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Knowledge acquired and decisions made: triadic interactions during allogrooming in wild bonnet macaques, *Macaca radiata*

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The pressures of developing and maintaining intricate social relationships may have led to the evolution of enhanced cognitive abilities in many nonhuman primates. Knowledge of the dominance ranks and social relationships of other individuals, in particular, is important in evaluating one's position in the rank hierarchy and affiliative networks. Triadic interactions offer an excellent opportunity to examine whether decisions are taken by individuals on the basis of such knowledge. Allogrooming supplants among wild female bonnet macaques (*Macaca radiata*) usually involved the subordinate female of a grooming dyad retreating at the approach of a female dominant to both members of the dyad. In a few exceptional cases, however, the dominant member of the dyad retreated; simple non-cognitive hypotheses involving dyadic rank differences and agonistic relationships failed to explain this phenomenon. Instead, retreat by the dominant individual was positively correlated with the social attractiveness of her subordinate companion (as measured by the duration of grooming received by the latter from other females in the troop). This suggests that not only does an individual evaluate relationships among other females, but does so on the basis of the amount of grooming received by them. Similarly, the frequency of approaches received by any female was correlated with her social attractiveness when she was the dominant member of the dyad, but not when she was the subordinate. This indicated that approaching females might be aware of the relative dominance ranks of the two allogrooming individuals. In logistic regression analyses, the probability of any individual retreating was found to be influenced more by her knowledge of her rank difference with both the other interactants, rather than by their absolute ranks. Moreover, information about social attractiveness appeared to be used in terms of correlated dominance ranks. The nature of knowledge acquired by bonnet macaque females may thus be egotistical in that other individuals are evaluated relative to oneself, integrative in that information about all other interactants is used simultaneously, and hierarchical in the ability to preferentially use certain categories of knowledge for the storage of related information from other domains.

Keywords: social knowledge; bonnet macaque; allogrooming; social cognition; *Macaca radiata*

1. INTRODUCTION

Extensive social interactions between individuals of different ages, sexes, dominance ranks and kinship are typical of many nonhuman primate societies (for a review, see Smuts *et al.* (1987)). The development and maintenance of such complex social relationships have been expected to select for enhanced cognitive abilities in individuals living in such groups (Humphrey 1976; see also Chance & Mead 1953; Jolly 1966). These may include, amongst others, a knowledge of the dominance ranks of other individuals, an awareness of the social bonds between other members of the group, and possibly even more important, an ability to evaluate one's own position in the prevailing rank hierarchy and affiliative networks.

That social interactions between individual primates are indeed affected by mutual observations of previous, active engagements between the present interactants and other individuals of the group have, in fact, been borne out by a number of experimental and observational studies on baboons (Kummer 1968; Bachmann & Kummer 1980; Smuts 1985), macaques (Judge 1982; Datta 1983; Ogawa 1995), vervets (Cheney & Seyfarth 1980, 1986, 1989), and chimpanzees (de Waal & van Roosmalen 1979; de Waal 1982).

Individuals can obviously know about the relationships of their social companions by observing their interactions with other individuals. What is not entirely clear from the previous studies, however, is the nature of inferences that allows such knowledge to be acquired. Does an individual evaluate the social bonding between each of the interacting pairs of individuals relative to itself? Or, is it simply aware of the extent of the affiliative relationships enjoyed by another group member without specifically remembering each and every pair bond? At a more functional level, what is the relative importance of the frequency of affiliative interactions as opposed to the time spent in these interactions for such an assessment?

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Most of the above studies have provided good, but indirect or circumstantial, evidence for the influence of dominance ranks, kinship and other interpersonal bonds on complex behaviours such as aggression, reconciliation and alliance formation. What often needs to be directly analysed, however, is the precise extent and complexity of an individual's knowledge that provides flexibility in taking a specific social decision. For example, if a macaque female is aware of both, the dominance rank and the social relationships of her interacting partner, are these domains of her knowledge used in a hierarchical manner to take a particular decision? Moreover, it is also conceivable that the priorities afforded to these domains of her social knowledge may alter when decisions are made under different circumstances.

In an early experimental study that attempted to conceptualize social relationships, Bachmann & Kummer (1980) showed that a hamadryas baboon male (*Papio hamadryas*) was less likely to challenge a female possessed by another male, the stronger her affiliation with her companion. Hamadryas males were thus apparently able to assess the social choice of females, but the experiment could not exclude the possibility that the entire relationship was read from the behaviour of only one of the group members. In other words, it is still not clear whether an individual can conceptualize the multiple relationships of a potential adversary, information which cannot obviously be obtained on the basis of the behaviour of a single individual alone. Extending this problem further, if knowledge about the social relationships of a number of group members can be simultaneously acquired, is an individual able to integrate information about all interactants when involved in a complex social interaction with more than one partner?

Yet another important functional aspect of knowledge acquisition and use involves the specific aspect of an attribute that an individual evaluates as it takes a particular decision. When a macaque female acts on her knowledge of the dominance ranks of her social companions, for example, does she take into account their absolute ranks independent of her own, or does she evaluate their respective positions in the dominance hierarchy relative to her own particular rank? Cheney & Seyfarth (1986) provided evidence that vervet monkeys may redirect aggression on the basis of their knowledge of social alliances not involving themselves. It is still not known, though, whether non-egotistic knowledge of this kind can be extended to other domains, like dominance relationships, and whether decisions are made on the basis of this kind of knowledge in other social situations as well.

This paper investigates individual decision making during a specific triadic social interaction—competition for access to grooming partners—in adult female bonnet macaques (*Macaca radiata*). It analyses the evidence for an adult female's knowledge of the social status and dominance ranks of the other females in the group and attempts to examine the possible mechanisms that could underlie her perception of the affiliative bonds of her social companions. Finally, it provides evidence for a hierarchy of evaluations made by an individual before taking a particular decision during a complex social interaction.

2. METHODS

(a) *The bonnet macaque*

The bonnet macaque (*Macaca radiata radiata*, Geoffroy), an endemic cercopithecine occurring ubiquitously in peninsular India, commonly lives in multi-male, bisexual troops of about 15 to 60 individuals (Prater 1971). Females of this species, like those of many other cercopithecines, remain in their natal group throughout their lives, and during adulthood, form stable, linear dominance hierarchies that can be unambiguously assigned on the basis of the direction of approach–retreat and aggressive interactions. Allogrooming and other affiliative interactions occur at typically high frequencies among adult females, although unlike all other cercopithecines described so far, they appear to be primarily directed down the dominance hierarchy (Sinha 1998).

This study was conducted on a free-ranging troop of bonnet macaques inhabiting about 1 km^2 of dry deciduous scrubland forest in the University of Agricultural Sciences, GKVK Campus, Bangalore, southern India. At the time of observations, the troop consisted of 44–52 individuals with 8–11 adult males, 11 adult females and 22–30 juveniles of both sexes. Data were obtained during a period of two years, from March 1993 to February 1995, and are based on observations from approximately 269 h of focal animal sampling (Altmann 1974), with a mean (±s.d.) of 24.45 (±2.78) h per female, on the 11 adult females in the troop.

(b) *Allogrooming*

Allogrooming (subsequently used interchangeably with grooming) commonly refers to the manipulation of the fur and skin of another individual with the fingers, mouth, or teeth to remove bits of dirt, dead skin, ectoparasites or dried blood from wounds. The initiation of an allogrooming event by an individual and the duration of the subsequent grooming session have been considered as the basic data for the analysis of grooming relationships in the study troop (Sinha 1998). Allogrooming frequency has been expressed as the number of grooming events initiated by an individual towards another per hour. Grooming time has been computed as:

$$P_{ij} = \frac{t_{ij}}{T_{ij}}, \qquad (1)$$

where, P_{ij} is grooming time spent by individual i towards individual j, t_{ij} is total time spent by individual i in grooming individual j, and T_{ij} is total time that dyad i–j was observed.

This measure has also been interchangeably expressed as the duration of grooming given to another individual.

(c) *Allogrooming supplants*

Competition for access to an allogrooming partner in this group usually occurred whenever one female approached two females who were grooming, supplanted one of them, and then groomed or was groomed by the remaining individual. Only females dominant to either one or both the grooming individuals were ever observed to initiate such an interaction. Supplantation often involved aggression, but could also occur without any aggression

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when one of the two grooming females retreated before the approaching female could reach them, and sometimes even when she was more than 3 m away.

A total of 122 such non-aggressive allogrooming supplants were observed. Out of these, 47 interactions involved the approach of an individual intermediate in dominance rank between the two grooming females and these invariably resulted in the retreat of the most subordinate individual. In the other 79 supplants, an individual dominant to both the grooming females approached them; in four of these instances both the subordinate females retreated, while in the remaining 75 cases only one of the grooming partners did so. These latter instances appeared to involve active decision making by the two grooming individuals and have been further analysed in this paper with particular reference to the underlying knowledge that such individuals may possess and use during such interactions.

A total of 58 incidents of aggressive supplants were also observed during the observation period. Of these, 34 instances involved approaches made by females intermediate in rank to the two grooming females and were almost invariably characterized by the approaching female attacking the subordinate individual. In addition, there were 17 incidents when a dominant female approached two allogrooming individuals, both subordinate to her, and proceeded to show aggression towards one of them. These latter instances, which clearly involved a choice made by the approaching female in displaying aggression towards a particular target individual, have also been analysed in this paper.

(d) *Aggression*

Aggressive interactions have been calculated in terms of the cumulative frequency per hour of stares, eye flashes, open-mouth threats, head jerks, ground slaps, warning growls, aggressive screamings, lunges, chases, hold downs, pushes, pinches, slaps, and aggressive bites shown by an individual towards another over the entire observation period (A. Sinha, unpublished ethogram).

(e) *Data analysis*

Logistic regression analysis was performed as described by Shanubhogue & Gore (1987). Independent variables such as the dominance rank and social attractiveness of the different individuals involved in the triadic interactions were assumed to influence the probability of retreat by either of the two allogrooming individuals who were approached such that:

$$\ln \frac{p}{(1-p)} = \beta_0 + \Sigma \beta_i X_i. \quad (2)$$

The equation:

$$p = \frac{e^{\beta_0 + \Sigma \beta_i X_i}}{1 + e^{\beta_0 + \Sigma \beta_i X_i}}, \quad (3)$$

was solved by using the maximum likelihood criterion:

$$L = ({}^{m}_{i=1}\Pi p_i)({}^{n}_{i=m+1}\Pi[1-p_i]), \quad (4)$$

where p is the probability of an individual retreating and $(1-p)$ the probability of her staying, β_0 the intercept, β_i the regression coefficients, X_i the input variables, L the likelihood, and $(1-m)$ are individuals who retreat, and $(m+1-n)$ those who do not.

The goodness-of-fit of the models was tested as follows: p, the probability of retreating was computed for each individual by using the above equations. Dividing all probability values from 0 to 1 into 20 equal probability classes, the mean p values of all the individuals falling in any probability class multiplied by the total number of observed individuals would yield the expected number of retreating individuals in that probability class. The expected number of non-retreating individuals in each probability class could be similarly calculated. The observed number of retreating and non-retreating individuals among all individuals falling in each probability class being known, a χ^2 test was then performed.

Statistical tests were two-tailed unless otherwise specified, and carried out according to Sokal & Rohlf (1981). The test for difference in proportions was performed as described by Spiegel (1982). Significance was tested for Pearson's product moment correlation using a permutation procedure (1000 samples), again as described by Sokal & Rohlf (1981).

(f) *Computer simulations*

To determine whether the 12 cases of allogrooming supplants where the subordinate females did not retreat when approached (see results) could have been obtained by chance alone, a computer-based bootstrapping simulation was carried out. Ten thousand samples of 12 cases each were randomly drawn from the pool of the total 75 observed cases, the distribution of the particular values characterizing these samples for the parameters under study determined, and the properties of the observed cases compared with this distribution. The null hypothesis that the observed properties could have arisen due to stochastic events was rejected if they did not lie in the inner 95% of the distribution of the expected (simulated) values.

3. RESULTS

(a) *Knowledge of allogrooming relationships*

There were 75 observed instances when a dominant female (henceforth to be referred to as 'dominant') approached two of her subordinates during competition for access to grooming partners. In 63 of these (84% of the cases, or the 'usual' cases), the more subordinate of the two individuals that were approached (henceforth to be referred to as 'subordinate') retreated even before the dominant female could reach them, while in the remaining 12 instances (16% of the cases, or the 'exceptional' cases), the more dominant member of the dyad (henceforth to be referred to as 'intermediate') moved away. As the majority of these supplants consisted of the subordinate individual retreating, it is plausible that such females prefer to avoid two higher ranking individuals in such situations. Assuming that this is indeed true, what factors could have motivated the intermediate individual to retreat instead in the exceptional cases?

A simple hypothesis could be that triadic interactions are not different from dyadic ones (in which an individual is approached by another), and that retreats during grooming supplants could be guided by the outcome of simple one-to-one interactions which are so much more

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Table 1. *The proportion of retreats by intermediate and subordinate individuals to approaches by dominant females during dyadic and triadic interactions*

	retreated	not retreated	proportion of retreats
(*a*) Intermediate individuals			
dyadic interactions	35	366	8.7
triadic interactions	12	63	16
			$\chi^2=4.97, p<0.05$
(*b*) Subordinate individuals			
dyadic interactions	61	513	10.6
triadic interactions	63	12	84
			$\chi^2=425.14, p<0.001$

Table 2. *Rank differences between the dominant, intermediate and subordinate individuals, and aggression shown by the dominant individuals in the usual and exceptional cases*

(Aggression has been measured in terms of the frequency of aggressive acts shown per hour. All comparisons have been made by the two-tailed Mann–Whitney *U*-test.)

	usual cases ($n=63$)	exceptional cases ($n=12$)	
rank difference between			
dominant and intermediate	3.2 ± 1.8	2.5 ± 1.4	$U=284.5, p>0.15$
dominant and subordinate	5.8 ± 2.3	6.3 ± 2.2	$U=325.5, p>0.40$
intermediate and subordinate	2.6 ± 1.7	3.8 ± 2.4	$U=263.5, p>0.05$
aggression shown by			
dominant towards intermediate	0.102 ± 0.108	0.118 ± 0.171	$U=350.0, p>0.60$
dominant towards subordinate	0.092 ± 0.064	0.119 ± 0.069	$U=240.5, p<0.05$

frequent between pairs of adult females. The proportion of retreats exhibited by the intermediate and subordinate individuals during triadic interactions were, however, different from what would be expected on the basis of their behaviour during dyadic approaches (table 1). Decisions made by grooming individuals either to retreat or to remain in place during supplants thus appeared not to be influenced by those made when they were individually approached by the same dominant females.

The outcome of behavioural interactions between adult cercopithecine females often depend on the respective positions that they occupy in the dominance hierarchy. In addition, interindividual aggression is invariably directed down the hierarchy and usually serve to reinforce the dominance status of each female. Could grooming females being supplanted decide to remain in place or retreat on the basis of their dominance ranks? Rank difference between the specific dominant, intermediate and subordinate individuals involved, considered in pairs, did not differ significantly across the usual and the exceptional cases (table 2). Aggressive interactions initiated by the dominant females towards their intermediate and subordinate counterparts, examined across the entire observation period, also could not explain the behavioural difference of the supplanted females in the two situations (table 2). In fact, the significantly greater aggression shown by the dominant individual towards the subordinate in the exceptional cases is contrary to what would be expected if agonistic relationships guided the decision made by the subordinate individual to remain behind in these cases.

Could the intermediate individual in the exceptional cases be avoiding the approaching dominant female since she is aware of a preference of the latter for the subordinate individual as a social partner? Interestingly, the dominant females did exhibit a marked preference in directing their grooming towards the subordinate individuals in the 12 exceptional cases over that shown in the 63 usual cases. This was, however, evident only when the duration of grooming was considered (figure 1*b*; Mann–Whitney *U*-test, $U=202.5$, $n=12, 63$, $p=0.01$); frequency of grooming events initiated by the dominant towards the subordinate did not differ across the two situations (figure 1*a*; $U=257.5$, $p>0.05$). Moreover, no such difference could be discerned in the allogrooming relationships between the dominant and the intermediate individuals (figure 1*c*,*d*; frequency: $U=300$, $p>0.25$; duration: $U=321$, $p>0.40$).

Dominant females did not, however, appear to discriminate between the subordinate and the intermediate individuals as grooming partners with regard to time spent in grooming them respectively, either in the usual (Wilcoxon's matched-pairs signed ranks test, $T=867$, $n=63$, $p>0.40$) or in the exceptional cases ($T=32$, $n=12$, $p>0.55$) (figure 1, compare between *b* and *d*). This would make it unlikely that, in the exceptional cases, the intermediates are retreating because of a preference of the dominant females for the subordinates over them. Moreover, the dominant individual actually showed greater affiliation, in terms of total time invested in allogrooming

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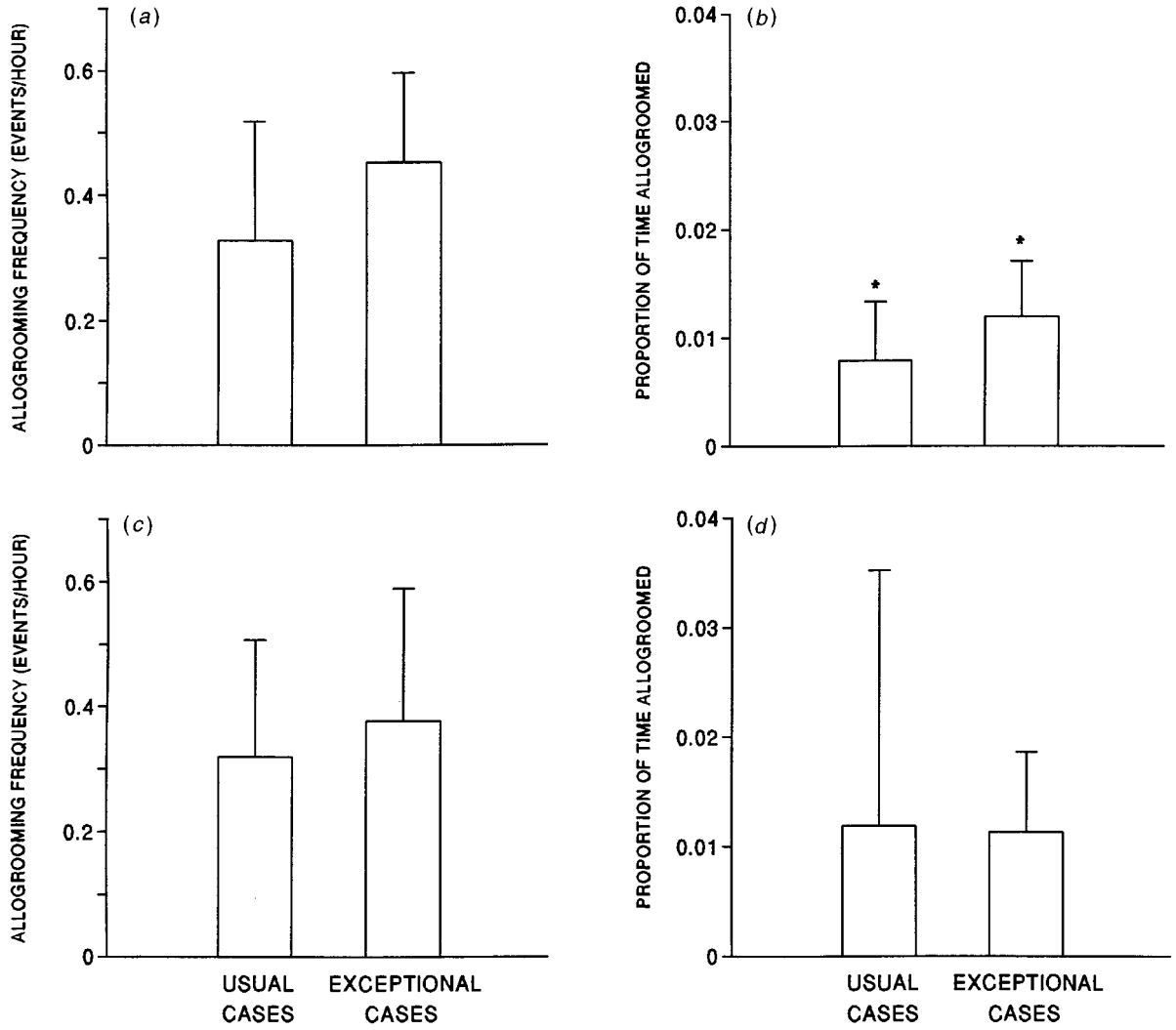

Figure 1. Allogrooming directed by dominant females towards subordinate and intermediate individuals in the usual and exceptional cases. (*a*) and (*b*): grooming frequency and duration (proportion of observed time spent in grooming) towards subordinates; (*c*) and (*d*): grooming frequency and duration towards intermediates. Error bars represent standard deviation. The asterisk denotes a statistically significant difference between proportion time spent grooming subordinates in the usual ($n=63$) and exceptional ($n=12$) cases (Mann–Whitney U-test, $U=202.5$ $p=0.01$).

over the entire observation period, towards the intermediate than towards the subordinate in 6 out of the 12 exceptional instances in which the intermediate had moved away.

Could there nevertheless be a difference in the levels of preference of the dominant for the subordinates relative to that for the intermediates, in these same 12 instances, that the latter could be aware of? Computation of the ratio of the grooming time spent by the dominant female with her preferred partner (the individual whom she has groomed more over the observation period) to that with the other individual, however, failed to show any significant difference (median: 1.59 in the six cases where the subordinate was preferred, and 1.15 in the six cases where the intermediate was preferred; Mann–Whitney U-test, $U=26$, $p>0.20$); this would make it unlikely that individuals were able to perceive any marked preference of the approaching female for their allogrooming companions relative to themselves.

A different perspective to the decision-making process during triadic supplants could involve the act of not retreating performed by the subordinate female. When the identities of all the subordinate individuals involved in these 75 interactions were examined, a significant negative correlation could be found between their coefficients of variation for allogrooming duration received (from all other females in the troop) and their propensity not to retreat when approached, measured as the proportion of all approaches received (as the subordinate member of the triad) in which they were not supplanted (Pearson's product moment correlation, $r=-0.6493$, $n=9$, $p=0.03$). There were no significant correlations, however, between the propensity of the subordinate individuals to remain behind and their dominance ranks ($r=-0.4583$, $p>0.10$), or other, more direct, measurements of grooming duration such as the mean ($r=0.5364$, $p>0.05$), the reciprocal of the mean ($r=-0.5133$, $p>0.05$), or the standard deviation ($r=0.1551$, $p>0.35$) of the grooming received from other females in the group.

The coefficient of variation (standard deviation/mean) of the allogrooming that an adult female receives from other females can be minimized by decreasing values of

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the standard deviation, increasing values of the mean, or a combination of both factors. High values of this measure thus indicate a relatively greater variation in the grooming received by an individual. Its reciprocal, in contrast, represents the consistency with which an individual is preferred as a grooming partner by other females, and can, therefore, be used as an index of social attractiveness of that particular individual. Such indices were computed in terms of both, the frequency and the duration of allogrooming received by these individuals, and have been accordingly used in subsequent analyses.

The above interpretation, therefore, implies that the subordinate member of a supplanted dyad was less likely to retreat, on being approached by a dominant female, when she was more socially attractive than her dominant grooming partner. This relationship, however, held only when social attractiveness was considered in terms of allogrooming time received by these individuals (figure 2; Pearson's product moment correlation, $r=0.6784$, $n=9$, $p=0.015$; linear regression, $r^2=0.46$, $p<0.05$, $Y=0.2695X+0.2442$), but not with respect to the frequency of grooming received by them ($r=0.5578$, $p>0.05$). Moreover, no relationship could be discerned between the propensity to remain in place when approached and social attractiveness for the intermediate females of the triads (grooming time received: $r=0.2813$, $n=8$, $p>0.20$; grooming frequency received: $r=0.2447$, $p>0.25$).

It was also important to determine whether random sampling of subordinate females from those involved in the 75 observed supplants could yield the significant correlation described above. Results from the bootstrapping simulations confirmed that the observed correlation coefficient of the proportion of times that a subordinate female did not retreat when approached and her social attractiveness in terms of allogrooming duration was indeed significantly different from that expected by chance alone ($p=0.0003$). On the other hand, as was expected, simulations which took into account social attractiveness of the subordinates in terms of the frequency of grooming received by them, yielded correlation coefficients that were not different from those obtained by random sampling ($p>0.05$).

The subordinate individuals involved in the supplants could also be classified into two groups with the qualitative criterion of those who had invariably retreated on being approached and those who had remained behind at least on a single occasion. In accordance with the results obtained above using the quantitative relationship, the five females who had invariably retreated were significantly less socially attractive in terms of grooming duration received than those four who had failed to retreat at least once on being approached (Mann–Whitney U-test, one-tailed, $U=18$, $n=5, 4$, $p<0.05$). The two groups of females did not differ, however, when they were compared either in terms of the mean ($U=14$, $p>0.10$) and standard deviation ($U=11$, $p>0.10$) of the grooming duration received from the other females in the group, or their social attractiveness in terms of grooming frequency ($U=17$, $p>0.10$).

In addition, females who were more socially attractive (for grooming duration) than their grooming companions formed a significantly greater proportion of the non-

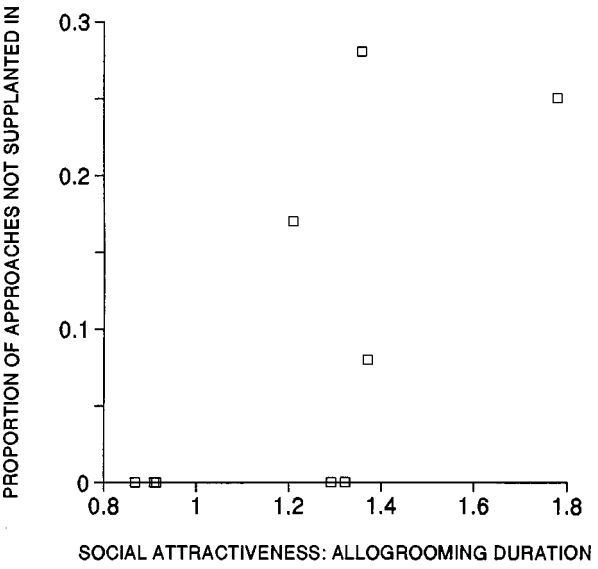

Figure 2. Correlation between the proportion of approaches, received by subordinate females, that did not result in them being supplanted and their social attractiveness in terms of allogrooming duration received (Pearson's product moment correlation, $r=0.6784$, $n=9$ individuals, $p=0.015$).

retreating individuals in the exceptional cases (9 out of 12, or 75%) than they did in the 63 usual cases (25 out of 63, or 39.7%) (test of difference in proportions, one-tailed test, $p<0.01$). Moreover, the subordinate individuals in the exceptional cases exhibited a tendency (though not significantly so) to be more consistently attractive than their intermediate counterparts (figure 3; Wilcoxon's matched-pairs signed ranks test, one-tailed, $T=20$, $n=12$, $p=0.07$); no such trend was, however, apparent for the usual cases ($T=816$, $n=63$, $p>0.20$). In accordance with these results, bootstrapping simulations showed that the Wilcoxon statistic for the observed 12 exceptional cases was indeed significantly different from that obtained by chance alone ($p<0.0001$), while it was not so, as expected, for the 63 usual cases ($p=0.15$).

(b) *Knowledge of dominance ranks*

When all the 75 cases of competition for allogrooming partners were considered, there was a strong positive correlation between the frequency of approaches a female had received as the intermediate member of the triad and her social attractiveness in terms of grooming frequency received from all the other females in the group (figure 4; Pearson's product moment correlation, $r=0.8389$, $n=8$, $p=0.006$; linear regression, $r^2=0.70$, $p<0.01$, $Y=0.2947X+0.0301$). This was inspite of the fact that the intermediate and subordinate individuals in the approached dyads did not differ in their social attractiveness (frequency: Wilcoxon's matched-pairs signed ranks test, $T=1212$, $n=75$, $p>0.25$; duration: $T=1075$, $p>0.05$). The correlation was, however, weaker and the regression non-significant when attractiveness was measured in terms of grooming duration received (Pearson's product moment correlation, $r=0.6606$, $p=0.045$; linear regression, $r^2=0.44$, $p>0.05$, $Y=0.4455X+0.1476$). In contrast, no relationship could be discerned at all between these parameters and the frequency of approaches received by the

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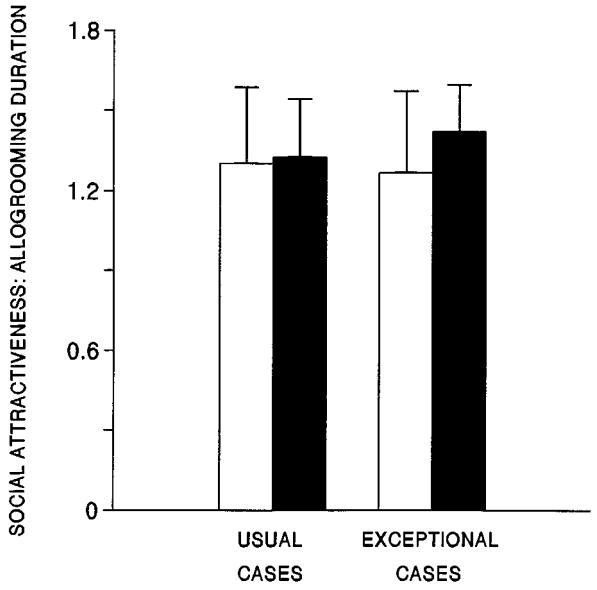

Figure 3. Social attractiveness, in terms of allogrooming duration received, of the intermediate and subordinate individuals in the usual and exceptional cases. A comparison has been made for the usual ($n=63$) and the exceptional ($n=12$) cases independently. Open bars: intermediate individuals; filled bars: subordinate individuals; error bars: standard deviation.

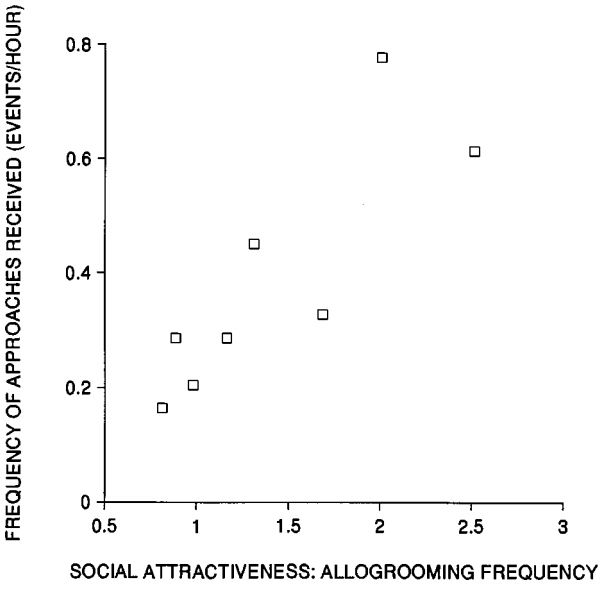

Figure 4. Correlation between the frequency of approaches received by intermediate females and their social attractiveness in terms of allogrooming frequency received (Pearson's product moment correlation, $r=0.8389$, $n=8$ individuals, $p=0.006$).

subordinate members of the allogrooming dyads (Pearson's product moment correlation, grooming frequency: $r=0.2818$, $n=9$, $p>0.25$; duration: $r=0.3760$, $p>0.20$).

The above results indicate that individuals who are more socially attractive as grooming companions for the females in the group (in terms of grooming frequency received) are approached at comparatively greater rates by more dominant individuals only when they are the dominant members of the supplanted dyads. Note that there was no consistent difference between the intermediate and the subordinate females in their social attractiveness either generally to other females in the group, or specifically to the approaching dominant female (see above). Nevertheless, support for the possibility that there may indeed be a preference for the intermediate females comes from the direct observations of 25 instances when a dominant female approached two allogrooming subordinates and proceeded to herself groom one of them. The dominant member of the dyad was preferentially groomed on a significant majority of 20 of these occasions; the subordinate received attention in only five instances ($\chi^2=9.000$, $p<0.005$). Consequently, these results would argue that the approaching female may be specifically attending to the more dominant member of the approached dyad, and therefore, she must be aware of the relative ranks of the two approached individuals.

The conclusion that an adult bonnet macaque female might indeed be aware of the dominance ranks of the other females in the group is also supported by data from yet another kind of triadic interaction. On 17 occasions, a dominant female approached two of her grooming subordinates and supplanted one of them through aggressive interactions. In 13 of these instances, the more subordinate of the two females was attacked, while the intermediate individual received aggression on the remaining four occasions. Aggression was thus more significantly directed towards the subordinate individual than would be expected if the dominant female were to attack either of the females randomly ($\chi^2=4.765$, $p<0.05$).

An attempt was made to examine the factors that could motivate approaching females to preferentially exhibit aggression towards more subordinate females when supplanting a member of a grooming dyad. The dominant females, involved in these 13 particular interactions, did not show any inherent preference in directing grooming towards the intermediate individual over that towards the subordinate one over the entire observation period (grooming frequency: Wilcoxon's matched-pairs signed ranks test, one-tailed, $T=30$, $n=13$, $p=0.15$; grooming duration: $T=27$, $p=0.10$). The intermediate females were also not more socially attractive than were their subordinate companions (grooming frequency: $T=34$, $p=0.20$; grooming duration: $T=27$, $p=0.10$). Finally, as compared to their intermediate counterparts, the subordinate females had not necessarily received more aggression from these particular dominant individuals in dyadic interactions over the observation period ($T=44$, $p>0.45$).

Is it nevertheless possible that the dominant female was aware of a differential response made by individuals of different ranks to aggression show by her during dyadic interactions? The proportion of approaches received by females from more dominant individuals to which they retreated did not, however, correlate with their absolute ranks (Pearson's product moment correlation, $r=-0.5482$, $n=10$, $p>0.05$); dominant females may not thus be able to use such behavioural responses as cues to the relative ranks of their subordinates. There was also not a single instance (during the entire 269 h of observation) when any of the intermediate females, though often close in rank to the dominant individuals, had ever been observed to threaten or attack any of the latter. On the other hand, a surprising

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Table 3. *Logistic regression analysis: determinants of the probability of any member of an allogrooming dyad retreating when approached by a more dominant individual*

(Goodness-of-fit of the model with the observed data: $\chi^2=2.753$, d.f.$=2$, $p>0.1$, $^{*}p<0.05$, $^{**}p<0.01$.)

variable	estimated coefficient	standard error	z
1. intercept	0.7211	1.8180	0.3967
2. its own dominance rank	−0.3643	0.1847	−1.9724*
3. rank difference with approaching individual	−0.8180	0.1447	−5.6527**
4. rank difference with allogrooming companion	0.2198	0.1348	1.6306
5. its own social attractiveness[a]	0.0050	0.1612	0.0313
6. ranked difference in attractiveness[a] with allogrooming companion	0.0465	0.1049	0.4433

[a] In terms of duration of allogrooming received.

result was that dominant females were significantly more likely to attack subordinates of higher rank than those of relatively lower ranks during dyadic interactions (Pearson's product moment correlation, $r=0.6227$, $n=10$, $p=0.001$); this was in complete contrast to their behaviour during triadic interactions. Taken together, these results suggest that the a dominant individual may be well aware of the ranks of two grooming females and may choose to show aggression more towards the subordinate member of the dyad when she has a choice of supplanting one of them.

(c) *Decision-making during allogrooming supplants*

Knowledge of dominance ranks and social attractiveness could thus be important factors which influence the probability that an individual will decide to either retreat or stay back during grooming supplants. It was, of course, clear that neither of these factors, by themselves, were of absolute importance since, in each case, it was not necessarily the dominant or the more attractive individual which failed to retreat. It thus became of interest to understand which of these aspects of an individual's social knowledge of her grooming companion correlate with the decision to retreat during a triadic interaction.

Each member of the 75 approached dyads either retreated or failed to do so; the dependent variable was thus a binary one and could be influenced by a number of independent variables. Logistic regression analysis (Cox 1970; see also Shanubhogue & Gore 1987) was used to determine the factors that may critically influence the decision of a female in an grooming dyad to retreat when approached by a more dominant individual. The independent variables that were considered in these analyses included the individual's own dominance rank, rank of the approaching dominant female, rank difference with the approaching female, rank of the grooming companion, rank difference with the grooming companion, the individual's own social attractiveness in terms of the duration of grooming received by her from other females and the ranked difference in attractiveness with the grooming companion. Social attractiveness was considered only for duration of grooming received since this measure was found to be important for the macaques' knowledge of allogrooming relationships. Regression was carried out with all these variables taken one at a time as well as with all of them considered together. The influence of the absolute dominance rank or social attractiveness was investigated by two slightly different approaches: once by including these variables directly as such, and once by including the difference in rank or attractiveness between the two individuals in the set of independent variables.

The first set of models examined the relative influence of the different variables on the probability that any female in an allogrooming dyad would retreat when approached by a more dominant individual. One of the successful models for this regression analysis is shown in table 3. Two regression coefficients, namely those associated with an individual's own dominance rank and with rank difference with the approaching female, were significant. According to this model, therefore, an individual had an increased probability of retreating as its position in the rank hierarchy fell, as it did when the approaching individual was relatively closer to it in rank. In contrast, an alternate model which incorporated the absolute dominance rank of the approaching female, instead of that for rank difference with her, failed to explain the observed patterns of retreats; none of the coefficients in this model were significantly different from zero (data not shown).

It is important to note here that since these models include decision-making by both the members of the grooming dyad as the dependent variable ($n=150$, derived from 75 interactions), they would consistently fail to distinguish between the knowledge of one's own rank or attractiveness and that of the corresponding properties of the grooming companion. Knowledge about oneself was, however, preferentially incorporated into the tested models since it is less cognitively demanding.

To examine more explicitly the combined influence of social attractiveness and dominance rank, the following alternate approach was also explored. Models were constructed using, as the binary dependent variable, either the decision of the dominant member of the grooming dyad or that of the more socially attractive one to retreat or not to do so, but maintaining the same independent variables as above. Absolute rank and attractiveness of the grooming companion could also be now legitimately incorporated into these models as independent variables.

Rank difference with both, the approaching individual and the allogrooming companion, were found to significantly influence the probability of retreat of the more dominant member of the dyad in a model described in table 4. Such an individual was, therefore, more likely to retreat when the approaching female became relatively

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Table 4. *Logistic regression analysis: determinants of the probability of the dominant member of an allogrooming dyad retreating when approached by a more dominant individual*

(Goodness-of-fit of these models with the observed data could not be calculated since the number of merged classes were less than three $^{*}p<0.05$, $^{**}p<0.01$.)

variable	estimated coefficient	standard error	z
model I			
1. intercept	5.0487	4.7162	1.0705
2. its own dominance rank	−0.0278	0.4078	−0.0682
3. rank difference with approaching individual	−2.0578	0.6362	−3.2346**
4. rank difference with allogrooming companion	1.7240	0.7437	2.3181*
5. its own social attractiveness[a]	0.7064	0.4546	1.5537
6. ranked difference in attractiveness[a] with allogrooming companion	0.4039	0.3234	1.2491
model II			
1. intercept	−2.2007	2.7769	−0.7925
2. its own dominance rank	0.4910	0.2932	1.6744
3. dominance rank of approaching individual	−0.2628	0.2916	−0.9012
4. dominance rank of allogrooming companion	−0.3490	0.2652	−1.3161
5. its own social attractiveness[a]	−0.0029	0.1240	−0.0233
6. social attractiveness[a] of allogrooming companion	0.1792	0.2196	0.8158

[a] In terms of duration of allogrooming received.

Table 5. *Logistic regression analysis: determinants of the probability of the more socially attractive member of an allogrooming dyad retreating when approached by a more dominant individual*

(Goodness-of-fit of both the models with the observed data: $\chi^2=2.838$, d.f.$=1$, $p>0.05$, $^{**}p<0.01$.)

variable	estimated coefficient	standard error	z
model I			
1. intercept	1.3595	2.1555	0.6307
2. dominance rank of approaching individual	−0.0619	0.1696	−0.3647
3. its own dominance rank	−0.1790	0.1723	−1.0389
4. dominance rank of allogrooming companion	0.4420	0.1481	2.9842**
5. its own social attractiveness[a]	−0.0038	0.2013	−0.0187
6. social attractiveness[a] of allogrooming companion	−0.0433	0.1478	−0.2930
model II			
1. intercept	1.3595	2.1555	0.6307
2. dominance rank of approaching individual	−0.0619	0.1696	−0.3647
3. its own dominance rank	0.2630	0.2330	1.1289
4. dominance rank of allogrooming companion	0.4420	0.1481	2.9842**
5. its own social attractiveness[a]	−0.0471	0.2014	−0.2337
6. ranked difference in attractiveness[a] with allogrooming companion	−0.0433	0.1478	−0.2930

[a] In terms of duration of allogrooming received.

less dominant to her, while the grooming companion became progressively more subordinate. An alternate model which incorporated knowledge of the absolute dominance ranks of the approaching individual and the grooming companion as well as the social attractiveness of the latter instead of their values relative to one's own, however, failed to reveal a significant influence by any of the independent variables (table 4).

Why would a dominant female retreat more often when she was with a relatively more subordinate individual? One solution to this problem possibly lies in the strong positive correlation that was observed between the rank difference of the dominant members of the dyads with their subordinate companions and their difference in social attractiveness in terms of grooming duration received (Pearson's product moment correlation, $r=0.2729$, $n=75$, $p<0.01$). Increasingly more subordinate companions were, therefore, relatively more attractive as grooming partners to all the females in the group, and the retreating dominant females may have been aware of this relationship.

Finally, regression models were constructed to examine the influence of the different independent variables on the probability of the more socially attractive member of the grooming dyad retreating. Either of two alternative models, which surprisingly yielded identical estimates for the respective significant variables, could explain the observed behavioural patterns (table 5). It was not possible, therefore, to determine which of the two

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variables—dominance rank of one's companion or rank difference with her—was more important in influencing the behaviour of these individuals. An alternative model which used these two variables alone was found to yield a good fit with the observed data, but failed to assign priority to any of them (data not shown). It may also be noted that rank difference with the approaching female was no longer a significant factor in these models. These last set of models, thus, clearly show that the more socially attractive member of an allogrooming dyad was more likely to retreat (inspite of her popularity) as her companion became increasingly dominant to her.

4. DISCUSSION

Primate groups, being unusually socially complex, would demand that individuals be aware not only of their own relationships with others, but also of the social bonds that develop between other individuals in the troop. This becomes particularly important since such societies are typically characterized by both competition and cooperation; each individual therefore has to consistently evaluate its own position in the prevailing social network of affiliative and dominance relationships.

(a) *Knowledge of allogrooming relationships*

If individuals do indeed possess information about the attributes of other members of the society such as their dominance ranks or their social relationships, they would presumably act on this knowledge while taking social decisions. A commonly observed triadic interaction among adult cercopithecine females involves a competition for grooming partners in which one of the members of the mutually grooming dyad retreats when a more dominant female approaches them. In this study, as in others (e.g. Cheney & Seyfarth 1990), it is usually the more subordinate member of the dyad which moves away. Cheney & Seyfarth (1990, p. 82) argue that this would require a knowledge on the part of the intermediate female about her position in the rank hierarchy so as not to retreat. A simpler non-cognitive hypothesis to explain this interaction would however suggest that only the female who is subordinate to both the other individuals independently needs to move away. This argument can explain the 63 instances out of the total of 75 such cases (84%) in this study (and 29 out of the 30 instances reported for vervet monkeys by Cheney & Seyfarth (1990)) where the most subordinate individual does indeed retreat.

But why, in the remaining 16% of the cases, does the dominant member of the approached grooming dyad move away? Results from this study show that the proportion of times that a subordinate female remains in place during an allogrooming supplant is not affected by her dominance rank, rank differences with the approaching female and her grooming companion, or the agonistic relationships between these individuals. It also does not appear to be influenced by her corresponding behaviour when approached by dominant females during dyadic interactions.

The tendency of these subordinate individuals to remain behind (and the corresponding dominant partners to retreat) is however negatively correlated only to the coefficient of variation for the duration of grooming received (but not to the mean, the reciprocal of the mean, or the standard deviation) by these individuals from all the other adult females in the troop. Because this coefficient can be minimized by decreasing values of the standard deviation or increasing values of the mean of the grooming received or both, the reciprocal of this measure could represent, in some sense, the social attractiveness of a particular individual, or the consistency with which she is preferred as a grooming companion by the other females in the group. This would strongly indicate, therefore, that the intermediate female (i.e. the dominant partner of the dyad) may actually be aware of the social attractiveness of the individual that she is currently with, and accordingly tend to retreat when approached by a still more dominant female. In support of this hypothesis, the subordinate members of the dyads in the exceptional cases did exhibit a marked tendency to be more socially attractive than their dominant counterparts; no such difference could be discerned in the usual cases (where the subordinate females retreated).

It must be pointed out that the macaque females in this troop did not appear to recognize and/or react to the social bonds that apparently exist between particular pairs of females (A. Sinha, unpublished observations). This is borne out by the fact that in the exceptional instances where the intermediate individuals retreated, the approaching dominant females did not appear to discriminate in directing grooming towards the subordinate and the intermediate individuals either with regard to the frequency of initiated events or the subsequent duration of grooming given to them. What is illuminating, however, is that these females nevertheless appeared to be responding to the social attractiveness of their partners as evaluated by the uniformity with which the latter received grooming from the other troop members. It is not only the mean grooming time received by the target individual nor the variation in the number of troop members who groom her that are independently being taken into account, but a combination of both factors.

Bachmann & Kummer's (1980) classic study on the hamadryas baboon was one of the earliest attempts to demonstrate that primates may be aware of the social relationships of others and take decisions on the basis of such knowledge. Their experiments, however, could not distinguish whether it was indeed the social interactions that were providing cues to the observer, or simply the behavioural patterns of either of the two interacting individuals. This particular study, however, shows that bonnet macaque females might be aware of the allogrooming that other individuals might be receiving from different members of the group. Knowledge of this kind, encompassing the multiple social relationships of target individuals, clearly needs to be acquired from observations of the actual social interactions of all the individuals involved in these relationships. It is very unlikely that the macaque females are simply reacting to the behavioural cues being provided by each observed individual in the troop.

In order to react to particular social relationships between pairs of group members, an individual would have to memorize the pattern of interactions among each pair. Observation and memorization could suffice in small groups which are relatively stable over time, but would obviously place increasingly difficult cognitive demands on an individual either as the group size increases or its

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composition changes (see also Seyfarth & Cheney 1987). An alternative strategy which bonnet macaque females seem to have evolved is to obtain an impression of the social attractiveness of another individual with regard to its affinity to the other group members without specifically remembering each and every pairwise interaction. Such an ability would obviously appear to make the task of evaluating one's own position in the group's social network much less cognitively demanding.

But what do individuals actually observe and memorize? Whenever dominant females in the allogrooming dyad took a decision to move away, they appeared to do so primarily on the basis of the consistency with which the other females in the troop spent grooming time with her subordinate partner. It is interesting that the females seem to be reacting more to the duration of grooming that the other individual receives (as measured by the total time spent by her in this activity), than the actual frequency of the initiated events. This would require that the observer simply scan the target individuals periodically to note whether she is being groomed instead of remembering the actual number of times that an individual has been groomed. Again, this calls for a cognitively simpler mechanism to obtain the desired information. In addition, individuals also apparently need to remember whether different group members are uniformly grooming the target female during these scans.

A problem that should be noted here concerns the small sample of 12 exceptional cases on which the analysis of the macaques' knowledge of allogrooming relationships is based. Small samples may often be subject to stochastic events that may or may not be of any significance to the hypotheses being investigated. In order to at least examine whether these small number of exceptional cases could have arisen by chance alone, bootstrap simulations were conducted. The validity of the reported conclusions appear to be supported by the results of these simulations which rule out the possibility that the exceptional cases could have arisen randomly.

It is also not clear from the present analysis whether the observed patterns could be strongly affected by the females' interactions with one particular individual. Statistically, attempts were made to reduce this possibility by analysing the pattern of allogrooming supplants from three perspectives. First, the proportion of times that subordinate females remain in place were considered as a continuous variable possibly dependent on the social attractiveness of these particular individuals. Second, threshold effects were implicitly assumed when a comparison was made between the social attractiveness of two groups of individuals—those who had invariably retreated when approached and those who had remained behind at least on a single occasion. Finally, logistic regression models were constructed to quantitatively examine the probability distribution of an individual's decision to remain behind, when approached, as a function of her knowledge, different aspects of which were represented as continuous independent variables. All these methods of analysis yielded similar results, an indication that the reported patterns were statistically robust inspite of being obtained from a rather small data set.

(b) *Knowledge of dominance ranks*

Besides their knowledge about the grooming relationships of different individuals, macaque females also appear to possess information about the relative ranks of others in the dominance hierarchy. Results obtained in this study clearly show that the greater the social attractiveness (in terms of grooming frequency received) of the more dominant member of a grooming dyad, the greater are the number of approaches that she receives from a still more dominant female. The important point here is that this does not hold true for the same females if they are the subordinate members in the supplanted dyad. The approaching dominant females thus appear to be well aware of the relative dominance ranks of the two approached females, both subordinate to her. Further evidence that females may indeed be aware of the relative ranks of the other individuals in the troop comes from those instances where grooming supplants do not occur, and the dominant individual preferentially grooms the intermediate female although both the approached females are equally socially attractive.

Data in support of this conclusion is also provided by the patterns of preferential aggression shown by the approaching dominant female towards the more subordinate member of the supplanted dyad. This is rather surprising since, during dyadic interactions, aggression is more directed towards comparatively less subordinate members of the troop. These contrasting behavioural patterns seem to suggest that females may be aware of the relative ranks of their adversaries, and may choose different strategies depending on the prevailing situation; a more subordinate female is thus attacked only when another female is present.

Because, in those instances when an actual supplant does not occur, the dominant female appears to prefer the intermediate individual as a grooming companion, why does the latter retreat when she is with a more socially attractive subordinate? A solution to this apparent contradiction may lie in the relative frequencies with which dyadic and triadic interactions occured in the troop. Triadic allogrooming sessions, where the dominant individual groomed the intermediate female in preference to the subordinate one, were relatively rare; such interactions occurred at a frequency of about 0.09 events per hour during the entire observation period of 269 hours. In contrast, dyadic grooming was much more frequent, with a mean rate of 2.5 events per hour; females in the study troop were also much more likely to groom relatively more subordinate individuals during these dyadic sessions (Sinha 1998). In addition, subordinate females also tended to be more socially attractive than their dominant counterparts. It is therefore possible that most females never received an opportunity to learn that they might be preferred as grooming companions by more dominant individuals during triadic supplants, and were, therefore, more likely to be guided by their observations of dyadic interactions in their responses to more dominant females.

How do macaque females assess individual ranks? Do they follow a brute force method by which individuals observe and remember dyadic interactions between each and every pair of troop members and then conclude a linear hierarchy? Alternatively, are bonnet macaques capable of inferring linear orders by associative transitivity

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(Treichler & Van Tilburg 1996)? Such processing of serial information would be advantageous in allowing them to deduce individual ranks in the hierarchy from partial knowledge of agonistic relationships without having to observe interactions between every pair of individuals (for a discussion, see Cheney & Seyfarth 1990). Future studies under controlled conditions in the laboratory may provide an answer to this dichotomy.

(c) *Decision-making during allogrooming supplants*

What particular aspects of a bonnet macaque female's knowledge directly influence the probability of her making a decision to retreat or remain behind during a grooming supplant? Logistic regression analysis indicated that the two most important factors that were taken into consideration for such a decision to be made included knowledge of the subject's own dominance rank and her rank difference with the approaching dominant female. A model which incorporated the absolute rank of the latter failed to explain the observed behavioural patterns. Individuals, thus, clearly appear to be aware not only of their own positions in the rank hierarchy, but also of that of the other females in the troop. What is more interesting, however, is that this knowledge of another individual's dominance rank seems to be acquired only relative to one's own; a female knows of her rank difference with another female but does not appear to be aware of the absolute position of her adversary in the rank hierarchy.

This finding reinforces the view that social knowledge of primates might primarily be of an egotistical nature in that knowledge of another individual's attributes is best acquired and conceptualized in terms of the subject's own attributes. Knowledge of the absolute is likely to be more cognitively demanding than knowledge of the relative, especially that based on the self. Knowledge of this kind can also be easily obtained when the subject actively interacts with another individual; its acquisition does not require that she observe and memorize social interactions between other individuals and which do not involve her.

Rank difference with the approaching female and with the grooming companion appeared to be important motivating factors when the more dominant member of an allogrooming dyad decided to retreat on being approached. Individuals are clearly able to simultaneously process information about all their interacting companions and then use this knowledge effectively during complex social interactions. The computations involved in this particular situation are further complicated by the fact that the intermediate female in a grooming supplant chooses to retreat as the approaching individual becomes relatively less dominant to her while her grooming companion is comparatively more subordinate.

Females in the study troop became increasingly socially attractive to others as they occupied progressively lower positions in the dominance hierarchy. A possible reason, therefore, for the intermediate female retreating inspite of being more dominant was the increasing attractiveness of her grooming companion. Again, the more socially attractive individual in the grooming dyad decided to leave only when her companion became progressively more dominant to her. Taken together, it seems evident that high dominance ranks of individuals can compensate for their lower attractiveness and vice versa during grooming supplants. Individuals thus appear to be capable of not only integrating information about both their partners, but seem to be simultaneously accessing different domains of their knowledge—those for dominance ranks and for social relationships—while making a decision. Surprisingly, however, the logistic regression models failed to ascribe direct significance to knowledge of social attractiveness, either of one's own or of that of others, in the decision-making process. Is it then possible that information about social bonds is acquired in terms of their correlated dominance ranks? If this is true, it would suggest that, unlike in humans, certain categories or domains of knowledge could be much more easily accessible than others to primates, and that these domains could be preferentially used for the storage of related information from other categories.

Finally, in conclusion, it should be stressed that relationships and interactions between adult females in a typical cercopithecine society are strongly guided by a number of definite rules mainly centred around the dominance hierarchy. This would, in turn, give rise to a hierachical organization in the acquisition and use of information, in terms of its different domains. Thus, knowledge of one's own position in the rank hierarchy and that of others would be preferentially gathered and applied when making social decisions, especially those involving individuals dominant to oneself. This would, however, tend to obscure the discovery of social decisions that are made by these individuals on the basis of cognitive information processing even should they occur. In this particular study, for example, subordinate members of allogrooming dyads retreat and are supplanted by more dominant females in the majority of cases. The dominance hierarchy clearly reigns supreme. However, there are a few exceptional cases where the rule is broken and it is the dominant member of the dyad who decides to leave instead. If and when this happens, however, it might actually be on the basis of cognitively acquired and processed information that this decision is made.

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