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Male bonnet macaques use information about third-party rank relationships to recruit allies

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Social challenges may have driven the evolution of intelligence in primates and other taxa. In primates, the social intelligence hypothesis is supported by evidence that primates know a lot about their own relationships to others and also know something about the nature of relationships among other individuals (third-party relationships). Knowledge of third-party relationships is likely to play an especially important role in coalitions, which occur when one individual intervenes in an ongoing dispute involving other group members, by helping individuals to predict who will support or intervene against them when they are fighting with particular opponents, and to assess which potential allies are likely to be effective in coalitions against their opponents. To date, however, there is no evidence that primates make use of knowledge of third-party relationships when they form coalitions. Here, I show that male bonnet macaques, *Macaca radiata*, use information about third-party rank relationships when they recruit support from other males. Males consistently chose allies that outranked themselves and their opponents, and made such choices considerably more often than would be expected by chance alone. The analysis shows that the data do not fit simpler explanations based upon males' knowledge of their own relationships to other males or males' ability to recognize powerful allies.

A growing body of evidence suggests that natural selection has favoured the evolution of intelligence in primates and other taxa as a means to meet the challenges of social life (Jolly 1966; Humphrey 1976). According to the social intelligence hypothesis, which was first articulated by Jolly (1966) and Humphrey (1976), complex social interactions (including cooperation, competition, manipulation and deception) can occur when animals live in large and stable social groups. Natural selection favours the evolution of cognitive abilities that enable individuals to operate effectively in this complex world. The social intelligence hypothesis is supported by evidence that the degree of encephalization among primates, particularly the relative size of the neocortex, is correlated with the size of social groups, which may reflect the cognitive demands of managing social relationships in groups of different sizes (Dunbar 1992, 1995; Barton & Dunbar 1997). Similar correlations between brain size and sociality have also been found in bats and carnivores (Barton & Dunbar 1997).

Further support for the social intelligence hypothesis comes from the observation that monkeys and apes are skilled in negotiating social relationships (reviewed by Cheney & Seyfarth 1990; Tomsello & Call 1997). They seem to understand certain things about their own relationships to other group members, including maternal kinship, relative dominance rank, and the quality of social bonds. They also appear to have some knowledge of the relationships between other group members (third-party relationships). Knowledge of third-party relationships may play a particularly important role in coalitions (Tomasello & Call 1997), helping individuals to predict who will support or intervene against them when they are fighting with particular opponents, and to assess which potential allies are likely to be effective in coalitions against their opponents. Tomasello & Call (1997) speculated that knowledge of third-party relationships may enable primates to form more complex coalitions than other animals do (Harcourt 1992). Although evidence of the ability to make use of information about third-party relationships is currently limited to primates, it is possible that other animals with complex social interactions, such as cetaceans, may have similar abilities.

Our knowledge of other primates' understanding of third-party relationships is limited, partly because it is so difficult to determine what other animals know about the world and how information is represented in the mind.

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However, several experimental studies provide convincing evidence that monkeys make use of some kinds of information about third-party relationships. In the laboratory, juvenile longtail macaques, *Macaca fasicularis*, were trained to choose pictures of a single familiar mother–offspring pair over pictures of various other pairs of unrelated group members (Dasser 1988a). Later, these juveniles consistently chose pictures of other mother–offspring pairs over unrelated pairs, and matched pictures of offspring to pictures of their mothers. The juveniles also succeeded in choosing the correct match when they were trained on a similar procedure with sibling pairs (Dasser 1988b). Cheney & Seyfarth (1980) played tape recordings of juveniles' distress vocalizations to vervet, *Cercopithecus aethiops*, females. While mothers responded strongly to their own offspring's calls, other females also responded. Other females looked at the juveniles' mothers, often before the mothers themselves had reacted. Thus, longtail macaques and vervets seem to be able to make connections between mothers and their offspring and between siblings.

Playback experiments conducted in the field indicate that female baboons, *Papio cynocephalus*, have some knowledge of the relative ranks of other females (Cheney et al. 1995). In this experiment, females heard a sequence of tape-recorded vocalizations. Females responded more strongly when they heard a sequence of calls that simulated a higher-ranking female responding submissively to a lower-ranking female's grunt than when they heard a sequence of calls simulating a lower-ranking female responding submissively to a higher-ranking female's grunt. Control experiments excluded the possibility that females were simply reacting to the fact that they had not heard a particular sequence of calls before. Experiments conducted on captive hamadryas baboons, *Papio hamadryas*, suggest that monkeys also have some knowledge of other group members' social relationships. Male hamadryas baboons do not attempt to compete for strange females that show preferences for rival males (Bachmann & Kummer 1980).

These experimental results are supported by observational evidence that suggests that monkeys and apes have some knowledge of third-party relationships (reviewed by Cheney & Seyfarth 1990; Tomasello & Call 1997). This body of data is less compelling than the experimental data, partly because the observational data were collected (and sometimes analysed) with other questions in mind. Consequently, the observations suffer from certain liabilities. One problem is that it is often difficult to rule out alternative, 'less cognitively generous' (Tomasello & Call 1997, page 200) explanations for a given observation. For example, when female hamadryas baboons threaten higher-ranking females, they sometimes simultaneously present to males that outrank their opponents (Kummer 1967). This form of behaviour, called a 'protected threat', is sometimes interpreted to mean that females understand the rank relationships between their opponents and their protectors (Tomasello & Call 1997). However, if all hamadryas males outrank all adult females, then females might follow a simple rule: 'present to males when challenging higher-ranking females' which requires no understanding of others' rank relationships.

The second problem with the observational data is that interpretations are sometimes based upon very small samples of events and are not tested rigorously. For example, Smuts' (1985) observation that male baboons sometimes redirect aggression against the friends of their former opponents is sometimes cited as evidence that baboons know something about the social relationships between other group members. However, Smuts witnessed only five cases in which males redirected aggression towards friends of their former opponents (from Table 6.2 in Smuts 1985). To be certain that males understood the nature of the other animals' friendships, it is necessary to demonstrate that males redirected aggression against their opponent's friends more often that would be expected by chance.

Baboon females' interest in apparent rank reversals provides the most unambiguous evidence that monkeys understand third-party rank relationships, but other observations are suggestive. Cheney & Seyfarth (1990) suggest that the formation of linear dominance hierarchies in which all triadic relationships are transitive may be based upon an understanding of third-party rank relationships. They also note that, in some groups, the extent of competition over grooming partners is correlated with each partner's rank. This may mean that females recognize other females' dominance relationships. However, both transitivity and competition over high-ranking partners may have simpler explanations, as Cheney & Seyfarth point out.

Data derived from a study of coalition formation among bonnet macaques, *Macaca radiata*, provide an opportunity to assess monkeys' knowledge of third-party rank relationships systematically. Male bonnet macaques frequently intervene in ongoing conflicts among other males (Simonds 1974; Rahaman & Parthasarathy 1978; Silk 1992a). Over a 13-month period, the mature males in a large and stable captive group intervened in nearly one-quarter of the ongoing contests among their peers (Silk 1992a). Males were most likely to intervene in ongoing contests when they outranked both of the original contestants (Silk 1993). High-ranking allies were also more effective than low-ranking allies, as males were less likely to be defeated in coalitions when their allies outranked their opponents (Silk 1992a).

Males that were involved in aggressive conflicts sometimes recruited support from other males by turning their heads rapidly from the potential ally to the opponent and back again. Similar kinds of recruitment behaviours occur in baboons, chimpanzees, and other macaques ('side-directed behaviour': Packer 1977; de Waal & van Hooff 1981; Smuts & Watanabe 1990; Noë 1992). Males typically direct solicitation gestures to only one or two other males in a given dispute, so their recruitment efforts may provide insight about their knowledge of the nature of dominance relationships between other males. Because males are most likely to intervene when they outrank the original participants and intervention is most effective when the ally outranks the opponent, males are expected to solicit selectively males that outrank themselves and their opponents. Males' conformity to this prediction would provide strong evidence that males make use of knowledge of third-party rank relationships.

The analyses described below are based upon observational data that were originally collected with other purposes in mind. Thus, the problems that confound analyses and interpretations of other observational data might also apply to this analysis. However, I have made an effort to avoid the kinds of problems that confound interpretations of other observational data. Fortunately, males recruited potential allies often, so the analysis is based upon a fairly large number of recuitment events (*N*=309). Whenever possible, 'cognitively generous' explanations are explicitly compared against more parsimonious explanations. In addition, I have constructed a series of Monte Carlo simulations to evaluate the likelihood that observed patterns might have occurred by chance. Thus, the results provide a rigorous, albeit nonexperimental, test of the hypothesis that males make use of information about third-party relationships when they choose their allies.

METHODS

I conducted a 13-month study of coalition formation among male bonnet macaques at the California Primate Research Center at the University of California, Davis. The group was housed in an outdoor enclosure which measured approximately 33 × 66 m. The study group was established in 1970–1971, and was maintained for behavioural research over the next two decades. Management policies were designed to replicate demographic features of free-ranging groups. No unfamiliar females were introduced into the group after it was initially established. Maturing males were periodically removed from the group to simulate emigration, and mature males were introduced occasionally to simulate immigration. Due to natural recruitment, the group grew in size and eventually exceeded the capacity of the enclosure. Five years before the present study began, the group was divided. In an attempt to mimic fission in free-ranging macaque groups (Chepko-Sade & Sade 1979), a number of the lowest-ranking females and all of their immature offspring were moved to another enclosure. At the time the study began, the group was composed of 70 animals, including 16 mature males (6–19 years of age) that were the subjects of this study.

Data Collection

The events described here are drawn from ad libitum observations of coalitions. A coalition occurs when one monkey intervenes in an ongoing dispute between two or more other monkeys. Although ad libitum data are subject to certain biases, this data set is likely to represent an unbiased sample of coalitions for several reasons. First, coalitions are conspicuous behavioural events, so it is unlikely that a substantial number of coalitions were missed. Differential visibility of individuals is unlikely to bias the data because males were recognized easily from a distance and coalitions usually occurred in open areas of the cage. Furthermore, focal samples were conducted on all of the mature males, so all males were seen regularly.

In each coalition, the identities and activities of all participants were recorded. The analyses presented below are based upon the identities of three individuals: the 'solicitor' (SOL) attempts to recuit support from a 'potential ally' (PAL) against an 'opponent' (OPP).

The results presented below are based upon recruitment for support in contests that originally involved one male initiator and one male target of aggression. This is the same set of events on which previous analyses of coalition behaviour in this group were based (Silk 1992a, b, 1993, 1994).

Dominance rank

Males' dominance ranks were based upon the outcome of dyadic agonistic encounters, and were determined independently of the polyadic encounters described in this report. All dyadic contests observed during focal samples and ad libitum in a given calendar month that had clearly decided outcomes were entered into a square matrix. I manipulated the ordering of males to minimize the number of entries below the diagonal. Separate matrices were prepared for each month of the study, and males' ranks in each month were computed according to this procedure.

Statistical Analysis

Males' ranks changed over the course of the study (Silk 1993). Therefore, in most analyses reported below, dominance ranks of participants in coalitions were based upon their position in the dominance hierarchy during the month in which the coalition occurred. However, to assess the correlation between male rank and participation in coalitions, I computed each male's rank by taking the average of his rank in all the interactions in which he was involved as a solicitor, opponent, or potential ally.

I used matrix correlation methods to assess the relationship between recruitment and aid received. I used a row-wise correlation test (*Kr* test; de Vries 1993) to determine whether males selectively solicited males that supported them most often, and a partial row-wise correlation test (de Vries 1993) to determine whether male rank influenced the relationship between solicitations and support. The MatMan software package (de Vries et al. 1993) was used for these computations. The results are based upon 2000 simulations.

I conducted Monte Carlo simulations to determine whether males selected allies at random. In these simulations, an ally is chosen at random for each of the observed solicitor–opponent pairs in the sample. Each randomly chosen ally is evaluated to determine whether he fits the predicted pattern. For example, one simulation tests the prediction that males choose allies that outrank themselves and their opponents. In all simulations, dominance ranks of participants in coalitions were based upon their position in the dominance hierarchy during the month in which the coalition occurred. This process is

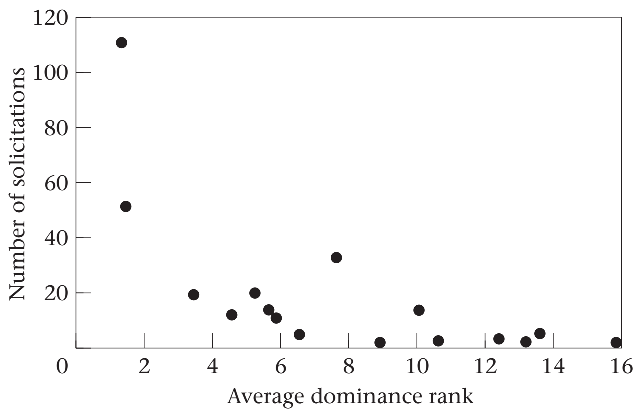

Figure 1. High-ranking males received more solicitations than lower-ranking males.

repeated for each of the solicitor–opponent pairs in the sample. The proportion of randomly chosen allies that satisfy the predicted pattern is tabulated and recorded. This process was repeated 10 000 times to generate a distribution of values. Then the observed value is compared against the results of the simulation to examine the likelihood that the observed value occurred by chance. Each test is based upon 10 000 simulations. Programs for the simulations were written in Visual Basic.

RESULTS

Patterns of Recruitment Behaviour

Male bonnet macaques intervened in approximately 22% of all dyadic aggressive interactions among males (N=2619; Silk 1992a). Protagonists in these dyadic contests attempted to recruit support from other males 309 times. Males succeeded in obtaining support from the males that they attempted to recruit 24% (74/309) of the time. In most cases (84%, N=309), the solicitor was the male that initiated the aggressive interaction. All mature males were represented in the sample as solicitors, opponents and potential allies.

Solicitations were directed towards high-ranking males significantly more often than to low-ranking males (Spearman rank correlation: $r_s = -0.788$, N=16, P<0.001; Fig. 1). The significance of this correlation did not rest upon the one high-ranking male that was solicited twice as often as any other male because the correlation remained high when this male was removed from the sample ($r_s = -0.742$, N=15, P=0.002).

Males were most likely to solicit the males that supported them most often (Kr=467, P<0.001). Fourteen of the 16 correlations for individual males were positive (Table 1), indicating that nearly all males preferentially solicited the males from whom they received the most support. This pattern might be an artefact of male dominance rank because high-ranking males intervened in ongoing disputes more often than lower-ranking males and were solicited more often than other males were. However, when male rank was controlled, the relationship between solictation and support remained significant (partial Kendall row-wise correlation=0.3561; P<0.001).

Table 1. Matrix correlation test results

Male	Kendall's tau	Weight	Contribution
24	0.35	48.91	17
61	0.50	46.18	23
79	0.34	50.65	17
BG	−0.03	68.925	−2
CA	0.49	92.27	45
DW	0.55	79.60	44
ED	0.40	72.00	29
GR	0.72	86.72	36
JI	0.58	87.43	63
JK	0.44	82.84	48
MA	0.40	86.87	38
OR	−0.19	68.21	27
RN	0.49	85.08	−16
RO	0.44	72.02	35
RU	0.44	92.27	41
ST	0.40	54.99	22

Knowledge of Third-party Rank Relationships

The correlation between male rank and the frequency with which males were solicited suggests that males knew something about the rank relationships among other males. While males were expected to solicit support from males that outranked themselves, they were also expected to solicit support from males that outranked their opponents. To conform to this prediction consistently, males would have to evaluate the relative ranks of other pairs of males.

Males solicited support from males that outranked them and their opponents 84% of the time ($Rank_{PAL}$>$Rank_{SOL}$ and $Rank_{OPP}$). All males attempted to recruit males that outranked them and their opponents more often than they attempted to recruit other males ($\bar{X}\pm$SE=0.85 ± 0.038, range 0.64–1.00).

I conducted a Monte Carlo simulation to determine the likelihood that observed recruitment patterns occurred by chance. This simulation tested the prediction that males selectively solicited allies that outranked them and their opponents ($Rank_{PAL}$>$Rank_{SOL}$ and $Rank_{OPP}$). The results indicate that the observed value (84%) was significantly higher than expected if males chose allies at random with respect to their rank (P<0.0001; Fig. 2a).

These results do not necessarily mean that males made use of information about third-party relationships to choose allies. If solicitors consistently outranked their opponents, the same pattern would be observed if males simply chose allies that outranked them ($Rank_{PAL}$>$Rank_{SOL}$). If so, conformity to the predicted pattern ($Rank_{PAL}$>$Rank_{SOL}$, $Rank_{OPP}$) would decline when opponents outranked solicitors. One hundred and twenty-six coalitions met the condition $Rank_{OPP}$>$Rank_{SOL}$. Most of the males in the group were involved in these coalitions as solicitors (N=15), opponents (N=14), or potential allies (N=14). When opponents outranked solicitors, solicitors

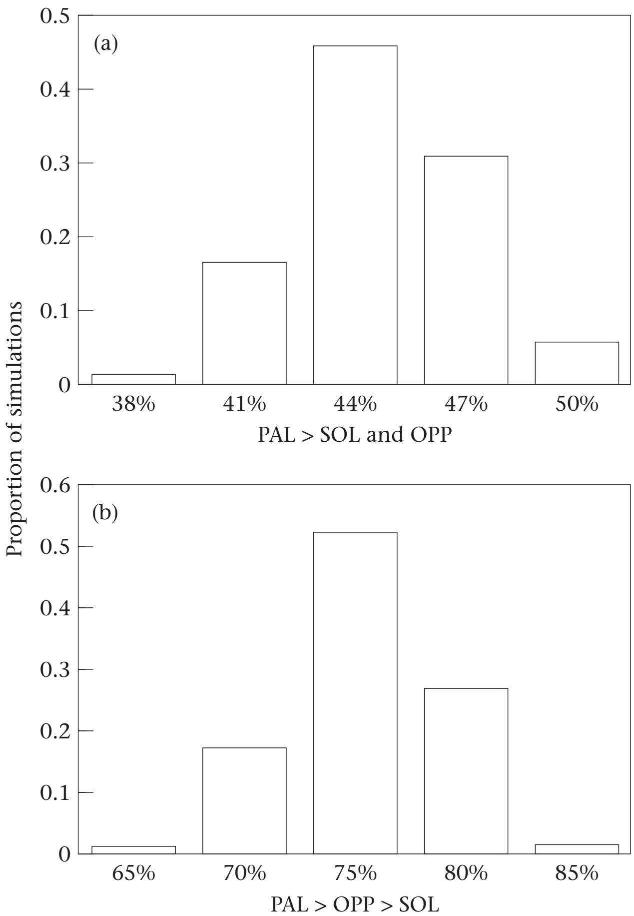

Figure 2. Results of Monte Carlo simulations. (a) In these simulations, an ally was chosen at random for each of the 309 observed solicitor–opponent pairs, and then tested to determine whether he outranked both the solicitor and the opponent. The number of allies that met this condition was tabulated. The values plotted here represent the results of 10 000 simulations. The observed value, 84%, was significantly higher than expected if males chose their allies at random with respect to their rank. (b) This simulation was based upon coalitions in which $Rank_{OPP}>Rank_{SOL}$. Solicitors were constrained to select allies that outranked them, and then allies were tested to determine whether they also outranked the solicitors' opponents. The distribution of values generated by these simulations is plotted here. The observed value, 84%, was significantly higher than expected if males simply chose allies that outranked themselves.

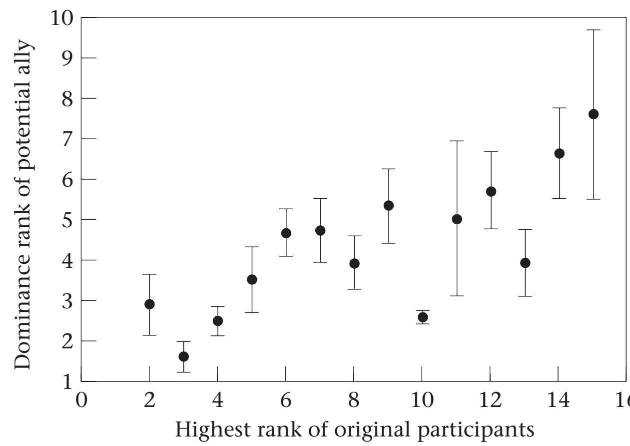

Figure 3. Males chose lower-ranking allies more often when they were involved in conflicts with low-ranking males than when they were involved in conflicts with higher-ranking males. The rank of the higher-ranking of the original participants (SOL, OPP) was positively correlated with the average rank of the potential ally. Means and standard errors are plotted.

still recruited support from males that outranked them and their opponents 84% of the time.

I modified the Monte Carlo simulation to test whether males were choosing allies that outranked them or allies that outranked them and their opponents. Here, an ally was chosen at random for each of the solicitor–opponent pairs in which $Rank_{OPP}>Rank_{SOL}$. I assumed that males always chose allies that outranked them, so potential allies were evaluated to determine whether they met the condition $Rank_{PAL}>Rank_{SOL}$. If not, a new ally was randomly chosen. This process was repeated until an ally was selected that satisfied the criterion. The results of this simulation indicate that the observed value was significantly higher than expected if males simply chose allies that outranked themselves ($P<0.005$; Fig. 2b).

The observed pattern may also have arisen because males focused recruitment efforts on the highest-ranking male. If top-ranking males were distinguished by their posture, condition or behaviour, then they could be identified without making use of information about third-party relationships.

I tested the hypothesis that males chose top-ranking allies by examining the correlation between the rank of the initial participants and the rank of the potential ally. If males consistently chose the top-ranking allies, there would be no correlation between the rank of the higher-ranking of the two participants (SOL, OPP) and the rank of the potential ally. On the other hand, if males consistently chose allies that outranked them and their opponents, then the rank of the potential ally should be positively correlated with the rank of the original participants. The observed correlation was significantly positive ($r_s=0.776$, $N=14$, $P=0.001$; Fig. 3), indicating that males chose higher-ranking allies against high-ranking opponents more often than against low-ranking opponents.

DISCUSSION

Taken together, these data suggest that males make use of information about other males' dominance relationships. Males chose allies that outranked themselves and their opponents much more often than expected if they chose allies at random with respect to their relative rank. Males did not simply choose allies that outranked themselves; when faced with higher-ranking opponents, males chose allies that outranked both them and their opponents. Moreover, males did not simply recognize the highest-ranking males in the group and recruit their support. Males chose higher-ranking allies more often when they were involved in confrontations with high-ranking males than in confrontations with low-ranking males. This task was complicated by the fact that the relative ranks of pairs of males often changed from month to month (Silk 1993).

These data do not tell us how males mentally represented information about other males' ranks or what males 'understood' about other males' dominance ranks. Thus, the possibility that there is some less cognitively generous explanation for males' recruitment behaviour cannot be excluded. It is possible, for example, that males assess other males absolute dominance or power, but do not draw inferences about other males' positions in the dominance hierarchy. However, to recruit consistently allies that outrank themselves and their opponents, males would still need to assess the relative status of other males.

Bonnet males' strategic recruitment of allies provides further evidence of the complexity of primate coalitions. Monkeys and apes cultivate relationships with powerful supporters (Simpson 1973; Cheney 1977; Fairbanks 1980; Seyfarth 1983; Harcourt 1992), compete for powerful allies (Seyfarth 1977; Silk 1982; Cheney & Seyfarth 1990; Harcourt 1992), prevent rivals from forming potentially disruptive alliances (Kummer 1971; de Waal 1982; Nishida & Hiraiwa-Hasegawa 1987; Chapais et al. 1995), and minimize risk to themselves when they intervene in coalitions among nonkin (Chapais 1983; Silk 1993). Here, males put their knowledge of their own relationships to other males and their knowledge of relationships among other males to good use. By selectively soliciting males that most frequently supported them and males that outranked them and their opponents, males focused their recruitment efforts on the males that were most likely to intervene on their behalf and those whose support was most likely to be effective in defeating their opponents.

Males did not direct all solicitations to the highest-ranking male in the group, even though the two males that held the top-ranking position over the course of the year were most likely to intervene and were most effective in defeating their opponents. Why did male bonnet macaques ever solicit support from other males? There are a number of possible reasons for this. In some cases, males may have solicited males that helped them often in the past rather than the male that held the highest-ranking position. On some occasions, the top-ranked male may have been involved in other activities, such as consortships, that limited his availability to participate in coalitions. It is also possible that the top-ranked male may have already intervened on behalf of the solicitor's opponent and was unlikely to switch sides. In some cases, males may not have expected the alpha male to support them against certain opponents. Some males consistently supported particular males and rarely intervened against them (Silk 1992b). Males' may have avoided soliciting top-ranking males that were more 'loyal' to their opponents than to themselves. This would require that males had some knowledge of the patterning of support among other males, another kind of third-party knowledge.

These data are important because they extend our knowledge of primates' use of information about third-party relationships. They are also useful because they demonstrate that we can obtain rigorous evidence about third-party relationships from nonexperimental studies. Recruitment behaviour provides a fruitful source of information about monkeys' knowledge of their own relationships and their relationships with others. Packer (1977) demonstrated that male baboons preferentially seek support from the males that most often seek their own support in attempts to disrupt consorts. When juvenile pigtail, *M. nemestrina*, and rhesus, *M. mulatta*, macaques scream to recruit support, their calls provide information about their own relationship to their opponent (Gouzoules et al. 1984; Gouzoules & Gouzoules 1989). The data presented here indicate that recruitment behaviour also provides a useful means to assess knowledge of third-party relationships.

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