

MODES OF COOPERATION DURING TERRITORIAL DEFENSE BY AFRICAN LIONS

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Cooperation during territorial defense allows social groups of African lions to defend access to resources necessary for individual reproductive success. Some forms of cooperation will be dependent upon cognition: reciprocity places greater cognitive demands on participants than does kinship or mutualism. Lions have well-developed cognitive abilities that enable individuals to recognize and interact with others in ways that seem to enhance their inclusive fitness. Male lions appear to cooperate unconditionally, consistently responding to roaring intruders regardless of their male companions' kinship or behavior. Female lions, however, do keep track of the past behavior of their female companions, apparently using the reliability of a companion as one means of assessing the risks posed by approaching intruders. Some "laggard" females may exploit the cooperative tendencies of "leaders" during territorial encounters. Although leader females clearly recognize laggards as such, the costs of tolerating laggards may be less than the benefits leaders gain through territorial defense behavior. Thus, although lions clearly have the cognitive ability to base cooperation on reciprocity, territorial defense cooperation appears instead to be based primarily on mutual benefits to participants for both male and female lions.

KEY WORDS: African lion; Cognition; Communication; Cooperation; *Panthera leo*; Leader; Laggard; Roaring; Territorial defense

In group-living species, cooperation during territorial defense requires that individuals take on costs associated with defense (e.g., the risk of injury or

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death) while providing benefits for all group members (e.g., access to resources, protection from intruders). By defecting on a cooperating companion, an individual may be able to avoid the short-term costs of territorial defense while gaining the long-term benefits of territory ownership. Natural selection should favor behaviors that benefit individuals the most while costing them the least. Thus, the presence of cooperative behaviors despite this temptation to defect demands an evolutionary explanation. Three different explanations have been widely proposed: kin selection (Hamilton 1964), reciprocity (Axelrod and Hamilton 1981; Trivers 1971), and mutualism (Dugatkin et al. 1992; Lima 1989; Maynard Smith 1983). Which of these evolve in a particular situation will depend on the costs and benefits of cooperation, and the pattern of cooperative interactions between individuals. It will also depend on the cognitive abilities of the participants, for the different types of cooperation have different cognitive requirements.

Cooperation based on kinship requires that individuals preferentially interact with genetic relatives (Hamilton 1964). Kinship-based cooperation thus requires at least the ability to recognize relatives. By doing so, individuals can restrict the benefits of cooperation to genetic relatives while minimizing the costs of territorial defense to any one participant. Inclusive fitness benefits of cooperating with close relatives can outweigh the temptation to defect, allowing the payoff for cooperation to exceed that of defection when a companion cooperates (Hamilton 1964). By reducing the net cost of cooperation, inclusive fitness benefits may also make the outcome of cooperation positive even in the event of defection by a close relative. Thus, kinship-based cooperation should be relatively tolerant of "cheaters," unlike reciprocity.

Reciprocity puts greater cognitive demands on individuals since they must base their decision to cooperate on the past behavior of their companions, thereby restricting the benefits gained by cooperation to those that have previously incurred its costs (Axelrod and Hamilton 1981; Trivers 1971). Not only must participants be able to recognize and preferentially interact with certain individuals over an extended period of time, they must also be able to remember the past behaviors of companions and cooperate only with proven reciprocators. Additionally, reciprocators may use different currencies of exchange or may devalue rewards over time (Stephens 2000). Reciprocity is likely, therefore, to require sophisticated cognitive abilities. In contrast, mutualism makes only minimal cognitive demands of participants. Unlike kinship and reciprocity, mutualism is unconditional, in that choosing to cooperate will always give the highest payoff regardless of the identity or behavior of companions (Dugatkin et al. 1992; Maynard Smith 1983).

In this article I examine the costs and benefits of cooperation during ter-

territorial defense by African lions, a species well known for such behaviors (Schaller 1972), and the links between cognition and cooperation. The results presented here are based on a population of lions that has been studied more or less continuously since 1966 in a 2,000 km² part of Serengeti National Park, and in the adjacent Ngorongoro Crater, Tanzania. I will review the evidence for cognitive abilities in African lions, test for the three types of cooperation introduced above, and discuss the role of cognition in cooperation by African lions.

BACKGROUND

Both male and female African lions gain reproductive benefits from belonging to cooperative social groups. The links between cooperation and reproductive success are the same for the two sexes: cooperation with group members reduces the costs faced by each participant, thereby protecting companions and preserving group size necessary for acquiring and defending access to resources critical for reproductive success (Figure 1). The resources for which groups compete, however, and the specific mechanisms leading to reproductive success, differ for males and females. Males form coalitions that compete amongst each other for exclusive access to female prides, the resource necessary for male reproductive success. Competition can be intense, with rival groups chasing, wounding, and even killing each other (Schaller 1972). Larger groups dominate smaller groups, giving larger coalitions an advantage in the competition for pride ownership (Grinnell et al. 1995). Larger groups have a greater probability of



Figure 1. Generalized scheme illustrating the long-term mutual benefits to lions of cooperation during territorial defense.

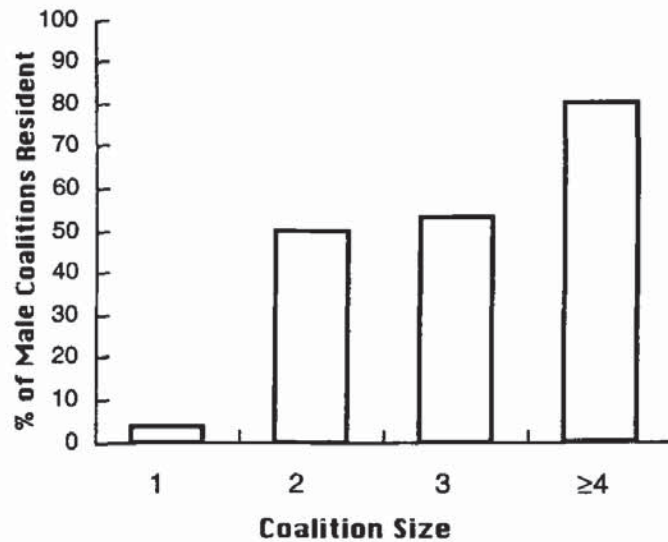


Figure 2. Probability of gaining residence by coalition size. Larger coalitions are significantly more likely to gain tenure than smaller coalitions: for the singletons, 1 of 29 gained residence; for pairs, 13 of 26; for trios, 9 of 17; for groups of four or more, 16 of 20 ($\chi^2 = 36$, $p < 0.0001$). Data are from all coalitions in Serengeti and Ngorongoro study areas whose members were seen before and at least once after the age of three ($n = 92$ coalitions: 1966–1990).

becoming resident in a pride (Figure 2), and members of a larger group first gain residence at a younger age than do those of smaller coalitions (Pusey and Packer 1987). Larger coalitions also remain resident for longer periods (Figure 3) and sire more surviving offspring per male than do smaller coalitions (Figure 4: Bygott et al. 1979; Packer et al. 1988), although the variance in individual male reproductive success increases with coalition size (Packer et al. 1991). Membership in a coalition is thus of vital importance to male lions, and individual males often spend years wandering nomadically before they join with other nonresident males in a coalition able to take over their first pride (Pusey and Packer 1987). On average, however, a coalition has a reproductive lifespan of only about 2.8 years (Figure 3: Packer et al. 1988), just enough to raise one cohort of cubs to independence before being evicted by a rival coalition (Packer et al. 1988; Pusey and Packer 1987). In a very real sense, therefore, male lions will often have only one chance at reproductive success in their lifetimes. Such limited reproductive opportunities appear to have selected for an extreme response to intruders: Grinnell and colleagues (1995) found that male residents aggressively approached the loudspeaker from which roaring of outside males emanated in all 28 playback experiments in which resident defenders were challenged by similar numbers of intruders, and even in three of eight experiments in which a single defender was outnumbered by three to one.

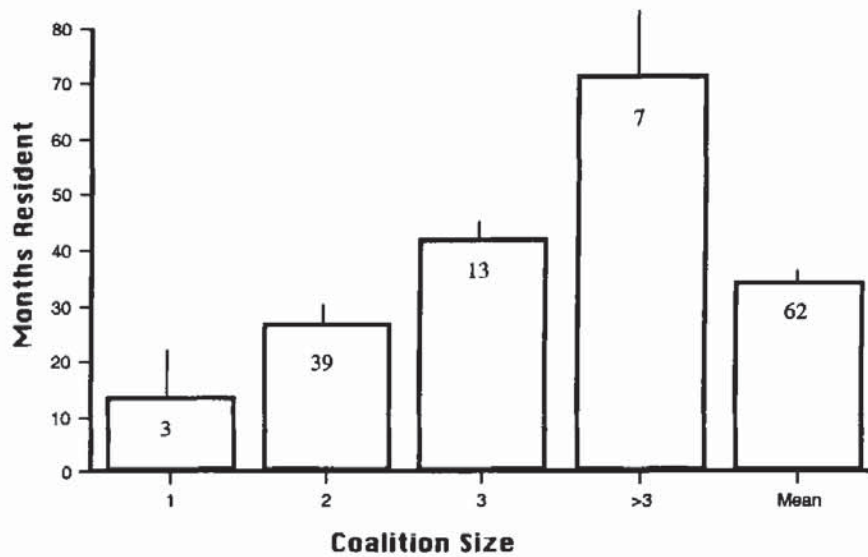


Figure 3. The effect of coalition size on length of residency in one or more prides. Data from 62 Serengeti coalitions resident in the study area for at least 3 months (1966–1990). Numbers inside the bars correspond to numbers of coalitions in each size category. Mean residency for each coalition size (mean \pm SE) in months: singletons, 13.57 ± 9.28 ; groups of two, 26.64 ± 3.07 ; groups of three, 42.05 ± 4.01 ; groups with four or more, 71.54 ± 11.80 ; mean for all sizes: 34.31 ± 3.12 . Mean tenure lengths are significantly different (ANOVA: $F(3,58) = 11.90$, $p < 0.001$).

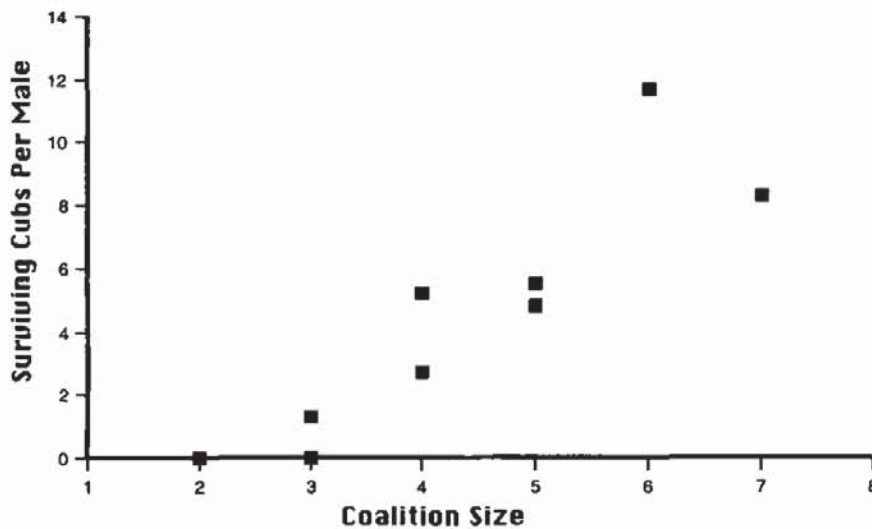


Figure 4. The effect of coalition size on male reproductive success. Data are from 15 coalitions in the Serengeti study area for which complete residency and lifetime reproductive data exist. These coalitions were either born into the study or were first seen at <3 years of age and subsequently became resident in one or more study prides (1966–1990).

The selective pressures on female lions are considerably different. Whereas male groups compete to hold onto a pride, female prides compete to hold onto a territory. Females are born into a pride that defends a traditional territory that is handed down through generations. Female reproductive success depends on translating a territory's resources into cubs and on keeping the cubs alive. Grouping by females facilitates both. By grouping, females are able to defend a territory collectively against other prides of females (McComb et al. 1994), thereby maintaining access to important resources such as secure denning sites, dry-season water sources, and a prey base (Packer 1986). Grouping also makes females more successful than solitary females at defending their cubs against potentially infanticidal males from outside the pride (Grinnell and McComb 1996; Packer et al. 1990). Whereas females without cubs spend considerable time alone and associate with pride companions in a "fission-fusion" pattern (Packer 1986), females with cubs of a similar age pool their offspring into a "creche" and associate together almost constantly (Packer and Pusey 1983; Packer et al. 1990). Packer and colleagues (1990) found that by doing so, mothers in groups of two or more were much more successful at defending their cubs against infanticidal males than were solitary females. Nonresident, potentially infanticidal males respond to groups of females roaring in chorus much more cautiously than to single females roaring alone, reflecting the increased ability of females to repulse threatening males when they are with companions (Grinnell and McComb 1996). Companions are thus important to females for success both in interpride competition for territory and in keeping their cubs from being killed by outside males. I will argue that the benefits of maintaining group size and thus of keeping companions alive determine to a great extent the type of cooperation present in both female and male lions.

African lions are well known for cooperative behaviors ranging from communal nursing (Packer et al. 1990; Pusey and Packer 1994) and cooperative hunting (Stander 1992) to territorial defense (Bygott et al. 1979; Packer 1986). Territorial defense is characterized by many behaviors that could be considered cooperative, including patrolling the territory (done predominantly by males), scent-marking (males and females), roaring in chorus (males and females), and chasing / attacking like-sexed intruders (males and females). Of these, the last entails the most obvious risk to participants, and it is on this behavior that I will focus here.

EXPERIMENTAL EVIDENCE OF COGNITION

In most animals, the cognitive abilities of group members will dictate the complexity of social organization (chemically controlled societies, such as

those of the eusocial insects, are an exception). By social complexity, I mean here a social system in which an individual interacts with many different members of the social network and whose interactions are frequent, of diverse kinds, and conducted over an extended period. Humans, chimpanzees (de Waal 1982; Goodall 1986), and elephants (McComb et al. 2000) characterize one extreme, in which cognitive abilities and social complexity are both highly developed. Complex social relationships rely on the abilities of individuals to recognize, remember, and interact in different ways with different individuals within and outside of their social groups. Though most apparent in primates, this complexity is also true of some other social animals, such as African lions. Lion social organization requires pride and coalition members to be able to recognize, remember, and bias their behavior towards group members in order to limit the benefits of a group and its territory to relatives (in the case of females) or long-term cooperators (males) and to deal effectively with classes of individuals that are a threat to reproductive success. In the case of females, lions must also remember the past behavior of their companions in order to minimize the costs of responding with them to territorial threats (see below).

My colleagues and I have tested the cognitive abilities of lions through the use of playback experiments (for details of methodology, see cited references). Briefly, our playback protocol was as follows (see also McComb 1992). Recordings of known individuals roaring in known contexts were broadcast over an amplified loudspeaker to one or more subject lions when they were neither feeding nor near lions of the opposite sex. The speaker was placed in vegetative cover 200 m from the subject lions; playbacks commenced 20 to 30 minutes before sunset, at a time of day when it would not be unusual for lions to roar (Schaller 1972) and when it was still light enough to videotape the subject's responses. Responses were recorded in field notes and on videotape whenever possible, and in most cases playbacks to any particular individual were separated by at least 7 days to avoid habituation. Recordings were considered unfamiliar to subject lions if they were made of individuals living more than 30 km away, or individuals who had died before the subject lion was born.

Do Lions Assess the Sex and Number of Individuals Roaring?

Grinnell and McComb (1996) compared the responses of extrapride (nonresident) males to playbacks of roaring from unfamiliar males and unfamiliar females. They found that nonresident males were attracted to the roars of females but avoided the roars of male lions (Table 1). In addition, nonresident males were much more likely to approach, and would approach faster, when the playback consisted of the roaring of a single female rather than a chorus of three females. Whereas this demonstrates the

Table 1. Responses of Nonresident Males to the Roars of Male and Female Lions (counts are of number of different coalitions that gave each response)

| <i>Sex of roarers</i> | <i>Approach</i> | <i>Don't approach</i> |
|-----------------------|-----------------|-----------------------|
| Male | 0 | 6 |
| Female | 10 | 3 |

The average number of roarers per playback was similar for both male and female playbacks: male: 2.0 ± 0.45 ; female: 2.1 ± 0.28 . Fisher's Exact test: $p = 0.0062$, two-tailed (data from Grinnell and McComb 1996).

value of grouping by females when potentially infanticidal males are listening, it also indicates that lions are, not surprisingly, capable of discriminating male from female, and one from many, roarers. In studies of territorial defense by males and females, respectively, Grinnell et al. (1995) and McComb et al. (1994) found that both sexes respond to simulated intruders by approaching the loudspeaker more consistently and more quickly when faced with fewer opponents.

Do Lions Recognize and Remember Group Members?

In a study of 15 male coalitions in Serengeti National Park, I compared the responses of resident males to either (a) the broadcast roaring of a temporarily absent male companion ($n = 5$ coalitions) or (b) one of eight different recordings of an unfamiliar male ($n = 10$ coalitions). In each of the five cases in which resident males heard an absent companion roaring they remained stationary and/or roared in chorus with the playback. In contrast, the 10 coalitions that were played the roar of an unfamiliar male all approached the loudspeaker silently (Fisher's Exact Test: $p = 0.007$, two-tailed; Table 2). Coalition males are thus clearly able to recognize and remember each other's voices, probably using this ability to coordinate movements, recruit aid, and broadcast group membership to listening rivals when separated (Grinnell 1994).

Table 2. Responses of Resident Males to Playback of a Single Coalition Partner or a Single Unfamiliar Male

| | <i>Roar with playback</i> | <i>Don't roar with playback</i> |
|-----------------|---------------------------|---------------------------------|
| Partner's Roar | 4 | 1 |
| Stranger's Roar | 0 | 10 |

Counts are of number of different coalitions that gave each response. Fisher's Exact test: $p = 0.007$, two-tailed.

Pride females likewise are efficient discriminators of pride males from unfamiliar males. By comparing the responses of females with cubs to the roaring of the cubs' fathers, of unfamiliar males, and of unfamiliar females, McComb et al. (1993) found that mothers reacted with agitation to the roars of unfamiliar males, with aggression to those of unfamiliar females, and with unconcern to those of their cubs' fathers (Table 3). Females with cubs clearly gain fitness benefits from differentiating between potentially infanticidal males and the fathers of their cubs.

Do Lions Remember Past Behavior of Group Members?

Pride females cooperate in territorial defense by approaching the roaring of unfamiliar females in their territory (McComb et al. 1994). Members of the responding group will often approach at different speeds, such that some lions arrive in the vicinity of the roar ahead of the others. After conducting 6–15 playbacks of unfamiliar females to the same eight prides over a period of two years, Heinsohn and Packer (1995) found that many pride females had consistent behaviors during approaches; some females would consistently lead an approach while others would consistently lag behind. By opportunistically simulating roaring intruders to "leaders" when paired with other leaders or with "laggards," they found that leaders approached the loudspeaker more slowly, and monitored their companion more carefully, when paired with laggards than when paired with other leaders. Leaders thus seemed to recognize certain individuals as unreliable, suggesting that lions have the cognitive ability to keep track of their companions' past behavior.

Do Lions Have the Cognitive Abilities for Conditional Cooperation?

Female lions are able to recognize and remember individuals and their behaviors, allowing them to bias their cooperative behaviors toward kin (Hamilton 1964). They also appear to have the cognitive abilities to implement the "score-keeping" necessary for cooperation by reciprocity (Axelrod and Hamilton 1981). This finding should not be surprising, given the degree of sociality shown by lions and their multifaceted reliance on cooperation. In fact, Hemelrijk (1996) has argued that the cognitive demands

Table 3. Responses of Females with Cubs to Playback of Either a Familiar ("Father's Roar") or an Unfamiliar Male's Roaring

| <i>Response</i> | <i>Father's Roar</i> | <i>Unfamiliar Male's Roar</i> |
|----------------------|----------------------|-------------------------------|
| Retreat and/or snarl | 0 | 9 |
| No retreat or snarl | 9 | 2 |

Fisher's Exact test: $p = 0.0003$, two-tailed. Data from McComb et al. (1993).

of reciprocity have been exaggerated and that reciprocity and social structure could instead be the result of simple rules used by individuals. In any case, although lions appear to have the cognitive abilities required for conditional cooperation, they may not rely on them for cooperation during territorial defense.

EXPERIMENTAL TESTS OF COOPERATION HYPOTHESES

Cooperation during Territorial Defense by Male Lions

Male lions make good subjects for tests of cooperation hypotheses because they form coalitions that may be composed entirely of relatives, non-relatives, or a mixture of the two (Packer et al. 1991; Grinnell et al. 1995). Resident males father all cubs sired in the pride, but the reproductive success of individual coalition members becomes increasingly skewed with increased coalition size (Gilbert et al. 1991; Packer et al. 1991). Males thus appear only to join unrelated lions to form coalitions of two or three; larger coalitions are composed entirely of relatives (Packer et al. 1991). By cooperating with kin, males can gain inclusive fitness benefits even if they are unable to reproduce themselves (Hamilton 1964; Packer et al. 1991). However, once an individual lion has joined a coalition, kinship does not appear to influence his behavior.

Through a series of playback experiments, Grinnell et al. (1995) tested predictions based on kin selection, reciprocity, and mutualism in a sample of 15 resident coalitions. They found that resident males approached the loudspeaker when challenged with unfamiliar males roaring in all of 36 playback experiments except for three of eight experiments in which a single individual was challenged with three intruders. In a multivariate model predicting the time until lions reached the speaker after playback, the authors found that the number of defenders, the number of simulated intruders, and the degree of cover were significant predictors. Theories of cooperation based on kinship and reciprocity predict that cooperation will depend on the relatedness or the behavior of an individual's companion, respectively. However, relatedness had no significant effect on the rate or the probability of approach. If reciprocity is important, cooperators should monitor the behavior of their companions, approaching when companions do and holding back when they lag behind. Because kinship could favor cooperation in the absence of reciprocity, nonrelatives should monitor their companions' behavior more than relatives should. Grinnell et al. (1995), however, found no effect of kinship on either the number of times a lead lion would glance back at a follower or the proportion of the 200 m approach to the loudspeaker in which lions walked side by side, when partners could be monitored continuously.

In the absence of any evidence for reciprocity or kinship, the authors concluded that mutualism is the best explanation for cooperation in male lions. Because each male's reproductive success depends directly on his membership in a coalition large enough to maintain access to females, a male's companions are valuable to him and must be preserved. Thus, there should be no temptation to defect during a challenge by rival males because a male's ability to repulse intruders, and hence to hold onto his pride, would be reduced if his companions were wounded or killed. Defection during territorial defense could thus result in the forfeiture of a male's entire lifetime reproductive success: since throughout their lifetime males typically hold a pride for only 2–3 years (Packer et al. 1988), losing a companion could lead to the loss of their only opportunity for reproduction.

The evolution of cooperation by mutualism is likely when (1) singletons have a low probability of success, (2) there is a low probability of replacing the current (same-sex) partner(s), and (3) partners interact repeatedly over a long period of time (Lima 1989). These three conditions match those seen in male lions: the reproductive success of solitary males is low (Bygott et al. 1979; Packer et al. 1988), finding companions may entail years of a nomadic existence (Schaller 1972; Pusey and Packer 1987), and, once formed, a coalition persists for the life of its members.

These selective pressures may be similar to those that promote territorial behaviors by male chimpanzees. Male chimpanzees form coalitions that cooperate in competition against neighboring male groups (Goodall 1986). These groups are kin-based, but the three conditions listed above (Lima 1989) may still apply. This intergroup competition can take the form of lethal raiding, a phenomenon in which the males of one community move stealthily together into the territory of a neighboring group and attack and often kill neighboring males (Wrangham 1999). Success in these raids is clearly group-size dependent; when an attacking coalition significantly outnumbers the victims, the costs to each attacker may be very low and the probability of success high (Wrangham 1999). Males apparently benefit from eliminating rival males because it enables them to annex neighboring territory and females (Goodall 1986; Wrangham 1999). As with male lions, there is no indication of defection by males during these chimpanzee group attacks (Goodall 1986), suggesting that the mutual benefit of reducing the strength of rival groups may be driving individual participation in the raids.

However, even where individual participants gain long-term mutual benefits from participating in territorial encounters, some individuals may gain short-term benefits by lagging behind during such encounters. In their study, Grinnell and colleagues (1995) found consistent laggards in five of eight coalitions that were the subjects of two or more experiments. If leaders are more likely to be attacked (as is true for females: Heinsohn

and Packer 1995), laggards may reduce the risk of injury to themselves while increasing the risk of injury to their leading companion. Without detailed observation of actual encounters (which are infrequently observed: Grinnell et al. 1995), the real consequences of lagging behind will be unclear. However, two observations suggest that male laggards do contribute to intercoalition encounters. First, in those encounters between resident coalitions that have been observed, the outcome has always been group-size dependent, with larger coalitions dominating smaller ones (Grinnell et al. 1995). Second, single males approach three simulated intruders much more slowly than when they have one or more companions (Grinnell et al. 1995). Other possible explanations for the presence of leaders and laggards will be considered after a discussion of the dynamics of female cooperation.

Cooperation during Territorial Defense by Female Lions

Female lions cooperate to repulse non-pride females from their territory (Schaller 1972; McComb et al. 1994). As in males, the outcome of intergroup competition is group-size dependent, with larger prides dominating smaller prides in the competition for territory (Schaller 1972; Packer et al. 1990). Females gain long-term mutualistic benefits from having sufficient companions to defend a territory from rival prides (McComb et al. 1994), defend cubs from extrapride males (Packer et al. 1990), and hunt large prey (Scheel and Packer 1991). Defection during territorial defense, as in males, could lead to the loss of companions that are not easily replaced. Since pride size increases only through the birth and retention of offspring, each female should benefit from unconditional cooperation during territorial encounters by protecting her companions from injury and death and preserving the size of the pride. Only when a pride is larger than the reproductive optimum of 3 to 10 individuals (Packer et al. 1988) might we expect the benefits from protecting companions to be reduced.

Cooperation during territorial defense can be thought of as entailing two decisions that must be made by defenders upon hearing an intruder's roaring. First, do individual defenders approach and confront the intruders, or not? And second, if approaching, how fast does a lion approach? Both decisions will depend upon the perceived risk to the defenders, and this risk will depend upon the number of intruders relative to defenders (the "odds") and the reliability of one's companions (i.e., if a companion is a known cooperator or a possible defector). The amount of risk an individual lion is willing to assume when confronting territorial intruders is very different between males and females: on average, females are willing to assume much less risk than are males. This is evident in their behavior with respect to both decisions presented above.

In a study by McComb et al. (1994), female lions consistently approached a simulated threat (first decision) only when the defenders outnumbered the intruders. In contrast, male lions always approached simulated intruders when the odds were similar, and even in three of eight cases when the defender was outnumbered by 3 to 1 (Grinnell et al. 1995). Where competition for territory is intense because of high lion population densities (as in Ngorongoro Crater: Van Orsdol et al. 1985) and its value is consequently increased, the probability of females approaching intruders may increase (Heinsohn 1997). Likewise, females may approach simulated intruders more quickly (second decision) when the value of the territory is greater (e.g., in Ngorongoro Crater: Heinsohn 1997). Thus, a more valuable territory may make accepting greater risk in its defense worthwhile. However, females even in Ngorongoro Crater respond more cautiously than do males in the Serengeti (Grinnell et al. 1995; Heinsohn 1997). This difference may reflect the contrasting selective pressures on males and females: whereas males are defending what may be their lifetime reproductive success, females are negotiating long-term territory boundaries with neighboring prides. Since female reproductive success is not at risk with every interpride encounter, will female cooperation still be based on the long-term benefits of mutual protection? The answer appears to be yes, although the details of female cooperation show it to be more conditional—and more complex—than was expected (Heinsohn and Packer 1995).

Heinsohn and Packer (1995) tested for reciprocity by leader and laggard females (see above). During approaches of simulated intruders, leaders apparently mistrusted laggards more than they did other leaders: leaders monitored laggards more carefully and approached the intruders more slowly than when teamed with another leader (Table 4). The behavior of leader females thus appears to be conditional on the presence and cooperative tendencies of their companions, both when deciding to approach (only approaching when sufficient companions are present to bias the odds in their favor: McComb et al. 1994; Heinsohn 1997) and in the behavior during the approach (approaching quickly and with less monitoring when paired with another leader: Heinsohn and Packer 1995). However, during approaches, leaders did not conform to the predictions of reciprocity because they failed to “punish” laggards by refusing to approach without them (Axelrod and Hamilton 1981; Mesterton-Gibbons and Dugatkin 1992). Leaders continued to approach and arrived at the loudspeaker well before their lagging companion (48 to 106 seconds ahead at midpoint), putting themselves at significant risk of being attacked before a laggard could catch up to help (Heinsohn and Packer 1995). Because females benefit mutualistically from having many pride companions (as described above), we might expect laggards to contribute most to territorial defense when their participation was most needed. Heinsohn and Packer (1995) found that this

Table 4. Responses of Six Female "Leaders" to Playback of a Single Unfamiliar Female When Paired with Either Another Leader (Top) or a "Laggard" (Bottom)

| <i>Pair</i> | <i>Approach time of leader (s to 100 m)</i> | <i>Lag time (s)</i> | <i>Glances (n)</i> |
|-----------------------|---|---------------------|--------------------|
| LEADER-LEADER | | | |
| CS55-CS63 | 128 | 1 | 2 |
| CSN-CS46 | 185 | 1 | 0 |
| L75-L78 | 55 | 25 | 0 |
| MSF-MKN | 134 | 9 | 3 |
| MKU-MKT | 91 | 6 | 1 |
| Nymph-Nell | 65 | 20 | 0 |
| LEADER-LAGGARD | | | |
| CS55-CS60 | 224 | 86 | 7 |
| CSN-CS27 | 304 | 58 | 4 |
| L75-L72 | 191 | 80 | 2 |
| MSF-MKS | 174 | 106 | 5 |
| MKU-MKO | 126 | 48 | 4 |
| Nymph-NW15 | 134 | 56 | 4 |

Leaders approached more slowly, got farther ahead of their companion, and glanced back at their companion more when with a laggard than when with a leader (Wilcoxon Signed Rank: $p = 0.031$, two-tailed. Data from Heinsohn and Packer 1995).

was true of three of the twelve laggards in their study. Termed "conditional cooperators," these females lagged least when their participation would shift the likelihood of success in their favor. However, three others (termed "conditional laggards") lagged most when most needed, and the remaining six ("unconditional laggards") did not alter their behavior according to the ratio of intruders to defenders.

Given that female lions are sensitive to the risk involved in approaching intruders (McComb et al. 1994), and that leaders take on additional risk when paired with a laggard, why should a female leader approach at all? As with male lions, there is some evidence that female laggards are trusted to contribute when needed. Three of the laggards identified by Heinsohn and Packer (Trifle, SBC, and LK23) were half of a pair of defenders that was played roars simulating three intruders. The fact that they approached, rather than remaining motionless or retreating (as did two of the three singletons played similar roars simulating three intruders by McComb et al. 1994), suggests that although the lead female recognized her companion as a laggard, she nonetheless trusted her enough to risk confronting superior numbers.

LAGGING DURING TERRITORIAL DEFENSE

In the absence of unambiguous conformance to the predictions of reciprocity or mutualism, three other suggestions have been made to explain this diversity of female behavior (Packer and Heinsohn 1996): (1) leaders may specialize in territorial defense while laggards may specialize in other activities; (2) leaders gain more than laggards from territorial defense (Jahn 1996); (3) leaders may be better fighters than laggards, and thus risk less by leading. While none of these suggestions can be ruled out with certainty given available data, there is little evidence to support any of them.

Specializations

In male lions, the five laggards reported by Grinnell et al. (1995: John, Hctr, Twp2, MM1, Joe) were all observed roaring with companions in group choruses, and four of the five were recorded leading chorused roars. While this behavior contributes to territorial defense by advertising group size and ownership, no other evidence supports a bartering of services to make up for lagging during intercoalition encounters. In females, there is no evidence from cooperative hunting data, for example, that laggards take lead roles in group hunts (Packer and Heinsohn 1996).

Unequal Benefits

There is also no evidence that female leaders gain additional benefits from leading. There is no dominance hierarchy among females that would allow resources to be divided asymmetrically (Packer and Pusey 1985); all females have equal access to all parts of the territory (Packer et al. 1990); and males show no mating preferences for particular females (Packer and Pusey 1983). In male lions, individual reproductive success becomes increasingly skewed as coalition size increases (Packer et al. 1988); thus male laggards may be members of larger coalitions that have been unable to sire cubs and therefore have less motivation to defend the pride. No data on reproductive success are available to test this proposition; however, three of the five identified male laggards (Hctr, MM1, Joe) were in coalitions with only two members, and both males in groups of this size usually have similar reproductive success (Packer et al. 1988).

Unequal Abilities

If larger lions have greater fighting ability, leaders should be larger than laggards. However, Heinsohn and Packer (1995) found no relationship between body size and whether a female lion was a leader. In addition, leading and lagging strategies appear to be set in an individual female by the

age of eight months, well before adult body size is attained (at two to three years), and they appear to be stable over time (Heinsohn and Packer 1995).

COOPERATION BY FEMALES AND MALES

Reciprocity requires that laggards give something back to the leaders to make up for the extra costs associated with leading. The three explanations mentioned above are attempts to explain how this may occur. However, a laggard may in fact never reciprocate, but may instead be a sort of "scrounger" to the leader's "producer" (Barnard 1984). In this scenario, producers make available resources that can be exploited by a scrounger (e.g., a territory). If scroungers are rare and producers abundant, the long-term benefits to producers may exceed the cost of tolerating scroungers. In the case of female lions, the cost of tolerating laggards may be less than the cost of not defending one's territory, especially since the laggards are close relatives.

Even with the diversity of cooperative behaviors shown by females, the largest payoffs to group-living and cooperation still appear to be based on mutualism. Cooperation by females within prides gives long-term reproductive benefits to all group members, while allowing some individuals to gain additional short-term benefits at the expense of their more cooperative companions. The benefits gained by laggards are clearly frequency-dependent, however: if too few females take on leadership roles, all will lose as the territory is lost. If enough females participate in territorial defense, all gain the benefits of a communal territory, even if some females avoid some of its costs (Heinsohn and Packer 1995; Packer and Heinsohn 1996). Within this framework of mutual benefit, however, females make short-term decisions based on conditions that influence the risk associated with territorial defense behaviors: they approach intruders when the odds are in the defenders' favor, and approach more cautiously when with a possibly unreliable companion.

Male lions reflect similar, but more extreme, selective pressures towards mutualistic cooperation. With their entire lifetime reproductive success potentially at stake with every territorial intrusion, males are under intense pressure to respond aggressively and cooperatively during intercoalition encounters. Laggards exist among male defenders, but the degree of lagging is unrelated to the odds faced by defenders (Grinnell et al. 1995). The only correlate of lagging time found by Grinnell and colleagues (1995:102) was cover density. In thicker cover, laggards should find it easier to defect without being detected by leading males, yet leaders monitored laggards no more in thick than in light cover (Grinnell et al. 1995). This suggests that leaders trusted the laggards to contribute when needed (cf. females: Heinsohn and Packer 1995) and/or gained sufficient benefits from cooperation

(i.e., continued cub survival and pride residence) to cooperate regardless of the behavior of their companions. In contrast, the benefits to females of territorial defense may outweigh the costs of engaging rival females only when sufficient trustworthy companions are present to bias the odds in their favor. Females consistently approach intruders only when defenders outnumber intruders, and they monitor their companions more when faced with three intruders than with one (McComb et al. 1994). Additionally, in Ngorongoro Crater, where territories are more highly contested, females appear to approach intruders when the odds are against them more readily than do Serengeti females (Heinsohn 1997). Females thus are more sensitive to the costs and benefits of territorial defense than are males, and this process of assessment may result in the more diverse strategies of cooperation observed by Heinsohn and Packer (1995).

THE ROLE OF COGNITION IN COOPERATION DURING TERRITORIAL DEFENSE

Cognition plays an important role in the structure of lion society by enabling group members to recognize, remember, and preferentially interact with pride and coalition members, and to assess the risks and benefits of cooperating with different pride companions. Because of their cognitive abilities, individuals can roar to locate and recruit distant companions and can join from a distance in choruses that advertise group membership and territory ownership (Grinnell 1994; McComb et al. 1994). Assessing the roars of unknown individuals facilitates the defense of cubs by females (McComb et al. 1993; Grinnell and McComb 1996) and triggers behaviors in defense of territory and pride in both sexes (Grinnell et al. 1995; Heinsohn 1997; McComb et al. 1994). As demonstrated by the conditional behavior of female lions during playback challenges (Heinsohn and Packer 1995), lions clearly have the cognitive abilities to base cooperation on reciprocity through "score-keeping." However, it is unclear whether laggard females reciprocate to make up for the increased risk that lagging puts on leaders. In addition, females that lead territorial responses fail to punish known laggards by requiring reciprocity before approaching a potentially serious threat (Heinsohn and Packer 1995), and males approach intruders without regard to the behavior of their coalition companions—and even in the absence of any companions (Grinnell et al. 1995). Rather than through reciprocity, both male and female lions appear to gain mutual long-term advantages from territory ownership that benefit all pride members—even if it does allow some individuals to exploit the cooperative behaviors of others for additional short-term gain. The role of cognition in territorial defense cooperation probably differs between males and females. Both males and females derive benefits from mutualism (see Figure 1)—a form

of cooperation that makes few cognitive demands. However, females also use their cognitive abilities to assess the risks posed by intruding lions given companions of various degrees of reliability. Thus, even in a system driven primarily by mutualism, lions appear to make good use of their well-developed cognitive abilities.

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