Female	Male	Female
Tail-up marking:				
with scraping	X	—	X	X
with treading	X	—	—	—
Rear-end down:				
marking	—	X	X	X
urination	X	X	X	X
with scraping	X	—	X	X
<i>Inspected by:</i>	<i>Cheetah</i>		<i>Lion</i>	
	Male	Female	Male	Female
Tail-up markings of:				
male	X	X	X	X
female	n.a. <sup>a</sup>	n.a.	X	X
Rear-end down markings of:				
male	—	—	X	X
female	X	—	X	X
	<i>Cheetah</i>		<i>Lion</i>	
	Male	Female	Male	Female
Scraping with defecation	X	—	—	—
Olfactory inspection of feces	X	X	—	—

n.a. = not applicable.



Figure 4-6 The Flehmen response in the lion is highly exaggerated and pronounced. (Photo: R. L. Eaton.)

Although male lions mark more frequently than females and respond to a proestrous female's urine with more *Flehmen* responses than other females, both sexes do exhibit the same spectrum of response to marks and urine. The actual motor patterns of *Flehmen*, and postures of marking and urination are the same in both sexes. The differences are purely quantitative in degree of intensity, that is, frequency of occurrence.

Cheetahs of both sexes display *Flehmen* identically, but it has been observed less frequently in females in response to marks. Males and females exhibit the same frequencies of *Flehmen* to dummy cheetahs, human urine, and novel objects or odors, for example antiseptic spray on other cheetahs.

Exactly why the motor patterns of the *Flehmen* response are so strikingly different in cheetah and lion is not known, unless the more elaborate expression in the lion acts as a visual releaser (Fig. 4-6). On many occasions a lion exhibited *Flehmen* and thereby attracted others to him, whereupon they inspected the same urine marking and also showed *Flehmen*. In these cases the other lions were up to 50 meters or more away and appeared to be responding visually to the *Flehmen* expression.

Lions take odors both from the air and by extending the tongue to touch and pick up the odiferous substance before eliciting *Flehmen*. Cheetahs acquire airborne and surface-bound chemicals also prior to *Flehmen*; however, there is a difference in the motor patterns involving the tongue.

The lion's tongue is extended straight outwards and brought back into the oral cavity. The movement is rapid and only the very tip of the tongue contacts the surface. The cheetah's tongue is used in a lapping type movement in which a large portion of the dorsal surface of the tongue comes into contact with the surface.

## DEFECATION AND RESPONSE TO FECES

Cheetahs lack the sanitary control found in lions. They defecate on tops of logs, rocks, or simply in the shady areas where they lie up (Fig. 4-7). The lions at Lion Country Safari get up, walk away from the lying-up area of the pride, and defecate. Cheetahs are adapted for a near-constant rate of travel around their home range and selection has not acted to bring about the sanitary habit found in lions, which frequently use the same resting spots or remain sedentary for longer periods of time. Consequently, at Lion Country Safari, with wide-ranging movements artificially inhibited, cheetah feces are highly concentrated at resting spots.

Feces conceivably could carry scent and act as markings. Cheetahs are known to inspect feces and have been observed in the wild to scrape with the hind feet when defecating, which implies feces may carry olfactory information. Lions are, like cheetahs, social, but show no response to feces.

The explanation for difference in response to feces in lions and cheetahs relies on our knowledge of their spacing behavior in the wild. Cheetahs move much more from day to day around their home range, and unlike lions, they do not have a more-or-less fixed geographic territory. Instead, cheetahs employ a time-plan spacing system which allows several groups or individuals to occupy the same home range concomitantly, without disruption of hunting efforts. The system is effective because fresh markings are responded to as warnings and the course of direction is changed. Scraping, though rarely associated with defecation, may be responded to visually. Observation of scraping in the wild and the inspection of feces by cheetahs at Lion Country Safari implies that defecation also plays a role in spacing, or at least is communicative.

Lions rarely exhibit scraping with defecation, and I have never seen them inspect feces. In fact, I have introduced the fresh feces of foreign lions to the lions of another pride, at times only inches from the nose, and there was no inspection. In the defense of a large territory, the deposition of feces would hardly be important compared with the highly efficient use of small amounts of urine.

In the cheetah system of spacing, maximized marking would be expected since exact territorial boundaries do not exist and cannot



become well known to foreign individuals. There is a greater probability of one cheetah group not being aware of another's whereabouts. For this reason, defecation has evolved as an additional spacing mechanism in cheetahs.

In the way of summary of information available that is pertinent to spacing systems in the cat family, Table 4-3 is provided. It can be seen that there are correlations in these data which begin to tell us more about the "whys" of spacing differences and similarities across several species.

Several species—cougar, tiger, leopard, lynx, bobcat, and serval—lead a relatively solitary way of life. They all live in forest and/or forest edge habitats that produce far less biomass of terrestrial prey than the more open savanna and grassland plains. These species cannot afford to live in social groups. The smaller species, for example lynx, bobcat, and serval, kill prey smaller than themselves, which could not adequately feed several adults. Furthermore, several individuals hunting together would be less effective, in that they would create more disturbance and frighten off prey.

In their evolution, the cats specialized primarily in stealth and stalking to capture prey, quite unlike the dog family, in which the prey is typically



Figure 4-7 Cheetah inspecting feces on top of a log. (Photo: R. I. Eaton.)

TABLE 4-3 SUMMARY OF INFORMATION RELEVANT TO SPACING SYSTEMS\*

Animal	Habitat Preference	Social Organization	Home Range Size (Square Miles)	Spacing Mechanisms (M = Male; F = Female)		Source
				M	F	
Cougar	Forest, scrub, edge	Female and young; single adults	10-25	Urine: M, ? Feces: — Scraping: — Scratching: —	—	Hornocker (1969)
Tiger	Forest, edge	Female and young; single adults	10-15	Urine: M, F Feces: M, F Scrapes: M, F Vocalizations: M, F	—	Schaller, 1967 Singh, 1971 D. Shorey, pers. comm.
Leopard	Forest, savanna	Female and young; single adults	10-30	Urine: M, ? Scrapes: M, ? Vocalizations: M, ? Scratching: M, F	—	Myers, 1971; Muckenhirn and Eisenberg, 1973 York, 1973
Serval	Forest, edge, scrub	Female and young; single adults	?	Urine: ? Scrapes: ? Urine: M, F	—	Berrie, 1973
Lynx; Bobcat Housecat	Forest, edge Open fields	Female and young; single adults	12-20; 1-5	Feces: F, ? Urine: M, ? Scrapes: M, F	—	Provost, 1973 Leyhausen and Wolff, 1957 Eaton, 1970a
Cheetah	Open plains, savanna, open woodland	Female and young; adult groups; pre-dominantly males, and single adults	20-50+	Urine: M, — Feces: M, F Scrapes: M, —	—	Schaller, 1969; Schenkel, 1966; Eloff, 1973; Eaton, 1973
Lion	Plains, savanna, miombo woodland, montane, desert	Entended matriarchy—sex and age classes, usually fewer adult males than females	20-100+	Urine: M, F Scrapes: M, F Vocalizations: M, F Active aggression: M	—	

\* (?) = unknown; (—) = not found.

chased and run down. For most cats to be successful they must hunt alone. In less productive biotopes, such as the forest, a large cat can kill and depend on prey as large or larger than itself, but group hunting would not be any advantage. It would lead to a lower hunting success not to mention more bellies to feed. A cougar kills about one deer per week, on which it feeds for several days. An adult group of cougars would scare off disproportionately more game than they could collectively acquire for food.

For those reasons most cats are solitary, and they require a relatively large hunting area to provide adequate food resources. A fixed territory is the best way to achieve the following:

1. Hunting success—other individuals hunting in the same area would disrupt and thwart the resident's own hunting success.
2. Adequate resources—a large enough area will ensure that even during resource scarcity, an adequate population of prey is available to the territorial occupant.
3. "Prudence"—the entire predator population is thus spaced out over an area in such a way that they will not overeat their prey resources, and thereby kill off the prey and themselves.

These cats more or less defend their areas in the same way, utilizing chemical and visual warnings that communicate their presence without having to physically threaten or aggress intruders. Besides, it would be impossible to keep tabs on the entire territory at the same time. Thus, other means have evolved to replace and represent the proprietor's rights and intent to defend his area against conspecifics. In all these same species we see that males are wider ranging but that females maintain more stringent boundaries against other females. This too makes sense in that a female must provide an area, and its resources, sufficiently large to feed her young without competition from other family groups. The males are at an advantage the larger the territory is. The more territories of females that can be encompassed by a male the more offspring he can procreate. It goes without saying that natural selection favors a higher reproductive success. The result is a population with fewer territorial males than there are adult males, many of which are transients and forced to "wait their turn." It can be seen why a territorial male has a territory larger than what he requires for food alone, which is the major factor determining size of female territories.

In a different biotope, the grassland plains or savanna, we find in the cats:

1. different social organizations;
2. larger home ranges; and
3. different hunting techniques.

The open areas are more productive. The density and biomass of prey are greater here; however, in this habitat, hunting in the typical cat fashion would be less effective, for the prey have better visibility. This is one reason that the cheetah evolved its fantastic specializations for great speed. There was a niche for a predator on smaller, swift antelope. The plains of Africa have a great diversity of medium and smaller sized prey species most of which are hunted by pack-living predators, for example wild dog and hyena, that employ running and/or speed more than stealth.

When the many larger ungulates evolved in the late Pleistocene, the *Panthera* group of cats also evolved, apparently as a "response" to new predatory niches. The leopard, lion, and tiger all appeared most recently in felid evolution.

The lion became the largest predator in Africa, living primarily on the plains; the tiger became largest in Asia, living primarily in its vast forested regions. The lion had few competitors for the larger African prey such as adult wildebeeste, zebra, and buffalo. Stealth is certainly used by lions to capture and kill equally large or larger prey, which feeds several lions for several days. Also employed by lions is cooperation in which one lion puts prey to flight directly toward other lions.

The availability of large prey in dense populations might itself have been conducive for early evolution of group life; however, additional factors soon become operative. The group would have to maintain a large enough area to supply game year round. The prey populations respond in terms of densities and movements to the annual cycles of rainfall and drought, so that during some periods of the year, game is relatively scarce and a larger hunting area is required. This is why lion prides often have such large territories. Defense of this area is critical not only for food resources but also to protect young since intruding male lions have no inhibition about killing and eating a pride's cubs. One other factor favoring sociality in lions is protection of cubs against the many other predators. While one female hunts and kills, another female actively babysits the cubs.

Regarding the cheetah it can be seen that where prey is abundant brothers may stay together into adulthood and be able to survive on what they kill. They tend to kill larger prey than single adults. The female must live away from other adults since the size of prey she can kill is smaller, and she must be able to feed four or five cubs for about one year. The cheetah cannot live in prides. They are unable to kill large prey, owing to specializations for speed which have reduced the cheetah's overall size, power, and killing tools—the teeth and claws.

Their specializations for a limited range of prey size and a specific hunting habitat require that the cheetah be able to cover a large area. A small group (three or four) of adults or a family could not economically defend the area required. A fixed territory is not practical, thus a spacing system has evolved which temporarily separates cheetahs. It is a time-plan system with boundaries that move as the warnings lose their effect. This same pattern was seen in the Kalahari lion, which also requires an area too large to demarcate and maintain absolute boundaries. Again, this is the result of availability of prey, quite low in an arid habitat.

It has been shown that a variety of mechanisms are employed to achieve spacing in the cat family. The advantages to spacing may be food, mating, population control, or some combination of these. Regardless of the system, whether it is a fixed territory or a time-plan, or a combination, the particulars of how each species remains spaced out in the environment are understandable only in terms of "defensibility." Ability to defend an area, directly or indirectly, must be economical so that the expense of time and energy does not outweigh the advantages to the individual.

The above generalizations do not include discussion of special social classes, for example nomadic lions (Schaller, 1972). And the unusual patterns of spacing brought on by varying ecological conditions are not treated, rather, what appears to be the basic system is presented.