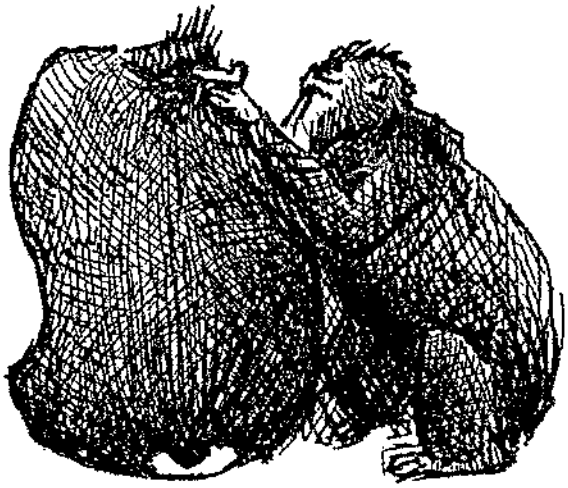
THE EFFECTS OF DOMINANCE, KINSHIP AND SEXUAL STATE ON THE GROOMING BEHAVIOUR OF BLACK MACAQUES.

(*Macaca nigra*)



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This study was carried out with the cooperation of Jersey Zoo.
Cover illustration by Michael Shanahan.

ABSTRACT

The social interactions of a captive group of black macaques were studied in order to assess the factors affecting the distribution of social grooming (allogrooming). The animals exhibited a linear dominance hierarchy and grooming was directed up the hierarchy with dominance rank being strongly correlated with grooming received (r_s=0.93) and number of animals groomed by (r_s = 0.86). This supported Seyfarth's (1977) model of monkey grooming patterns. Seyfarth's second prediction that most grooming would occur between adjacently ranked individuals was not upheld. As predicted by the theory of kin selection, closely related animals groomed more frequently than unrelated individuals but this trend was not statistically significant. The female undergoing sexual cycling received most grooming at the peak of her sexual receptivity and this was accompanied by the greatest proportion of grooming directed to her sexual skin indicating a sexually related function of grooming. Indeed 63.6 % of sexual mounts were preceded by the male grooming the female and it is proposed that this behaviour allows the males access to mount the females. Finally the majority of allogrooming was directed to parts of the body inaccessible to the recipient animal suggesting a utilitarian function of allogrooming.

INTRODUCTION

In a model of social grooming, Seyfarth (1977) has identified five causal factors which influence the distribution of grooming in cercopithecine monkeys. These are dominance, preference among genetic relatives, changes in reproductive state, time available and individual differences in attractiveness.
The aim of this study was to examine the former three factors on the grooming behaviour of captive black macaques (*Macaca nigra*). Additionally the benefits associated with social grooming were to be explored with respect to aggression and support between grooming partners.
Each of Seyfarth's selected factors shall be introduced in turn. Regarding dominance, Seyfarth argues that monkeys will groom one another because such behaviour increases the likelihood of beneficial behaviour (e.g. coalitions) between a given pair of animals in the future. As high ranking animals are the most successful in supporting others, they become the most attractive grooming partners and lower ranking individuals compete for access to them. The top ranking (alpha) individual can thus distribute its grooming as it pleases. All those ranking below will compete for access to the alpha animal with the lowest ranked animals gaining least access and grooming least. Instead, lower ranking animals will groom those nearest to them in rank due to less competition (i.e. In a group of ten monkeys, the lowest ranked will compete with eight others for access to the alpha individual but with only one for access to the eighth ranked animal). Seyfarth's theory gives rise to the two main predictions of his model. These are a) that grooming will be directed up a dominance hierarchy and b) that the majority of grooming will occur between adjacently ranked individuals.
Concerning preferences among genetic relatives, Sade (1965), Seyfarth(1976), and Baker & Estep (1985) in studies of rhesus macaques, savannah baboons and black macaques, observed greater than expected grooming frequencies between related animals. These observations have been attributed to being due to kin selection (Hamilton 1964, Maynard Smith 1964) in action. According to this theory, animals which act in a manner that will increase the reproductive success of kin will increase the frequency of their own genes in future generations due to the fact that they have genes in common with such kin animals. This phenomenon will occur only in such situations when the cost to an animal's fitness does not exceed the benefits (Baker & Estep 1985).
Changes in sexual state of female monkeys may also influence their grooming interactions. Rowell (1968) found that oestrus female macaques groomed less and received less grooming whilst Seyfarth (1976) found no relationship between grooming and sexual state in savannah baboons. A third pattern, of increased grooming received by oestrus black macaques is reported by Dixson (1977).
Social grooming among primates serves a range of functions. Grooming may reduce aggression by serving as a gesture of appeasement (Chalmers 1979), bring support in future agonistic encounters (Seyfarth 1977) or allow males

access to sexually receptive females prior to mating (Dixson 1977). However at its simplest, grooming may have a strictly utilitarian function. For an animal's skin to function correctly, it must remain clean (Sparks 1967) and thus grooming keeps the recipient animal's fur and skin clean and reduces the number of ectoparasites present. Baker (1985) in a study of grooming site preferences in a range of primates, including black macaques, found that the distribution of allogrooming was complementary to that of autogrooming with the allogrooming being concentrated on regions inaccessible or invisible to an autogrooming individual. This suggests that where the utilitarian, asocial autogrooming cannot occur, allogrooming is used instead to maintain cleanliness of the skin and fur.

The species under study (*Macaca nigra*) occurs only on the island of Sulawesi (formerly Celebes). The macaques are black in colour and possess a long crest of hair on the head which may be erected or flattened in display. Specialized thickenings of skin (ischial callosities) are present on the rump and are an adaptation to the animals spending long periods sitting on rocks or trees. In common with many other primates (see Pagel 1994), the females of the species possess a sexual skin - a hairless area surrounding the perineum which swells considerably during the oestrus cycle as a signal of sexual receptivity.

With respect to the grooming behaviour of black macaques, the following predictions are made:

1. *Grooming will be directed up the dominance hierarchy (if present).*
2. *The majority of grooming will occur between adjacently ranked individuals.*
3. *Related animals will groom more frequently than unrelated animals.*
4. *Females will receive most grooming from males at the peak of their oestrus cycles.*

Regarding the function of social grooming, the following predictions are made:

1. *An animal that receives grooming is less likely to show aggression to the grooming animal.*
2. *An animal that receives grooming is more likely to support the grooming animal in agonistic encounters.*
3. *The majority of grooming will be directed to areas inaccessible to the recipient animal.*

METHODS

Subjects

The study group was composed of 12 black macaques living in a captive social group of 18 individuals at Jersey Zoo. The subjects were selected on the basis of age with each animal being over three years of age at the start of the study. The remaining six animals were not included in the study as they were similarly sized and very hard to tell apart.

The age-sex composition of the study group is presented in Table 1. The identities and genealogies of all subjects were provided by the zoo and each animal had a name given by zoo staff.

Subject animal	Sex	Age at start of study
Poubelle	Female	26y +.
Masamba	Male	12y, 7m, 10d.
Wesi	Female	9y, 2m, 5d.
Morelia	Female	8y, 6m, 29d.
Kulawi	Female	8y, 5m, 11d.
Clint	Male	6y, 9m, 3d.
Frodo	Male	5y, 9m, 5d.
Imandi	Female	5y, 1m, 28d.
Gimpy	Male	4y, 11m, 23d.
Pixie	Female	4y, 10m, 10d.
Gizmo	Male	3y, 9m, 12d.
Murgo	Male	3y, 0m, 1d.

Housing

The animals were housed in a combination shelter/outdoor enclosure at Jersey Zoo. The interior of the building measured 360 cm. x 540 cm. whilst the exterior had an area of approximately 1800 m^2 and was landscaped with grassy hillocks, climbing logs and an artificial stream. The enclosure was the recipient of the 1990 Universities Federation for Animal Welfare (UFAW) captive animal award. The outdoor area was surrounded by a four feet high electrified fence (4.5 kV). The animals were fed four times daily on mixed fruit and vegetables and standard monkey chow.

Data Collection

The study was carried out between 23 August and 13 September 1994. Two days of initial observation were spent during which the identities of the subject animals became familiar. With the assistance of zoo staff, individuals were distinguished by differences in pelage, size, facial features and in females, size and state of sexual skin.

The data collection was carried out over the remaining 19 days and all observations were taken from beyond the electric fence. Each day, six 30 minute focal animal samples (Altmann 1974) were taken. Each animal received a total of 300 minutes of observation with the scheduling of each animal's focal samples throughout the study period being based on a table of random numbers. This helped to eliminate any sampling error due to the confounding effects of the time of day on an individual's behaviour. During each focal sample, the focal animal was followed around the enclosure and the following behaviours were recorded on a check sheet (Bateson & Martin 1993). The behaviour definitions are modified after O'Brien (1993) and Fairbanks (1990).

- **Autogrooming:** Manipulation by an animal of its own fur and skin to remove dead skin, dirt, ectoparasites etc.
- **Allogrooming:** Manipulation of fur and skin of one animal (the recipient) by another (the groomer) to remove dead skin, dirt ectoparasites etc.
- **Displacement:** The approach of one (dominant) individual; and the subsequent movement away of a subordinate animal.
- **Aggression:** Display of stare or threat faces (Dixson (1977)),chases, kicks and biting between individuals.
- **Agonistic support:** Coalition formed between individuals to assist in aggressive action against other individuals.
- **Sexual mount:** Mounting of a mature female by a male and subsequent intromission (as opposed to the socio-sexual mounts described by Dixson 1977).

For all behaviours other than autogrooming, only dyadic behaviours (involving a pair of animals) were recorded. Triadic encounters, where three animals interacted, were treated as simultaneous dyadic behaviours and broken up into their constituent dyads and recorded separately.

For each behaviour, the identity of the interactant, direction of behaviour (whether performed or received by the focal animal) and the duration were recorded. In addition to the identity of the interactants, the animals' relatedness to each other and sexual state (if female) were recorded.

Kinship was measured using the coefficient of relatedness (r=0.5, 0.25, 0.125, 0). The sexual state of females could be divided into sexually cycling, pregnant or not cycling (following a birth for example). For those females undergoing sexual cycling, Dixson (1977) has described four easily recognisable changes in female black macaques' sexual skin. These are flat, inflating, fully swollen and deflating. These classifications correspond to females in the early follicular phase, later follicular phase, mid-cycle (peak receptivity) and luteal phase of the menstrual cycle.

The final information recorded was that of body parts receiving grooming during such behaviours. These were recorded as either arm, leg, flank, front, back, head, or sexual skin (in the case of females). These body areas were further classified as being accessible to the recipient animal (i.e. the former four) or inaccessible (the latter three).

All durations were timed with a digital stopwatch. On occasions when the focal animal went out of sight, the duration of this 'Time Out' (Altmann 1974) was noted and a corresponding period was added to the end of the sample to ensure that each period of observation lasted exactly 30 minutes. To assist in identification of individuals at distance, 8 x 21 binoculars were used.

RESULTS

Dominance.

The results of the displacement reactions between pairs of macaques are displayed in the dominance matrix below (Table 2). During the course of the study, 229 occurrences of displacement were observed. Of 66 dyads that could interact in this behaviour, 11 failed to do so. The dominance matrix obtained has no reversals and Landau's index of linearity (Bateson & Martin 1993) was calculated as *h* = 0.89.

	MAS	CLI	KUL	PIX	IMA	MOR	POU	WES	FRO	GIM	GIZ	MUR
MAS	-	12	1	5	4	5	0	0	5	0	2	1
CLI	0	-	8	2	4	6	2	4	12	12	6	3
KUL	0	0	-	0	16	10	10	4	7	6	3	3
PIX	0	0	0	-	7	5	0	3	0	1	2	1
IMA	0	0	0	0	-	6	1	6	1	2	1	3
MOR	0	0	0	0	0	-	6	0	1	2	1	1
POU	0	0	0	0	0	0	-	0	1	1	2	5
WES	0	0	0	0	0	0	0	-	1	1	0	0
FRO	0	0	0	0	0	0	0	0	-	7	3	1
GIM	0	0	0	0	0	0	0	0	0	-	2	0
GIZ	0	0	0	0	0	0	0	0	0	0	-	2
MUR	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. Dominance matrix based on observed displacements. Rows represent approaching animal, columns represent retreating animal.

Characteristics of grooming behaviour.

During 60 hours of observation, 8.63 hours of grooming were observed in 273 grooming sessions. These grooming sessions ranged in duration from 3 seconds to 747 seconds (mean.±.s.e = 114.8 .±.7.56 seconds). Of 66 dyads that could groom together, 20 failed to do so.

Predictions.

Grooming will be directed up the dominance hierarchy.

Figure 1 shows the total grooming received (during 10 focal samples) by each animal plotted against dominance rank. A significant positive trend exists, with dominant animals receiving the most grooming, supporting the above prediction. Further indicators of the effect of dominance rank on grooming are the ratio of grooming received to grooming performed by each rank (figure 2, $r_s = 0.94$), and the number of animals each individual was groomed by (figure 3, $r_s = 0.89$).
With respect to dyadic interactions, of the 44 dyads that groomed, in 30 of these the subordinate partner performed the greater amount of grooming ($X^2 = 10.52$, $p< 0.05$, d.f.=1).

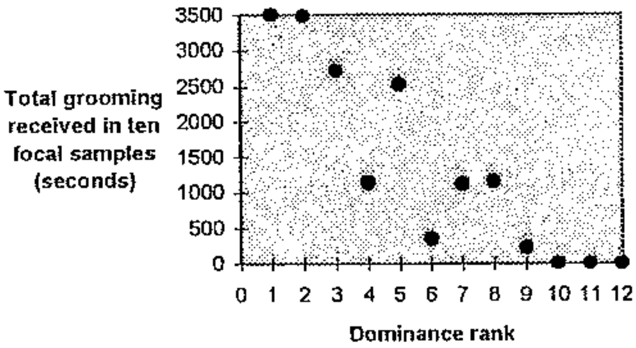

Figure 1. The relationship between dominance rank and grooming received during ten focal samples. $r_s = 0.93$, n= 12, p = 0.005

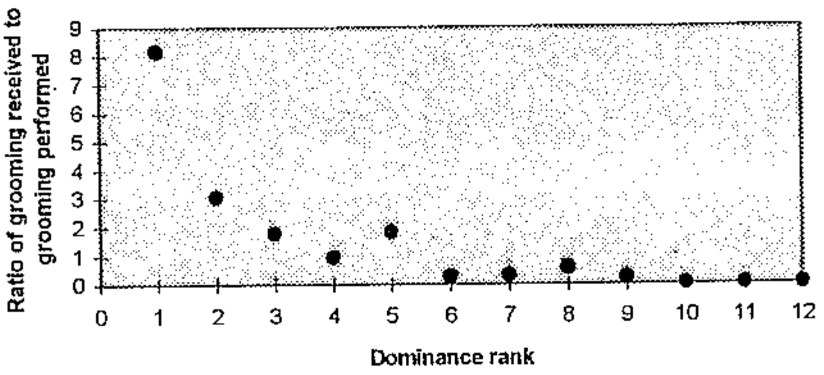

Figure 2. The relationship between dominance rank and the ratio of grooming received to grooming performed. $r_s = 0.94$, n= 12, p = 0.005

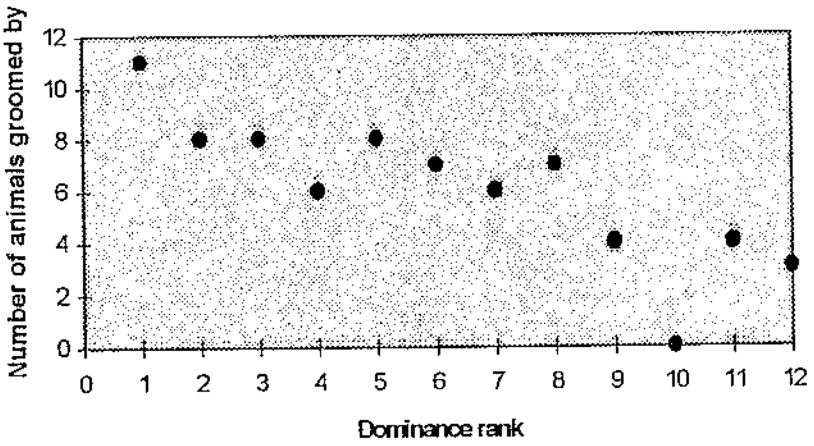

Figure 3. The relationship between dominance rank and the number of animals groomed by. $r_s = 0.89$, n = 12, p = 0.005.

The majority of grooming will occur between equally ranked individuals.

To test Seyfarth's second prediction, the durations of grooming between dyads were compared with respect to the individuals in the dyads being adjacently or non- adjacently ranked. The mean grooming duration of adjacently ranked dyads was greater than that of dyads composed of non adjacently ranked individuals (695.55 ± 311.06 and 443.33 ± 91.89 respectively, see figure 4). However non-parametric 'one-way ANOVA' showed no significant difference between the grooming durations of the two types of dyad ($H = 0.173$, $p > 0.05$).

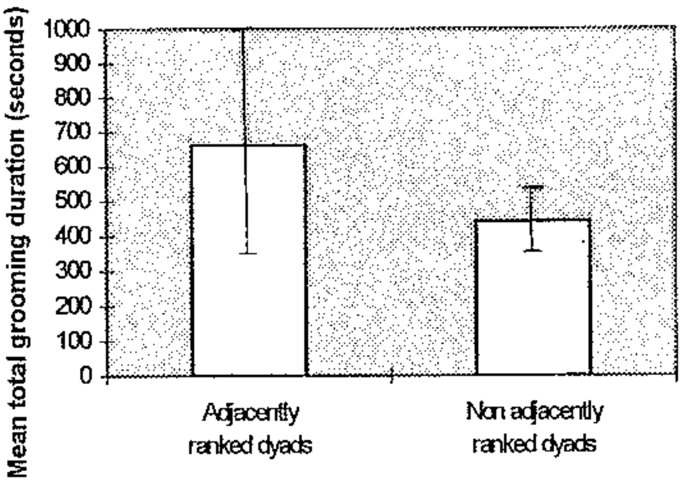

Figure 4. Mean total grooming durations of adjacently ranked and non adjacently ranked dyads. Non parametric 'One-way analysis of variance' showed no significant difference ($H = 0.173$, $p > 0.05$).

Related animals will groom more frequently than unrelated animals.

Figure 5 shows the relationship between the coefficient of relatedness (r) of members of dyads and the total frequency of grooming sessions. Between animals that were related (i.e. r = 0.125 to 0.5), grooming frequency increased as the extent of relatedness increased. However the total grooming frequency between unrelated animals was also relatively high and as a result, no significant trend was obtained ($r_s = 0.4$, n =4, $p > 0.05$).

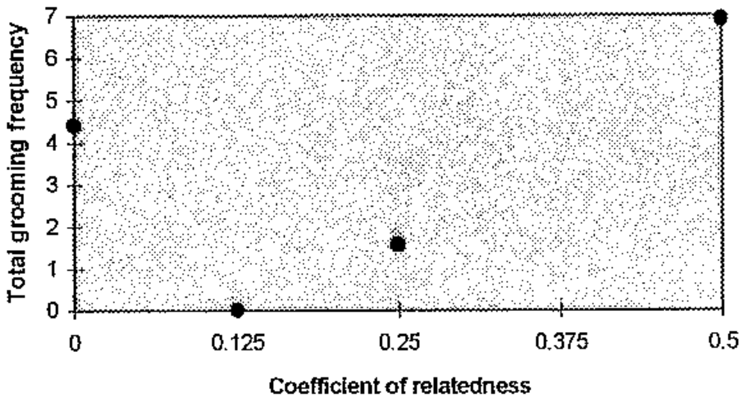

Figure 5. The relationship between the coefficient of relatedness (r) of dyads and the total frequency of grooming. No significant trend emerged ($r_s = 0.4$, n = 4, p > 0..05).

Females will receive most grooming from males at the peak of their oestrus cycles.

During the study, only one female (Imandi) underwent a full oestrus cycle exhibiting all four stages of sexual skin inflation. Of the remaining females, two were not cycling, one had just finished a cycle and two were suspected to be pregnant. Figure 6 shows the ratio of grooming performed and received by Imandi in each stage of her oestrus cycle and figure 7 shows for each stage of the oestrus cycle, the percentage of grooming sessions which included grooming of her sexual skin. Both figures show an increase in Imandi's attractiveness as a target for grooming as the peak of the oestrus cycle is reached and this attractiveness may be sexually based. Indeed, during the study, 11 sexual mounts were observed involving focal animals and of these, 7 were preceded immediately by grooming of the female by the male.

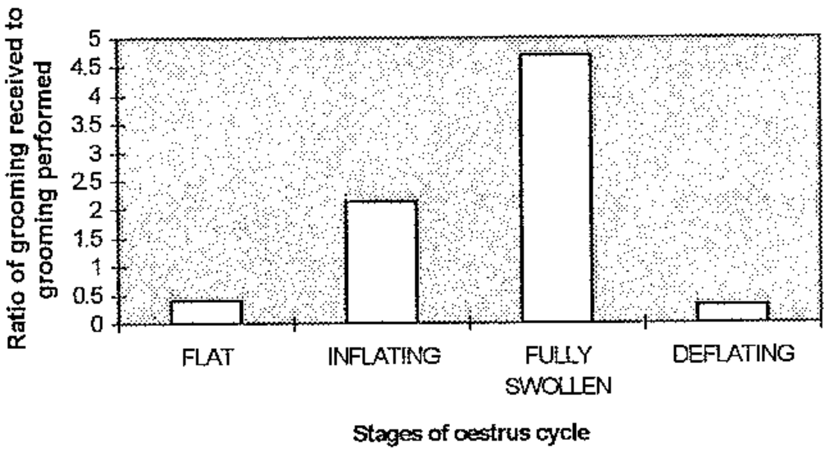

Figure 6. The ratio of grooming received to grooming performed, by Imandi at each stage of her oestrus cycle.

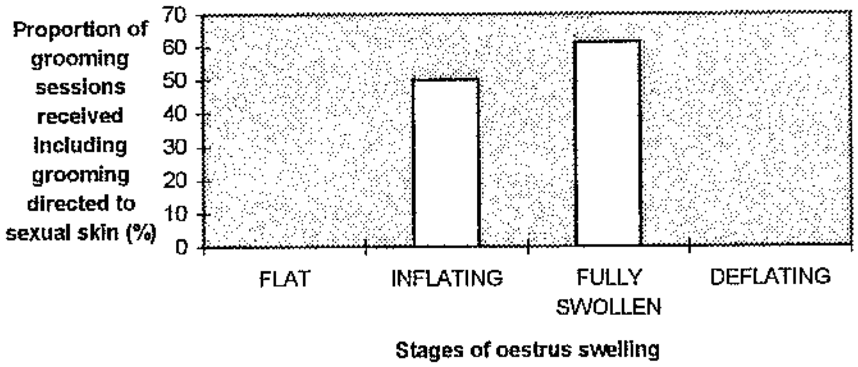

Figure 7. The proportion of grooming sessions received by Imandi which included grooming to her sexual skin. This proportion was greatest at the peak of the oestrus cycle when Imandi's sexual skin was fully swollen.

An animal that receives grooming is less likely to show aggression to the grooming animal.

It has been shown that grooming is directed up the dominance hierarchy (figures 1-3). One proposed benefit of grooming dominant animals is that of appeasing them and reducing aggression between individuals (see introduction). During this study, 30 occurrences of aggression involving focal animals were observed. In each case, aggression was directed from the dominant member of an interacting dyad to the subordinate member. Figure 8 shows the frequency of aggression plotted against the mean frequency of grooming directed towards the dominant member of a dyad. Generally, as the frequency of such grooming increased, the amount of aggression declined. However the pattern of results obtained had no statistical significance (specific 'one- way ANOVA' $z = 0.501$, $p > 0.05$).

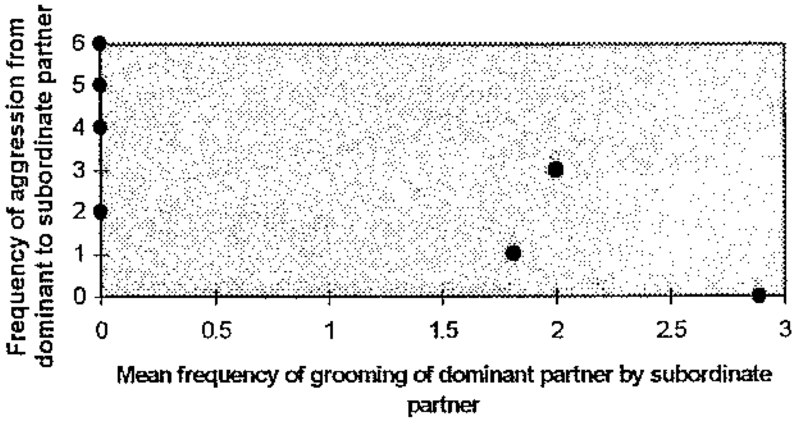

Figure 8. The relationship between grooming and aggression. Aggression was generally more frequent in dyads where the subordinate did not groom the dominant animal. However no significant pattern was obtained (specific 'one-way ANOVA' $z = 0.501$, $p > 0.05$)

An animal that receives grooming is more likely to support the grooming animal in agonistic encounters.

During 60 hours of observation, only 7 coalitions involving focal subjects were observed. These coalitions were concentrated in just four of the 66 possible dyads and in each case, the animal receiving support was subordinate to the animal giving support. Additionally, in each.case, the animal receiving support had groomed the one giving support. However, due to the small number of observations of such support behaviour, no statistically sound inferences can be drawn about the nature of the relationship between grooming and coalition formation.

The majority of grooming will be directed to areas inaccessible to the recipient animal.

Figure 9 shows the distribution of allogrooming about the body of the recipient animal. All of the body parts were groomed with the back being groomed most frequently (in 68.1 % of all grooming sessions). As expected, allogrooming was directed to areas that were inaccessible to the recipient animal significantly more frequently than to areas that the recipient could reach or see to groom itself (specific non-parametric 'one-way ANOVA' $z = 5.66$, $p < 0.05$).

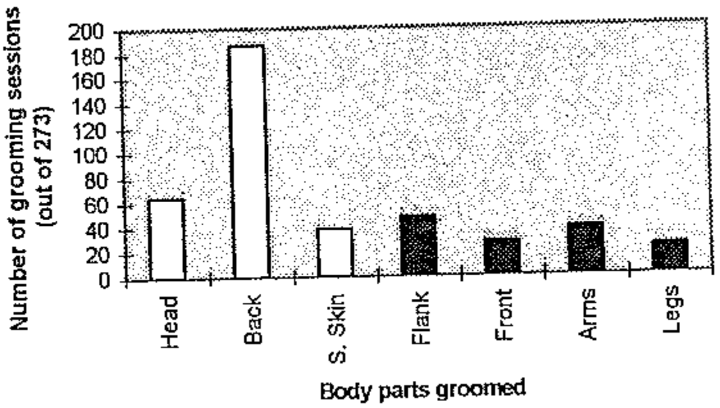

Figure 9. The distribution of allogrooming. Areas inaccessible to the recipient animal (white) received significantly more grooming than accessible areas (grey). Specific non-parametric 'one-way ANOVA' $z = 5.66$, $p < 0.05$.

DISCUSSION

The results obtained highlight the complex nature of the factors influencing grooming behaviour of black macaques.

The pattern of grooming with respect to the observed dominance hierarchy supported Seyfarth's (1977) initial prediction but not his second. Grooming was directed up the dominance hierarchy, with high ranking animals receiving the most grooming, being groomed by the greatest number of other animals and having the highest ratios of grooming received to grooming performed. In the majority of cases, for any given grooming dyad, it was the subordinate partner which performed the greater proportion of the grooming.

According to Seyfarth's model, this pattern is a result of attraction of individuals to those ranked above them in the hierarchy. Such attraction is proposed to be due to the benefits that high ranking animals can give to groomers in the future. Investigation of such possible benefits showed that animals which formed grooming relationships with higher ranking individuals were less likely to receive aggression from them. However this finding was not statistically significant. Aggression was a relatively rare behaviour and the short timescale of this study may be reflected in the lack of comprehensive results regarding any possible interplay between grooming and aggression. Similarly, very few instances of agonistic support were observed during the focal samples and no conclusions can be drawn about the relationship between grooming and coalition formation.

Seyfarth's second prediction, that most grooming will occur between adjacently ranked individuals was not upheld by this study. Although the mean total duration of grooming relationships between adjacently ranked individuals was greater than that of relationships between non- adjacently ranked animals, once more, the results were not significantly different.

Regarding the effect of kinship on grooming behaviour, the expected pattern of kin grooming more frequently than unrelated animals was not clearly observed. Closely related animals(i.e. siblings or parents and offspring) groomed with the greatest frequency. However unrelated dyads groomed more frequently than those dyads which were made up of half-sibs. High frequencies of grooming between closely related animals can be supported by the theory of kin selection (see Hamilton 1964, Maynard-Smith 1964) but such behaviour may be less apparent in the artificial environment of a zoo. Because of plentiful food supply, veterinary health care and an absence of predators, all individuals born into a captive group have considerably higher chances of surviving to adulthood than in the natural situation (see Burghardt 1975). Because of this the benefits to an individual of preferentially grooming kin, may be less than the costs of not grooming potential allies or aggressors. This may cause animals which are related but not very closely (i.e $r < 0.5$) to compromise their behaviour.

A clear pattern of increased grooming received by the female Imandi at the peak of her oestrus cycle was observed. This coincided with an increased proportion of the grooming she received being directed to her sexual skin. These observations support the findings of Dixson's (1977) study of black macaques and can be explained as sexual behaviour. 63.6 % of the observed sexual mounts were immediately preceded by grooming of the female by the male and it can be postulated that by grooming a female, a male gains access to mount her. Such grooming may increase the likelihood of a male's sexual advances being accepted by the female.

The final aspect of this study's findings to be discussed is the observed distribution of grooming about the body of the target animal. The results show that the majority of allogrooming is distributed to those parts of the body that an individual would not be able to either reach or see if it had to rely on autogrooming to maintain the clean state of its skin and fur. These results support Barton's (1985) study of various primates and suggest that allogrooming has a utilitarian function. If the purpose of allogrooming was solely to reinforce social bonds then the behaviour would be distributed more evenly over the body of the recipient animal. It can be postulated then that allogrooming as a behaviour originated as a utilitarian behaviour and that as it has developed, other functions have become associated with it.

In summary, it has been shown that black macaques exhibit a strict dominance hierarchy and that social grooming is directed up this hierarchy. The purpose of this direction of behaviour has not been clearly illustrated by this study. However the basis of relationships between grooming and reduced aggression, and grooming and coalition formation, although not significant, were apparent. Due to the relative infrequency of aggression and coalitions, it is the recommendation of this work, that further studies operate on a longer time-base to allow fuller investigation of these supposed relationships. Closely related animals groomed most frequently as predicted by the theory of kin selection. However, unrelated animals also groomed with a relatively high frequency and it is proposed that in the closed environment of the zoo, the benefits of an animal grooming kin do not outweigh the costs of not grooming non kin. Grooming appears also to have a sexual function, with the greatest grooming received occurring at the same time as the peak of a female's sexual receptivity. Such a trend can be linked to male pre-coital behaviour with males gaining access to females through grooming them. Finally data on the distribution of allogrooming about the recipient's body suggests a utilitarian function and that this was the original purpose of social grooming and that the other factors associated with it as the primates' social life developed.

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