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editors

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SERENGETI CHEETAH PROJECT

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1. OVERVIEW

Over the past 11 years, the Serengeti Cheetah Project has sought to determine the numbers of cheetahs living in the ecosystem and monitor changes in the population size over time. This is achieved by having personnel collecting demographic records in the field on a continuous basis. Our long term records indicate that perhaps only 600 cheetahs inhabit the whole ecosystem, half of these on the Plains. In contrast, approximately 4000 spotted hyaenas and 1500 lions use the same area. This raises two questions: why are cheetah numbers so low and what are the principal factors limiting cheetah numbers in the wild? These questions have important consequences for conservation because the cheetah is endangered, and for management because visitors are keen to see this species.

We have used three approaches to answer these questions. First we have investigated the social behaviour of this species to determine whether intraspecific mortality reduces cheetah numbers. Second, we have examined the interaction of cheetahs with their principal food, Thomson's gazelle. And third, we are investigating the causes of cub mortality. Our findings show that cub mortality and social behaviour are the most important factors limiting cheetah numbers in Serengeti.

Update on Work Since Last Biennial Report

During the last 2 years, progress in the cheetah project has been made on three fronts: (1) Tim Caro has made extensive inroads into completing his monograph on the social behaviour of cheetahs, he also came out to Serengeti in June-July 1988 and May-June 1989 to make further field observations. (2) Clare FitzGibbon finished writing her PhD dissertation on the antipredator behaviour of Thomson's gazelles in relation to cheetahs. (3) Karen Laurenson carried out an in-depth investigation of the causes of mortality and costs of reproduction of cheetahs in Serengeti, and continued to collect demographic records.

2. CHEETAH SOCIAL BEHAVIOUR

Female cheetahs

In order to understand the factors that limit cheetah numbers in the wild, it has been crucial to understand cheetah social behaviour. Cheetah females live alone or with their dependent cubs, while males either live alone or in small permanent groups of 2 or 3, termed coalitions. The reasons that female cheetahs and most other felines live by themselves is not fully understood, but it is now known that the cost of having cubs accompany their mother for 12-20 months is a huge drain on maternal resources. Observations show that, in Serengeti, mothers are always far hungrier than adult females, with large cubs consuming as much as 75% of the food that mothers catch for them. If female cheetahs were to become social, they would find it difficult to feed additional group members because they are already at the upper limit of the time they can devote to hunting. They also experience difficulties in catching large prey and would
be unlikely to increase hunting success if other females were present.

**Cheetah cubs**
One of the principal factors limiting the reproductive rate of females is the length of time that cubs remain dependent on their mothers. Contrary to belief, quantitative analyses of the development of hunting skills by cubs show that there is little improvement in hunting behaviour with time; mothers catch virtually all the food for the family. This is the case despite mothers actively encouraging their offspring to develop hunting skills by releasing prey in front of them. When cubs emerge from the den at 2 months of age they are also critically dependent on their mothers defending them against a variety of predators, especially lions and spotted hyaenas. We have now seen many litters attacked by these predators. Moreover, cubs' vigilance does not develop until they are nearly a year old making them poor at spotting danger ahead of time. But the long period of cub dependence is due primarily to cubs' inability to hunt properly.

**Adolescent cheetahs**
Cheetahs only start to become competent predators at approximately two and a half years old, a year after leaving their mothers. Adolescents hunt easy-to-catch neonate gazelles and hares almost exclusively when they first gain independence. Their hunts on larger prey failed because they are often seen by prey as they approach it, and they do not dare knock prey over at the end of a chase.

Adolescent cheetahs of both sexes remain together as stable units for several months after separating from their mother. These groups of littermates attempt to catch larger prey than do adolescents living alone and, by chasing prey simultaneously, one member is on hand if its partner does not dare knock prey over. However, groups of adolescents have to share prey that they catch so feeding benefits cannot explain why they stay together. Rather, adolescents in groups gain safety in numbers because they are harassed far less by other predators than are singletons.

**Male cheetahs**
Although some male cheetahs live alone, others live in amicable coalitions of two or three members, usually brothers. Coalitions are very egalitarian associations with no one male obtaining greater access to food or to any of the females that they encounter. Males are distressed when they lose their partner suggesting that it is important for them to be in a group. The reason is that coalitions are far more likely to become territory holders than are single males. Indirect evidence shows that groups of males win fights against single males and that mortality during such fights reduces the male population to almost half that of females. Territorial animals encounter more females than do non-territorial animals and probably have greater reproductive success.

As a consequence of living in small groups, males hunt together. Observations show that males living in larger groups do not have greater hunting success than single males because they do not hunt cooperatively, but they do prefer to hunt large prey such as wildebeest rather than smaller Thomson's gazelles. This necessarily results in large prey making up a greater proportion of their kills and as a result they eat more per unit time than males living alone. Thus the feeding consequences of living in a group are different for males than they are for groups of adolescents.

In summary, the behaviour of cheetahs does affect their population size through slowed reproduction of adult females as a consequence of having cubs, increased mortality of adult males through fighting, and possible reduced survivorship of adolescents as a result of incompetent hunting.

**3. INTERACTIONS BETWEEN CHEETAH & THEIR PREY**

**The importance of prey's vigilance**
Cheetahs normally catch their prey using a concealed approach followed by a sudden dash. Thus the degree to which prey, usually Thomson's gazelles, is vigilant has a dramatic effect on cheetahs' hunting success and ability to eat. When gazelles are in smaller groups, individuals scan the environment for predators more often; they are also
more vigilant in tall vegetation. Thomson's gazelles also benefit from joining groups of Grant's gazelles that are extremely vigilant and see approaching cheetahs at great distances. The importance of individual vigilance is shown by the fact that cheetahs chose to hunt those gazelles that are less vigilant than their neighbours. Also, cheetahs select male Thomson's gazelles more often than females because males tend to be on the edge of gazelle groups and are less vigilant than females.

**Fawns**

Approximately 60% of gazelles killed by cheetahs are immature animals, mostly youngsters born in the last 6 weeks. To counteract this disproportionate selection by cheetahs, fawns hide from them in vegetation which decreases the probability that they are found by cheetahs. Also, when fawns are chased they drop out of sight and lie prone which also lowers likelihood of capture. This is especially true if fawns drop down at a long distance from the predator. Since those fawns that drop down have mothers which detect predators further away, vigilance by mothers once again can be seen to have important consequences for increased survivorship of gazelles.

There was no evidence to suggest that the Thomson's gazelle population (approximately 300,000 animals) limits cheetah numbers in Serengeti. Calculations show that they take approximately 8% of the adult population annually. Nevertheless, the seasonal birth of Thomson's gazelles and their distribution has subtle impacts on different segments of the cheetah population. Single adolescents rely almost exclusively on fawns, mothers in dens concentrate on this age class, and all cheetahs are hungrier in the wet than in the dry season.

In summary, the prey's behaviour has major consequences for cheetahs' hunting and feeding behaviour, but Thomson's gazelle numbers are unlikely to be the most important factor keeping cheetah numbers at low levels in Serengeti.

**4. REPRODUCTIVE SUCCESS & THE CAUSES OF CUB MORTALITY**

Our long term records suggested that litter size had fallen in the Serengeti population by almost a third to approximately 2.0 cubs per litter in 1986. This decline is being investigated by examining the problems that reproductive females must surmount in order to raise litters of cubs successfully. In the course of this work, cheetah cub mortality is being documented and its causes ascertained. In order to be able to relocate individual females regularly, it has been necessary to fit a very limited number of radio-collars. These are being removed once observation schedules are completed. Since December 1989, 12 mothers have tried to raise 25 litters and we have been able to collect behavioural and physiological data when the females are pregnant, when they have cubs in the lair and when their cubs had newly emerged from the lair.

**5. RESULTS**

**5.1 Lairs**

For the first 7-8 weeks of cheetah cubs lives, cubs are concealed in a lair chosen by the mother. Observations show that females locate a suitable site within the general area of their home range that they had been using during pregnancy, determined by the position of the migratory Thomson's gazelles. Of the known lair sites, 10 have been in the middle of marshes, 5 under bushes in dried up river beds, 8 amongst long grass or tall herbs and shrubs and 1 in a kopje. All sites had good cover, were not on existing animal tracks, and almost all were close to standing water.

In most cases the mother was observed or known to move her cubs. So far there seems to be a high degree of variability between individual mothers as to how often this occurs and also what factors may precipitate the move.

As mothers must return virtually daily to suckle their cubs it appears that the choice of den site, in terms of the availability of prey, can be critical to the survival of the cubs. In two cases mothers have been seen to abandon cubs, probably due to poor hunting success and having to travel long distances to find prey.
5.2 Changes in Hunting and Feeding Behaviour during Lactation

Lactating females have been found to spend far more of their daily time budgets hunting and searching for prey than do females without young. Furthermore, there is an increase in the number of kilograms of meat eaten each day, and mothers continue to hunt after eating small prey items, instead of then resting. Prey choice may also alter at this time although more data are required, as choice is obviously affected by prey availability. In addition, choice of prey will affect hunting success as small prey items such as Thomson's gazelle fawns or hares are virtually always caught.

5.3 Activity Patterns

Females with cubs in lairs have different activity patterns from other females. They spend the first, cooler hours of the day with their cubs. It is not until later that they start moving to search for prey which may result in greater energy expenditure in the heat of the day. As females have to then return to their cubs after feeding, the total distance travelled each 24 hours is increased when compared to non-lactating females.

An increase in time spent drinking of over 300% has been seen when females were lactating. The presence of water nearby is probably important when choosing lair sites, particularly in the dry season.

5.4 Physiology

The energetic costs of lactation are high in most mammalian species and often cause a female to lose condition. One purpose of this study is to discover whether this is reflected in physiological changes during lactation in cheetahs. Blood samples were obtained when collar and decollaring and haematological, biochemical, genetical and virological parameters are being analysed. An important aspect of these results will be to compare them with those from cheetahs being bred in captivity where lactational costs are much reduced.

5.5 Cub Mortality

5.5.1 Pre-Emergence

Mortality during the first 8 weeks of cheetah cubs lives has never before been studied in the wild. This study is showing that mortality at this time is high. 18 out of 25 (72%) litters have died before 8 weeks of age and emerging from the lair. In many cases information as to the cause of death is available or the observer's understanding of mothers' behaviour in certain circumstances has led to the possible causes being narrowed down. Lion predation, hyaena predation, fire and the abandonment of litters by mothers have all been witnessed.

<table>
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<th>Cause</th>
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<td>3</td>
<td>1</td>
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In this and previous studies predation was found to be a major cause of mortality after the cubs had emerged from the lair, but it now appears that predation is a keen source of mortality at earlier stages as well. One litter was seen to be killed by a passing lioness who chase the mother from the lair. In 3 other cases predation was considered the most likely cause of death when mothers were found in the early morning lying in the vicinity of the lair, but no cubs could be found. One mother was seen to return to the area to search and call for 4 days after the known demise of her cubs.

A dry season grass fire was the cause of death of another litter. Two females had denned within 800m of each other. One night a raging and extensive grass fire swept through the area. Next morning the female with 4 week old cubs was found sheltering in bushes 500m away from the previous den. As only 2 of 3 cubs were with her, she repeatedly
went out and searched for the other. She eventually found the lost cubs, still alive but all the cubs appeared singed and burnt. The younger litter was found dead within a metre of the lair, perhaps because they were too young to walk. Both mothers were unharmed.

In two, and a possible third, mothers were seen to abandon cubs. Both had chosen lairs in an area where few prey animals were available. In one case the mother was observed closely when the cubs were 5 weeks old. By then the nearest gazelles were 8km off, so several hours walking were required before a hunt could even be attempted. Over 3 days only 2 hares were caught despite several unsuccessful hunts. During this time the mother did not return to her otherwise healthy cubs. On the fourth day the cubs were still alive but by the fifth they had been killed by predators. The mother still had not returned.

The high mortality at this stage of cub's lives is corroborated by the long term records we have of the population where females have been seen lactating repeatedly but no cubs were subsequently seen.

5.5.2 Post-Emergence

If cubs survive until 7-8 weeks of age, the mother will lead them from the lair. They are, however still extremely vulnerable at this age. Although they are now able to follow their mother and eat meat at kills, they are still too young to outrun predators. Additionally, they have insufficient experience to recognise danger.

The first week post-emergence seems to be a particularly critical time. Of the 7 litters that successfully emerged, 3 whole litters and a further 5 out of 14 cubs were killed in the first week. Only 5 cubs were seen to be killed, and all by hyaenas, but circumstantial evidence gives further weight to the hypothesis that predation by lions and hyaenas is very much the major cause of mortality at this time. In the following 6 weeks, by the time the cubs are 3.5 months old, a further 7 cubs disappeared and only 2 are known to have survived to 6 months of age. With an average litter size of 3.5 and 25 litters born, this gives as overall morality rate of about 97%.

Clearly, with such a high rate of mortality, the principal cause of which is predation, changes in the population size of the major predators such as lions and hyaenas could severely affect the cheetah population in the park. Predation, in fact may be the most important factor limiting cheetah numbers in this ecosystem and possibly also elsewhere.

LIST OF PUBLICATIONS FROM THE CHEETAH PROJECT


male cheetahs (*Acinonyx jubatus*). *Journal of Zoology* 221, 89-105.


