Frame GW. 1980. Cheetah social organization in the Serengeti ecosystem, Tanzania. Annual Meeting of the Animal Behavior Society, Colorado State University, Fort Collins, Colorado, 9-13 June 1980. Session on the Structure and Evolution of Carnivore Social Systems.; 20 p.

Keywords: 1TZ/Acinonyx jubatus/behavior/cheetah/ecosystem/evolution/Serengeti/social behavior/social system

Abstract: At least 82 percent of the cheetah sightings in the Serengeti were composed of lone adults, mothers with cubs, or sub-adult littermates who had not yet separated. Cheetah cubs were born in all months of the year. Mean litter size was 3. By 23 months of age all females had separated from their littermates, but males littermates sometimes stayed together for 5 years or longer. Females had home ranges of about 800 square kilometres, which largely overlapped those of their mothers and sisters. Females actively avoided each other, but they were not territorial. Young adult males emigrated from their mother's range. Some adult males were territorial, which territories of 12 to 36 square kilometers. Adult males who were not littermates sometimes joined together. About half of the adult males lived in groups. Among adults there were twice as many females as there were males; this is partly due to some males being killed in fights with other male cheetahs. The forming of social groups by half of the adult male cheetahs seems to be a strategy of gaining strength in numbers for competing with other male cheetahs.

Invited paper presented at the annual meeting of the Animal Behavior Society, Colorado State University, Fort Collins, Colorado, 9-13 June 1980.
Session on the Structure and Evolution of Carnivore Social Systems.

Title: Cheetah Social Organization in the Serengeti Ecosystem, Tanzania.

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This is a report on some of the results of a cheetah study that I did in northern Tanzania, East Africa, from late 1973 until early 1978. Other aspects of the cheetah research are still in preparation.

Specifically, I will here describe the cheetah social groupings, ranges, dispersal, territoriality, and evidence of hierarchies within male groups. Then I will speculate on why this social system evolved.

The study area covered about 5,200 square kilometers of grasslands and acacia woodlands in the southeastern portion of the Serengeti National Park and the western portion of the Ngorongoro Conservation Area. Observations were made from a vehicle. Sometimes the cheetahs were searched for and watched on a daily basis, and at other times they were followed continuously day and night for several days.

Cheetahs were photographed, and each individual was identified by the unique pattern of spots on its face and legs. I began my fieldwork with a photo file of 22 cheetahs, which Brian Bertram had compiled while doing a lion study. I cataloged an additional 420 different adults and cubs. For some of the cheetahs I was able to maintain records over a span of four generations.

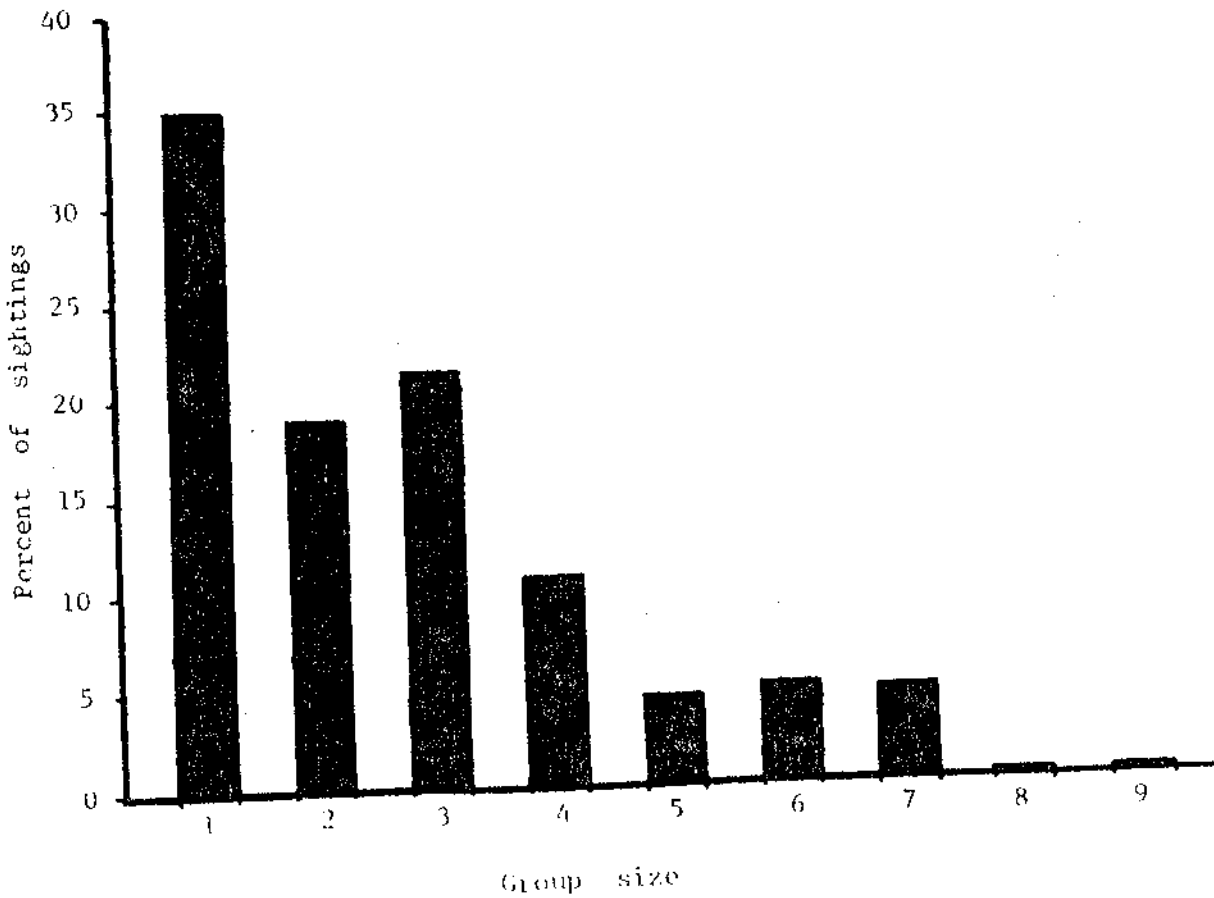
I recorded 1,260 cheetah sightings (Figure 1). These involved more than 200 different adults and as many cubs. The sample covers the years 1969 through 1979. It includes cheetah sightings recorded by Brian Bertram before

I began my fieldwork in 1973, and by Anne Pusey and Craig Packer after I completed my fieldwork in 1978. Tim Caro arrived in the Serengeti early in 1980 to carry on cheetah studies.

The group sizes ranged from 1 to 9, with 1 being the most frequent. Two-thirds of the sightings were of groups, but most of these were mothers with cubs, or young adult littermates who had not yet separated.

The one group of 9 cheetahs was an instance of two mothers with cubs who lay together for several hours. And the one group of 8 was a brief meeting between a mother with cubs and a territorial male.

Figure 1. Frequency of group size from 1,260 cheetah sightings in the Serengeti ecosystem, Tanzania.



In the 1,260 cheetah groups recorded, at least 82 percent of the sightings, i.e. the first five lines of Table 1, were either mothers with cubs, lone adults, or else littermates less than 23 months old who had not yet separated from each other. At least 7 percent of the sightings were of adult male groups. And 3 percent were of adult female-male groups of temporary association, such as courtship. [redacted] of [redacted] (the rate was about 1 in 500 sightings), and when they did associate it was only for several hours at most.

Table 1. Composition of 1,260 cheetah groups sighted* in the Serengeti ecosystem, Tanzania.

Association		Percent
Adult female with cubs		40
Lone adult female	19	35
Lone adult male	6	
Lone adult sex unknown	10	
Group of littermates, separated from mother		7
Group of adult males		7
Group of adults, sex and relationship unknown		8
Adult female with non-littermate adult male(s)		3
Total		100

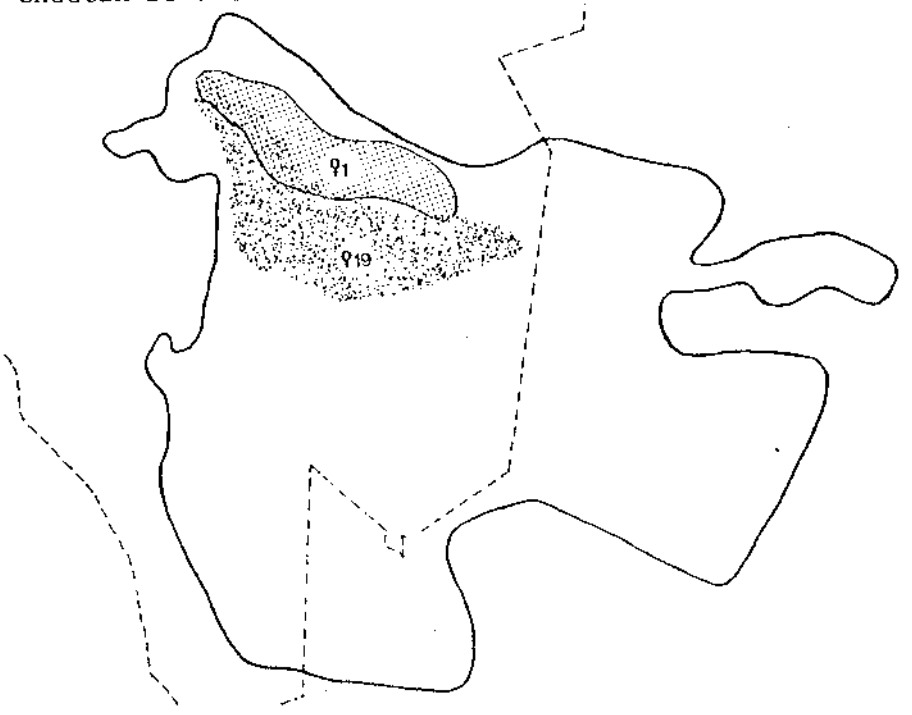
* Sightings recorded by Brian C.R. Bertram 1969-1973
George and Lory Frame 1973-1978
Craig Packer and Anne Pusey 1978-1979

Records from 91 different litters show that cheetah cubs were born throughout the year. Litter size ranged from 1 to 6 cubs, with a mean of 3 cubs per litter at the time each litter was first seen. The mode was 2 cubs per litter.

Cubs separated from their mothers between the ages of 13 and 20 months. The littermates stayed together for several months after leaving their mother, but all females left their littermates between 17 to 23 months of age. Some males separated from their male littermates, and other males stayed together for several years or longer.

In Figure 2, the map's heavy solid line represents the limits of our study area. The irregularities of the boundary were defined mainly by mountains, dense woodlands, and rivers. The dashed line shows the southeastern and southwestern boundaries of the Serengeti National Park. The study area was approximately 60 to 100 kilometers in diameter.

Figure 2. Cheetah study area in the Serengeti National Park and Ngorongoro Conservation Area, Tanzania. The ranges of two cheetah female littermates are shown.



Numerous resightings of known cheetah individuals showed the pattern of dispersal. Females remained in approximately the same area as their mother, but there was a partial shift in their ranges.

The known ranges of two female littermates over a period of 11 years are shown in Figure 2. Their mother's range is not indicated, but it partly overlapped the ranges of these two daughters. The range of ♀1 was approximated by drawing a polygon around the outermost of 80 point locations. And the range of her sister, ♀19, was estimated from 31 point locations.

The ranges of ♀1's two grown daughters, ♀2 and ♀4, during the four years after they left their mother, are shown in Figure 3. Their ranges are 50 to 65 kilometers long. Most females had known home ranges of about 800 square kilometers, but it is likely that the full extent of their ranges was even larger. Each adult female traveled her range in an annual cycle, and appeared to use the same range year after year.

Males, in contrast, did not remain in their mother's range. Instead, they emigrated. In this example, ♀2 and ♀4 had three male littermates. Two of the males, ♂3 and ♂5, were last seen on an apparent emigration west of their mother's range within several months after separating from their mother and sisters. The third male disappeared.

Another example of the dispersal pattern of young adults is ♀11's litter of three cubs (Figure 4). In the three years after ♀14 separated from her mother, she continued occupying nearly the same range as her mother; both mother and daughter had ranges at least 50 kilometers long. However, the two male cubs, within months of separating from their mother, emigrated more than 18 kilometers south of their mother's range.

The brothers, ♂12 and ♂13, displaced two males, and began marking their new small range of about 13 square kilometers. By the time our study ended, ♂12 and ♂13 had been resident three years. More recently, two strange male cheetahs were found within hours of being killed in ♂12 and ♂13's range

Figure 3. Ranges of a mother cheetah, ♀1, and her two adult daughters. Two young adult sons emigrated.

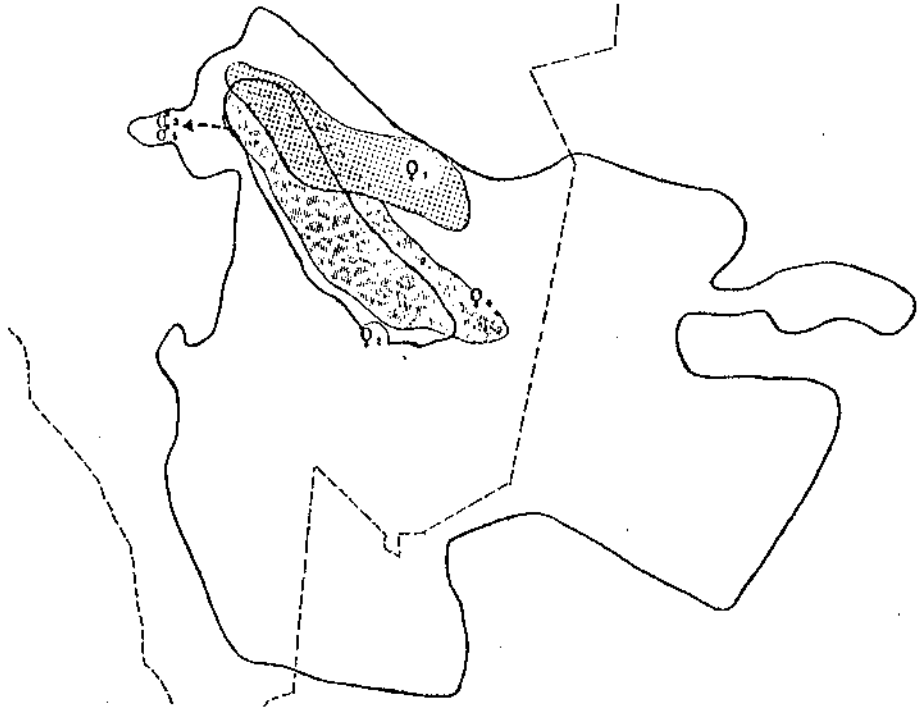
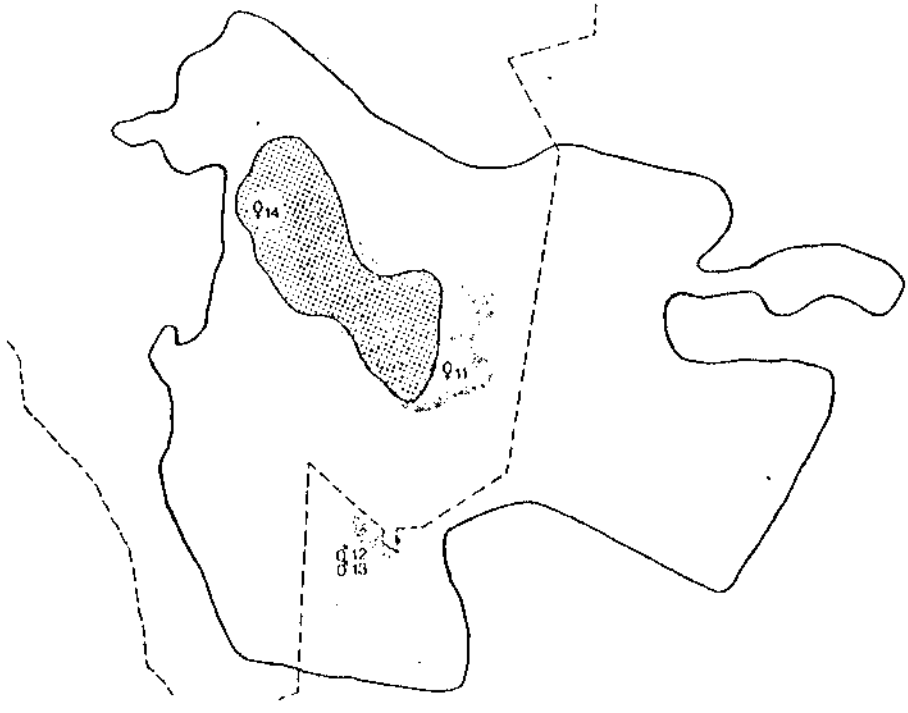


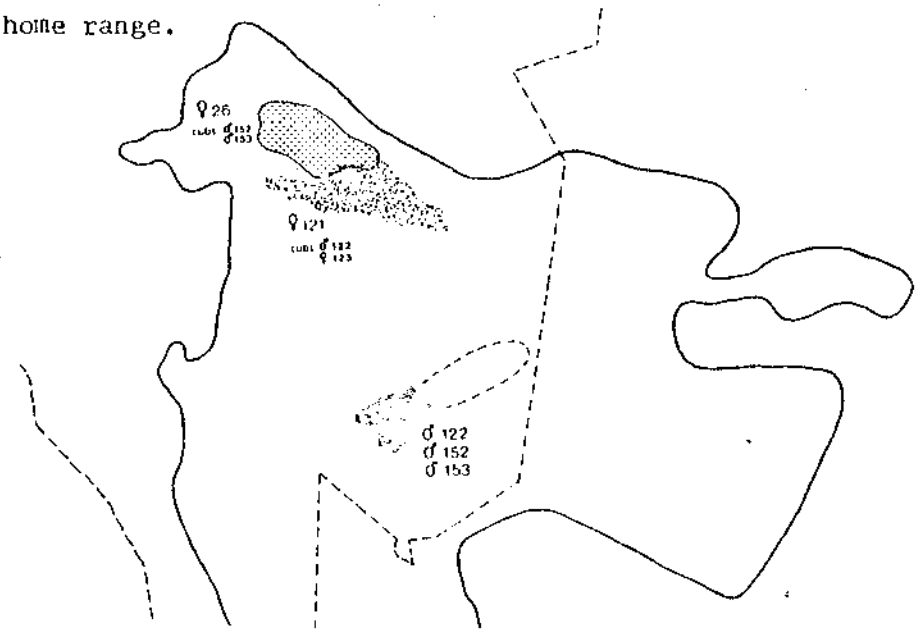
Figure 4. Ranges of a mother cheetah, ♀11, and her adult daughter. Two young adult sons emigrated and established a territory more than 18 kilometers south of their mother's range.



A third example of the emigration of male cheetahs is shown by two mothers and their cubs (Figure 5). The ranges of the mothers, shown in the upper left, are underestimated. Both ranges probably extended northward out of the study area. ♀26 had a litter of two males, ♂152 and ♂153. And ♀121's litter consisted of ♂122 and a sister. Shortly after the litters separated from their mothers, ♂122 joined ♂152 and ♂153 while they were all still in their mothers' ranges.

The three males emigrated together to the area shown by the cross-hatching (Figure 5). They marked and defended at least part of this range of 36 square kilometers. After 14 months, at a time when prey were scarce, they extended their range to include the area denoted by the dashed loop--an additional 22 square kilometers. A month later, the 3 males were seen again in the original area denoted by cross-hatching.

Figure 5. Ranges of two mother cheetahs whose male offspring joined together and emigrated. The group of three young adult males established a territory more than 20 km south of their mothers' home range.



Before discussing the territorial behavior of males, it would be useful to review the data about male groups. Among the 442 cataloged cheetah individuals, 58 were adult males (Table 2) and 111 were adult females. The remainder were mostly cubs and a few adults of undetermined sex.

The adult females lived alone or with cubs. They did not form social groups. Males, however, were more gregarious. As Table 2 shows, nearly half of the 58 known adult male cheetahs lived alone, and the rest lived in groups of 2 or 3.

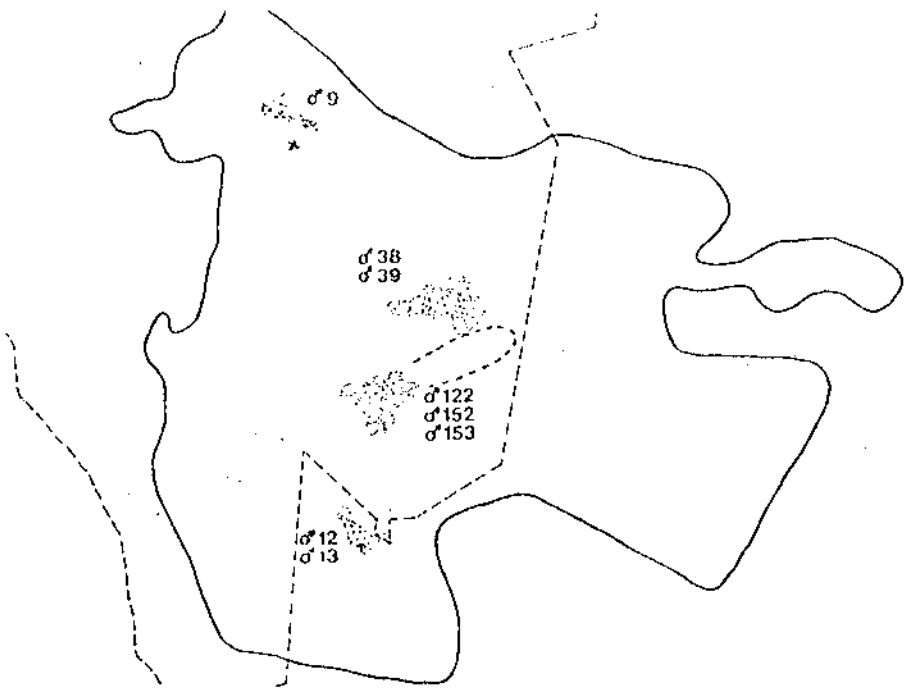
Some male groups consisted of littermates, and some of males who were not littermates. Among the 91 litters that I recorded, only about a third could be followed in detail as they grew up and dispersed. Only six of these litters had more than one male in them at the time they separated from their mother. In four of the six litters, the males did not stay together.

Table 2. Grouping of cataloged adult male cheetahs in the Serengeti ecosystem, Tanzania.

Group composition	Number of groups	Number of males
Alone	27	27
Two littermates	2	4
Two littermates with one non-littermate	3	9
Two non-littermates	1	2
Two, relationship unknown	8	16
	Total	58

Figure 6 shows four territories (represented by the stippled areas) that were recognized through frequent observations of the indicated males. Other males were seen in most portions of the study area, but were not observed often enough or with sufficient detail to determine whether or not they had territories. In saying that some male cheetahs are territorial, I mean that they regularly scent mark a well-defined area, that they leave the area only rarely in search of food or water, and that they kill or chase away intruding male cheetahs.

Figure 6. Map of four territories held by cheetah males.



We can see from the males listed on the map (Figure 6) that territories were held by lone males and by groups of 2 or 3 males. ♂9 held his territory for at least 4 years. ♂38 and ♂39 were of unknown relationship; they maintained their territory at least 1½ years. ♂122, ♂152, and ♂153, as we discussed in an earlier figure, were an alliance of two brothers and a male of the same age who had been born to a different mother; they held their territory for at least 1½ years. Finally, ♂12 and ♂13, which we also saw in an earlier figure, were brothers who were known to maintain their territory for at least 3 years. In all four cases, the known existence of territories ranged in duration from 1½ to 4 years, and it is likely that the males continued to defend their territories even longer than this. The sizes of the territories were between 12 and 36 square kilometers. These male-held territories were in areas of good vegetative cover, such as drainages and kopjes, and with good availability of prey.

The sex ratio of the Serengeti cheetahs is suggestive of a differential dispersal or mortality of males. In the 1,260 recorded sightings the sex ratio was 1♂:1.69♀ (Table 3). Many of those sightings were repeat observations of the same individuals. Based only on the cataloged individuals, i.e. known adults and cubs, where there was no repetition, the sex ratio was 1♂:1.4♀. Dividing the cataloged cheetahs into the two categories of "cubs only" and "adults only" is more enlightening. The sexes at birth were approximately equal in number. By the time the cheetahs were adult, however, there were nearly twice as many females as there were males.

The territorial behavior of males explains why the cheetah sex ratio shifts from unity at birth to twice as many females as males among adults. We know for certain that some males were killed in territorial disputes. There could also have been a differential emigration from the study area.

Table 3. Sex ratio of cheetahs in the Serengeti ecosystem, Tanzania.

1 ♂ : 1.62 ♀	All individuals in the 1,260 sightings (adults and cubs)	
	850	males
	1,375	females
	1,115	sex unknown (mostly small cubs)
	3,340	Total
1 ♂ : 1.43 ♀	All cataloged individuals (adults and cubs)	
	116	males
	166	females
	160	sex unknown (mostly small cubs)
	442	Total
1 ♂ : 0.93 ♀	Cataloged cubs only	
	54	males
	50	females
	150	sex unknown
	254	Total
1 ♂ : 1.91 ♀	Cataloged adults only (older than 23 months)	
	58	males
	111	females
	10	sex unknown
	179	Total

One morning while I was observing the group of three territorial males, I saw them chase a group of three intruding males. They caught one intruder, and attacked him viciously. The victim's gestures were defensive, and he made almost no effort to fight back and no attempt to escape. The three territorial males cooperated in attacking. They tore out fur, and directed hundreds of bites to all parts of his body. After 17 minutes of vigorous fighting, the three territorial males lay down to rest, just a few meters from the victim. By this time the victim was lying quietly with deep irregular breathing.

During the fighting I tried to quantify behavioral differences among the three territorial males. Recall that ♂122 was not a brother. ♂122 fought most intensely, thrashing his head from side to side as he bit the victim. He often leaped vertically, more than one meter into the air as he attacked. Whenever either companion attacked the intruder too vigorously, ♂122 turned and swatted them or bit an ear. Also, ♂122 was the only one who crouched and sniffed the ground in several places near the intruder. And when a spotted hyena came too close, ♂122 chased it away.

All three males rested 20 minutes and then resumed their attacks. But they fought only a few minutes more before ♂153 killed the intruder with a suffocating bite on the underside of the neck--the same bite that is used in killing prey.

After killing the first intruder, the territorial males went to the other two who were watching from several hundred meters away. They fought for a minute; then ♂153 chased one of the intruders at least 1 kilometer. But after a few minutes they rested, only three meters apart, until they were rejoined by ♂153.

As ♂153 returned, he was met by his companion, ♂122. ♂122 stalked and charged toward him, swatted several times, ran circles around him, and then sniffed the ground. ♂153 was accepted, and they lay down together for half an hour.

The three territorial males then resumed their attack on the remaining intruder, who was still lying nearby. They fought vigorously for a minute with ♂122 leading and fighting most. The victim gave squealy yelps and meows, very much like a housecat. ♂122 fought most, and ♂153 fought second most; these same two males sniffed the ground around their victim.

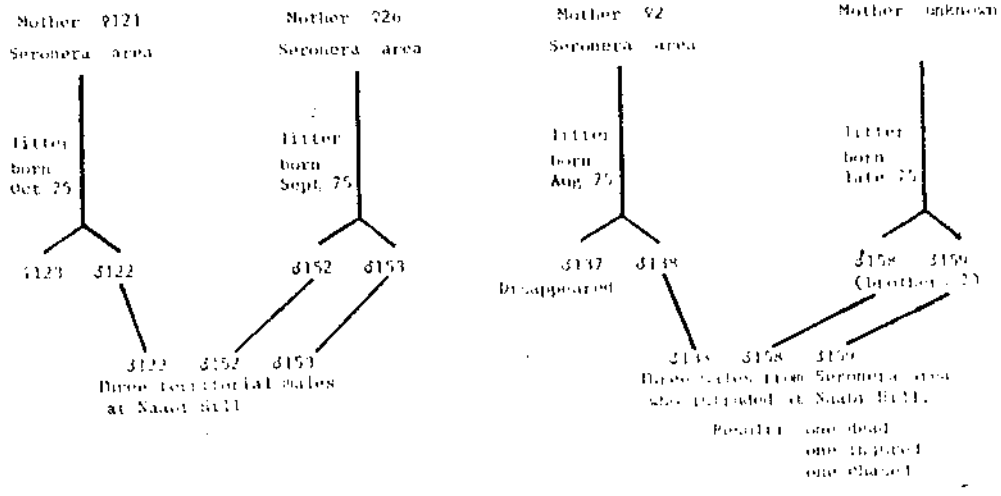
By then the territorial males were tired and hot, so they left their victim. ♂122 led toward the shade trees in the center of their territory; his mouth was bleeding from the fighting. The intruder lay still, watching his attackers leave. He did not appear to be seriously injured, and that evening he sneaked away.

In this fighting, it appeared that ♂122 was the leader and the dominant. That is, he took most of the initiatives, and was the only one who sometimes attacked his own companions.

The family relationships of the males are shown in Figure 7. The left half of the diagram shows the three territorial males. ♂152 and ♂153 were littermates, and ♂122 was born to a different mother. Their mothers were not littermates.

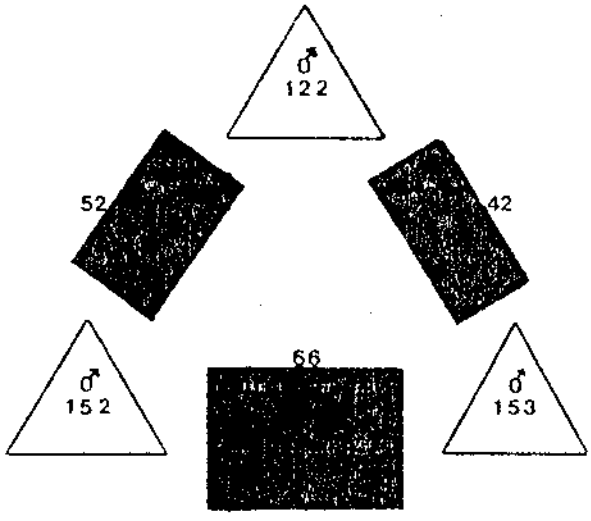
The right half shows the three intruding males. Like the territorial males, the nomadic males were born to at least two different mothers. ♂138 originally had a brother, ♂137, but he disappeared when they separated from their mother.

Figure 7. Relationships of two groups of male cheetahs who fought at Naabi Hill, on the Serengeti Plains, Tanzania.



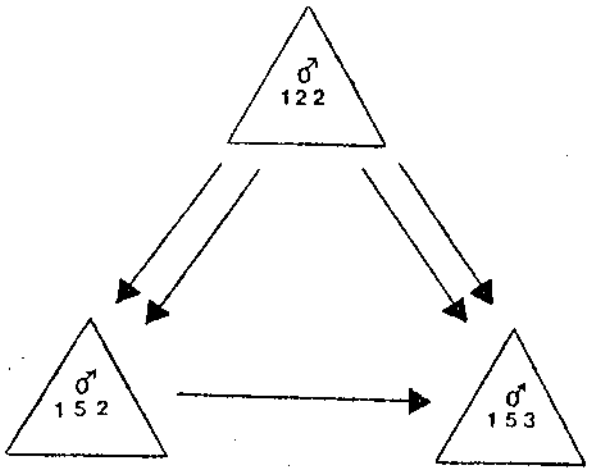
It is of interest to look more closely at the social relationships between the three territorial males. The proximity diagram (Figure 8) shows the males' affinity for resting together, about three months after they established their territory. Sampling was done over a five day period. Proximities were recorded at 15 minute intervals. Among the three dyads there was a significant non-random pairing, as shown by a χ^2 test with a P of about .02. The two brothers showed the greatest tendency to rest together. ♂122 rested least near ♂153, who seemed to be his closer rival.

Figure 8. Proximity associations within a group of three territorial male cheetahs in the Serengeti ecosystem, Tanzania. Sample of 160 associations in which cheetahs were touching or within reach.



During 38 hours of the same 5 days of observation, I saw only five cheek rubs between the three males (Figure 9). The unrelated male, ♂122, who I thought was highest ranking, directed two face rubs to each of the other males. ♂152 directed one face rub to his brother. But ♂153 did not initiate any face rubs. χ^2 shows no statistical significance with a P of about .5. This greeting gesture is generally interpreted to symbolize peaceful intentions and a sense of acceptance.

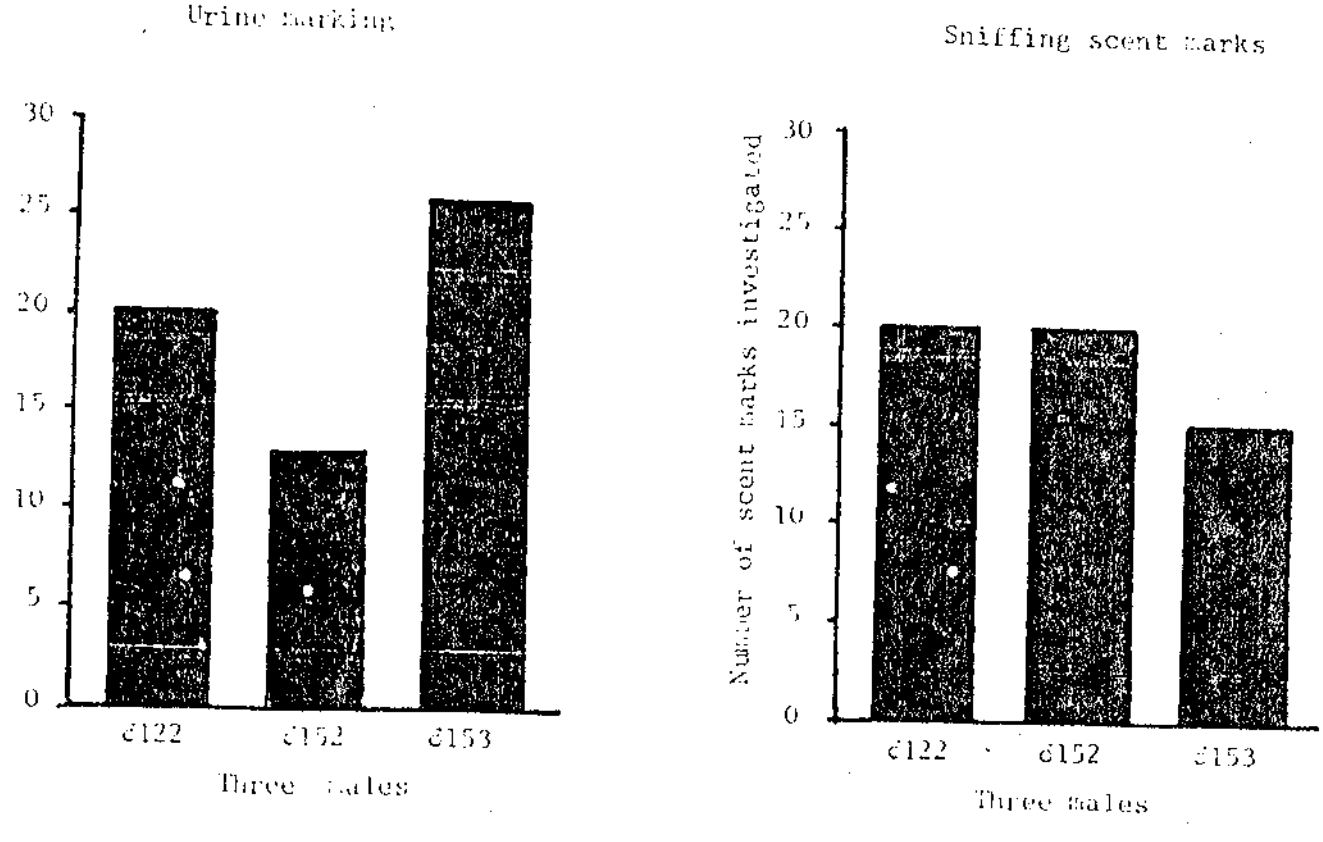
Figure 9. Cheek rubbing within a group of three territorial male cheetahs in the Serengeti ecosystem, Tanzania. Sample of 5 cheek rubs in 38 hours of observation.



The number of urine marks made by each of the three territorial males during the five day sample period are shown in Figure 10. χ^2 shows a non-random distribution for a P of about .05. ♂153 urine-marked most frequently, and ♂122 did the second most.

Figure 10 also shows the number of instances in which scent marks were sniffed. The differences among the males was not statistically significant, with χ^2 giving a P value of about .4.

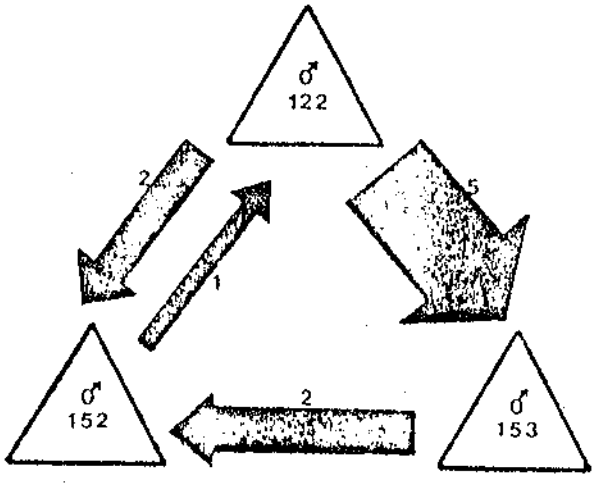
Figure 10. Urine-marking and investigation of scent marks by a group of three territorial male cheetahs in the Serengeti ecosystem, Tanzania. Sample of 59 urine marks and 55 scent marks sniffed in 34 hours of observation.



The rate of interaction between the three males was low. In a five day observation period, the only aggressive interactions occurred when ♂122 briefly attacked his companions during their fight with the intruding males. There was one play bout, and that was between the two brothers; it lasted only a minute, and consisted of slow wrestling and mutual grooming.

On ten occasions play invitations were initiated (Figure 11). The χ^2 test shows this to be non-random with a P of about .02. ♂122, the presumed highest ranking male, sent most of the play invitations, and his contribution to the χ^2 value was alone enough to give a P of .05.

Figure 11. Play invitations initiated within a group of three territorial male cheetahs in the Serengeti ecosystem, Tanzania. Sample of 10 invitations in 34 hours of observation.



From the various measures, it is apparent that a significant social relationship existed between ♂122 and ♂153. The non-brother, ♂122, seemed the most active in maintaining the social relationships with the other two via cheek rubs and play solicitation. Yet his low proximity association plus his high levels of aggression toward his companions (during their attack of the intruding cheetahs) suggested that he was dominating them. This was further born out by his leadership in attacking the intruders.

A solitary life for cheetahs seems favored because their slender build and small jaws tend to limit prey to a size that will fill the stomachs of no more than one adult, or a mother with small cubs. Cheetahs hunted by careful stalking. I recorded 493 hunts in which 203 kills were made. Nearly 60 percent of the kills were Thomson's gazelles. Only 40 percent of the Thomson's gazelles that were stalked were then chased. Of those chased, 49 percent were caught.

I found no evidence that cheetahs grouped together for the purpose of hunting larger prey. However, when adult male cheetahs were already grouped for social reasons, or when a mother cheetah was with her nearly full-grown cubs, they then sometimes hunted larger prey. Otherwise the groups would have had the energetically inefficient alternative of killing the usual small prey every day, and sometimes twice per day, to get enough to eat. This would have necessitated hunting almost all day long, every day.

The sociality shown by some adult males appears to be a strategy to increase their success in gaining and holding a territory. Their territories seemed to be in the best habitat, that is, in moderate cover with water and prey. Females tended to gravitate to this kind of habitat. Thus, territorial males may have an increased chance of meeting females--an advantage for a species that lives widely scattered. We might, therefore, expect territorial male cheetahs to have greater success in breeding, but this remains a speculation.

SUMMARY

At least 82 percent of the cheetah sightings in the Serengeti were composed of lone adults, mothers with cubs, or sub-adult littermates who had not yet separated.

Cheetah cubs were born in all months of the year. Mean litter size was 3. By 23 months of age all females had separated from their littermates, but male littermates sometimes stayed together for 5 years or longer.

Females had home ranges of about 800 square kilometers, which largely overlapped those of their mother and sisters. Females actively avoided each other, but they were not territorial.

Young adult males emigrated from their mother's range. Some adult males were territorial, with territories of 12 to 36 square kilometers. Adult males who were not littermates sometimes joined together. About half of the adult males lived in groups. Among adults there were twice as many females as there were males; this is partly due to some males being killed in fights with other male cheetahs. The forming of social groups by half of the adult male cheetahs seems to be a strategy of gaining strength in numbers for competing with other male cheetahs.

ACKNOWLEDGEMENTS

Lory Herbison Frame and I worked together in most of this joint field study of cheetahs and African wild dogs. A large portion of these results about cheetahs is, therefore, credited to her.

Our research was authorized by the Tanzania National Scientific Research Council. We especially owe thanks to David S. Babu (Chief Park Warden of the Serengeti National Park), Anthony N.J. Mgina (Chief Conservator of the Ngorongoro Conservation Area Authority), and Tumaini Mcharo (former Director of the Serengeti Research Institute) for their cooperation and assistance.

The East African Wild Life Society donated a new Toyota Land Cruiser to the Serengeti Research Institute for us to use in our cheetah research. Funds for petrol, repairs, and other research expenses were contributed by the African Wildlife Leadership Foundation, the Shikar-Safari Club, the Max Planck Institut für Verhaltensphysiologie, Sigma Xi: The Scientific Research Society of North America, the Fauna Preservation Society, the Explorers Club, the Zoological Society of Philadelphia, the New York Zoological Society, the World Wildlife Fund, Don Meier Productions Inc., the Fund for Animals Inc., Wolfgang Bayer Productions Inc., and Baron Hugo van Lawick.

A cheetah research program began in the Serengeti in 1969, when Brian C.R. Bertram started identifying individual cheetahs that he encountered while doing his lion and leopard research. From then, until we began our fieldwork in late 1973, Bertram accumulated 146 sightings of 22 different individuals. These records he gave to us, to provide a foundation for our research. All of Bertram's sightings are included in our analyses.

While we were doing our fieldwork, from late 1973 through early 1978, many other researchers and visitors helped by contributing photographs and notes of their cheetah sightings. Considerable assistance was provided by David Bygott, Jeannette Hanby, Jon and Hazel Rood, and Reinhard Leo Künkel. Additional sightings were contributed by Dieter Schmidl, Robin Pellew, Sean and Sam McNaughton, Helmut and Sue Epp, Tjapko Jager and Marjolyn Jager-van Deursen, Aadje Geertsema, Warren and Genny Garst, Alan and Joan Root, Leon Joe Folse, Hugo van Lawick, Patricia Moehlman, Jerry Rilling, Dirk Kreulen, David Pratt, Virginia Anderson, and others. Their help saved us considerable searching time and expense, and provided details which we might otherwise have missed.

After we left the Serengeti, Craig Packer and Anne Pusey photographed 28 sightings that they made during 1978 and 1979. Their sightings, through March 1979, are included in our analyses.