

Cooperation and competition within coalitions of male lions: kin selection or game theory?

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Male lions form cooperative coalitions which compete against other coalitions for exclusive access to female groups^{1,2}. This cooperation and the apparently low level of intra-coalition competition over oestrous females, have been considered to be due to the close genetic relatedness of the males in the coalition¹⁻³. However, we now present evidence that breeding coalitions of male lions include non-relatives much more commonly than was generally supposed, that intra-coalition competition over females is widespread and that kinship is not the primary factor determining levels of competition.

Between July 1978 and May 1981 we studied the population of lions in the Serengeti, Tanzania, described by Schaller⁴, and all the lions resident on the floor of Ngorongoro Crater. Lion prides are stable social groups composed of 2-18 adult females, their dependent offspring and a coalition of 1-7 adult males (which can simultaneously control more than one group of females). Genealogical records have been maintained since 1966 for two prides in the Serengeti⁵ and since 1974 for another 13 prides in the Serengeti and Ngorongoro². We made daily censuses of as many prides as possible and recorded the incidence of fresh wounds, the consort partners and mating activity of each male, and the presence of non-consorting males ('rivals') within 200 m of each consort pair. We collected over 500 h of behavioural data on consort pairs during 2 h watches at dawn and dusk.

Theoretical analyses of male coalitions have assumed that they are always composed of relatives^{1,2}. However, there are examples of unrelated males becoming companions^{2,5}, and our data show that 42% of breeding coalitions of known origins contained non-relatives (Table 1). This proportion is higher than the 10% reported by Bygott *et al.*⁶, because their data included cohorts that had not yet gained a pride (J. D. Bygott, personal communication). There is considerable mortality among subadult and nomadic males so that by the time they gain a pride their initial companions may have been lost and new ones found.

Competition for individual oestrous females between males from the same coalition consists primarily of competition for temporary 'ownership' of the female. When a female in a pride comes into oestrus, the first male that encounters her forms a consortship with her and this confers temporary dominance

Table 1 The composition and origins of the 20 male coalitions having tenure in prides in the Serengeti and Ngorongoro during 1978-81

Coalition sizes	Origins
6, 5, 5, 4, 3, 2, 2	Unknown
3	Pair of unknown origins with son
7, 4, 4, 4, 3	Cohort from same natal pride
3, 2	Full siblings
3, 2, 2, 2	All unrelated
3	Sibling pair with unrelated third

Males were considered relatives if they came from the same natal pride or joined their probable fathers, and non-relatives if they were known not to have come from the same natal pride or if they had associated with a variety of male partners for over a year before coming together (consistent with the behaviour of males known to be from different prides and completely unlike that of males of the same natal pride).

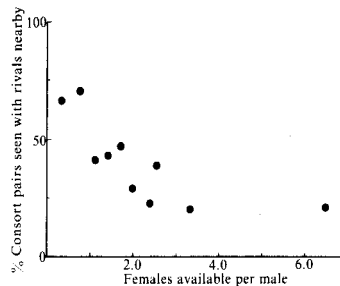


Fig. 1 The proportion of sightings ($n = 222$) in which non-consorting males ('rivals') were seen within 200 m of consort pairs plotted as a function of the number of potentially oestrous females available to those males elsewhere (number of unconsorted females not pregnant or with cubs/number of non-consorting males). Only data taken from coalitions which had sole control of a pride are used and points were taken at least 4 days apart. Eight of nine coalitions showed trends similar to the overall result ($P < 0.04$) and there was no difference between the Serengeti and Ngorongoro, so all data were pooled and cells combined to give a $k \times r$ matrix with sufficient sample size to test for heterogeneity ($\chi^2 = 23.87$, 9 d.f., $P < 0.01$). The trend for rivals to be present more often when fewer females are available elsewhere is significant ($r_s = 0.89$, $n = 10$, $P < 0.01$).

on the consorting male^{5,6}. The consorting male maintains proximity (usually < 1 m) to the female, herds her and prevents other males of his coalition from moving too close to her. Behavioural oestrus (days with mating) lasts about 4 days, during which time copulation occurs once every 25 min; the inter-oestrus interval is about 16 days⁷. The male sometimes guards the female for 1 or 2 days before mating and for up to 6 days after mating has ceased⁷. Males occasionally 'mistake' a potentially oestrous female, guarding her for a day or two and then leaving her after she fails to come into oestrus.

As both coalitions containing relatives and those containing non-relatives were common, it was possible to determine whether kinship affected intra-coalition aggression over oestrous females. Threats without contact by consorting males towards other males were common and occurred mainly when the other males were within 15 m of the consorting male's female (84%, $n = 63$ threats). Most of these threats (53%) were the direct result of the female attempting to move closer to rivals (or other consorting males). Kinship had no effect on the frequency of threats by consorting males to rivals (calculated per minute spent by a rival within 15 m of a consorted female and based on six consorting males whose unrelated companion(s) spent any time within 15 m of his consort partner, and on 12 males whose related companion(s) spent time within 15 m; $U = 36$, $P > 0.50$), or the time spent by rivals within 15 m of the consorted female (based on 10 males who had unrelated consorting companions, and 19 males who had related consorting companions; $U = 76$, $P > 0.20$). The fact that rivals spent any time as close as 15 m to the consort pair was due primarily to the behaviour of the female. Their presence at more moderate distances, however, depended on the behaviour of the rival, and rivals were more likely to be within 200 m of a consorted oestrous female as the availability of other possibly oestrous females declined (Fig. 1).

More serious intra-group fights over females included slapping and biting and frequently resulted in wounding of one or both males. Such fights were observed nine times and could be inferred another five times from fresh wounds on one or both males together with a change of consort partners. Serious fights were no more common between non-relatives than between relatives ($P > 0.50$); rather, they were context specific: of 13 fights where the context was known or could be inferred, eight

occurred when 'ownership' of the female was undecided or unclear and four involved two consorting males. Ownership was 'undecided' when two males simultaneously came into the vicinity of an unconsorted, potentially oestrous female; and was 'unclear' when the consorting male moved further from the female than was the rival. There was usually a race between males to arrive first at a female. On arrival, the loser would defer to the winner though in subsequent consortships the previous consorting male might be a rival to the new consorting male (also see ref. 5). Lion males can consort simultaneously with two females and females being consorted by different males occasionally tried to come into close proximity to each other. In such cases one consorting male sometimes tried to take over the other's female.

Males also competed in a less direct manner to be the owner of a female when she came into oestrus. Males guarded non-oestrous females, probably in anticipation of the female's oestrus, and this was most common when the availability of oestrous females was lowest. When only one female in a pride was being consorted, the consorting male was more likely merely to be guarding a non-oestrous female than on days when several females were being consorted ($T = 40$, $n = 19$ males observed consorting at least twice in each condition, $P < 0.05$).

Males in Ngorongoro Crater guarded non-oestrous females more frequently than did males in the Serengeti. When only one female was consorted, the female was not in oestrus on 80% of occasions in the Crater (based on the behaviour of 11 consorting males) but on only 42% of occasions in the Serengeti ($n = 24$, $U = 69$, $P < 0.025$). Guarding of non-oestrous females may be more common in the Crater because it is less costly. Consort pairs rarely hunt and therefore feed infrequently⁷, but prey density in the Crater is so high and pride ranges so small⁸ that consort pairs can more easily join pride mates at kills.

Because fights over oestrous females are so rarely observed, males of a coalition have been said to 'share' females and to do so because they are relatives (see refs 1, 2). However, two factors should be taken into account when attempting to measure differential reproductive success among males of a coalition. First, females in a pride tend to come into oestrus at

the same time^{5,6}. In our study, on the first day of 43% of oestrous periods other females in the pride were also in oestrus ($n = 150$). Second, females tend to move to additional mating partners after their first mating partner loses interest in them at the end of oestrus⁷. Subsequent partners show only a brief interest in the female and females seek additional partners most often when their fertility is lowest⁷. Thus calculating the relative mating activity of males without controlling for either the number of females in oestrus or the order in which males consorted with a particular female (as in refs 1, 2) biases against finding any differences in reproductive success.

The extent of differential male reproductive success was measured in 11 coalitions using data that eliminated these biases (Table 2). Coalitions consisting solely of relatives did not 'share' females more equally than did coalitions containing non-relatives. However, differences in competitive ability did result in differential male reproductive success. Disparities in consorting success were greater in coalitions in which the males were of markedly different ages or sizes than in those where all the members were evenly matched (Table 2). In all six of the former coalitions, the non-prime (either very young or old) and small individuals consorted less frequently with oestrous females than did their larger or more vigorous companions.

The high proportion of coalitions containing non-relatives is not surprising. Because singleton males almost never gain control of a pride and coalitions of three or more father more surviving offspring per male than do smaller coalitions⁷, selection will favour singletons and pairs forming coalitions with additional males. As females are frequently in oestrus simultaneously, even subordinate males often have access to females.

Males would benefit even by cooperating with non-relatives but should prefer relatives as partners^{9,10}. We know of no case where a male with related companions left them for an unrelated companion, although there were cases where additional relatives were not accepted. A group of three relatives prevented three younger relatives from joining them, and incorporation of sons into the coalition was known or suspected only when the number of older males was one or two ($n = 4$ coalitions). In coalitions of three or more, incorporation of sons has never been seen, even though such large coalitions are more likely to maintain tenure long enough to father surviving sons². Because large coalitions can control prides without additional companions, they would be expected to exclude additional members when an added male would reduce each male's reproductive success (but not when the exclusion results in a loss in inclusive fitness). This is especially important if the new male would become disproportionately successful as in the case of ageing males being joined by males nearing their prime.

Costs to males of direct competition for oestrous females can be high: one-to-one fights typical of such encounters often result in wounds to the face and eyes and sometimes in blinding⁵. Even in a gang attack on a single individual, the lone animal can wound several of its opponents. Furthermore, the loss of a companion through fighting may shorten tenure in the pride¹. Game theoretical analysis predicts that when costs of fighting are high, contests may be settled 'conventionally' through recognition of asymmetries such as 'owner versus rival' or 'large versus small', rather than through overt aggression¹¹⁻¹³. As differences in size or vigour exist in only about one-third of male coalitions (7 of 20), the 'respect' of ownership in lions is particularly important. Males were seen to compete for females indirectly by anticipating oestrus in a female in order to be the 'owner' when she eventually came into oestrus and they did this more often when costs of guarding and availability of oestrous females were lowest. Fights were virtually restricted to occasions when ownership was unclear or when two consorting males were in close proximity.

In conclusion, the low levels of aggression observed within coalitions of male lions, which had been ascribed to kin selection, are not affected by the degree of genetic relatedness of

Table 2 Extent of differential mating success in each coalition

Mating success of respective males	Includes non-relatives?	All same age and size?	I_T
3, 0, 0	Unknown	No	2.00
3, 0, 0	Unknown	No	2.00
5, 5, 0, 0, 0	Unknown	No	1.50
4, 0	Yes	No	1.00
2, 0	Yes	No	1.00
3, 3, 0, 0	Unknown	No	1.00
7, 4, 3, 2, 2, 1, 1	No	Yes	0.47
7, 4, 2, 2	No	Yes	0.30
3, 2, 1	No	Yes	0.17
2, 1, 1	Yes	Yes	0.13
2, 2	Yes	Yes	0

Each line gives data on a different male coalition. For each male in each coalition, the number of oestrous periods is given in which he consorted with a female who was the only oestrous female available to that coalition on the day when she was first observed mating. Only the first male to mate with the female in each of these periods is considered, unless a male was seen to win the female from another male in a fight—in these cases the victor was also included. Only coalitions in which the average number of such periods is one or more per male are included. For each coalition a measure of differential mating success, I_T (ref. 14), was calculated. Large values of I_T indicate unequal mating success; smaller values indicate evenly distributed mating success. Coalitions containing members of different size or age showed significantly more unequal mating success than coalitions with equally aged and sized members ($n_1 = 6$, $n_2 = 5$, $U = 0$, $P < 0.01$), but there was no significant difference between coalitions consisting solely of relatives or including non-relatives ($n_1 = 3$, $n_2 = 4$, $U = 6$, $P > 0.50$).

the males and may be better understood in terms of game theory.

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