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Abstract: Cheetah social organisation is probably unique among mammals, females live singly, males in permanent associations of three, in pairs or alone. Cheetah male coalitions confer no much advantages because solitary females have overlapping home ranges and pass through a number of male territories during the year. Because of female dispersal and relative asynchrony of oestrus, a male that kept close to a single female over an extended period would suffer lowered reproductive success to one that searches for a number of females over that time. Unless there are unknown benefits to forming a coalition. This study sets out to determine those benefits.

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CHEETAH MALE COALITIONS

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Final Report

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INTRODUCTION

Cheetah social organization is probably unique among mammals, females live singly, males in permanent associations of three, in pairs or alone. Male lions accrue benefits from coalitions through extended pride tenure and enhanced ability to take over prides (Bygott, Bertram & Hanby 1979; Packer & Pusey 1982). Cheetah male coalitions confer no such advantages because solitary females have overlapping home ranges and pass through a number of male territories during the ~~year~~ course of the year. Because of female dispersal and relative asynchrony of oestrus, a male that kept close to a single female over an extended period would suffer lowered reproductive success to one that searched for a number of females over that time.

Leopard males do not form coalitions yet females live singly and have home ranges that overlap to some extent as in cheetah (Bertram 1978). It appears therefore that there is something peculiar to cheetah alone among felids that allows at least some males to benefit from permanent associations. Cheetah social organization cannot therefore be described as "intermediate" between lions and leopards.

If, other things being equal, each member of a coalition of males shared an equal proportion of the matings that coalitions obtained from oestrus females, then a member of, for instance, a pair would only leave half as many offspring as would a singleton male; unless there are unknown benefits to forming a coalition. This study sets out to determine those benefits.

CHEETAH SOCIAL ORGANIZATION

On the Serengeti Plains of Tanzania and its woodland border (see Sinclair 1979 for a general description), female cheetah move over wide areas (800 sq km) (Frame 1980) closely following the migration of

their main prey species, Thomson's gazelle (Schaller 1972). Male cheetah divide up the Plains into exclusive non-overlapping territories with sharp boundaries over which neighbours will not normally trespass. Territory holders are identified by repeated sightings in the same area and by their scent marking. Transient males or "floaters" are found in other males' territories where they seek out females. They are chased out by resident males and a number have been found wounded and incidents of male cheetah killed by conspecifics have been reported (Frame 1990; Moelhan and Tanzania National Park rangers pers com). Indeed the adult sex ratio in the Serengeti is low (Frame 1980) as in other cheetah populations (McVittie 1979), indicating a high male mortality and/or emigration.

Competition between cheetah males thus appears severe but single males do manage to hold territories (Table I). It is likely that smaller coalitions of males will lose fights against larger ones. It is thought that territories occupied by pairs of males are normally replaced by pairs, those occupied by trios are replaced by triplets, and singletons by solitary males. Thus there appears to be something specific to an area of the Serengeti that determines which kind of male association will occupy it. To reinforce such an hypothesis, transient trios have been seen ~~in~~ passing through a singleton territory but not attempting to occupy it.

GROUP SIZE BY DEFAULT?

In order to eliminate superficial explanation for group size it is important to determine the number of males present in the ecosystem. If there are very few, then solitary males and duos may simply be the result of there being too few partners available to form trios. Even though the sex ratio is low, there appear to be more than enough available partners to form large groups. Single males often meet and do not join up. Long term records (Bertram 1978; Frame 1980) allow the determination of

kinship relations among Serengeti cheetah and it is known that a number of male coalitions consist not only of brothers but of unrelated males of different ages. This group size is not simply a reflection of litter composition at independence. Some males actively join groups.

BENEFITS OF COALITIONS

A number of possible benefits derived from coalition formation have been examined.

TERRITORY SIZE AND LENGTH OF TENURE

Because male cheetah move large distances at night they are difficult to follow. Most territories straddle the plains-woodland border and the thick vegetation there makes relocation difficult next morning. Thus the full extent of males' territories is not known yet. Preliminary results indicate that singletons do not hold smaller territories than groups of males and that territory size does not increase with group size.

Males have been ousted from a number of territories since the study began but because males occupy territories for a number of years it is too early to say whether larger coalitions hold tenure for longer periods. Table II shows no overall trend starting from March 1980. Long term monitoring of all the territories will have to occur to show whether larger coalitions do gain reproductive benefits in this way.

DO MALE GROUPS HAVE ACCESS TO A BETTER DIET?

Detailed analysis has not been completed but results indicate that there are few differences in prey availability or diversity of prey species on territories occupied by males of different coalition size. Male coalitions can capture proportionately larger prey than singleton cheetah. Groups of males regularly select yearling and two-year old wildebeest, also hartebeest and topi whereas single males' diet consists primarily of adult

Thomson's gazelle and newborn wildebeest, although some single males have been seen to attempt to capture adult male wildebeest. In some instances group living males topple large prey using their combined weight. Detailed observations reveal that although food is shared unequally among group members, the larger prey size means certain and perhaps all members of a coalition eat more kilograms of meat per kill and may have to hunt marginally less often than singleton males.

Although groups of males do not defend carcasses from spotted hyaenas or lions, males from every kind of association have been seen scavenging, often from female cheetah (see Caro 1982).

ARE GROUPS OF MALES MORE VIGILANT?

Preliminary evidence suggests no marked differences in much the cheetah group scans the environment for prey or females when different sized coalitions are compared. Individuals within the groups do not scan the environment much less than do solitary cheetah (see Bertram 1980 for a comparison with ostrich groups).

DO GROUPS OCCUPY BETTER QUALITY TERRITORIES?

Male reproductive success is limited by the number of females they can inseminate (Trivers 1972), so the research has focussed on the number of females that males encounter on different territories. Four measures are being used to determine this.

(1) Numbers of females

The most important measure is the number of females found by the observer in each territory. These figures are standardized for the distance that the observer spends searching in each area. Subsequently the reproductive status of the females will be used to adjust the figure so that the number of potentially oestrus females available to each member of a coalition can be estimated.

Behavioural data taken when male coalitions encounter females

show that although coalition members all pin down a female by surrounding her, one male wins low level agonistic encounters that frequently occur in her presence. Dominance at kills is not indicative of dominance in the presence of a female but as no mating have been witnessed in coalitions it is not known whether the male that stays nearest the female is the one that is more successful in getting copulations.

(ii) Thomson's gazelle

Not all females can be located in a territory: they may be shy and natural obstacles easily obscure their presence. Female cheetah on the Serengeti Plain feed almost exclusively on Thomson's gazelle (Schaller 1972) and so the number of Thomson's gazelle provide an alternative measure for estimating the number of females. Male cheetah diet is far more catholic and Thomson's gazelles are not a good indicator of the number of males in the area. Monthly gazelle counts are being made in a minimum of four points in each territory allowing the migratory patterns of the gazelle to be closely monitored. Mean numbers and annual variance of the gazelle will subsequently be compared between territories.

(iii) Rainfall

The amount of rainfall directly affects the Thomson's gazelle distribution (see Bradley 1977) because Thomson's gazelle move to areas where new grass shoots appear. Monthly rainfall figures will be compared between territories.

(iv) Vegetation

Gross vegetation cover over the whole Plains has been quantified from aerial photographs taken by previous scientists. The grass-herb ratio indicates the amount of potential forage available for Thomson's gazelles as they are primarily grazers. The woodland cover in each territory provides shade for both male and female cheetah but more importantly provides a year-round food buffer for males. A number of prey

species are resident in the woodlands throughout the year which can be utilized after the migratory gazelle and wildebeest have left the area.

All these measures directly or indirectly estimate the number of females available per territorial male per annum. The prediction is that larger coalitions of males will encounter more oestrus females on their territory.

TRANSIENT MALES

Not all single and group living males hold territories. Transient males or floaters are found all over the Plains moving in and out of males' territories. Floaters have been found to consist of two or possibly three categories.

Firstly there are young males (known from past sightings as cubs) who are usually of small body size and are presumably either not big enough or are too inexperienced at fighting to challenge a territory holder.

Secondly there are territory holding males that have temporarily vacated their own territory. The demographic and ecological data collected during the course of the study will enable the causes of temporary abandonment to be delineated. For example, may leave and search for females elsewhere when there are few females to be found within their territory confines.

There may be a third class of males which are permanent floaters. These males may have opted not to hold territories; they are not individuals that have recently been evicted or males that have temporarily vacated territories unknown to the observer outside the study area. Knowledge of the identity of such adult males would be strengthened if it could be shown that there are suitable parts of the Plains that are not occupied by males. Then one could be sure that these males were actively selecting to float rather than being unable to set up a territory because everywhere was occupied. This hypothesis is currently being investigated.

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TABLE I

Number of known territories on the Serengeti Plains

<u>Male group size:</u>	<u>1</u>	<u>2</u>	<u>3</u>
Number of known territories	2	5	2

TABLE II

Male takeovers since March 1980

Male group size:	1	2	2	2	2	2	3	3
Has a take over occurred?	No	Yes	Yes	Pos sibly	No	No	Yes	No