

Cooperation in male lions: kinship, reciprocity or mutualism?

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Abstract. Playback experiments simulating the presence of intruder male lions elicited cooperative behaviour of male coalitions resident with prides of females. Resident males approached the broadcast roars on all occasions when more than one male was present for the experiment, and only failed to approach in three of eight cases when a single male faced the roars of three intruders. Three routes to cooperation were tested: kinship, reciprocity and mutualism. These results suggest that approaching the roars of strange males is a cooperative behaviour, and that this cooperation is not conditional on either the kinship or the behaviour of a male's companions. Cooperation in male lions instead appears to be based on mutualism.

Cooperative behaviour can evolve by one of three major routes: kin selection (Hamilton 1964), reciprocity (Trivers 1971; Axelrod & Hamilton 1981) and mutualism (Maynard Smith 1983; Lima 1989). In a Prisoner's Dilemma, both individuals would benefit from mutual cooperation, but each individual would benefit more from defecting when its companion cooperated. When the payoffs of each interaction follow a Prisoner's Dilemma, cooperation will be conditional on a companion's identity or behaviour and thus can only evolve by kin selection or reciprocity. When individuals interact with close kin, the inclusive fitness effects of cooperation can outweigh the temptation to defect, allowing the payoff for cooperation to exceed that of defection when a companion cooperates (Hamilton 1964; Maynard Smith 1982). Reciprocity requires repeated interaction between individuals that base their decision to cooperate on the recent behaviour of their companion: reciprocating with cooperators and excluding non-cooperators from further cooperative acts (Trivers 1971; Axelrod & Hamilton 1981). Lima (1989) has shown that while many cooperative exchanges may appear to involve a Prisoner's Dilemma, the payoffs are in fact mutualistic once the advantages of grouping are incorporated into a dynamic model. In mutualistic interactions, there is no temptation to defect: cooperation always yields the highest payoff regardless of the opponent's behaviour (Maynard Smith 1983; Packer & Rutan 1988; Dugatkin et al. 1992).

Although these three different routes could superficially lead to similar behaviour, the precise form of cooperative relationships will be quite different. Both kinship and reciprocity lead to conditional cooperation, where the exchange of cooperative acts depends on the identity or behaviour of the companion. However, where cooperation has evolved through mutualism, individuals are expected to behave cooperatively without any regard for the kinship or cooperative tendencies of their companion.

African lions are well known for their cooperative behaviour (Schaller 1972). Lions hunt together (Scheel & Packer 1991; Stander 1992) rear their cubs communally (Packer et al. 1990; Pusey & Packer 1994a) and defend joint territories (Bygott et al. 1979; Packer 1986; McComb et al. 1994). Although female pridemates are always close relatives, male coalitions are often composed of non-relatives as well as close kin (Packer et al. 1991a). Male lions thus provide a valuable opportunity to test evolutionary models of cooperation.

Background and Rationale

Male lions cooperate to maintain exclusive access to groups of females (Bygott et al. 1979; Packer et al. 1988). Competition between coalitions is intense, with only a small proportion of males ever gaining residence in a pride, and few coalitions are able to maintain residence long

Table I. All observed encounters between resident coalitions and their outcomes

Date	No. of males:no. of males	Result
23 August 1978	3:1	3 chase 1
8 December 1967	2:1	2 chase 1
29 September 1978	2:1	2 chase/attack 1
31 March 1981	2:1	2 chase 1
September 1983	2:1	2 kill 1
4 August 1987	2:1-2	2 wound 1; attack ends upon arrival of singleton's companion
January 1971	9:6	1 of 6 killed, 1 of 9 wounded
14 November 1967	2:2	Back and forth chasing
9 January 1989	2:2	Back and forth chasing, roaring

Note: there have been numerous observations of resident males chasing nomadic males over the years; almost all of which involve groups repelling single strangers. Such encounters have been excluded because of a possible resident advantage.

enough to rear even a single set of cubs. Males kill all small cubs when they first take over a pride (Bertram 1975; Pusey & Packer 1994b), and thus prolonged residence is essential for successful reproduction. Lions are primarily nocturnal, and thus direct observations of inter-coalition encounters are rare. However, male lions commonly receive wounds typical of such fighting, suggesting that these encounters are frequent. Table I summarizes all direct observations of encounters between rival coalitions. These data emphasize the role of male-male cooperation in inter-group competition: large coalitions dominate smaller coalitions. As a result of such size-related effects, large coalitions gain considerable reproductive advantages: large coalitions are more successful in gaining residence in a pride, maintain residence for longer periods and sire greater numbers of surviving offspring than small coalitions (Bygott et al. 1979; Packer et al. 1988).

Resident males father all offspring sired during their tenure in a pride, but the individual reproductive success of coalition partners becomes increasingly skewed with increasing coalition size (Gilbert et al. 1991; Packer et al. 1991a). Consequently, males only team up with unrelated companions to form coalitions of two to three males; all larger coalitions are composed entirely of close kin (Packer et al. 1991a). Males would only benefit from remaining as non-breeders in large coalitions if their participation in the coalition enhanced the reproductive success of their close kin. Although kinship may thus influence each male's decision to join a coalition with a particular partner, prior studies have been unable

to detect any consistent effect of kinship on behaviour within the coalition (Packer & Pusey 1982).

Male lions only roar when they have been in recent association with females (i.e. if they are resident: unpublished data); thus a strange roar in a resident male's territory should be interpreted as a serious threat, indicating that a rival coalition is willing to defend the same area. By broadcasting the roars of strange males in a resident's territory we can simulate encounters between coalitions that would otherwise rarely be observed.

Resident males respond to playback experiments as they would to a real intruder: advancing cautiously towards the speaker and looking alertly around (see also McComb et al. 1994). Whenever a taxidermically mounted young male lion was included in a playback experiment, at least one of the resident males always attacked the 'dummy', lunging up and biting it on the lower back (Fig. 1), the same part of the body where male lions are most frequently wounded. We consider males that collectively approach the broadcast roars of strange 'intruder' males to be acting cooperatively because both risk injury and both benefit each other (as well as absent companions) by lessening the partner's risk of injury and by defending the reproductive potential of the entire coalition. Because only resident males roar, and residents will chase, attack and kill rival coalitions, males should treat opponents that roar within their territories as a serious threat. Approaching such a threat is therefore potentially risky, especially when outnumbered.

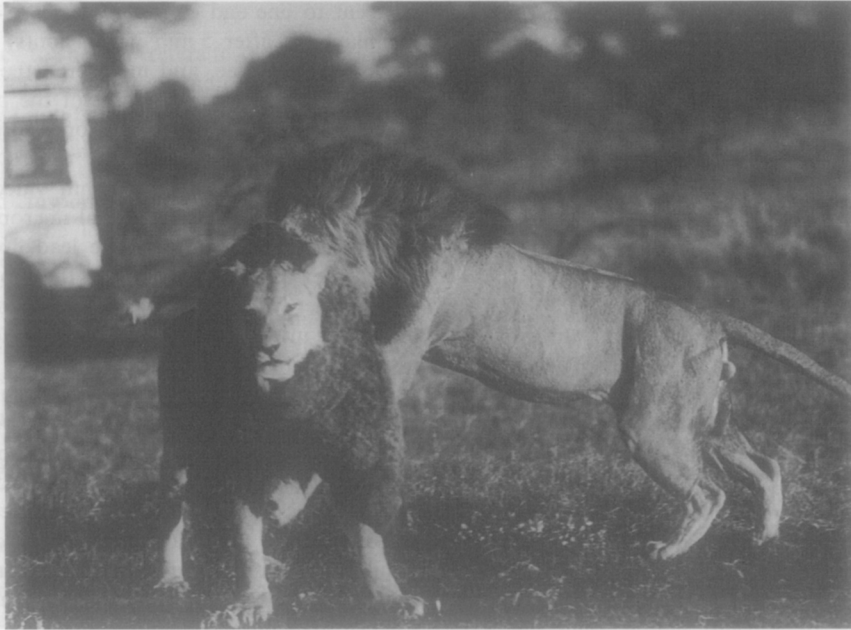


Figure 1. A male lion approaches and attacks a stuffed lion after hearing the recorded roar of a single male intruder. A total of three playbacks that included a dummy were performed: in two playbacks, one of the residents attacked the dummy and in the third both did so.

We report here the results of experimental studies that elicited cooperative territorial responses by male coalitions of known kinship. We test for evidence of kin-biased cooperation, reciprocity and mutualism.

METHODS

Study Site and Population

The study population includes 200 lions in about 20 prides over a 2000-km² area of the Serengeti National Park, Tanzania (Packer et al. 1988). All lions are individually identifiable from natural markings, and continuous demographic records have been maintained on all study prides since 1975 (Hanby & Bygott 1979) and for three prides since 1966 (Schaller 1972; Bertram 1975). About one-third of the males were born into the study, while the remaining two-thirds immigrated from outside the study area (Packer et al. 1991b). The degree of kinship within each coalition is known either from long-term demographic records or by DNA-fingerprinting techniques (Packer et al. 1991a; J. S. Martenson, personal communication). All study animals were habituated to the presence of vehicles.

Playback Experiments

Between July 1987 and July 1990 we performed 40 playback experiments on a total of 15 resident male coalitions. The general playback protocol follows that of McComb et al. (1994). Playback experiments were performed using roars recorded on a Panasonic SV 250 portable digital audio tape-recorder through a Sennheiser MKH816T directional microphone. These roars were of adult males recorded on still nights while facing the microphone from a distance of at most 30 m. We played back recordings of a single bout of roaring of one to three lions lasting 30–65 s from digital tape through a Proton 100 W/channel amplifier and either one ($N=36$) or two ($N=4$) Klipsch Heresy speaker(s) placed 200 m from the subject lions. Peak sound pressure levels were 116 dB at 1 m.

Each playback commenced approximately 20 min before dusk. We controlled the tape and amplifier from within the vehicle and concealed the speaker in vegetation 80–100 m away; if there was no suitable cover we placed the speaker

adjacent to one end of the vehicle. We repeated the playback after 5 min if the lion(s) had not moved in that time, and monitored the subjects for at least 1 h from the onset of the playback. Successive experiments to any one subject were separated by at least 7 days.

Using a Sony CCD-F40 8 mm video-camera equipped with a JVC directional microphone we videotaped the response of the lead lion(s) and scored the type of cover between the subjects and the speaker with reference to potential hiding places for intruder lions. The cover scale was: 0: no cover, grass less than 30 cm high; 1: grass 30–60 cm in height; 2: grass greater than 60 cm, erosion terraces; 3: bushes; and 4: trees. We scored cover according to the predominant cover type modified by the presence of another dominant type if necessary. For example, scattered bushes surrounded by tall grass would be scored 2.5. Similarly, short-grass savannah was scored 0.5 if the predominant cover type was very short grass with sparsely distributed trees.

We played back choruses of one, two and three roaring males to groups of one to four resident coalition males. All playbacks were performed while the residents were well inside their normal pride range. We used 13 recordings of 10 coalitions in the experiments: five three-male, four two-male and four single-male roars. Within these size categories, we chose recordings according to geographic location of the subjects (e.g. a recording of lions resident in the north would only be played to lions in the south) and how often each recording had been played to a certain coalition or in the study as a whole; care was taken to intersperse recordings both within and between male groups as appropriate. Recordings were always of males resident at least 30 km away or that had died before the target lion entered the study area. To control for the identity of males whose roars were used during the playback, recordings of the same males were used in playbacks of both solitary and chorus roars whenever possible. Four of the nine two- and three-male recordings were assembled from the roars of one or two males using standard sound mixing techniques: recordings were mixed from digital source tapes onto an analogue Uher stereo tape-recorder, then back to digital tape for broadcast. In these cases, care was taken to place the recordings on the tape in a realistically staggered manner, using natural choruses as templates.

Playback Responses

'Latency to speaker' refers to the length of time between the beginning of the recorded roar until the subject lion reached the speaker. Elapsed time was automatically recorded on the videotape when filming the playback response. Other measured responses included: the number of glances by the lead lion towards his following companions; the proportion of time that the approaching lions walked side by side; and the number of times each subject animal stopped before reaching the speaker. Each of these behaviour patterns is presented as the number of events during the latency to speaker. In addition, we noted the number of times that each subject roared in the hour following the playback.

Experimental Design

We presented each coalition, where possible, with three-, two- and one-male roars to simulate contexts exceeding, equal to, and less than the coalition size. As coalition companions are often found apart from one another, we used subsets of coalitions to increase the sample sizes of odds categories. For example, a coalition of three males might be played a three-male roar when the entire coalition was present (odds of 3:3), a three-male roar when only two coalition males were present (odds of 2:3) and a two-male roar when two males were present (odds of 2:2). For any one of these odds classes, each coalition appears in the analysis only once. Out of a total of 40 playbacks, four experiments duplicated odds classes for three coalitions. In these cases, we averaged coalition responses into a single score for the purpose of analysis, reducing the total sample size to 36.

Statistical Analysis

Linear regression models were fitted using the Statistix (Siegel 1985) microcomputer package. In all analyses, we used only one mean value per playback, rather than the separate response of each lion, to avoid the pseudoreplication inherent in measuring the behaviour of a group. Means were used instead of the latency of the lead lion to avoid any purely probabilistic influences on the rate of approach in larger coalitions, although all results presented here remain qualitatively unchanged with either measure. As we were

unable to play the same roar types (e.g. three, two and one intruder) to each coalition, by chance some groups will be represented in these analyses more than others. However, as we could detect no effect of coalition identity on rate of approach, we treat each of the 36 playback events as statistically independent for purposes of the multivariate analyses. All *P*-values are two-tailed.

RESULTS

Recordings

While the size of a recorded chorus produced consistent responses in playback subjects (see below), the identity of the actual recording had no consistent or significant effect on subject responses: when included as dummy variables in a multiple regression model none of the recordings were associated with a particular latency. Similarly, while the sound quality of digital original recordings used in the playbacks was superior to that of the four recordings assembled through sound mixing, lions showed no differences in response to natural and 'dubbed' recordings when the numbers of defenders and 'intruders' were equal (Mann-Whitney *U*: $U=37$, N_1 (natural)=12 playbacks, N_2 (dubbed)=5, $P>0.20$).

Risk Assessment

Resident males were sensitive to the number of apparent intruders in their territory. The latency of approach by resident males when alone was significantly longer when faced with three roaring intruders than with just one ($\bar{X} \pm SE$, three: 45.55 ± 4.34 min; one: 7.67 ± 1.01 min; Table II). Out of the 36 playbacks performed in this study, in only three cases did the subject(s) fail to approach, and all three cases were of one male with three intruders.

We fit multiple regression models of latency to speaker on the independent components of odds (number of defenders present and number of intruders) and the 12 other explanatory variables listed in Table III. These results exclude the three cases in which the subject did not approach the speaker (leaving $N=33$ playbacks); however, all results remained essentially unchanged when these were included as latencies of 66.6 min (the hour monitored plus the median approach of 6.6 min).

Table II. Latency (approach time) in min for playbacks of one and three intruders to single males

Coalition male	Three intruders	Coalition male	One intruder
Blnd	30.03	Clvn	9.00
Hctr*	54.58; NA	Glfb	7.07
MS12	52.03	Trmn	5.58
Cpot	NA	Smth	4.57
Cktl	48.00	Cktl	11.45
PNE	NA	PNE	8.33
MM2	43.12		
Mean	45.55		7.67

Playbacks to individual males in the absence of females or coalition partners: Mann-Whitney U -test, $U=42$, $N_1=7$, $N_2=6$, $P<0.002$; with each male included only once: $U=30$, $N_1=6$, $N_2=5$, $P<0.004$. NA: Never approached. *Hctr was the subject of two experiments.

Table III. Effect of each independent variable when included in a cumulative model describing latency for all numerical playback experiments that elicited an approach

Variable	Model r^2	Δr^2	F	k	P -value	P in full model*
No. present	0.255	NA	10.59	1	<0.003	0.0001
No. intruders	0.503	0.248	14.97	2	<0.001	0.0002
Cover	0.639	0.136	10.95	3	<0.003	0.0025
Full model			17.11	3		0.0001
No. subadults in pride	0.668	0.029	2.484	4	NS	
No. speakers	0.666	0.027	2.241	4	NS	
Coalition IDs	0.839	0.200	1.330	17	NS	
Month of playback	0.759	0.120	1.093	12	NS	
Season (wet/dry)	0.647	0.008	0.670	4	NS	
Recording	0.730	0.091	0.552	14	NS	
Coalition size	0.644	0.005	0.410	4	NS	
Relatedness	0.644	0.005	0.410	4	NS	
No. females in pride	0.643	0.004	0.316	4	NS	
Females nearby	0.642	0.003	0.258	4	NS	
No. cubs in pride	0.641	0.002	0.128	4	NS	

Only the first three variables were significant in the multiple regression model, and all three contributed significant independent effects; variables were included in the multi-variate model if the increases in the model r^2 (as shown by the Δr^2 value) produced a significant F -statistic (Sokal & Rohlf 1981). k : Number of parameters included in the model.

*Probability value associated with each parameter when included in a single model.

Of those parameters tested in Table III, only three showed a significant effect on the latency to approach the speaker: the number of defenders present, the number of intruders, and nearby cover (Fig. 2). For all analyses, the rate of approach was not significantly influenced by the presence or number of cubs, subadults or females in the males' pride, by the month or season during which the playback occurred, or by the absolute size of the resident coalition irrespective of the number of males present at the playback (Table III). The relatedness of coalition members similarly had no significant effect (Table III).

When the playback contexts were matched for number of participants (i.e. 1:1, 2:2, or 3:3), group size showed no significant influence on the rate of approach (Fig. 3). Males always approached the speaker in these matched-context experiments, even when alone.

Behaviour During the Approach

During an approach, males could walk side by side or in tandem. The proportion of the distance approached side by side could be a measure of the need to monitor the companion's behaviour. If

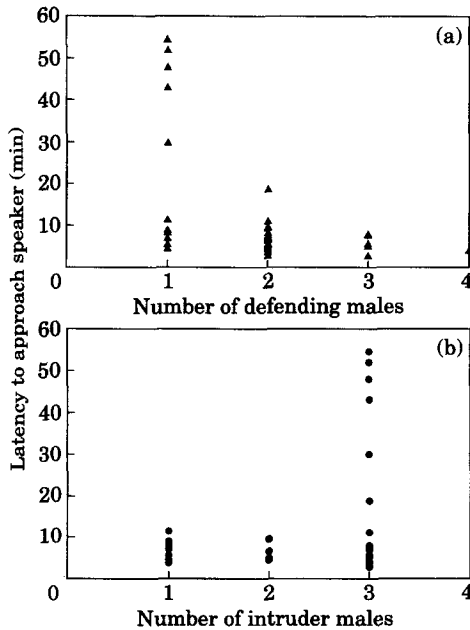


Figure 2. Effect of (a) number of defenders present and (b) number of intruders on the latency to approach speaker. Both variables shown (as well as cover) have significant effects on the latency to speaker. Statistics are presented in Table III.

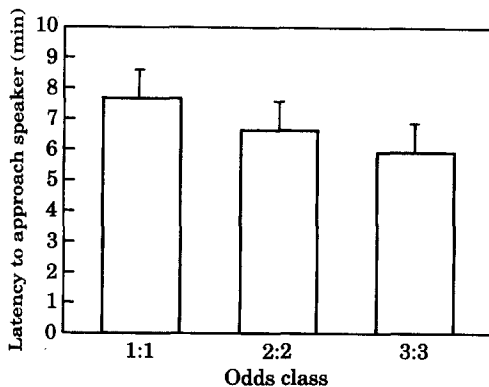


Figure 3. Latency to approach speaker for even-odds playbacks with one, two and three males present. Group size did not significantly affect rate of approach: Kruskal-Wallis: $H=1.19$, $N_{1:1}=6$, $N_{2:2}=6$, $N_{3:3}=5$, $P>0.40$.

cooperation between non-relatives is based on reciprocity, non-relatives should show more parallel approaches than relatives, because relatives could expect greater levels of unmonitored cooperation from their companions. However, no

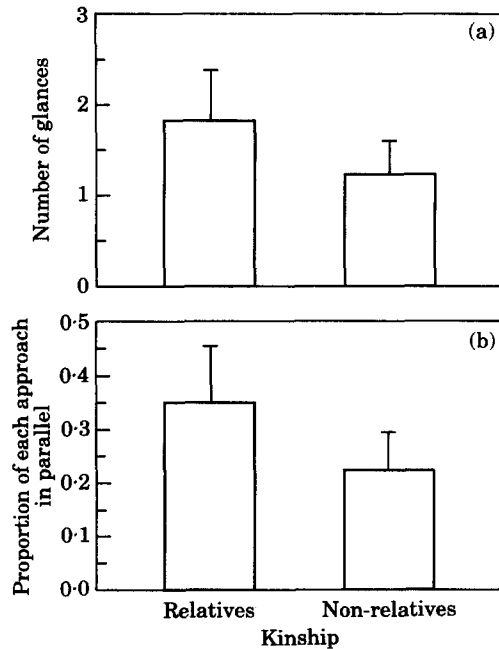


Figure 4. Effect of kinship on (a) proportion of approach-distance walked in parallel and (b) number of glances during a playback approach. Non-relatives and relatives walked in parallel equally often: Mann-Whitney U -test: $U=81.5$, N_1 (relatives)=10 playbacks, N_2 (non-relatives)=13, $P>0.20$. Non-relatives and relatives also glance at followers equally often: U -test: $U=83.5$, N_1 (relatives)=11, N_2 (non-relatives)=12, $P>0.20$.

relationship was found between kinship and the proportion of approach-distance that males walked in parallel (Fig. 4a). No tested variable had a significant effect on the formation in which males approached the speaker.

Similarly, the number of glances from a lead lion towards a following companion could be interpreted as a measure of distrust, but again no relationship was found between glances and kinship (Fig. 4b). Multiple regression models also showed no relationship between number of glances and relatedness, number of intruders, cover, or the ratio of the number of defenders to the number of 'intruders'.

McComb et al. (1994) found that female lions that were separated from their prides roar more frequently during the first hour following a playback, apparently to recruit distant companions. However, males did not show a similar

trend. Male lions frequently roared in the first hour irrespective of whether the entire coalition was present ($\bar{X} \pm \text{SE}$, all present: 2.79 ± 1.28 roars/h; not all present: 2.00 ± 0.60 roars/h; Mann-Whitney U : $U=128.5$, $N_1=14$, $N_2=19$, NS).

Individual Variation in Latency to Approach Speaker

In most playbacks, male coalition partners arrived at the speaker at different times. The time interval between the arrival of the leader and the follower varied from 0.0 min (all participants arrived at the speaker simultaneously) to 4.07 min (Table IV). Neither relatedness, coalition size, body size nor length of residence in the pride explained the time-lag between the lead lion and the last lion, but the regression of time difference on cover was significant ($F=4.30$, $P=0.05$), indicating that lions spread out more in thicker cover.

When we included all the playback experiments averaged together into single scores per odds class (see Experimental Design in Methods) or previously excluded due to insufficient data or differences in protocol, we obtained data on eight coalitions that were subjects of more than one playback experiment when two or more males were present. We could detect consistent variation between partners in five of these. Certain males habitually followed and never led an approach toward the speaker (Table IV). The most striking example involved the trio JMS; the lion John lagged in every one of six playbacks (binomial test: $P=0.003$). However, we could find no feature in common between the laggards of these respective coalitions.

DISCUSSION

Male lions approached the recorded roars of extra-pride males at virtually every opportunity. Although male behaviour was clearly cooperative during these playback experiments, what do the results tell us about the evolutionary basis of male-male cooperation? Males did not appear to condition their cooperation on either the relatedness or the behaviour of their companions. Kinship did not influence the speed with which companions reached the speaker, the extent to which males monitored each other's behaviour or

the degree to which males spread out while approaching the speaker. Similarly, males did not appear to base their responses on the behaviour of their companions. While all lions with companions approached the speaker during playback experiments, the lead lions approached even when followers lagged far behind and they did so without monitoring their companions' actions. Despite the opportunity for single males to defect on pride defence when their behaviour could not be monitored by an absent companion, males nevertheless approached the playback. During approaches in thick cover, when it might be easier to defect on a companion unnoticed, males showed no more tendencies to monitor the behaviour of their partners through glances or parallel walks than when in open terrain. These results suggest that neither kinship nor a Tit-for-Tat-like reciprocity (Axelrod & Hamilton 1981) is important in maintaining male-male cooperation.

Although the behaviour of male lions does not appear to be conditional on the identity or behaviour of their companions, it does appear to be sensitive to two major variables: the number of intruders compared to their own group size and the degree of cover.

Resident males appear to assess the risk involved in approaching the roars of intruders by judging their relative numbers. Theoretical studies predict that contestants should assess the competitive ability of their opponents and avoid confrontations that they cannot win (Parker 1974; Maynard Smith 1982). Coalitions are more likely to be chased or attacked by numerically superior rivals (Table I) and our experiments show that males are slower to approach the speaker both when the number of defenders is low and when the number of roaring intruders is high. The ratio of the number of defenders to the number of intruders has a highly significant effect on the latency to approach the speaker ($r^2=0.224$, $P<0.005$: unpublished data): males approach more slowly when they are outnumbered.

When cover was thick, male lions approached the speaker more slowly and also spread further apart during the approach. This can be interpreted in a number of ways. At one extreme, males may be more cautious while approaching opponents that they cannot see because of thick cover. However, if they were fearful, they might be expected to approach in tight formation. At the

Table IV. First and last males to approach the speaker in each playback experiment when two or more males were present, and the difference in their approach times

Coalition	Lead lion	Last lion	Coalition size	No. males present	Close kin?	No. intruders	Time difference (min)	Mean difference (min)
TRMN	Trmn	Cktl	3	2	N	3	3.13	3.13
	Gfjb	Bbob	3	2	Y	3	2.79	2.79
	PNE	Timo	3	3	N	3	2.67	2.67
	Mnrd	John	3	3	Y	3	4.05	2.30
JMS	Smith	John	3	3		3	2.5	
	Mnrd	John	3	3		3	1.8	
	Smith	John	3	3		3	0.83	
	Mnrd	John	3	3		3	†	
	Mnrd	John	3	3		3	†	
	Mnrd	John	3	3		3	2.83	1.78
	Mhwk	Hctr	2	2	N	2	2.00	
	Mhwk	Hctr	2	2		2	0.5	
	Mhwk	Hctr	2	2		1	†	
	Mhwk	Hctr	2	2		1	†	
LTWIRP	Twp1	Twp2	3	3	N†	3	1.16	1.46
	Twp1	Twp2	2	2		2	1.63	
	Twp1	Twp2	2	2		2	1.60	
	L21*	Twp1*	2	2		3	0	
	Twp1*	L21*	2	2		2	0	
	MM2	MM1	2	2	Y	3	2.03	1.23
MSMS	MM2	MM1	2	2		1	0.42	
	MS12	MS21	9	2	Y	1	1.28	1.13
	MS10	MS12	4	4		3	0.98	
	Snag	Norm	2	2	N	2	1.4	0.58
SNORM	Snag	Norm	2	2		1	0.67	
	Snag	Norm	2	2		1	0.5	
	Norm	Snag	2	2		3	0.22	
	Norm	Snag	2	2		2	0.13	
	Blnd	Blick	2	2	N	1	0.58	0.58
	Blick	Blnd	2	2		3	†	
	GI	Joe	2	2	N	2	0.38	0.25
	GI	Joe	2	2		3	0.05	
BCS	GI	Joe	2	2		3	0.32	
	BC2	BC4	3	3	Y	2	0.17	0.17
	SBI	SBN	2	2	Y	2	0.05	0.05
MGS	MG12*	MG08*	3	3	Y	3	0	0

Note: this table includes playbacks excluded from other analyses due to slight variation in protocol or insufficient data.

Y: All members related; N: all unrelated; N†: related pair with unrelated third.

*Arrived simultaneously; lead and last positions arbitrary.

†Precise times not available.

other extreme, they may be using the cover to their own advantage and hence are being more stealthy, surrounding their opponents and searching possible hiding spots. Lions often spread out while hunting their prey (Schaller 1972) and there is often a persistent division of labour during cooperative hunts (Stander 1992).

Although males might superficially appear to be facing a Prisoner's Dilemma when confronted by a challenge to their residency, each male's reproductive success depends directly on his membership in a coalition large enough to maintain access to females. His coalition partners are therefore necessary to him and must be preserved to help defend the pride. Packer et al. (1988) have calculated that each additional member of a coalition increases individual reproductive success by 0.64 surviving cubs per male.

There should thus be no temptation to defect completely during an outside challenge, because a male's ability to repulse intruders, and thus to hold onto his pride, would be reduced if his partner is wounded or killed. Male coalitions are typically resident in a pride for only 2–3 years and once evicted by a rival coalition they rarely gain residence again (Packer et al. 1988). Defection by a male during an inter-coalition encounter could thus lead to the forfeiture of his entire lifetime reproductive success.

These are exactly the conditions predicted by Lima (1989) to lead to cooperation through 'mutual dependencies'. In Lima's model, three factors influence the tendency to cooperate within pairs or groups: a low probability of success when alone, a low probability of replacing the current partner and a large number of interactions before the end of the association. For male lions, the reproductive success of solitary is typically low (Bygott et al. 1979; Packer et al. 1988); finding a partner often entails years of a nomadic existence (Schaller 1972; Pusey & Packer 1987); and a coalition persists for the life of its members.

The importance of protecting current reproductive effort is emphasized by the contrast in behaviour between males and females towards the roars of like-sexed intruders. McComb et al. (1994) found that female lions only approach intruder females when the relative odds are heavily biased towards the defenders. Whereas males compete for the exclusive access of a pride and typically father only a single cohort of young,

females negotiate long-term territorial boundaries and breed repeatedly over their lifetime (Packer et al. 1988, 1990).

Cooperation among male lions thus appears to be a matter of unconditional self-interest, and it is not surprising that their responses to intruders are not dependent on the number of females, cubs, or subadults in the pride (cf. McComb et al. 1994, for the behaviour of females). When such a large proportion of male lifetime reproductive success is at risk, males should respond aggressively and cooperatively to each intruder regardless of their pride's composition, their own kinship, or their companions' behaviour.

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