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Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model

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Seyfarth (1977, *Journal of Theoretical Biology*, **65**, 671–698) proposed an influential model that explained the long-term patterning of grooming relationships between female primates in terms of an interaction between the idealized grooming objectives of females and competition for valuable grooming partners. A critical test of the model requires a demonstration not only that competition for partners exists, but also that females do have an underlying target for the amount of grooming that they would like to receive relative to the amount they need to give. As it is not possible to stipulate a priori what this target is, or to detect it directly, we assessed its applicability by making a set of predictions, within the framework of Seyfarth's model, as to how observed grooming patterns should change with changes in the intensity of resource competition. We tested these predictions with data from a troop of baboons, *Papio hamadryas ursinus*, for which the within-bout structure of grooming has already been shown to be sensitive to changes in resource competition (Barrett et al. 2002, *Animal Behaviour*, **63**, 1047–1053). We found no evidence of competition for grooming partners and our results do not support the predictions of the modified model with respect to the existence of underlying grooming objectives. The findings that the grooming of female baboons is more diverse and that the mean rank distance separating partners increases when resource competition is greater, together with the absence of rank effects on long-term patterns, are, however, supportive of the recent biological market approach to social interactions.

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In the absence of language, friendly engagement between adult nonhuman primates is confined essentially to the grooming that one animal can provide or request from another. No attempt, therefore, to describe primate sociality or to determine its organizational principles can succeed without an understanding of how and why grooming is deployed in the service of reproductive success. By far the most influential analytical framework has been provided by Seyfarth (1977, 1980). His conceptualization of the strategic significance of grooming for

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female primates within a closed social world has been of great heuristic value (Schino 2001), and, by establishing a set of mechanistic parameters that guide individual action, is a cornerstone of modern accounts of the higher primates as social tacticians (Harcourt & de Waal 1992).

Two apparently ubiquitous features of female monkey social interaction are that higher-ranking females get more grooming than they give and that more grooming than expected occurs between females who are close in rank (Schino 2001). Seyfarth's model, as it is known, sets out to provide an explanation for this. To do so, it makes the following assumptions: (1) grooming has both hygienic and social value (specifically with regard to coalition formation); (2) there is an optimal ratio of grooming received to grooming given (with the former more valuable than the latter), for which females strive; (3) the time available to pursue grooming opportunities is limited; (4) females are attracted to one another and this is mediated by rank, and higher-ranking females are more attractive because of their value as coalition partners; (5) when two females wish simultaneously to groom a third,

the higher-ranking has priority of access (POA). Within this framework, resource competition, making coalition formation advantageous, leads to competition for access to valuable partners. Grooming competition, therefore, is the mechanism by which the observable outcomes, i.e. the directionality of grooming (up or down the dominance hierarchy) and its distribution among potential partners, are achieved.

The model itself is a simulation of outcomes in which ranked females within a cohort of given size are limited in the amount of grooming they can give and receive, which it is their goal to optimize by obtaining a desired amount of grooming (A_r) in relation to the grooming they are willing to give (A_g). This predetermined ratio (A_r/A_g) of desired grooming outcomes produces a long-term pattern of observed grooming interactions. Changes in A_r/A_g between simulation runs therefore generate quantitatively different patterns of grooming allocation. Comparison of these patterns with those observed in real social groups are then used to determine the range of A_r/A_g values where the model matches empirical data.

The distribution of the highest-ranking female's grooming is calculated first, since her allocation is unconstrained by the rank of others. She begins by grooming the second-ranking female until either her allocated time for giving grooming (A_g) or the second-ranking female's time for receiving it (A_r) has been met. If the second-ranking female's time is up, and the highest-ranking female still has time available, she continues to groom down the dominance hierarchy, grooming each female in turn until her allocated time is used up. The second-ranking female's grooming distribution is then calculated. She distributes her grooming according to the attractiveness of others (in descending order of rank) and her allocation is constrained only by the prior distribution of the highest-ranking female's grooming. She might, for example, be disposed to give a certain amount of grooming to the third-ranking female, but be unable to meet this target, totally or in part, because of the grooming between the first- and third-ranking female that had preceded her attempt. The distributions of the grooming of all other females are calculated in the same way, giving rise to a grooming matrix that describes the actual amounts of grooming received (R) and given (G) in relation to the females' hypothetical goal (A_r/A_g). Although the main simulations assume that A_r/A_g is the same for all females, Seyfarth (1977) showed that the outcomes were robust to constrained, random assignment of values for A_r/A_g.

The simulated outcomes, where POA limits the achievement of desired outcomes, are that (1) females are more likely than expected to groom those who are very close in rank to them, and (2) high-ranking females get more grooming than they give (Fig. 1). These outcomes are argued to have general support from empirical data across a range of primate taxa (Schino 2001).

Chacma baboon, *Papio hamadryas ursinus*, females rarely form coalitions with one another (Barrett & Henzi 2002), even when resource competition is intense (Ron et al. 1996), and they persist with grooming when there is no manifest resource competition (Henzi et al. 1997).
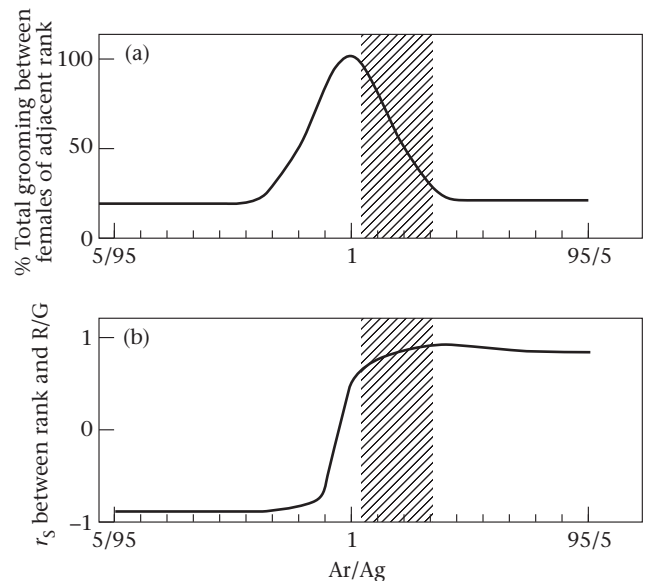

Figure 1. The simulated relationship between the desired ratio of grooming received to grooming given (A_r/A_g) and the ratio that is actually achieved (R/G). The figure is a summary version of that given in Figure 5 in Seyfarth (1977). (a) The effect of changing values of A_r/A_g on the extent to which a female's grooming allocation becomes directed to partners who are adjacently ranked. The closer that A_r/A_g is to unity, the more likely females are to have adjacently ranked partners. (b) The strength of the correlation coefficient between female rank and the ratio of grooming received to grooming given (R/G) achieved under different values of A_r/A_g. As the goal becomes increasingly biased towards giving rather than receiving grooming (A_r/A_g <1), higher-ranking females will give more grooming than they receive, but this outcome is reversed when A_r/A_g >1. Hatched area indicates the values of A_r/A_g for which outcomes were considered by Seyfarth to match empirical findings.

This finding has led us to assess the functional relevance of allogrooming within the framework provided by the theory of 'biological markets' (Noë & Hammerstein 1995). Here grooming is considered a commodity by virtue of its hygienic and hedonic value and, as such, is something that may be 'traded', either for itself or for some value equivalent (Barrett & Henzi 2001). Analyses of grooming then hinge on predictions about its allocation that derive from the structure of the local 'market', that is, the number of trader 'classes' and the relative availability of traders within each. So, for example, in the absence of competition, when grooming can be traded only for itself, we would expect females to get as much grooming as they give. Where grooming can be exchanged for another commodity, such as tolerance at a feeding site, we would predict a shift in the ratio of grooming received to grooming given, where this will be mediated by the availability of females who can provide the commodity required.

The relative success of attempts to analyse grooming interactions in this way, for both baboons (Barrett et al. 1999; Leinfelder et al. 2001; Henzi & Barrett 2002 and blue monkeys, *Cercopithecus mitis* (Payne et al., in press), together with doubts about the centrality of coalitions to the dynamics of female sociality (Henzi & Barrett 1999),

raise the possibility that free trade (i.e. unfettered by rank-related impediments) may be the organizing principle dictating grooming allocation by female monkeys. However, this conclusion needs further assessment for a number of reasons. First, our analyses have focused on individual encounters rather than the cumulative effect of such encounters, which is the express objective of the POA model (Seyfarth 1977). Although we discount the strategic capacity of which it has been assumed female monkeys are capable (Barrett & Henzi 2002), it is entirely possible that these individual encounters will, over time, build into the pattern of engagement predicted by the POA model, especially where resource competition leads to lower-ranking females providing grooming in exchange for some other commodity (Barrett et al. 2002).

Second, Seyfarth's emphasis on competition needs to be taken seriously in any attempt to extend or formalize biological markets theory, which has hitherto assumed that commodities are traded without impediment (Noë et al. 1991). Our own data indicate that high rank may enable a female to override market value (Henzi & Barrett 2002). It is therefore likely that no understanding of grooming dynamics will be complete without an assessment of the effects of competition (Barrett & Henzi 2001).

Third, given that it conceives of grooming being exchanged for support, Seyfarth's model is itself a biological markets model (Noë & Hammerstein 1994). However, it does not conform to more recent biological markets conceptualization in that it is entirely static and, more problematically, is not directly predictive about observed grooming outcomes. Although it is often assumed that the model predicts grooming up the hierarchy (Schino 2001), the values that it generates are actually coincident only with observed ratios of grooming received to grooming given (R/G) under some specific conditions (Seyfarth 1977). Seyfarth proposed that females set out to obtain a specific amount of grooming in relation to the amount they give (A_r/A_g) that is rarely realizable because of competition for access to grooming partners. So, rather than the model predicting R/G, it actually uses empirical values of R/G to support the conjecture that females set out to get more grooming than they give (i.e. $A_r/A_g > 1$). As such, the model is not readily falsifiable. Although instances where females groom down the dominance hierarchy (e.g. Parr et al. 1997) may be said to negate the assumption that females prefer to receive grooming than to give it, they disprove neither the underlying assumption that females have a goal 'in mind' nor the assumption that higher-ranking females have, or exercise, priority of access to grooming partners. It is clear from Fig. 1 that the model can accommodate observations of a negative correlation between rank and R/G, because this is predicted to occur when $A_r/A_g < 1$. Since there is no way of knowing where females set this ratio, a direct evaluation of Seyfarth's model requires proof not only of grooming competition but also of the assumption that females operate with an underlying, optimal ratio in mind. As this is not directly determinable, it can be tested only by making predictions about the effect of changing levels of ecological competition on female grooming goals, then comparing correlated changes in simulated R/G to observed shifts in grooming patterns.

Our objective, accordingly, was to generate a set of predictions explicitly within the framework of Seyfarth's model about the effects of changes in the intensity of resource competition on the allocation of grooming effort within a cohort of groomers. We then tested these five predictions using data from a troop of chacma baboons for which we have already demonstrated competition-related shifts in the within-bout structure of grooming interactions (Barrett et al. 2002). During the first phase of our study (period 1: April 1997–April 1998) one of our study troops (VT) foraged extensively for underground food items in a dry lake bed. The need to dig deep holes to obtain this food made contest competition profitable. In May 1998, the lake filled and the baboons were obliged to make much greater use of the surrounding scrub vegetation, where resources were more dispersed and contest competition less valuable. During period 2 (May 1999–October 2000), then, there was significantly less aggression and the effects of rank distance on the relative allocation of grooming within a bout significantly less pronounced (Barrett et al. 2002).

Mechanisms

The POA model is constructed on the assumption that females have some ratio of grooming received to grooming given (A_r/A_g) to which they aspire but which either active or passive competition for valuable grooming partners rarely lets them achieve. When competition is active, a higher-ranking female disrupts a grooming bout by displacing a subordinate. We predicted the following.

(1) There will be an increase in grooming disruption when resource competition increases, given an increase in the value of a high-ranking partner, and the rank of the disruptive female will lie between that of the targeted female and her grooming partner.

Most competition, however, is likely to be passive, where a female is prevented from grooming her partner of choice either because a higher-ranking female is already grooming her or because of a reluctance to approach and initiate grooming. Such inhibition may be expected if high-ranking females have nearest neighbours of similar rank and if these neighbours can be expected to prevent any attempt at initiation. As Seyfarth noted (1977), demonstrating passive competition is intrinsically very difficult. How can one show that the absence of grooming between two females is due to a decision not to engage because of the potential consequences?

We approached this by assessing changes in a measure of the likely resistance a female would meet should she attempt to groom a desired partner. On the argument that the close presence of a third, higher-ranking female will inhibit the approach of a potential groomer, we determined the frequency with which females of differing rank distances are nearest neighbours while the higher-ranking of the two females is resting and therefore at her most amenable to approach. If the target female and her nearest neighbour are both high-ranking (i.e. small rank

difference), it is reasonable to assume, if passive exclusion is a factor, that a third, lower-ranking female will not approach. Under such circumstances and using the same rationale that applies to the distribution of grooming itself, we would expect most near neighbours to be of similar rank. When resource competition increases, females should put more effort into maintaining close proximity to valuable partners, especially if grooming is exchanged for something like tolerance at a feeding site (Barrett et al. 1999).

(2) Therefore, when resource competition is high (period 1) the rank distance of nearest neighbours will be smaller than in period 2, when competition is reduced.

Outcomes

Determining the outcomes generated by constraints on grooming access within the POA framework requires a decision about where the A_r/A_g ratio is set, because this is the assumption on which predictions must be based and because there are substantial shifts in outcome with small changes in A_r/A_g (Fig. 1). We assume that the default ratio must sit somewhere in the band delineated by Seyfarth (Fig. 1), and that the effect of increased competition will be to shift it some indeterminable degree to the left; that is, as competition rises, so will the benefit accruing to increased investment in grooming others (Barrett et al. 2002). We therefore make the following prediction about the effect of resource competition on the relationship between rank and the observed ratio of grooming received to grooming given.

(3) As resource competition increases, there will be a reduction in the strength of the positive correlation between rank and R/G (Fig. 1). This is by necessity a limited prediction, since the strength of the effect depends on where A_r/A_g is set and how far it shifts.

The problems are exacerbated when we consider the relationship between A_r/A_g and the allocation of grooming to females of adjacent rank. Here, even a large shift in A_r/A_g could result in no change, since the relative representation of adjacent ranks is symmetrical about an A_r/A_g ratio of 1 (Fig. 1). However, it is possible to re-run Seyfarth's model, taking account of directionality in rank relationships rather than absolute rank differences, and to predict the following (Fig. 2).

(4) An increase in resource competition will be associated with a decreasing likelihood that the recipients of grooming will rank above the groomer. This is a more specific version of the following prediction, which derives from Prediction 2 above.

(5) The allocation of grooming to different partners in period 1 will be less diverse than in period 2, as a consequence of restrictions in gaining access to partners of higher rank. As a corollary, we would also expect grooming clique size (the number of grooming partners each female has; Henzi et al. 1997) to be lower in period 1.

METHODS

The data presented here come from one study troop of baboons (N=32–50) in the De Hoop Nature Reserve,
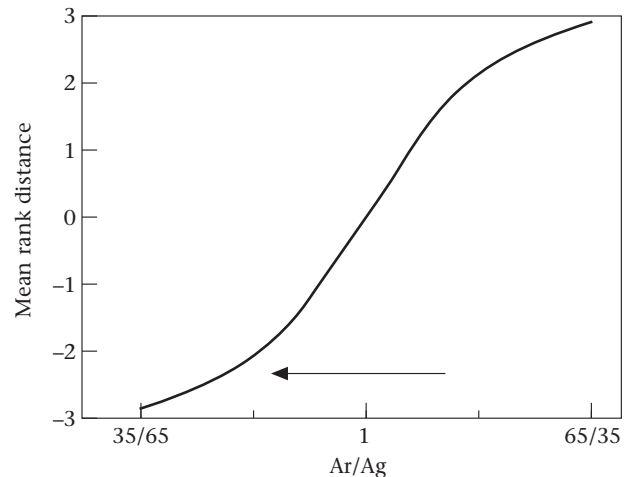

Figure 2. The effect of changing values of A_r/A_g on the mean rank of grooming recipients. Data were obtained by running Seyfarth's model for a cohort of 12 females, with each female allocated 100 units of time. A_r/A_g then represents the desired division of these 100 units into the reception and giving of grooming. We limited the range of A_r/A_g to those values across which change was realistic. Arrow indicates the hypothesized shift in A_r/A_g with increasing resource competition.

South Africa. We collected, from all fully adult females, 493 h of focal animal data (period 1: 215 h; period 2: 278 h) and 1745 h of scan data (period 1: 793 h; period 2: 952 h). The number of scans collected differed more markedly between periods 1 and 2 as a consequence of an increase in the distance between individuals and a decline in visibility. All individuals were recognizable from natural markings and were followed on foot at a distance of 5–10 m from dawn (0500–0730 hours) to dusk (1700–2000 hours) on each observation day. Instantaneous scan samples, during which we recorded the behaviour of all observable animals as well as the identity and distance of their nearest neighbours, were taken at 30-min intervals. Focal samples were 10 min long and distributed appropriately across subjects, time zones and months (Barrett et al. 2002). During each of these, we recorded all the social interactions of the focal female on a continuous basis. Here we use focal data only to determine levels of active competition for grooming partners.

We constructed a dominance hierarchy for the troop based on the outcome of decided agonistic events. During period 1, the troop contained 12 adult females. Some changes, however, occurred between the two study periods as a consequence of deaths, maturation and immigration. During period 2, there were 11 adult females in the troop, nine of which had been sampled during period 1. Females in the lower half of the hierarchy changed absolute rank but retained the same relative position, while the absolute ranks of females in the top half of the hierarchy remained the same across the two periods (Barrett et al. 2002). The highest rank was assigned the value of 1 and the rank distance between two females was calculated by subtracting one female's rank from the other. Rank distance could therefore have a

positive or negative value, with a negative value indicating that the target female's partner was lower-ranking than she was.

The comparison of the rank distance of nearest neighbours was based on the frequency distributions at group level and used absolute rank distance. The allocation of grooming across females was determined from the scan data for each female, with the relative frequency with which she groomed, or was groomed by, each other female. These frequencies were expressed as proportions of each female's time budget. We used the Shapiro–Wilk test to determine the normality of the data. Where sets deviated from normality, we log transformed the data. We used the Shannon–Wiener diversity index (H) to measure the proportion of grooming given by each female to every other female using the formula:

$$H = -\Sigma p_i (\ln p_i),$$

where p is the relative proportion of grooming given to the ith female. Note that diversity increases with the increasing value of H. We controlled for the effect of the small change in group size on H by using H_{MAX} as the divisor (Henzi et al. 1997), where:

$$H_{MAX n\ (i)} = \ln n(i).$$

In the absence of any deviation from normality (Shapiro–Wilk test), we did not apply a transform. All tests were conducted using the SPSS statistical package with alpha set at 0.05.

RESULTS

Disruption of Grooming

Of 427 female–female grooming bouts observed in period 1, 10 (2.3%) were disrupted by active intervention. Of these 10, three involved a grooming female who was higher-ranking than the intervening animal. In period 2, eight of 263 bouts (3.04%) were disrupted, with two involving a higher-ranking female. Disruption was therefore not common, nor did its relative frequency differ significantly between the two periods ($\chi^2_1 = 0.32$, NS).

Nearest Neighbour and Rank Distance

We compared the distribution of absolute rank distances of nearest neighbours using only those scans when the higher-ranking of the two females was resting. Although the difference was significant (Kolmogorov–Smirnov Z test: $Z = 1.63$, $N_1 = 1265$, $N_2 = 215$, $P < 0.05$), it went in the opposite direction to that predicted (Fig. 3). The cumulative distribution of the contribution of increasing rank distance rose more slowly in period 1, indicating that females of greater rank distance were more likely to be nearest neighbours when resource competition was greater.

Grooming Given and Received

There was no relationship between rank and R/G in either period (Pearson r, period 1: $r_{10} = -0.33$, NS; period
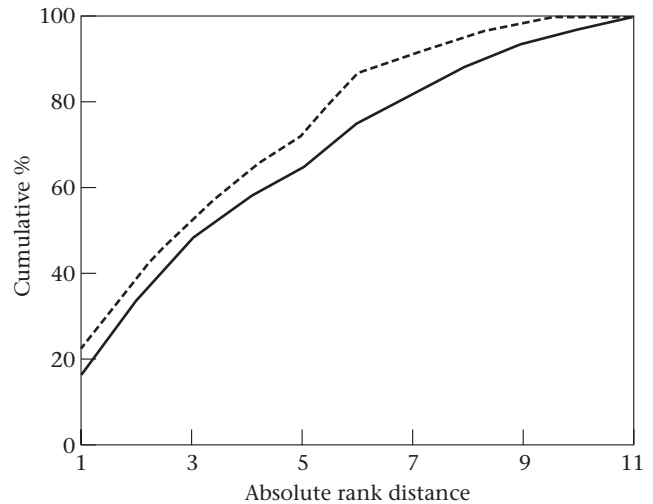

Figure 3. Cumulative allocation of grooming by females to partners of increasing absolute rank difference in period 1 (——), when resource competition is high, and period 2 (– – –), when it is low.

2: $r_9 = -0.23$, NS) or between the ratios and rank across periods (paired t test: $t_{11} = -0.25$, NS). Figure 4 suggests that this result is due to the tendency for high-ranking females both to receive and to give more grooming, although this trend reached significance in only one of the four comparisons (grooming received: period 1: $r_S = -0.7$, $N = 12$, $P < 0.05$; period 2: $r_S = -0.5$, $N = 11$, NS; grooming given: period 1: $r_S = -0.4$, $N = 12$, NS; period 2: $r_S = -0.5$, $N = 11$, NS). Since the data for the highest-ranking female were anomalous in three of the comparisons (Fig. 4b–d) and unduly influential (centred leverage values >0.2), we excluded her and repeated the analyses, thereby increasing the amount of explained variance (grooming received: period 1; $r_S = -0.7$, $N = 12$, $P < 0.05$; period 2: $r_S = -0.82$, $N = 10$, $P < 0.01$; grooming given: period 1: $r_S = -0.8$, $N = 11$, $P < 0.01$; period 2: $r_S = -0.75$, $N = 10$, $P < 0.05$).

Grooming Partners

We found no difference between the two periods, for the group as a whole, in the extent to which females received grooming from partners above or below them in rank ($\chi^2_1 = 1.73$, NS). Nor, more specifically, did we find a difference in the frequency with which nearest neighbours received grooming ($\chi^2_1 = 0.36$, NS). As this might nevertheless mask a constriction in the diversity of partners with increasing competition, we compared individual diversity scores (H/H_{MAX}) across the two periods. The means ± SE for the two periods ($X_1 = 0.67 \pm 0.047$; $X_2 = 0.5 \pm 0.049$) differed significantly (paired t test: $t_{10} = 3.55$, $P < 0.05$) although in the opposite direction to that predicted. Rank had no effect on diversity scores (period 1: $r_S = -0.05$, $N = 12$, NS; period 2: $r_S = -0.13$, $N = 11$; NS). Similarly, the difference in the size of grooming cliques across the two periods went against prediction (period 1: median = 7; period 2: median = 4; Wilcoxon signed-ranks test: $T = 11$, $N = 11$, $P < 0.05$). Rank had no effect on clique size (Spearman r, period 1: $r_S = -0.057$,
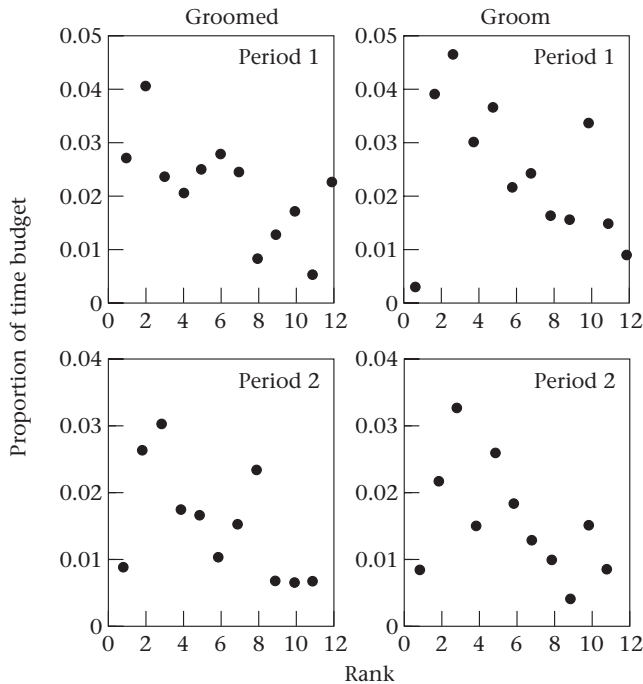
Figure 4. Relation between rank and time budget allocations of females to receiving grooming from and grooming other females when resource competition is high (period 1) and when it is low (period 2).

$N=12$, NS; period 2: $r_S= - 0.15$, $N=11$, NS). In summary, contrary to predictions, in the absence of a gross shift in the rank of grooming partners, the period of greater resource competition was marked by an increase in grooming diversity as well as in clique size (Fig. 5).

DISCUSSION

Our results support neither the contention that female relationships are underpinned by resource-driven competition for grooming nor that observed grooming allocations between females are derived from an implicit, preset objective. These are the central mechanisms by which observed outcomes are linked to Seyfarth's model and our findings, with those from other sites (Sambrook et al. 1995; Silk et al. 1999), indicate that, at the very least, they do not apply to baboons. Although it could be said that chacma baboons do not conform to the predictions because they rarely form coalitions, Sambrook et al.'s data on grooming outcomes are from a population of olive baboons, *P. h. anubis*, where coalitions are reported to be an important feature of female interactions (Barton et al. 1996). Even though in other regards they exemplify female-bonded species (Di Fiore & Rendall 1994), it may simply be that baboons are odd and that their relationships should not be seen as representative of those predicted to emerge under conditions of forced sociality and high within-group competition (van Schaik 1989).

To a large degree, of course, this is an empirical issue. The available data, although focused primarily on outcomes and not mechanisms, are sufficiently at odds to
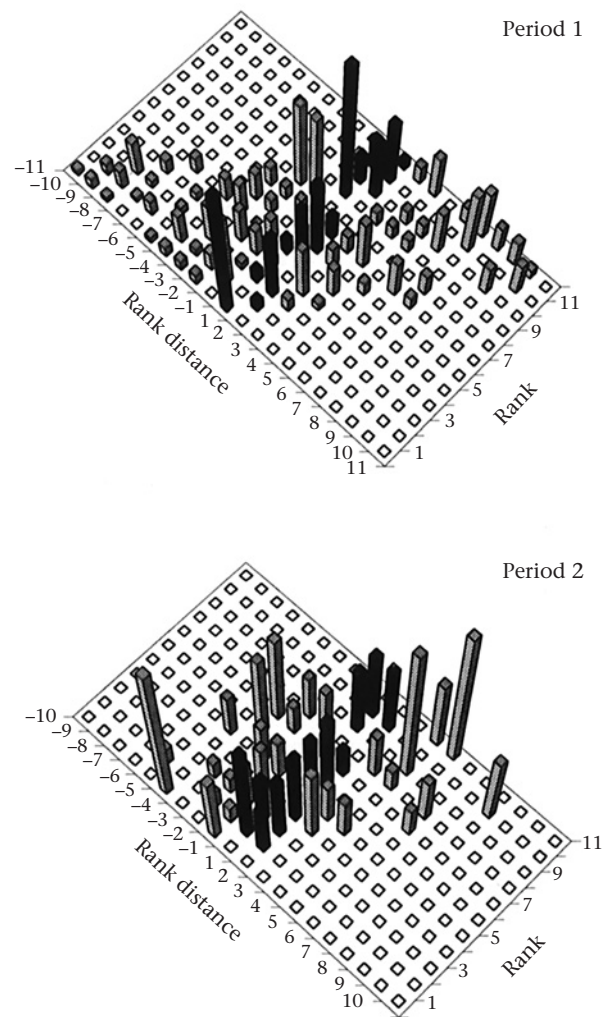

Figure 5. Relation between rank of the recipient of grooming and the rank distance of her adult female grooming partners when resource competition is high (period 1) and when it is low (period 2). The Z axis reflects the relative proportion of grooming received from each partner. Dark bars indicate female partners of adjacent rank. The illustration draws attention to the fact that the spread of partners beyond those adjacent in rank is marked in both periods although partner diversity is greater when resource competition is higher.

deny the assumptions in Seyfarth's model a general role in the structuring of female interactions. Although vervet monkeys, *Chlorocebus aethiops*, groom up the hierarchy, compete for resources and form coalitions (Seyfarth 1980), closely related blue monkeys, *Cercopithecus mitis*, do not, even though disruption of grooming bouts constitutes 16% of female–female agonism and females have ample resting time that they could divert to servicing relationships (Payne et al., in press). Female-bonded *Cebus* species direct grooming down the dominance hierarchy in both the wild (O'Brien 1993; Di Bittetti 1997) and captivity (Parr et al. 1997). Dominant females both perform more grooming than they receive and direct this grooming down the hierarchy. Schino's (2001) meta-analysis of the available primate data, on the other hand,

finds support for the POA prediction of grooming up the dominance hierarchy. However, since he also found that higher-ranking females give more grooming than lower-ranking females, this may mean that R/G is not rank related, which is what we have shown for the De Hoop baboons.

If trade in grooming is unimpeded by restrictions on access to partners, as the biological markets framework assumes and our data support, then the De Hoop females respond to changing circumstances precisely as one would expect. As resource competition increases, it pays females to exchange grooming for some commodity, such as short-term tolerance, with higher-ranking females (Barrett et al. 1999, 2002). We then see larger cliques and a greater diversity of partners, because a steeper power gradient means that more females will be able to exchange this commodity for grooming (Barrett & Henzi 2001). In the absence of strong competition, females need exchange grooming only for itself, which they are able to do with a smaller set of partners. The fact that nearest neighbours are less likely to be of similar rank when resource competition increases, can be read, in the absence of further analysis, as lower-ranking females either positioning themselves to groom when necessary or benefiting from their previous efforts through being tolerated at close proximity.

In any case, these findings confirm and extend the earlier results on the effect of resource competition on the internal structuring of grooming bouts (Barrett et al. 2002), giving added weight to the analytical value of the biological markets approach. Since they go in the opposite direction to the predictions derived from Seyfarth's model, it is clear that any reformulation of the grooming model needs not only to allow the value of grooming to be set by the market but also to assume that, temporal constraints to one side, access to partners is inalienable. To the degree to which it functions at all, grooming competition should be assumed to be more likely to distort the prevailing market than to structure it (Henzi & Barrett 2002). The biological markets framework now needs formalization for a number of reasons (Noë 2001); in the case of complex social systems, a predictive, dynamic model built on its principles will enable a better understanding of the general decision rules that interact with local environments to produce the patterns of engagement that we observe.

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