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Can simple rules account for the pattern of triadic interactions in juvenile and adult female sooty mangabeys?

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Several experimental and observational studies have investigated the pattern of triadic relationships in primates to demonstrate knowledge of third-party relationships (i.e. an individual recognizes the relationship that exists between two others). To date, all studies have investigated the recognition of third-party relationships in adult animals. Thus, we do not know whether juveniles have knowledge of third-party rank relationships or whether they use a set of simple rules until they learn the rank relationships of all animals within a group. Here, we present the first data on triadic interactions involving juveniles in a rainforest primate, the sooty mangabey, *Cercocebus torquatus atys*. In a group of 120 individuals, we found that (1) if two groomers were approached by an individual ranking higher than both, the higher-ranking member of the grooming dyad was significantly more likely to stay than the lower-ranking one; (2) when an animal intervened in a conflict, juveniles and adult females were significantly more likely to support the higher-ranking contestant; and (3) juveniles and females solicited help in conflicts significantly more often from potential allies that outranked them and their target than from allies that ranked below them and/or the opponent. Our results suggest that the triadic interactions of juvenile sooty mangabeys resemble triadic interactions reported for adult members of other species of Old World monkeys, but that most of the observed behaviour patterns could be explained by a set of simple rules instead of invoking higher cognitive abilities.

One of several hypotheses for the evolution of the primate brain suggests that the large neocortex of primates evolved as an adaptation to cope with social complexity such as kinship networks, friendships, dominance hierarchies and alliance formation (the 'social brain hypothesis'; Humphrey 1976). Some people have argued that primates differ from most other mammalian species particularly in their ability to recognize third-party social relationships: what an individual knows about the relationship between two others (Tomasello & Call 1997). However, recent studies have also demonstrated knowledge of third-party relationships in spotted hyaenas, *Crocuta crocuta* (A. Engh, personal communication) and possibly in birds and fish (Earley & Dugatkin 2002; Peake et al. 2002; Tobias & Seddon 2002).

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Several lines of evidence suggest that monkeys recognize kin and rank relationships that exist between others (kin: vervet monkeys, *Chlorocebus aethiops*: Cheney & Seyfarth 1980; baboons, *Papio cynocephalus ursinus*: Rendall et al. 1996; Cheney & Seyfarth 1999; pigtailed macaques, *Macaca nemestrina*: Judge 1991; longtailed macaques, *M. fascicularis*: Dasser 1988a, b; rank: baboons: Cheney et al. 1995a, b; bonnet macaques, *M. radiata*: Sinha 1998; Silk 1999; kin and rank simultaneously: baboons: Bergman et al. 2003). Harcourt (1988) argued that the recognition of third-party rank relations is especially important in regard to dominance and the formation of alliances. An alliance is defined as a relationship between two or more individuals that repeatedly form coalitions (i.e. show simultaneous aggression against a common target or opponent). Knowing third-party kin and rank relationships as well as alliances allows individuals to predict who will support them or intervene against them in an ongoing conflict with a particular opponent. It also allows individuals to choose coalition partners based on the relative ranks of their opponents and their allies, and thus increase the effectiveness of the coalition (Harcourt

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1988). As expected, individuals typically solicit support from other individuals that outrank them and their opponents (Cheney 1983; Sinha 1998; Silk 1999) and, moreover, refrain from soliciting relatives or 'friends' of the opponent (Dunbar 1983; Smuts 1985), suggesting that they have an understanding of third-party relationships.

Here, we present the first data on triadic interactions involving juvenile and adult female sooty mangabeys in the Taï National Park to examine whether juveniles have knowledge of third-party relationships. Sooty mangabeys are terrestrial forest monkeys that form relatively large, social groups (approximately 70–120 individuals) compared with baboons (approximately 40–80 animals), vervet monkeys (approximately 25 animals) and various macaques species (approximately 10–50 animals). We analysed three types of triadic relationships to test the hypothesis that such relationships in mangabeys are comparable to those among adult individuals in other Old World species. Furthermore, we investigated whether the observed patterns of triadic interactions could be sufficiently explained by the use of simple rules of thumb or whether knowledge of third-party relationships was necessary.

Competition for Social Partners

Competition for social partners occurs when one individual (A) approaches two others (B and C) that are grooming. In a subset of these encounters, individual A is of higher rank than B and C. Previous studies have found that the higher-ranking member (B) is more likely to stay than the lower-ranking member (C) (bonnet macaques: Sinha 1998; vervets: Cheney & Seyfarth 1990). It has been argued that, by remaining in place despite A's approach, animal B demonstrates knowledge of third-party relationships (Cheney & Seyfarth 1990). However, other explanations are possible. (1) The approaching animal may prefer to groom its closest associate or the individual nearest in rank and gives a clue indicating its preference, and thereby induces the other to leave. (2) C leaves because it is subtly threatened by B. (3) C becomes nervous in the presence of two higher-ranking individuals (Sinha 1998).

Coalition and Recruitment Behaviour during Agonistic Contests

Patterns of intervention

Several studies of coalitions in nonhuman primates have found that individuals are more likely to intervene in an ongoing conflict between others if they outrank both of the original contestants (e.g. bonnet macaques: Silk 1993; vervets: Cheney 1983). This pattern indicates that the supporter knows his/her own status relative to other group members; however, it does not necessarily show that the intervening animal understands third-party rank relationships, since the intervening animal could use the simple rule to intervene in the conflict only if he/she outranks both contestants. However, evidence that the intervening animal is always more likely to support the higher-ranking animal of the two contestants suggests that the intervener may have some knowledge of the rank relationship between the original contestants. A more parsimonious explanation would be that the intervener always supports the winner, which happens to be the dominant animal in most cases. Finally, it could also be explained by the concept of 'dependent rank' (Kawai 1958). For example, if an animal A always supports animal B against any other opponent in the group, then B may become close in rank to A and thus dominant to all opponents that rank below A.

Recruitment behaviour

Monkeys often solicit support from nearby animals by turning their heads rapidly from the potential ally to the opponent and back again ('show looking': de Waal et al. 1976; 'head flagging': Packer 1977). Since individuals are more likely to support another individual in a conflict when they outrank both the aggressor and the target, one would predict that individuals selectively recruit allies that outrank them and their target. Silk (1999) showed that male bonnet macaques conform to this prediction, thus providing evidence for third-party knowledge. However, at least some of the observed patterns can be explained by assuming that individuals only know the rank relationships of others relative to themselves and combine that knowledge with a set of simple rules (see below).

The observational studies reviewed above do not, in themselves, provide unambiguous proof that individual primates can recognize the rank relations of others. However, results of these studies are in agreement with playback experiments on baboons that provide stronger evidence for such recognition (Cheney et al. 1995a; Bergman et al. 2003; see Discussion).

METHODS

Study Site and Subjects

We studied a group of 120 free-ranging sooty mangabeys in the Taï National Park, Ivory Coast (6°20′N–5°10′N, 4°20′W–6°50°W). Visibility throughout the home range of our study group was 5–20 m.

During the study period, the group consisted of 6–10 adult males, 24–34 adult females, 29–34 juvenile males, 17–26 juvenile females and 4–22 infants. Individuals were defined as adult upon reaching their full size and sexual maturity. Juveniles were sexually immature males (1–6 years) and females (1–4.5 years) that foraged independently but also occasionally nursed from their mothers until 2 years old. Infants depended almost exclusively on nursing and usually stayed in close proximity to their mothers. All animals were well habituated to human observers and individually recognized. The group has been under study since 1997 and the mothers of most juveniles younger than 4 years were known.

Data Collection

The analyses presented in this paper are based on social supplants, agonistic supports and recruitment behaviour

recorded during focal animal and ad libitum sampling (Altmann 1974). Social supplants were recorded when one individual approached another individual involved in a grooming interaction and replaced that individual without overt aggression. Agonistic support occurred when one individual intervened in an ongoing conflict between two other monkeys. Agonistic support was often solicited by one of the individuals involved in the conflict through 'head flagging' (rapid, alternating gazing at another nearby individual and the target). During head flagging, the recruiting individual often growled but did not scream (for details on the vocalizations see Range & Fischer 2004).

We conducted 15-min focal samples with at least 60 min between consecutive samples of the same individual. We recorded the identity of the four nearest neighbours of each sex–age class (adult male, adult female, juvenile male, juvenile female) within 5 m of the focal animal each minute by means of instantaneous sampling (Altmann 1974). Social interactions were recorded continuously. Details of the ethogram are provided elsewhere (Range & Noë 2002). F.R. recorded focal animal samples for 24 adult females during April–July 2000, and for seven juvenile females and five juvenile males during August–December 2001 and during May–August 2002, with the exception of one juvenile female, who vanished in the beginning of 2002. We collected between 810 and 897 min of samples per adult female and between 1598 and 1673 min per juvenile (808 min for the juvenile female that vanished).

Between focal samples, we recorded all observed interactions between identified individuals (ad libitum sampling; Altmann 1974). In the case of conflicts, the nearest neighbours were recorded as mentioned above.

Dominance Relationships

Sooty mangabeys form linear dominance hierarchies with adult males outranking all other individuals in the group (Gust & Gordon 1994; Gust 1995; Range & Noë 2002; Range et al., in press). The relative dominance ranks of adult females in the dominance hierarchy remained stable during 1998–2002, as did the relative ranks of 14 of 16 juvenile females during 2001–2002 (F. Range, unpublished data). Two juvenile females switched ranks with an adult female, and in one case the adult female was the juvenile's mother.

Dominance rank was defined according to the direction of submissive behaviour (avoid, yield and supplant; for definitions see Range & Noë 2002). To determine the dominance relationships between all individuals in the group and establish a dominance hierarchy, we pooled focal animal and ad libitum data of three observers (F. Range, R. Peho and C. Fruteau). Because the relative dominance ranks of adult females remained stable over several years, we determined the rank of juveniles according to the rank order of the adult females for 2001 and 2002. Individuals were ordered to reduce the number of circular triads (de Vries 1995). If a relationship between individuals was unclear, we assigned the average rank to both. When juveniles are approximately 1.5–2 years of age (before they have attained adult size), they assume ranks that are similar to those of their mothers (F. Range, unpublished data). Thus, in females, there is no obvious relationship between rank and size and/or age (Gust 1995; F. Range, personal observation). Males start to move up the dominance hierarchy at an approximate age of 2–4 years (Gust 1995; F. Range, unpublished data). Thus, males older than 4 or 5 years are likely but not necessarily of high rank. Before they reach that age there is no relationship between size/age and rank.

Analysis of Coalition and Recruitment Behaviour

We based our analyses of agonistic interventions (i.e. unsolicited support) on the identities of the three participants: the 'supporter', the 'beneficiary' and the 'target'. When analysing recruitment behaviour, we identified the 'solicitor', the 'recruit' and the 'target'.

Because adult males outrank all adult females and juveniles, and juveniles were not observed to intervene in conflicts between adult males, we excluded all agonistic supports and recruitments involving adult males from the analysis. Moreover, we excluded all solicited agonistic supports from the analysis of intervention. The distribution of unsolicited agonistic interventions and solicitations per individual used for the analysis are presented in Table 1. All but three interventions and eight solicitations involved unique combinations of individuals and repeated combinations of individuals were separated by at least 1 day. We therefore considered all events as independent data points in our analyses.

To examine whether the age of individuals affected their choices, we analysed social supplants, agonistic interventions and recruitment behaviour separately for juvenile and adult actors. Because the number of observations (social supplant, agonistic support and solicitation) varied between individuals, we calculated the percentage of observed interactions per individual to control for these differences.

Statistics

Statistical analyses were performed with SPSS (1999) version 10.0.5 and by hand according to Siegel & Castellan (1988). All tests were one tailed since our predictions were directional. Alpha was set at 0.05; trends are reported for alpha less than 0.1. When we analysed subsets of data, probabilities were corrected by a sequential Bonferroni

Table 1. Distribution of agonistic interventions and solicitations across individuals

	Agonistic interventions		Solicitations	
Sex/age class	*N* (range)	*n*	*N* (range)	*n*
Juveniles				
Males	13 (1–10)	30	18 (1–6)	35
Females	14 (1–10)	58	18 (1–24)	125
Adult females	23 (1–6)	59	10 (1–6)	25

N is the number of individuals and *n* is the total number of cases.

procedure (Hochberg 1988). Statistical tests were calculated per individual. N is the number of individuals in the analysis and n is the number of cases.

RESULTS

Competition for Social Partners

We observed 66 social interactions in which a higher-ranking individual approached two lower-ranking animals that were grooming. In 51 cases, the lower-ranking animal of the grooming dyad moved at least 2 m away without any obvious threat (stare or lunge) from the approaching animal or from the higher-ranking grooming partner. In the remaining 15 cases, the higher-ranking individual of the grooming dyad left without any obvious threat from the other two animals. The higher-ranking animal of the grooming dyad was a juvenile in nine cases ($N = 8$ juveniles) and an adult female in 57 cases ($N = 26$ adult females). The proportion of juveniles that stayed when they were the higher-ranking grooming partners (8/9 cases) tended to be greater than the proportion of juveniles that stayed when they were the lower-ranking partners (1/9 cases) (Wilcoxon matched-pairs signed-ranks test: $T^+ = 31.5$, $N = 8$, Bonferroni corrected $P < 0.1$; Fig. 1). Similarly, the proportion of adult females that stayed when they were the higher-ranking grooming partners (43/57 cases) was significantly greater than the proportion of adult females that stayed when they were the lower-ranking partners (14/57 cases) ($Z = -2.468$, $N = 26$, Bonferroni corrected $P < 0.05$; Fig. 1). For adult females, preference for close associates and/or relatives could explain only nine of 43 cases in which the higher-ranking grooming partner stayed and only four of 14 cases in which the lower-ranking grooming partner stayed (for analyses of association pattern see Range & Noë 2002; F. Range, unpublished data). Excluding these 13 cases did not change our results ($Z = -2.408$, $N = 24$, Bonferroni corrected $P < 0.05$). For juveniles, relatedness could explain only one of eight cases in which the higher-ranking grooming partner stayed and close association could not explain any. Reanalysing of the data after excluding this data point (one individual) still yielded the same trend ($T^+ = 24.0$, $N = 7$, Bonferroni corrected $P < 0.1$).

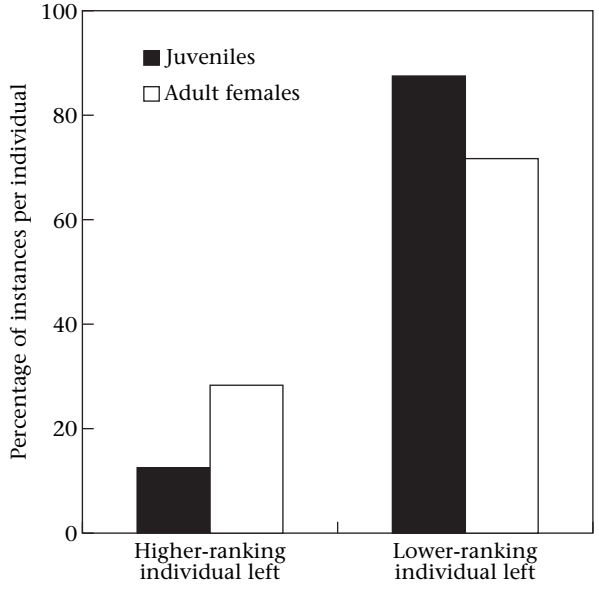

Figure 1. Competitive interactions for access to grooming partners by eight juvenile and 26 adult females. Histograms show the percentage of observed instances in which an individual approached two lower-ranking individuals that were grooming each other and either the higher- or lower-ranking of the two seated animals left.

Coalition and Recruitment Behaviour

During focal observations, 73 aggressive interventions and 81 solicitations were observed. The recruit supported the solicitor after only 23% (19/81) of the solicitations. During ad libitum observations, 135 agonistic interventions and 104 solicitations were recorded. Recruited animals supported the solicitor 42 times (40%) (data are summarized in Table 2). In three cases, the recruited animal supported the target instead of the solicitor. For all further analysis, focal and ad libitum data were pooled.

Pattern of intervention

Overall, the number of observations in which a juvenile or an adult female intervened on behalf of one of two contestants in an ongoing conflict varied significantly with the rank relationships between the animals involved (Table 3). Juveniles outranked both their beneficiary and the target in 52.4% of interventions. Less frequent were interventions in which the supporter was lower ranking than the beneficiary but higher ranking than the target (25.7%). Interventions in which the supporter was lower ranking than the target occurred the least frequently (21.8%) (Table 3). Adult females also tended to support others more often when they outranked both contestants (52.8%) than when they only outranked the target (22.2%) or when they were lower ranking than the target (24.9%) (Table 3).

The proportion of interventions in which a higher-ranking supporter supported the higher ranking of two contestants was significantly greater than the proportion of interventions in which a higher-ranking supporter supported the lower-ranking contestant (juveniles: $Z = -3.44$, $N = 19$, Bonferroni corrected $P < 0.01$; adult females: $Z = -2.92$, $N = 16$, Bonferroni corrected $P < 0.01$). However, in most cases in which intervening animals outranked both contestants, the higher-ranking individuals were also the aggressors in the conflict (91.1% for juvenile supporters and 91.2% for adult female supporters).

Pattern of recruitment

Because mangabeys mostly intervened in conflicts when they outranked both contestants, we examined whether individuals preferentially solicited agonistic support from animals that outranked them as well as the target to increase the probability that a recruit would intervene on their behalf.

Juveniles and adult females solicited agonistic support significantly more often from animals that outranked

Table 2. Summary of data collected during observation of agonistic interventions and solicitations involving juvenile and adult female sooty mangabeys

	Agonistic interventions		Solicitations		
Type of data collection	Total number of interventions	Unsolicited support given	Total number of solicitations	Solicited support given	Aggressor was solicitor
Focal observation	73	54	81	19	77
Ad libitum observation	135	93	104	42	98

them and their targets (69.7% and 72.1%, respectively; Table 4, Fig. 2). The target ranked below the solicitor in 91.1% of these interventions. In 20.0% and 16.2% of the observed solicitations, respectively, juveniles and adult females solicited recruits that ranked below them, but that outranked their opponent. Only in 10.3% and 11.7% of interventions did juveniles and adult females solicit help from an individual that was lower ranking than the target. The same pattern of solicitations was observed for individual juveniles (Fig. 2).

When an animal has only one potential ally nearby, the observed pattern of solicitations could be due to the circumstances and not to decisions made by the solicitor. In contrast, when several animals are present, the solicitor may preferentially solicit help from a recruit of higher rank than the target. To examine this possibility, we extracted the cases from our database in which juvenile solicitors had a choice of at least two individuals that could be recruited against the target (our data set for adult females was too small for this analysis). When there was the opportunity to recruit an individual of either higher or lower rank than the target ($n = 48$ cases), juveniles ($N = 18$) solicited help from the individual that outranked the target 87% of the time and solicited help from the individual of lower rank 13% of the time ($Z = -3.07$, $N = 18$, Bonferroni corrected $P < 0.01$). When we included only those data for individuals that solicited help at least four times, we still found a significant difference ($T^+ = 21.0$, $N = 6$, Bonferroni corrected $P < 0.05$). When both potential recruits outranked the target but one was of higher or lower rank than the solicitor ($n = 63$ cases), solicitors recruited the individual that outranked them significantly more often than they recruited the individual that outranked only their target ($Z = -3.141$, $N = 20$, Bonferroni corrected $P < 0.05$). Results were still significant when we excluded animals with less than four recruitments ($T^+ = 36.0$, $N = 8$, Bonferroni corrected $P < 0.05$). The results so far show that juveniles and adult females evaluate rank relationships when they recruit allies in conflicts. However, instead of recognizing third-party rank relationships, they could use the simple rule 'always fight an individual of lower rank and solicit help from an individual of higher rank'.

To examine whether juvenile sooty mangabeys have knowledge of third-party rank relationships, we analysed those cases in which the solicitor outranked both the recruit and the target ($n = 24$ cases) and when the solicitor ranked below both the recruit and the target ($n = 24$ cases). To make the 'right' decision in these cases and solicit a recruit outranking the target, an individual would have to evaluate the rank relationship between the recruit and target. In the first scenario, the recruit outranked the target significantly more often than the reverse ($Z = -2.17$, $N = 15$, Bonferroni corrected $P < 0.05$), whereas, in the second scenario, no significant difference was found ($T^+ = 64.0$, $N = 14$, $P > 0.1$).

'Mistakes'

In 160 solicitations, juveniles made 15 'mistakes', defined as enlisting help from an individual of lower rank than the target. Juvenile solicitors usually made these mistakes ($n = 13$) when the target was a young male older than 4 years of age. Juveniles between 1 and 1.5 years old solicited help 47 times in this study and made nine mistakes (19.15%; one female alone made six mistakes: 12.8%). Juveniles between 2.5 and 3.5 years old solicited help 106 times and made six mistakes (5.7%). Adult females made two mistakes in 25 solicitations (8%).

DISCUSSION

The results presented here show that the pattern of triadic interactions in sooty mangabeys is similar to that reported

Table 3. Results of tests examining patterns of agonistic support

	Friedman test				Multiple pairwise comparisons		
	N	χ^2	df	*P*	1	2	3
Adult females	23	7.32	2	<0.05*	*P*<0.05	*P*<0.08	*P*>0.1
Juveniles	27	6.70	2	<0.05*	*P*<0.08	*P*<0.08	*P*>0.1

We compared interventions in which (1) the supporter outranked the beneficiary and the target versus the beneficiary outranked the supporter and the target; (2) the supporter outranked the beneficiary and the target versus the target outranked the supporter; (3) the beneficiary outranked the supporter and the target versus the target outranked the supporter.
*Bonferroni adjusted.

Table 4. Results of tests examining of patterns of recruitment

	Friedman test				Multiple pairwise comparisons		
	N	χ^2	df	*P*	1	2	3
Adult females	10	9.44	2	<0.01	$P<0.05$	$P<0.03$	$P>0.1$
Juveniles	36	31.21	2	<0.01*	$P<0.03$	$P<0.03$	$P>0.1$

We compared interventions in which (1) the recruit outranked the solicitor and the target versus the solicitor outranked the recruit and the target; (2) the recruit outranked the solicitor and the target versus the target outranked the recruit; (3) the solicitor outranked the recruit and the target versus the target outranked the recruit.
*Bonferroni adjusted.

for other Old World monkeys. The higher-ranking animal in a grooming dyad was more likely to stay than to leave when approached by an animal that outranked him/her as well as his/her grooming partner. Sooty mangabeys were also more likely to intervene in conflicts when they outranked both contestants and were more likely to solicit help from animals that outranked them and their opponent. Although our data suggest that adult female and juvenile sooty mangabeys have knowledge of their own dominance status relative to others, they might otherwise rely on a fairly rigid set of rules for intervention and recruitment that largely determines their actions in triadic interactions. Supporters could intervene using the two simple rules: (1) intervene only when you outrank the target and (2) always intervene on behalf of the aggressor. Similarly, when recruiting allies in conflict, mangabeys could use a simple rule 'always fight somebody lower ranking than you and solicit help from somebody higher ranking than you'. However, several interactions could not easily be explained by this set of rules and might require higher cognitive abilities.

Because the pattern of social supplants could not solely be explained by an approaching animal's preference for one of the grooming partners, a middle-ranking individual may recognize that he/she outranks his/her grooming partner, but that the approaching individual outranks them both (Cheney & Seyfarth 1990). This ability would require that the intermediate individual has knowledge of its own position in the rank hierarchy and that of the relative rank relationships between the other two individuals involved. However, as noted in the Introduction, it is also possible that an approaching animal provides some cue to a lower-ranking animal that causes him/her to leave but is undetectable to a human observer.

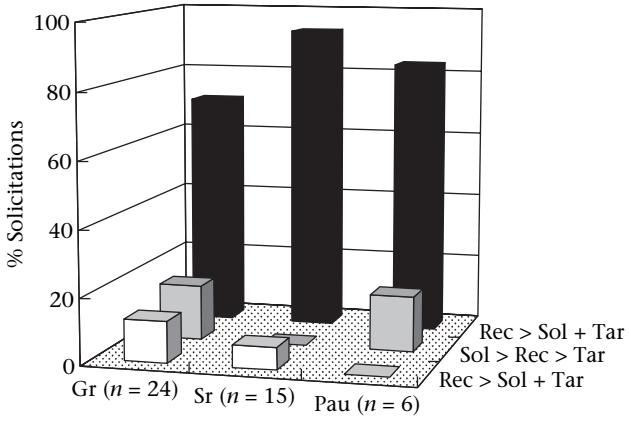

Figure 2. Solicitations by two juvenile females (Sr and Gr) and one juvenile male (Pau) to recruit help from a third party against a target of aggression. Sol = solicitor; Rec = recruit; Tar = target; *n* = the number of solicitations. The arrows denote rank relationships; A > B + C indicates that A outranked B and C.

We found that sooty mangabeys were more likely to intervene in disputes if they outranked both contestants. Although they could use the simple rule 'only get involved in an agonistic conflict when both contestants are lower ranking', the rule does not explain why they supported the higher-ranking individual significantly more often. However, another rule that they might use is 'always support the aggressor'. Because almost all threat behaviour in juvenile and adult female sooty mangabeys is directed down the dominance hierarchy (Range & Noë 2002; F. Range, unpublished data), the second rule would be very effective and would not require knowledge of third-party rank relationships. In 11.8% of the observed interventions by adult females, the adult female did not behave according to either rule but instead supported her offspring against a higher-ranking opponent. Juveniles did not conform to either rule in 5.7% of the interventions, but instead intervened against young males (4–5 years old).

Furthermore, we found that during agonistic interactions, adult females and juveniles solicited help significantly more often from potential allies that outranked them and their target. For juveniles, we found that these results were not due to chance. However, this method is very conservative for several reasons. First, due to practical limitations (having to write and observe at the same time), we could not record all individuals within 5 m, but only noted the four nearest individuals of each sex–age class. Second, we probably missed animals that were concealed from our view behind bushes, but could be seen by the animal recruiting agonistic support. Third, the solicitor could probably enlist individuals outside the 5-m radius. Thus, it is very likely that in almost all agonistic interactions ($n_{\text{Juvenile+Adult female}} = 185$), solicitors had the choice of enlisting agonistic support from several nearby individuals (not just the recorded neighbours), yet they still mainly solicited support from animals that outranked them and their targets.

The observed pattern of solicitations indicates that sooty mangabeys know their own status relative to other group members; however, it does not necessarily show that mangabeys understand third-party rank relationships.

Instead, they could use the simple rule 'always fight somebody of lower rank and solicit help from somebody of higher rank'. In 85.6% of all observed solicitations, the solicitor outranked the opponent, and in 70.6%, the recruited animal outranked the solicitor. Using this simple rule could explain 70.6% of the observed solicitations. When we tested whether mangabeys understand something about third-party rank relationships, results were only significant in the first scenario (the solicitor outranked both the recruit and the opponent), but not in the second (the solicitor ranked below the recruit and the opponent). Because the rank of the recruit is only relevant to the outcome of the interaction in the second case, this finding provides only very weak support for the idea that juvenile mangabeys recognize third-party relationships.

Moreover, the positive result in the first case may not be due to monkeys perceiving rank in a categorical way, but rather on a continuous basis. As a result, when two or more potential recruits are available, the solicitor may recruit the animal that it perceives to be the better fighter without having knowledge of the rank relationships between potential recruits. However, there is no evidence that rate of aggression or submissive behaviour is correlated with rank distance in mangabeys (F. Range, unpublished data), vervets (Seyfarth 1980; Cheney & Seyfarth 1990, page 82), or baboons (Seyfarth 1976). Moreover, animals may use the simple rule 'always solicit the highest-ranking animal present', which would also explain the behaviour. However, size and age in mangabeys is not correlated with rank except in older males (Gust 1995; F. Range, personal observation). Also, in instances where adult males were present during the conflicts, individuals did not necessarily solicit help from these adult males even though they were the most dominant animals present (F. Range, unpublished data).

Finally, we found that mangabeys made surprisingly few 'mistakes'. Most mistakes were made by relatively young individuals (<2.5 years) and/or when the potential recruit or the target was a young male. In sooty mangabeys, young males typically start the process of moving up in the dominance hierarchy when they are about 3 years old (Gust 1995; F. Range, unpublished data). Presumably, their ranks are very unstable during this time and might change swiftly, causing inaccuracies in our long-term dominance hierarchy that led us to mislabel these recruits as 'mistakes'.

The intervention and recruitment pattern in sooty mangabeys strongly resembles results found in a study conducted on 16 adult male bonnet macaques (Silk 1999). Our study demonstrates that even in a large group with up to 100 potential allies (excluding adult males), monkeys use the same information to recruit allies in conflicts. However, the data presented here suggest that juvenile sooty mangabeys could rely mainly on several 'rules of thumb'. This does not, however, imply conclusions about the source of the cognitive strategy used by mangabeys: innate, instrumental, learning or cognitive processing. The work of Gigerenzer et al. (1999), Todd & Gigerenzer (2000, 2003) and references therein on the use of 'simple heuristics', show that most decisions made by humans during cooperative interactions (such as trading) are governed by 'simple rules'. However, our data do not exclude the possibility that juvenile mangabeys have knowledge of third-party relationships either. The first suggestions of third-party recognition in primates historically came from observational studies. Only recently has third-party recognition in nonhuman primates been confirmed with the use of playback experiments (e.g. Cheney et al. 1995a; Cheney & Seyfarth 1999; Bergman et al. 2003). Unfortunately, to date, it has been impossible to conduct similar experiments on sooty mangabeys due to the political situation in the Ivory Coast. The results of our study suggest that juveniles could rely on a set of simple rules, but that in some situations they might use triadic knowledge. Playback experiments on juvenile mangabeys might either reveal (1) stronger evidence for triadic knowledge or (2) that juveniles really just rely on a set of simple rules and acquire knowledge about third-party relationships as they get older.

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