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Abstract: A study of cheetah group interactions reveals a spacing technique that works on a "time-plan". Marking appears to act as a means of defending any time. In this way, groups space themselves out, but this spacing system is not necessarily a population regulatory mechanism. The relationship between group size and mortality, and predation on cheetah as the factor most likely limiting cheetah numbers are discussed. A definition of territoriality is offered, and it is advocated that the "time-plan" of spacing is a special case of territoriality.

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Group Interactions, Spacing and Territoriality in Cheetahs

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With 2 figures

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Introduction

It is still controversial whether populations of predators are self-limiting, and thus do not over-utilize their prey (HAIRSTON et. al. 1960, SLOBODKIN et. al. 1967). Territoriality results in intra-specific spacing in many animals (NICE 1941, ERRINGTON 1946, HINDE 1956, ORIANS 1961, BROWN 1964, MARLER & HAMILTON 1966). The control or regulation of populations by spacing mechanisms such as territorality varies from species to species (NICE p. 469; ERRINGTON 1946, p. 228; 1956, p. 305; LACK 1954).

The traditional definition of territory as a fixed area is too narrow to describe territorial phenomena in many species. A "time-plan" spacing mechanism, under a broader territorial definition, can be considered as a special case of moving territory with time boundaries. The "time-plan" territory describes how several predator species may remain spaced.

This paper, the observations of which are taken from field data of a study of cheetah ecology, establishes that the cheetah employs marking as a means of defending a moving space. This work supports the theory of spacing by means of a "time-plan" advanced by LEYHAUSEN and WOLFF (1959) and further explained in LEYHAUSEN (1965). In addition it advocates that "time-plan" spacing can be considered a case of territoriality.

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Methods

Initially, photography was an important aid in determining the identity of individual cheetah. The spots on the left side of the face were used to identify individuals. However, cheetah soon became recognizable upon sight. A portable tape recorder was used for verbal descriptions whenever behavior sequences followed each other too rapidly for written descriptions.

Duplicate maps were used in the field to record daily movements and locations of various behaviors. A surveyor's field tape was used in measuring distances and for checking estimates for accuracy. Field work began October 15, 1966, and continued through February, 1967.

Area:

Data were collected in study areas of widely divergent habitat types. They were: (1) rolling *Themeda triandra* grassland *Acacia* savanna in Nairobi National Park, and (2) flat, dryer *Acacia* savanna in Masai Amboseli Game Reserve; both in Kenya. The greater part of the data presented here come from the northwest section of Nairobi National Park. The park is an area of about 44 square miles, closed in on 3 sides by tall fence and open on the south to the Athi-Kapiti Plains. It has a year-round supply of water from artificial dams. A dense forest lies in the extreme western border, and the park is sectioned north to south by strips of riverine bush along water runoff areas. Most of the park is short grass plains interspersed predominantly with short (4–7 ft) *Acacia drepanalobium.*

Results

Densities and Predation:

Nairobi National Park has the highest density, one cheetah for 2 square miles, known anywhere in the species' present distribution (GRAHAM & PARKER 1965). The cheetahs discussed here offered a variety of social groups including 3 adult groups of different sex and size compositions and a family group (♀ with cubs). The study area in the northwest section of Nairobi Park was an important part of each group's home range. It is preferred habitat for several probable reasons:

(1) The vegetation type of grass regularly interspersed with short *Acacias* is desirable stalking cover;

(2) several high dirt mounds and a surrounding bluff offer good "lookouts" from which game is located and sometimes hunted successfully, and

(3) This area harbors the man-made water supply that is partly responsible for maintaining dense game populations, especially during the dry season.

The Nairobi Park records of 3 litters and my observations of a litter in the park and in Masai Amboseli Game Reserve show that for 5 cheetah litters averaging 5 cubs at birth, half the cubs were killed in the first 8 months by other predators: lion *(Felis leo)*, leopard *(Panthera pardus)*, and hyena *(Crocuta crocuta)*. Predation was the only mortality factor in these litters, and several instances of attempted predation on adult cheetah are known (ANONYMOUS 1959), a few being successful. In one family, not mentioned above, the ♀ disappeared while hunting alone, possibly killed by lions, and the cubs, though half grown, were unable to hunt and must have starved to death.

Except for Nairobi Park, cheetah have low densities, one per 50 square miles being not uncommon (GRAHAM & PARKER 1965) and, roughly speaking, the park has the lowest densities of other large predators. Hyena and hunting dog *(Lycaon pictus)* are rare in Nairobi National Park; but where cheetah are scarcer, as in the Serengeti National Park, these 2 predators are more common. Nairobi Park cheetah sightings are most often of 3 individuals in a group, while in all other East African areas the most common sighting is of 1 and less commonly 2 cheetah (GRAHAM & PARKER 1965).

A total of 31 cheetah were observed more than once in the 2 study areas; however, the majority of the data presented here are from observations of the 15 cheetah of 4 social groups in Nairobi National Park.

These cheetah were all seen in the northwest section of the park, an area of about 8 square miles, within 48-hour periods on many occasions. Paths of one group often crossed the paths of other groups. Groups occasionally came into sight of one another, but actual inter-group association was not observed.

Group composition and Cohesion:

GRAHAM (1966 : 52) analyzed the data from questionnaires used in the Cheetah Survey (GRAHAM & PARKER 1965) and found that of 253 litters of young, 63 % were accompanied by 1 adult. It is presumed, since no sexing data were available, that these adults were ♀♀. My observations and those of J. B. FOSTER (pers. comm.) show that ♀♀ with litters will meet with ♂♂, apparently when in estrus, and copulate over a several-day period. The number of cases where more than one adult was seen with cubs is probably biased by greater likelihood of sighting. Those cases in which litters with more than one adult are observed are probably of ♂♂ pursuing ♀♀ rather than of second parental animal.

In the Cheetah Survey (GRAHAM & PARKER 1965), 15 adult groups of more than one individual were composed of 9 all-♂ groups and 6 with both sexes. Of 6 adult cheetah groups that I was able to sex by external observation, 2 were all male, and 4 included both sexes. Extensive observations of groups 2, 3, and 4 (Tab. 1) showed that one ♂ led each group. This individual determined the direction of movement, when 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 4 in November when the cubs were 3/4-full grown, at 11—12 months of age. In December one of the 3 ♂ cubs shared leadership with the mother, and in January (at 14 months age and sexual maturity) he was the sole leader of the group. This ♂ was more active and aggressive before, during, and after he became the leader. No contests or aggression was involved 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 ♂♂ when they attempted to mount her. This was the only aggression observed in the study. Early-morning and late-evening mock-fights were common in all groups, but this is best described as "play".

Of 1,225 sightings of 2,785 cheetah (corrected for duplicate observations to about 2,000 cheetah) in East Africa (GRAHAM & PARKER 1965) only one case of direct aggression was witnessed. That was described as the forcing away of a cub by an adult ♂ attempting to mate with the cub's mother. STEVENSON-HAMILTON (1947) in South Africa recorded overt aggression between cheetah twice, in both instances one ♂ killed another.

In groups 1, 2, 3, and 4 individuals seldom joined or left. Only group 3, the 2 ♂♂, separated temporarily but rejoined. Nairobi National Park records and several individuals' photographs show that these two ♂♂ originally hunted with 2 others for at least 2 years prior to the study, and they, too, broke up several times and rejoined. 2 of these 4 ♂♂ were not seen after the summer of 1966. It is believed by the Park Warden (D. KIERNEY, pers. comm.) that these four ♂♂ were litter-mates.

Marking and Response to Marks:

♂ cheetah are capable of directional urination as observed for tigers *(Panthera tigris)* and lions (SCHALLER 1967 : 251—3). The penis can be directed with accuracy at objects above or below the body (Fig. 1). ♂♂ in adult groups or singly pass small quantities of urine throughout the day on many objects, while ♀♀ appear to urinate heavily only occasionally as a purely excretory function. ♀ tigers and lions (SCHALLER 1967 : 252) emit wide sprays quite frequently. Both sexes in a cheetah group took great interest in the urination previously made by ♂♂ of other groups (Fig. 2). Where one group marked,

a)

b)

Fig. 1: Male cheetah marking a tree; note directional urination

another group inspected and then marked the same place. The ♀ with cubs took great interest in the markings of all other groups, and so did the cubs. ♂cubs of group 1, aged 4—8 months (ages after GRAHAM & PARKER 1965) during the study, were not observed to mark. The young ♂♂ of group 2 marked at 14 months, adulthood for cheetah.

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 homogeneous background of more common plants. For example, *A. drepanalobium* makes up at least 80 percent 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. drepa-*

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ings of the first group and as many as 21, with an average of 11. In no cases slowly and then warily in a direction different from the first group.

On 9 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 close-by markings before going on in a different direction than the first group. 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. 2). After all group members had paid great attention to the second-found marking, the group moved off, while marking, and proceeded slowly and then warily in a direction different from the first group.

On 5 occasions, 2 all-adult groups noticed each other while passing in opposite directions at 100—300 yards apart. Twice, 2 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. The lion watched the cheetah, but the cheetah were not aware of him. The expressions that cheetah make as group passes group closely fits the threatening behaviour of canines. In the cheetah, the ears are drawn back, the head is lowered, and the mouth is opened. In the observation of 2 ♂ cheetah approaching each other on opposite ridges about 100 yards apart, yelping (Tab. 2) and marking (J. B. FOSTER, pers. comm.) were frequent. The two ♂♂ 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 ♀ got up immediately and moved in the opposite direction from the 3 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.

Discussion

Although it is intended to describe the behavioral aspects of spacing in cheetah more than its ecological effects on populations, these topics are related and must be discussed. However, even if it is demonstrated that the spacing of 2 groups in close proximity is affected, this in no way necessarily implies a regulatory effect on cheetah numbers.

Population, Regulation, and Social Systems; Lions vs. Cheetah:

Data are scant, but it appears that there is a relationship between the size of local cheetah populations and the numbers of other predators. It also appears that size of adult groups is also related to the abundance of cheetah in an area. Since predation is mostly on cubs and cubs appear to remain together in adulthood, then it can be inferred that the average size of adult groups may be related inversely to predation pressure from other predators in a given area. This is especially noticeable in Nairobi National Park where at least some groups can be traced back as litter-mates. Also the absence of movement between cheetah groups indicates that members make up families. New groups are probably established as ♀♀ leave a group to give birth and raise young. It is not known if ♀♀ whose cubs are lost in some way re-enter their old groups or simply live alone until in estrus again at about 6 months after parturition. The first possibility is supported by the fact that, in a few groups, individuals left and rejoined after as long as 2 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 tenable; 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 then 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 behavioral castration (WOOLPY, 1968). That predation may be more important in controlling numbers than territoriality is shown, for example, in muskrats (*Ondatra zibethecus*). 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 1966) has eliminated the problem of predation on 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 is more important in limiting populations of lions than of cheetah. Aggression is also more important in the lion – pride members or territorial intruders are often killed (N. TINBERGEN, pers. comm., SCHENKEL 1966, 1967).

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, e. g. 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. Conversly, 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 or killed by adult ♂♂ in order for the pride to survive through the low part of a game cycle (which is related to the approximate 5-year rainfall cycle in East Africa, TALBOT & TALBOT 1963).

Marking in Lions and Cheetah:

Since members of lion prides often separate for periods while hunting (SCHALLER 1966), marking could be functional in reuniting members, e. g., to share a kill or for cooperative hunting efforts. Cheetah groups, on the other hand seldom have members leaving, with the exception of ♀♀ 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 must use markings to communicate estrous condition (BOURLIERE 1954). The cheetah ♀ when in estrous does pass scent that is of interest to ♂♂ wherever she sits or urinates; however, except during estrous, urination appears to occupy chiefly an excretory function most of the time. For lions, tigers, and

house cats vocalizations may act as important mating cues. Cheetah do not appear to vocalize to attract mates.

Threatening Behavior and Aggression:

The facial expressions of cheetah when two groups pass are typical threatening gestures. When threat behaviors are well established it is to be excepted that aggression between social groups is relatively rare. The observation of only 2 observed cases of overt aggression in cheetah (STEVENSON-HAMILTON 1947) indicates that the cheetah has a system that reduces the number of aggressive encounters. It is efficient in that strangers rarely meet. However, that threats are backed up by the potential of active aggression is indicated by the 2 observed fights, both of which resulted in death for one of the fighters.

Information Transfer in Markings:

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.

Selection for Differential Marking in the Sexes:

Female tigers and lions do mark (SCHALLER 1967), but ♀ cheetah apparently do not. Because ♀ cheetah always associate with ♂♂ except when they have cubs (GRAHAM & PARKER 1965), there may have been no selection for the development of the anatomical structures required for markings as found in ♂ cheetah. Social evolution in the tiger has probably led to a need for the ♀ to mark; however, that the degree of specialization has been limited by the ♀'s anatomy is shown by the ♀'s less efficient wide spray as opposed to the fine emission of ♂♂.

The ♂ in a cheetah group provides the chemical warnings, just as in many species of birds and mammals defense of territories is only by the ♂♂. A ♀ with cubs does not associate with other adults and therefore lacks a chemical warning system; perhaps ♀♀ with young are not spaced. According to LORENZ, (1946:243) "Where only one sex cares for the brood, only that sex is really aggressive toward members of the species". It is possible that ♀ with cubs, as in dogs, receive a "higher respect" from other adults. A ♀ in estrous was seen to ward off copulation attempts by her 3 adult sons. Her aggression was not returned by the ♂♂, one of which was the leader of the entire group. LEYHAUSEN (pers. comm.) observed what appeared to be marking by ♀ cheetah in captivity. Regardless, the ♀ does heed other group's markings and moves away from another group when they are sighted and thus remains spaced.

Efficiency of the Cheetah Spacing System:

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, [illegible] was not made and threat behavior patterns appear to function in this [illegible] hemical warnings were for a fixed area territorial scheme, they were [illegible]ve since the groups crossed marking paths constantly. The frequent [illegible] a route taken by cheetah probably serves as a means to prevent : 1) [illegible] from stumbling onto them (and interfering with their hunting), [illegible]bility of aggression from the encounter. The marking must be a [illegible]e capable, no doubt, of losing its information content over time [illegible]n this way, the warning is good only when needed. The mar[illegible]d a day after they are made, and later, but they are not re[illegible] robably 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 mark when so doing. Often these moves are just over short distances, at least 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.

Spacing Systems and Energy Budgets:

In thinking about spacing systems in cheetah it is helpful to ask why no fixed area territory is found. BROWN (1964) uses this approach with birds, and his ideas are generally 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.

Suggestions for Further Work on Territorial Behavior:

This "time-plan" of spacing has been found to date in at least one other species (the house-cat) by LEYHAUSEN and WOLFF (1959) and has been postulated for other species. It is interesting to note that the mountain lion appears to remain spaced by a time-space system (A. S. LEOPOLD, pers. comm.). To determine the function of marking in a species and its relation to spacing and/or territoriality is difficult. The cheetah group solidarity and habitat preference for the more open areas makes it, like feral house-cats, a suitable species to establish the meaning of social behavior patterns. In species such as the lion, where pride members come and go, or as in tigers, which dwell in the forest, it more difficult to confirm the presence of certain social behavior patterns. T use of bio-telemetric techniques to record various physiological parameters tl relate to aggression, e. g. blood pressure, could reveal the information cc of marking in the field or laboratory and other factors related to territor ng

g., to

The "Time-plan" of Spacing and Territoriality: e other

Since the cheetah is assuredly wild and is social, the applica ♀♀ for "time-plan" is extended to wholly natural populations and to s do not in- animals. It is an effective and substantiated means of spacing th lthough this sarily a population regulatory mechanism. I prefer to c . Many ani- spacing mechanism as a moving territory that is maintained . LIERE 1954). stituting temporary boundaries. This usage fits into the incl ♂♂ where- territoriality offered here: Territoriality is any behavio n appears to defense of any space in the home range against intruding cons s, tigers, and

All of the following observations indicate that an intraspecific spacing mechanism which appears territorial in nature is acting in the cheetah: 1) cheetah are highly specialized anatomically for marking, which they do frequently; 2) cheetah closely examine markings made by other cheetah; 3) 15 cheetah belonging to 4 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.

Summary

A study of cheetah group interactions reveals a spacing technique that works on a "time-plan". Marking appears to act as a means of defending any area against intruders. The markings are effective as warnings for only a short time. In this way, groups space themselves out, but this spacing system is not necessarily a population regulatory mechanism. The relationship between group size and mortality, and predation on cheetah as the factor most likely limiting cheetah numbers are discussed. A definition of territoriality is offered, and it is advocated that the "time-plan" of spacing is a special case of territoriality.

Zusammenfassung

Beobachtungen an den Auseinandersetzungen zwischen verschiedenen Gepardengruppen zeigten, daß die Tiere Zeitplan-Reviere haben (LEYHAUSEN 1959). Harnmarken scheinen als „Warnschilder" auf Eindringlinge zu wirken, aber nur für verhältnismäßig kurze Zeit. Auf diese Weise halten die einzelnen Gruppen Abstand voneinander. Diese Revierverhältnisse sind jedoch nicht entscheidend für die Populationsdichte. Die Gruppenstärke und die Sterblichkeitsrate hängen wahrscheinlich von der Anwesenheit und Anzahl anderer Raubtiere ab, welche Geparden schlagen (Löwe, Leopard, Hyäne). Eine Definition für Revierbesitz wird angeboten, bei der das Wahren eines Gruppenabstandes nach einem Zeitplan als Spezialfall gilt.

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