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Abstract: Cheetah (Acinonyx jubatus) data from our Serengeti field study were used to test Wrangham's model of the effects of the intraspecific mutualism on group composition. Wrangham predicted that when mutualists have negative effects on the reproductive success of other conspecifics (interference mutualism) they should comprise close mutualism, but about 1/3 of these coalitions did not fit the "close fit" prediction. When males have close kin they may prefer them, but often there were no close kin with which to incorporating this constraint.

POSTER PRESENTATION AND BACKGROUND PAPER FOR:

CHEETAH MALE COOPERATION: TEST OF A MUTUALISM MODEL

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Abstract for: 1984 Animal Behavior Society Meeting, Eastern Washington University, Cheney, Washington, August 13-17, 1984.

Abstract. Cheetah (*Acinonyx jubatus*) data from our Serengeti field study (ms. in prep.) were used to test Wrangham's model of the effects of intraspecific mutualism on group composition. Wrangham predicted that when mutualists have negative effects on the reproductive success of other conspecifics (Interference Mutualism) they should comprise close kin. Cheetah male coalitions were an example of Interference Mutualism, but about 1/3 of these coalitions did not fit the "close kin" prediction. When males have close kin they may prefer them, but often there were no close kin with which to associate. The model's generality would be increased by incorporating this constraint. Ref: Wrangham, R.W. 1982. Pages 269-289 in *Current Problems in Sociobiology*, Cambridge University Press.

Abstract for:
(1) Sigma Xi: The Scientific Research Society of North America, Fall 1984 Annual Meeting of the Utah State University Chapter, Logan, Utah; and
(2) Conservation Week 1985, College of Natural Resources, Utah State University, Logan, Utah.

Abstract. Cheetah (*Acinonyx jubatus*) data from our field study in the Serengeti ecosystem, Tanzania, were used to test Wrangham's (1982) model of the effects of intraspecific mutualism on group composition. Wrangham predicted that mutualists should be close kin if they have negative effects on the reproductive success of other conspecifics (Interference Mutualism). We found that 2/3 of the adult male cheetahs lived in coalitions that persisted for years. Most territories were held by male coalitions rather than solitary males, and intruding males sometimes were killed. Cheetah male colitions, therefore, were an example of Interference Mutualism. But about 1/3 of these coalitions did not fit the "close kin" prediction. Often there were no close kin with which to associate. In 96 litters the mode was 2, and 69% contained 0 or only 1 male. Even when there were brothers, they did not always survive as a coalition. These observations do not cause us to reject Wrangham's model. When males have close kin they may prefer them, but males do not always have that option. The model's generality would be increased by incorporating this constraint.

THE POSTER PRESENTATION:

THE MODEL

In an attempt to explain the tendency for close kin to associate, R.W. Wrangham defined two kinds of intraspecific mutualism:

Non-Interference Mutualism. Because it does not cost conspecifics outside the coalition, it neither favors nor disfavors kin as partners. An example is 2 hyenas cooperating to catch large prey.

Interference Mutualism. Because it costs conspecifics outside the coalition, it favors kin as partners. An example is two hyenas cooperating to exclude a third from access to a carcass.

THE TEST

In our field study of cheetahs in the Serengeti ecosystem, Tanzania, we identified 442 adults and cubs by their unique face-spot patterns. All females were solitary except while raising cubs. But two-thirds of the adult males lived in coalitions of 2 or 3 that persisted for years.

These cheetah coalitions provided a test for Wrangham's model. The two questions to be answered were:

(1) Whether coalitions were an example of Non-Interference Mutualism or Interference Mutualism; and

(2) Whether or not coalitions consisted of close kin.

If Non-Interference Mutualism, the groups should often contain non-relatives.
If Interference Mutualism, the groups should consist of close kin.

THE POSTER PRESENTATION:

RESULTS

RESULT 1. Male cheetah coalitions were an example of Interference Mutualism, because:

* Cheetah males killed in defense of their territory.

* Male coalitions held 70 % (7 of 10) of the territories. Only 13 % (3 of 23) of solitary males were territorial, while 37 % (7 of 19) of the coalitions were territorial.

Since Interference Mutualism is indicated, Wrangham's model predicts the coalitions should consist of close kin.

RESULT 2. Male cheetahs in coalitions were not always close kin.

* Some coalitions included males born to different mothers. We knew the relationships in 8 of 19 coalitions, and three of these included non-littermates.

We conclude that about one-third of the coalitions do not fit the "close kin" prediction of the model.

DISCUSSION

There appears to be a simple reason why few male cheetahs live with close kin: Males often do not have any close kin with which to associate.

* In 96 cheetah litters, the mode was two, and 69 % contained zero or only one male.

* Even coalitions of brothers suffered attrition after leaving their mother. In 4 of 6 brother pairs, one brother soon disappeared.

DISCUSSION (continued)

Cheetahs are not unique in having few close relatives. By the time they take over a pride, male African lion coalitions lose many of their closest male kin. Male turkey coalitions also are unlikely to consist of close kin only, due to high mortality.

The observations do not cause us to reject Wrangham's model of the effects of Interference Mutualism; they only point out an insufficiency. Animals do not always have the option of cooperating with close kin. The model's generality would be increased by incorporating this constraint.

THE BACKGROUND PAPER:

INTRODUCTION

An important question in formulating sociobiological theory is "Why, in many kinds of intraspecific groups (= mutualisms), do close kin associate?" Intraspecific groups form and persist when all participating individuals gain genetically (Alexander 1984). In other words, it "pays" some individuals to engage in mutualism.

Recently, R.W. Wrangham (1982) attempted to synthesize and classify the kinds of intraspecific mutualism. He observed that mutualism does not always result ipso facto in expense to conspecifics not belonging to the coalition. This he called "non-interference mutualism" (NIM). An example is two spotted hyenas (Crocuta crocuta) cooperating to catch large prey.

Sometimes mutualism results in direct cost to conspecifics outside the coalition. This, Wrangham (1982) called "interference mutualism" (IM). An example is two spotted hyenas cooperating to exclude a third from access to a carcass.

The two kinds of mutualism have different effects on inclusive fitness, because members of IM groups actively reduce the fitness (reproductive success) of conspecifics both directly and indirectly, while those in NIM groups do not. Wrangham modeled these effects with a view toward explaining how IM and NIM mutualism evolved, and he concluded that the following could be said about the composition of such groups:
(1) Non-Interference Mutualism neither favors nor disfavors kin as partners, and (2) Interference Mutualism favors kin as partners.

THE MODEL

In an attempt to explain the tendency for close kin to associate, Wrangham (1982) defined two kinds of intraspecific groupings:

Non-Interference Mutualism. There is no reproductive cost to conspecifics outside the coalition. Kin as partners are neither favored nor disfavored.

Interference Mutualism. This is reproductive cost to conspecifics outside the coalition. Kin are favored as partners.

THE TEST

The Data

In our field study of cheetahs (Acinonyx jubatus) in the Serengeti ecosystem, Tanzania, we identified 442 adults and cubs by their unique face-spot patterns. All females were solitary except while raising cubs. But two-thirds of the adult males lived in coalitions of 2 or 3 that persisted for years (see Appendix A). Some of the results of this field study were reported in Frame (1980 and 1984) and G.& L. Frame (1981).

The Prediction

These male cheetah coalitions provided a means of testing Wrangham's model. The two questions to be answered were:

(1) Whether coalitions were an example of Non-Interference Mutualism or Interference Mutualism; and

(2) Whether or not coalitions consisted of close kin.

If Non-Interference Mutualism, the groups should often contain non-relatives.

If Interference Mutualism, the groups should consist of close kin.

THE BACKGROUND PAPER:

RESULTS

RESULT 1. Male cheetah coalitions are an example of Interference Mutualism.

Cheetah sons dispersed farther from their mother's home range than did daughters. Many males vanished. We observed that while the sex ratio in cheetah cubs is 1 male:0.95 female (n = 117), it shifts to 1 male:1.91 females (n = 169) after adolescent cubs separate from their mother. This loss of cheetah males is consistent with our observation that male cubs disperse farther from their natal range than females do. Occasional reports of male cheetahs found dead of wounds suggests that male dispersal is not passive.

Our early documentation of possible male territoriality was limited to exclusive site-attachment, patrolling, and urine-marking. Females tolerated one another in broadly overlapping 800-sq-km home ranges, which overlaid the males' 30 sq km territories. Thus, territorial males were continually visited by a succession of females. If these males were effective in keeping other males out, then they benefited at the expense of others.

Male cheetah coalitions held 70 % (7 of 10) of the territories we knew. Nearly two-thirds of all male cheetahs lived in coalitions of 2 to 4, which persisted for years. Apparently male coalitions are more successful in possessing a territory. Only 13 % (3 of 23) of the solitary males were territorial, while 37 % (7 of 19) of the coalitions were.

The proof of Interference Mutualism came when a coalition of three male cheetahs, well known to us, discovered three intruding male cheetahs within their territory. The result was a violent confrontation in which one of the intruders was attacked and killed, and the other two were attacked and chased away (Frame 1980; Frame and Frame 1980).

We conclude that differential male mortality, territorial behavior, the observed fighting and killing, and male grouping apparently for defense, together indicate Interference Mutualism. According to Wrigham's model, these coalitions should, therefore, consist of close kin.

RESULTS (continued)

RESULT 2. Male cheetahs in coalitions are not always close kin.

Cheetah male coalitions sometimes contain non-littermates. An example is the three territorial males who fought with three intruders. Both trios consisted of two brothers and one non-littermate. In both cases the non-littermate was of similar age, but was born to a different mother. We knew the relationships in 8 of 19 coalitions, and three of these included non-littermates. Hence, coalitions containing non-littermates appear to be common in cheetah social organization.

Coalitions of males containing non-littermates appear to be common in cheetah social organization. We think it is significant that 3 of 4 male cheetah coalitions known to contain non-littermates were also territorial.

We conclude that about one-third of the male cheetah coalitions do not fit the "close kin" prediction of Wrangham's (1982) model. As Wrangham pointed out, where Interference Mutualism is favored, "...an important problem will be to explain why males do not associate with (close) kin."

DISCUSSION

There appears to be a simple explanation for why few male cheetahs live with close male kin: Male cheetahs often do not have any close male kin with which to associate.

The shortage of male kin is shown by our field data. We recorded 96 cheetah litters, the mean of which was 2.8 (range 1 to 6); the mode, however, was two. Furthermore, the 1:1 sex ratio was fairly consistent among litters, and there was not a disproportionate occurrence of all-male litters. About 69 % (37 of 54) of the litters we sexed contained just one (or no) male. Half the 42 litters that contained any males at all had just one male. Even coalitions of brothers probably were subject to the hazards of dispersal and conflicts with resident territorial males. We monitored the fate of six young-brother coalitions (in all cases they were pairs), and in four of these coalitions there was a rapid disappearance of one brother due to unknown circumstances. Males were often alone.

If Interference Mutualism is favored, then male cheetahs must sometimes form coalitions with non-relatives. Tolerance of non-littermates will be genetically rewarded. Cheetahs are not unique in having few close relatives. Young male African lions often lose close male kin, and form alliances with non-relative males, before taking over a pride (Packer and Pusey 1982). Male turkey coalitions also are unlikely to consist of close kin only, due to high mortality (Balph, Innis, and Balph 1980).

The phenomenon that does remain to be explained is how these male cheetah coalitions form. The initiation of mutualism between males who might otherwise kill each other is a fascinating topic, as well as a theoretically important one.

None of the above examples rejects Wrangham's hypothsis. Cheetahs that are not littermates may still be half-brothers or cousins. Even if they are not related, there is another consideration. As long as it is possible (statistically likely) that the non-littermate is kin (i.e. the groupmate is distantly related), then kin selection could account for his acceptance whether he is kin or not. It is not necessary for individuals to recognize kin for kin selection to occur. This is particularly likely when propinquity is a good indicator of genetic relatedness. Cuckoos and other nest parasites exploit this phenomenon. Feeding a nestling is kin-selected (parenting) behavior, although the baby cuckoo in the sunbird's nest is obviously not kin. In most birds and mammals, and certainly in cheetahs, female kin tend to raise their offspring relatively

near one another. Hence an alliance between males who meet perhaps for the first time as they leave their mothers could be kin-selected, while the acceptance by chance of non-kin is possible. Propinquity appears to be a factor in the formation of male cheetah coalitions. The cheetah trio that killed the intruder had grown up in adjacent home ranges and left their mothers at the same time.

The real problem is that models containing kin selection hypotheses may not be rejectable. This being so, models such as Wrangham's have limited utility in explaining present-day phenomena.

The observations do not cause us to reject Wrangham's model of the effects of Interference Mutualism; they only point out an insufficiency. Animals do not always have the option of cooperating with close kin. The model's generality would be increased by incorporating this constraint.

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APPENDIX A

CHEETAH MALE GROUPS

Male cheetah group size and group composition in the Serengeti ecosystem, Tanzania, were summarized in Frame (1980). Since then, we reinterpreted some of the data, and corrected several errors, resulting in the revised table which is presented below.

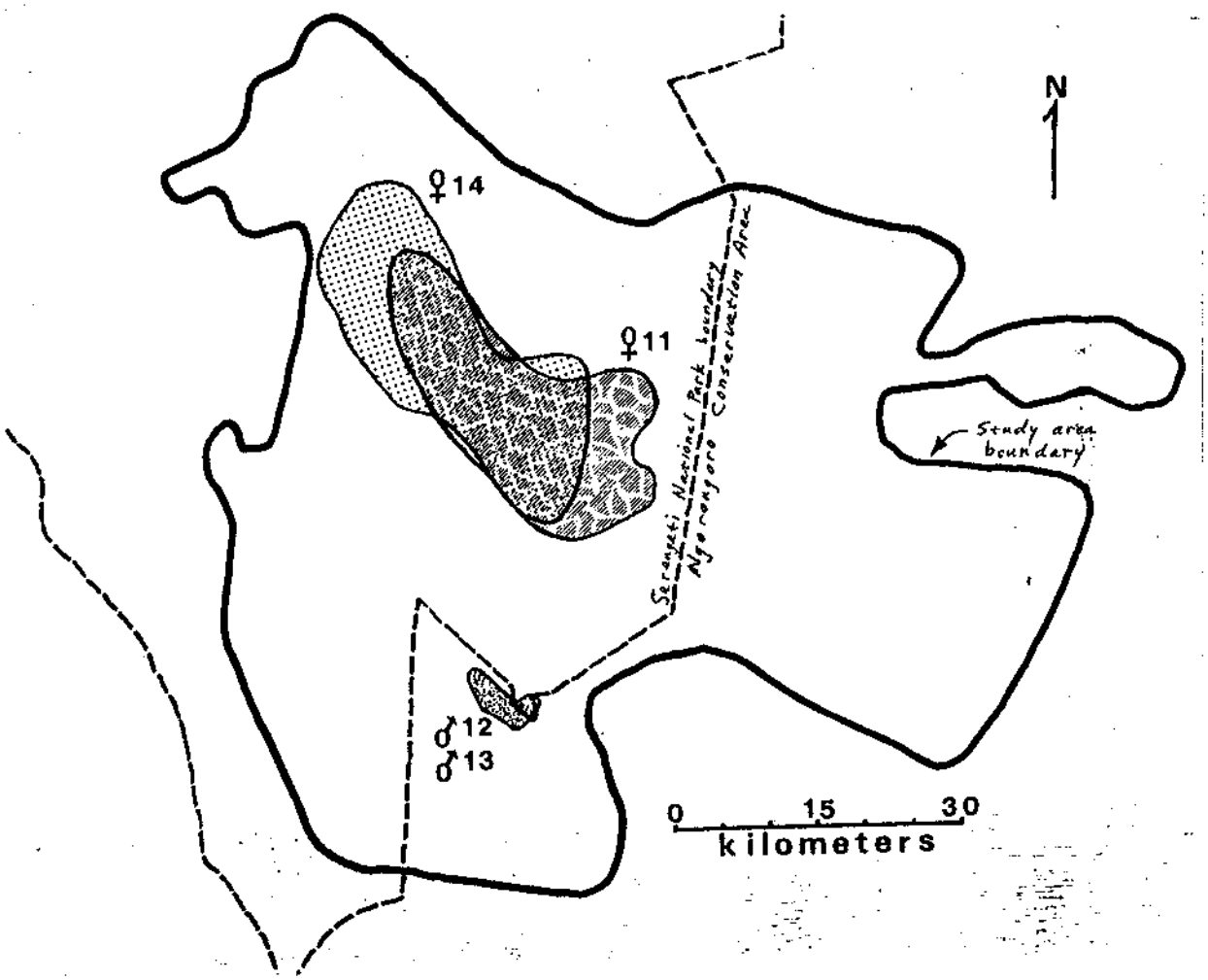
Table A.1. Cheetah male group size and male group composition in the Serengeti ecosystem, Tanzania, during the 1970s.

Composition of Male Groups	Number of Male Groups	Number of Males
Solitary adult male	23	23
Coalitions of adult males:		
Pair, littermates	5	10
Pair, non-littermates	1	2
Pair, unknown relationship	9	18
Trio, 2 littermates + 1 non-littermate	2	6
Trio, unknown relationships	1	3
Foursome, unknown relationships	1	4
	19	43
Totals	42	66

APPENDIX B

CHEETAH DISPERSAL

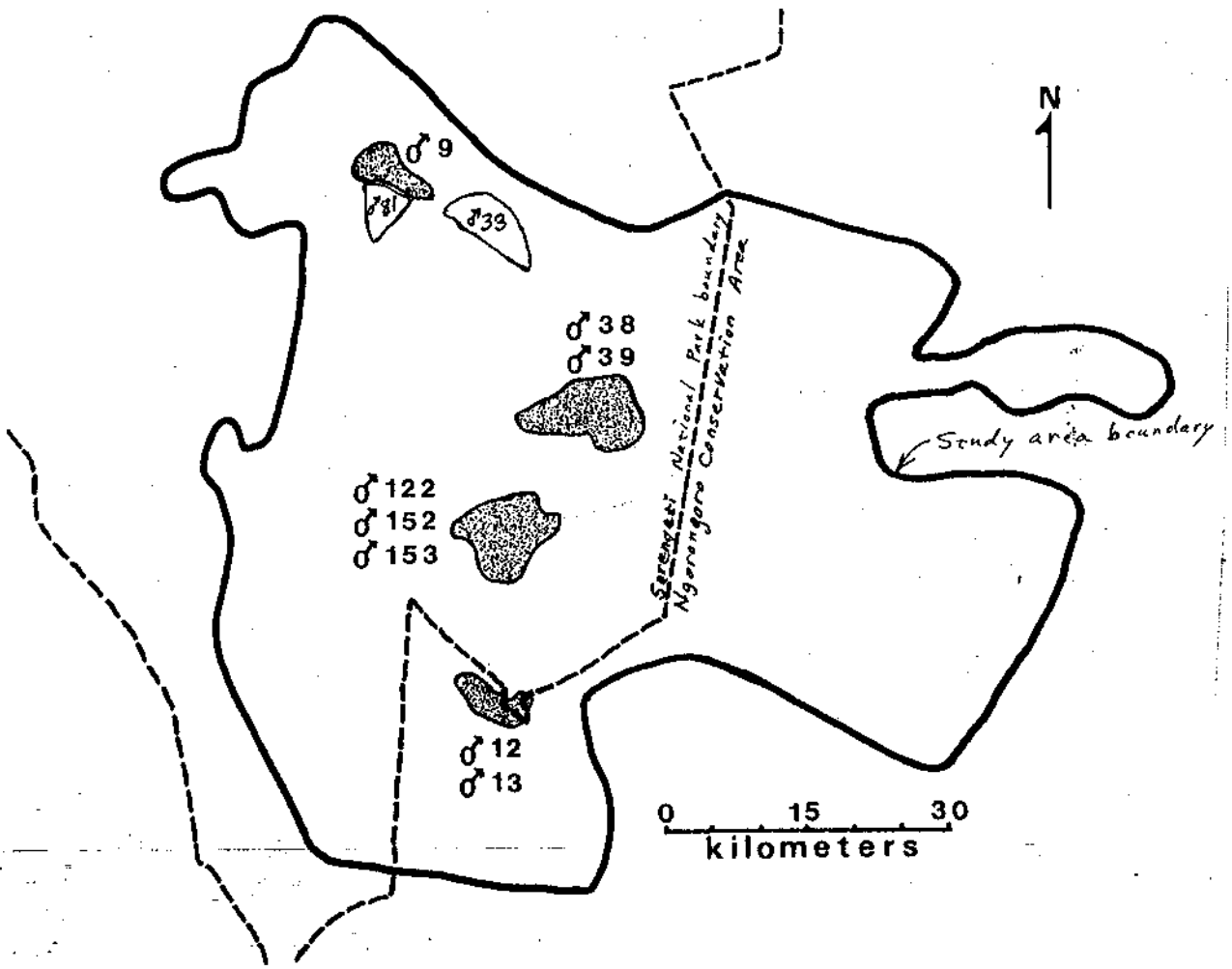
Cheetah sons disperse farther from their natal range than do the daughters. The map below shows the ranges of a mother (female 11), and her daughter (female 14) and two sons (males 12 and 13), on the Serengeti Plains and woodland edge. The ranges are based on sightings during the first year after the separation of the litter from their mother.



APPENDIX C

CHEETAH TERRITORIES

The territories of male cheetahs are relatively small compared with the home ranges of females and non-territorial males. The map below shows the location of cheetah territories on the Serengeti Plains and woodland edge. Some territories were held by lone males and others by coalitions of males. All the territories are in areas of dense cover, such as hills, kopjes, and a gorge. No territory was identified in the open grasslands.



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