

CONSTRAINTS ON RELATIONSHIP FORMATION AMONG FEMALE PRIMATES

by

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Summary

The notion that female primates' relationships are adaptive is an explicit assumption of socioecological models of primate sociality. Here, we point out that there are other, implicit, assumptions about female relationships that also need to be considered when investigating the ultimate value of social relationships. First, there is the assumption that the operational definition of 'relationship' used in primate studies is an accurate reflection of the way in which monkeys themselves view their interactions with their peers. We also note that a relationship-based approach encourages a focus on the outcomes of social processes, rather than their dynamics, and could generate a potentially misleading view of primate sociality. Related to this first point, we also question the assumption that females possess the cognitive capacities required to engage in the long-term strategic decision-making and are capable of a high degree of forward planning. We argue that, at least among monkeys, this is unlikely to be the case, and any long-term 'planning' is the product of an evolved 'rule of thumb' and not real-time cognitive processing. Finally, we highlight the fact that group life is inherently dynamic and that chance demographic effects can limit females' social options to a degree that suggests short-term contingent decision-making would be the more optimal strategy for

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females to adopt. We suggest that greater understanding of these three elements is required for a true understanding of the adaptive nature of female relationships.

Introduction

With respect to female primates, the question: 'What are friends for?' not only raises the issue of whether social relationships are adaptive (an assumption underlying a host of theoretical models, *e.g.* Wrangham, 1980; van Schaik, 1989; Dunbar, 1988; Sterck *et al.*, 1997), but also begs the further question: are animals really 'friends'? It has long been assumed that individual females form long-term, mutually beneficial alliances with specific individuals in order to buffer themselves against the negative effects of competition within their group. This buffering is thought to take the form of coalitionary support during agonistic interactions combined with the use of grooming to build trust and alleviate stress. This notion of strategic alliances or 'friendships' formed in order to protect against an uncertain future makes a number of assumptions that may not be warranted, and a critical evaluation of some of the more entrenched may well be valuable. Here, we present a discussion of the ways in which the assumptions made about the relationships of female monkeys lead, in turn, to further unsupported assumptions regarding the function of grooming, cognitive abilities, and freedom of partner choice, illustrating our points with data from chacma baboons. We finish with some suggestions for future directions in primate research.

Background to the De Hoop baboon study and methodology

Our ongoing study of chacma baboons (*Papio cynocephalus ursinus*) was established during December 1996 in the De Hoop Nature Reserve, Western Cape Province, South Africa. The area is dominated by coastal fynbos (literally 'fine bush') vegetation, a combination of hard and leathery bushes interspersed with tough spiky grasses. Fynbos is characterized by the presence of four primary vegetation types: *Proteaceae*, *Ericaceae*, *Restionaceae* and geophytes. Many species show xerophytic adaptations to intense summer drought, low soil nutrients, strong winds and recurring fire. As well as fynbos, the baboons' range encompasses woodland areas containing a high

density of *Acacia cyclops*, an extensive sand dune system and the dry bed of a large freshwater lake (known as a *vlei* in Afrikaans). De Hoop has a Mediterranean climate, with a mean annual rainfall of 428 mm and mean annual temperature of 17°C. Due to its southerly latitude De Hoop experiences considerable seasonal variation in day length, as well as rainfall and temperature.

Two groups of baboons ($N = 50$ and 21 respectively) were habituated at the start of the study and data collection began at the beginning of 1997. All individuals are recognisable from natural markings and are followed on foot at a distance of 2–10 m from dawn (05h00–07h30, depending on the time of year) to dusk (17h00–20h00) on each day of observation. While the larger of the two troops (VT) has been followed continuously since the study's inception, data collection on the smaller troop (ST) has been more sporadic since, during certain periods of the year, it ranges in steep gorges which are inaccessible to human observers. An outbreak of a disease epidemic in April 1998 resulted in a reduction of troop size in VT from 50 to 32 baboons (Barrett & Henzi, 1998). Immigration, emigration, births and deaths have resulted in group size fluctuating between 32 and 45 since then. At present, troop size is 38 animals.

In addition to specialized data collection for specific research projects, general activity budget data and ranging behaviour are collected on five days per month. Scans are taken every half hour, during which the age, sex and activity of all visible animals are recorded, as well as the distance to the nearest male and female neighbours and the identity of any grooming partners. For VT, the troop for which data is presented here, the database currently contains 35,496 half-hour scan records. We also collect basic demographic data (births, deaths, immigration and emigrations) on an almost daily basis. The database includes records of all births and deaths, plus the reproductive history of each adult female present in the troop (approximate date of conception, gestation length, length of lactation, inter-birth intervals).

As well as information from these long-term databases, we also present more detailed data collected on VT between August 1997 and October 1998 as part of a study of maternal investment and female social behaviour. All adult females ($N = 12$) were selected as focal subjects for this study. Three females died in the epidemic of April 1998 reducing sample size to nine after this date. The day was divided into four time zones and 10 minute focal animal samples were collected on each female at least once in each time

zone per monthly sample period to give a minimum of 80 minutes of data per female per month. Data used here are based on 1281 focal samples.

The nature of relationships

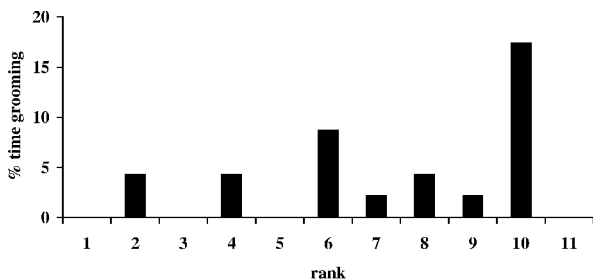
In a seminal work published in 1979, Hinde argued that a relationship was a quantity that could be abstracted from the set of social interactions that took place between two individuals. The nature of these interactions allowed one to classify relationships as affiliative or aggressive, weak or strong. From this set of relationships, one could then characterise the structure of a group as a whole. While this method has proved highly influential and has been successfully applied to a number of studies, there are three reasons why we should perhaps be cautious about its application. First, there is the problem that relationships so defined may be meaningful only to the observers who construct them and have no meaning in the lives of the animals themselves. This is something that is very hard to test, although there is evidence that animals have at least some understanding of the bonds that exist between others (e.g. Dasser, 1988; Cheney & Seyfarth, 1990).

What is lacking, however, are data on females' sensitivity to fluctuations in their social interactions with particular partners over time and how this affects their perception of their 'relationship' with another animal. As humans, we reify relationships, viewing them as solid and enduring even when we do not see a particular individual for many months or even years. However, it is not clear whether we should expect this to be the case for other primates, since it may require meta-representational ability to form such an abstract notion of a relationship. It seems more likely that monkey females perceive a relationship as a series of discrete events with a particular individual ('event perceptions': Donald, 1991), and are unable to sustain any concept of a relationship without the continued presence of the individual in question. This is not a problem for the relationship approach as such, as long as these limitations are borne in mind. However, the operational definition of relationships can be all too easy to confuse with the human concept of relationships, leading to the implicit assumption that they are, in fact, equivalent. This, in turn, may lead to an overestimate of species' cognitive abilities (see below).

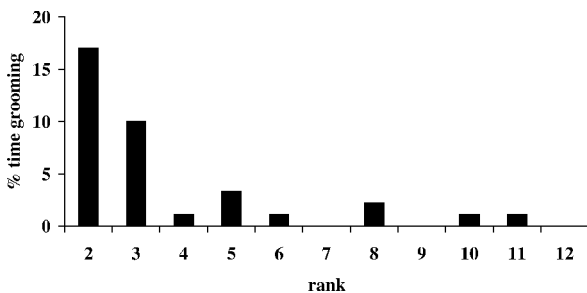
Second, although Hinde (1979) emphasised that relationships should reflect the sum total of a dyad's interactions, many authors (ourselves

included) have focussed exclusively on grooming as a way of identifying affiliative relationships. Indeed, grooming is often taken to be synonymous with adult social engagement (see *e.g.* works referenced in Dunbar, 1988). If this is indeed a valid metric for assessing the long-term value that animals ascribe to their associations, then this presents no problem. However, if grooming is not, in reality, a good measure of relationship strength, then it could lead to a false picture of female-female relationships and, by extension, overall group structure.

To illustrate this, Fig. 1 shows the grooming distributions for two females, one low ranking, DE, (Fig. 1a) and one high ranking, JU (Fig. 1b) taken from focal data collected between 1997-1998. Details of the calculations



(a)



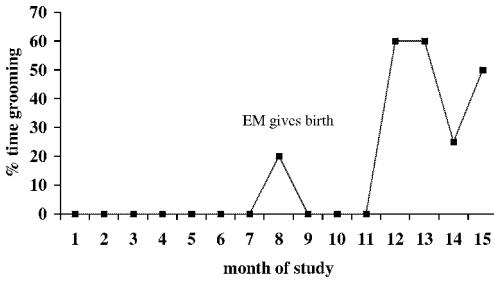
(b)

Fig. 1. Distribution of grooming across all other females for (a) a low ranking female, DE (rank 12) and (b) a high ranking female, JU (rank 1). Primary partners are those for which total grooming time is equal to or greater than 10%. To identify primary partners, the monthly allocation of each females' grooming time directed to all other females was calculated as a percentage. The overall frequency of grooming per dyad was then calculated as the mean of these monthly figures.

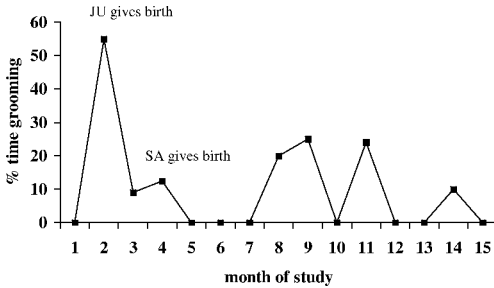
used are given in the figure legends. Both females show a preference for particular grooming partners; we designated these as 'primary partners' and defined such partners as females to whom more than 10% of their total grooming time was allocated. Dunbar (1984) suggests that females who maintain this level of grooming can be considered as a 'coalition', a long-term mutually supportive alliance. In the case of DE, one primary partner could be identified (ranked 10), whereas JU had two primary partners (ranked 2 and 3). However, when the distribution of grooming across months for each dyad is considered (Fig. 2a-c), it is clear that these preferences were not consistent across the fifteen months of the study, and were tied quite closely to the birth of an infant to one or other of the females. When data from all females were analysed, the proportion of time spent grooming when an infant was present was significantly higher than when there was no infant present (Fig. 3: Wilcoxon signed ranks test: $z = -0.254$, $n = 8$, $p = 0.012$). The presence of young infants thus appears to increase females' attractiveness to particular individuals. If such influences are not recognized and acknowledged, they may lead to a distorted view of the degree of affiliation between individuals over longer time scales.

Information from the long-term database seems to bear this out. Table 1 shows the primary grooming of the De Hoop baboon females over the period 1997-2000¹. Details of the methods used to determine primary partners are given at the foot of the table. It is clear that there is some variation across years in grooming partnerships (Table 1). On average, females changed their primary partner twice across the four years. Interestingly, there was much more variability among low ranking than high ranking females. For the four top ranking females (JU, SA, AL, GI) the median number of partner changes was 1 (and these four females formed an exclusive grooming clique), whereas the three bottom ranking females (BE, EM, DE) each changed partners three times (the maximum possible) (Mann-Whitney U -test: $U = 0.0001$, $p = 0.026$, 2-tailed). This increased consistency among high-ranking females implies that, as Seyfarth (1977) suggests, these

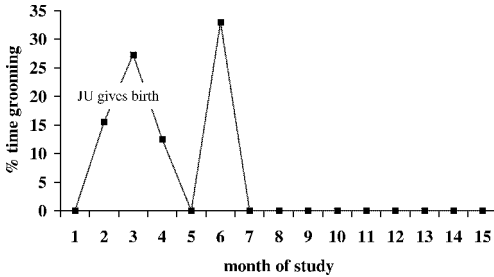
¹ Dividing the sample up into years is, of course, arbitrary and does not reflect 'baboon time' in any meaningful way; this would require dividing the sample up by events that, for example, led to a change in group composition or a change in ecological circumstances: see Barrett *et al.*, *subm.* However, since this is the time scale over which many observational studies are conducted, it seems reasonable to investigate the impact of this time scale on an assessment of relationships.



(a)



(b)



(c)

Fig. 2. Distribution of grooming between (a) DE and primary partner, EM (b) JU and primary partner, SA and (c) JU and primary partner, AL, across the 15 months of the study period.

individuals have greater flexibility and freedom to select their grooming partners than those of lower rank.

It is often suggested that proximity can also be used, either alone or in conjunction with grooming, to measure long-term affiliation. The rationale is that females will spend most time close to females with whom they feel comfortable and these will be females with whom they are affiliated. However, in this sample, proximity measures were equally as variable as

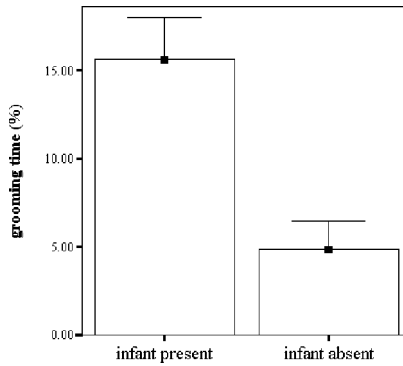


Fig. 3. Comparison of percentage of time spent grooming with primary partners when infant is present versus infant absent for eight pairs of primary partners. Error bars represent one standard error. The percentage time spent grooming was calculated for each of eight individual pairs of females during the period when a young infant was present (0-6 months) and when neither female had an infant.

grooming measures across the time period covered. Females displayed, on average, two changes in their primary proximity partners, although in this case there was no significant difference in this tendency between high and low ranking females (high rank = 3 changes, low rank = 2 changes; $U = 6.00$, $p = 1.00$). In addition, a female's primary grooming and proximity partners for any given year did not always coincide; on average, a female's primary grooming partner was also her primary proximity partner for only two out of the four years covered.

While this and the previous analysis are purely descriptive, the social fluidity shown by females across months and on a year-to-year basis suggests that grooming behaviour alone is not necessarily the best way to identify stable long-term relationships. One reason for this could be because there aren't, in fact, any long-term relationships to identify within this population, and short-term considerations alone drive female social behaviour. Alternatively, our analysis may have been too stringent in its use of primary partners alone. In a number of cases, females vacillated between the same two or three females over the years covered, suggesting that if one were to consider a female's top five partners instead, regardless of the amount of time devoted to grooming them, then it is possible that more consistency would be apparent.

However, even if this were so, it remains the case that there is a degree of variability in partner choice within and between years, suggesting that females vary in their importance to each other over time. 'Primary' partner-

TABLE 1. *Changes in primary grooming (G) and proximity (P) partners, 1997-2001*

I.D.	1997		1998		1999		2000	
	G ¹⁾	P ²⁾	G	P	G	P	G	P
AI (8/6) ³⁾	EM	JU	EM	AL	EM	FE	DE	DE
AL (3)	JU	JU	SA	AI	SA	FE	SA	SA
BE (9/7)	EM	SA	NA	NA	FE ⁴⁾	NA	EM	EM
DE (12/11)	BE	AY	EM	AI	BE	EM	AI	AI
EM (10/8)	BE	AI	AI	AI	AL	DE	BE	BE
GI (4)	SA	SI	AL	AL	SA	JU	SA	JU
JU (1)	SA	SA	SA	AL	SA	SA	SA	SA
NA (5)	GI	GI	BE	BE	FE	BE	EM	EM
SA (2)	JU	JU	AL	AL	AL	JU	AL	AL

¹⁾ Primary partners were identified for each year by calculating the percentage of each females' total grooming scans that were directed to each other female. Primary partners were defined as those individuals with whom a female spent >10% time grooming, following Dunbar (1984). Data are presented only for those adult females who were alive throughout the entire four year period ($N = 9$).

²⁾ The percentage of time spent in proximity to each of the other females was calculated from nearest neighbour scans. Primary proximity partners were identified as those with whom a female spent the highest percentage of her time as nearest neighbour.

³⁾ Female rank is given in brackets. Females with 2 values underwent an increase in relative, but not absolute, rank as a consequence of the death of higher-ranking females during April 1998.

⁴⁾ FE was a young adult female that immigrated following the epidemic in April 1998.

ships or 'coalitions' may not, therefore, be any such thing, but may instead represent a temporary response to the particular conditions that pertain in the market place of the group. Females' social responses may thus take place on a more short-term basis than is usually supposed and frequent partner changes may be the norm, rather than the exception. Increasing attention to the likely short-term benefits of individual action may therefore pay dividends when trying to explain the apparent goals of female sociality.

This brings us to our final cautionary point regarding Hinde's method, which is that it encourages a focus on *outcomes*, rather than on the dynamics of the interactions themselves (what we shall refer to here as *process*). This is seen most strikingly in another very influential model of female grooming relationships put forward by Seyfarth (1977). This model is an early prototype of a Biological Markets model (Noë *et al.*, 1991; Noë & Hammerstein, 1994); a fact we wish to emphasise since, in discussion

with others working in this field, we have discovered that our advocacy of biological market models has been taken to be in direct opposition to Seyfarth's (1977) model. While we disagree with the notion that grooming is necessarily related to coalitionary support, the model itself, based as it is on competition and partner choice, is a *bona fide* biological markets model.

Biological market models are designed to predict the manner in which animals trade valuable 'commodities' depending on their status within the market place, and the supply and demand of the commodities in question (see also Barrett & Henzi, 2001; Barrett *et al.*, 1999, 2000; Henzi & Barrett, 1999). In his early model, Seyfarth (1977) assumed that high ranking females would be more attractive than low ranking females due to their superior ability to provide support in agonistic interactions. He also assumed that individuals could use grooming to obtain such support from these animals. Finally, he assumed that this would lead to competition between females for access to high ranking grooming partners, such that lower ranking females would be more restricted in their ability to groom the partner of their choice than those ranked above them. Seyfarth (1977) used these 'rules' to predict the grooming distribution of a typical group of female monkeys subject to this constraint. This produced a grooming matrix which showed that, as a result of competition, females would spend most of their time grooming those next to them in the hierarchy, and that most grooming would be directed up the hierarchy to the highest ranking females because of their greater value as coalition partners.

Data on vervet monkeys confirmed the predictions of the model (Seyfarth, 1980; see also Hemelrijk, 1990), although tests of the model using data from other several other species have given somewhat inconsistent results (see review in Henzi & Barrett, 1999). Moreover, in cases where the model was supported, the direction of grooming up or down the hierarchy and the distribution of grooming across females of different rank was taken as sufficient evidence to support the model (*e.g.* Schino, 2001), with very few attempts to test its underlying assumptions (but see Fairbanks, 1980; Silk, 1982). However, it should be clear that different processes can potentially produce the same outcome. For example, high ranking females may 'demand' grooming from lower ranking females, rather than low ranking females competing for access to high ranking females. This would lead to the same outcome, but the process would be diametrically opposed

to that assumed by Seyfarth (1977). An analysis of the dynamics of inter-individual interaction, on the other hand, would be able to reveal such an effect.

In a similar fashion, adopting the more sophisticated biological markets model of Noë & Hammerstein (1994), with its greater emphasis on individual interaction, generates predictions which have a much greater potential to determine the value of social support to animals than a study of outcome alone. For example, the value of grooming will vary across individuals, such that very low ranking animals can be predicted to 'pay' a much higher price (spend much more time grooming) for potential support than an animal higher up the social scale (because the marginal value of any support gained would be greater for the lower ranking animal). This effect would be exacerbated by the level of competition from other animals, such that larger groups are predicted to display these effects more strongly than smaller groups. An understanding of market forces as determinants of social interactions thus allows more precise predictions to be made and tested. Overall, it seems that the overwhelming focus on relationships as the unit of analysis may be hindering our progress in understanding female sociality. The development of Seyfarth's model into a true biological markets model (*sensu* Noë & Hammerstein, 1994) seems essential to progress in this field.

Grooming and coalitions

The other effect that Seyfarth's model has had is to link inextricably grooming with coalitionary support. As we have argued elsewhere, most authors assume that the main function of grooming is to ensure coalitionary support from others, even though there is little empirical evidence to support such a view (Henzi & Barrett, 1999). Our own work on chacma baboons has shown that adult females do not support each other in agonistic interactions, although they maintain grooming at high levels (Henzi *et al.*, 1997; Ron *et al.*, 1996; see also Silk *et al.*, 1999). Thus, the notion that grooming functions as a means of cementing coalitionary alliances cannot be taken as a general explanation for primates as a whole. Given that this is the case, what is the value of grooming (and social relationships) for these animals? We have argued that grooming is valuable in and of itself (both for hygienic purposes and in that it raises levels of endogenous opiates) and that it does

not necessarily index a pre-existing bond. Instead, we suggest that chacma baboons use grooming as an exchange commodity to satisfy short-term goals. As the analysis above suggests, one such goal is access to infants. Adult female baboons are very interested in young (0-3 month old) infants and are keen to inspect and handle those of other females. As we have shown here, new mothers receive elevated levels of grooming (see also Altmann, 1980). We have shown elsewhere that the amount of time a female has to spend grooming a mother in order for her handling to be tolerated varies with the number of infants available in the group at the time: an example of a true market effect (Henzi & Barrett, in press). These results and our previous work therefore suggest that chacma female grooming interactions reflect the short-term exchange of commodities for a variable price, rather than the servicing of a friendship *per se*: females are 'business partners', not friends.

Cognition and relationships

This notion of short-term benefits as a driving force for behaviour brings us to another assumption regarding primate relationships. The large brain size of primates and their impressive cognitive abilities (see *e.g.* Tomasello & Call, 1997) have given rise to the presumption that the decisions that animals make with regard to their social interactions are a consequence of cognitive processes that take place in the animal's head in real time. Dunbar (1984), for example, in a study of gelada baboons, states that he makes 'frequent use of the language of *conscious* decision-making' (italics added) because '[it is] abundantly clear to me that strategy evaluation is precisely what animals are doing' (Dunbar, 1984; p. 4). With respect to their immediate goals, this might well be true. Monkeys' abilities to solve a wide variety of problems is impressive and well documented (see Tomasello & Call, 1997 for a review). However, there is no evidence to suggest that monkeys are capable of the 'mental time-travel' or 'off-line thought' (Tulving, 1983) required to plan ahead effectively and judge which animals will make the best alliance partner given a variety of possible futures. On the contrary, monkeys (like very young human children) appear to be trapped in the present, capable of responding only to their immediate needs and goals, or to objects presenting a current sensory stimulus (Tulving, 1983).

In humans, the ability to plan ahead, to contemplate the future and reflect on the past, are faculties associated with the pre-frontal cortex (see Fuster, 1980). Aspects of other higher cognitive processes such as Theory of Mind, self-recognition, autobiographical (episodic) memory and auto-noetic consciousness (the awareness that we are individuals who persist through time) are also associated with this region (*e.g.*, Fletcher *et al.*, 1995; Goel *et al.*, 1995; Stone *et al.*, 1998; Keenan, 2000). In humans, the pre-frontal cortex has greatly expanded to account for 33% of total cortical volume (Fuster, 1980). In the macaque, this area accounts for only 11% of total cortical volume. It seems likely that, along with their inability to recognise themselves in mirrors or pass ToM tests, monkeys are also unable to plan ahead with any effectiveness over time-frames longer than a few hours or to inhibit their behaviour in order to achieve long-term goals. The ability to plan strategically for the future in one's own best interest also seems to require a well-developed form of autobiographical or episodic memory; such a faculty does not develop in humans until around four years old (Pillemer & White, 1989) and may be linked to the acquisition of language and the development of metarepresentational thought; again these are abilities that monkeys are known to lack (we have already noted that a lack of metarepresentational abilities may limit the degree to which females can conceptualise their relationships). Interestingly, chimpanzees have a pre-frontal cortex intermediate in size to that of macaques and humans (17%), and they apparently show ToM abilities similar to those of a 3 year old child (O'Connell, 1995). We might therefore expect chimpanzees (and other apes) to show similarly enhanced planning abilities to monkeys.

This lack of planning ability therefore suggests that the formation of long-term relationships is not the result of strategic planning taking place within the head of an individual monkey, but reflects the operation of an evolutionary rule of thumb requiring very little in the way of advanced cognitive abilities. That is, when a gelada female forms a 'coalition' with her eldest daughter (see *e.g.* Dunbar, 1984), this is due, not to the weighing up of possible options by a cognitive process in the female's head, but to a 'rule of thumb' which states something along the lines of 'groom your oldest living female offspring'; a rule honed by natural selection and of which the female herself is unaware. This may seem pedantic since the ultimate outcome of either process is the formation of a fitness-enhancing grooming bond, but it does mean we have to view certain behaviours in a different light. That is, we

need to remember that not all primate behaviours are necessarily the result of 'smart thinking' in the here and now, and to pay greater attention to the extent to which evolutionary 'rules of thumb', similar to those that guide the behaviour of less cognitively well endowed species, also prevail within the primate order (see also Gigerenzer *et al.*, 1999).

Demography: a neglected constraint on behaviour?

Whether or not coalition formation is guided by evolutionary rules of thumb, it is nevertheless the case that the key element required is a suitable partner. This in turn depends on demographic processes and is subject to chance effects (Dunbar, 1988). To return to our female gelada, a coalition with an elder daughter is only possible if she actually has one in the first place. Understanding the value of female relationships should therefore involve comparing strategies between individuals whose partner choice options differ, as well as characterising the 'norm' for a particular species. In the case of gelada, females lacking female kin generally favour the unit male as their primary partner, whereas those with kin never groom preferentially with the male. It seems likely that the gains made by grooming female kin are greater than those made from grooming the male, although what these are is still not fully clear.

By the same token, the apparent focus on group males as grooming partners by chacma baboons in the Drakensberg mountains has been taken as an indication that this population is cross-sex bonded (Barton *et al.*, 1996). However, the low birth rates and slow rates of maturation in this habitat (Lycett *et al.*, 1998) mean it is unlikely that females have many living kin available to groom and that this so-called cross-sex bonding is determined by the size and demography of groups and the constraints on animals' time, rather than by a true preference for males. Indeed, data show that most females are, in fact, female-bonded (Henzi *et al.*, 2000).

Partner availability as a constraint on individual action is not explicitly acknowledged in most socioecological models of female sociality, even though demographic processes lie at the heart of many of them. This is not due to a lack of attention to this issue *per se*. Altmann & Altmann (1979), for example, have shown how chance demographic processes could have a profound and long-lasting effect on group structure and social relationships,

while several efforts have been made to model how demographic processes could lead to the matrilineal inheritance system of Japanese and rhesus macaques (Schulman & Chapais, 1980; Datta & Beauchamp, 1991; Datta, 1992; Hill, 1999) and the age-graded system of langurs (Hrdy & Hrdy, 1976). It is also true that Seyfarth's grooming model (1977; 1980) tackles this issue to some degree. However, the link between patterns of coalition formation across populations of the same species, and between different species, has not been related to demographic processes as such. In particular, there has been little, if any, recognition that differences in reproductive scheduling between females may determine the likelihood of coalition formation through time. With regard to chacma baboons, we suggest that a lack of partner reliability through time tips the balance against coalition formation in this sub-species.

During pregnancy, female chacma baboons become increasingly peripheral and asocial, avoiding most forms of normal social interaction. In particular, they engage in far fewer aggressive interactions (Barrett & Henzi, in prep.) and appear to avoid conflict. This may be a tactic to reduce stress and reduce the probability of miscarriage. Lactating females during the early post-natal period (0-6 months) show a similar avoidance of conflict (Barrett & Henzi, in prep), suggesting that they also attempt to safeguard against any threat to their reproductive output and hence fitness.

If females avoid conflict during periods when they are particularly vulnerable to high potential fitness costs, then they are unlikely to make effective or reliable coalition partners. The benefits of aiding a coalition partner would be far outweighed by the potential costs of losing or injuring their current offspring, such that females would be forced to defect on their partners for a proportion of the time. Since pregnancy in baboons lasts 6 months, a female would be out of action and unable to aid her partner for up to a year at a time. In addition, the fact that baboons are non-seasonal breeders means that potential coalition partners are likely to be pregnant/lactating at different times, which further reduces the likelihood that both individuals will be able to act as reliable partners for each other.

To illustrate this we have used the long-term demographic database to construct reproductive histories for all adult females present in the troop for the entire four year period (Fig. 4). We compared dyads that were classified as primary partners from the 97-98 database. In most cases, these were also identified as primary partners in at least two years in the long-term database.

For each dyad, we calculated (i) the percentage of time that both females would be free to come to each other's aid (neither female was pregnant or had a young infant under 6 months old), (ii) one female was potentially available to help the other (excluding periods when both were available) and (iii) the mean length of time during which only one female was available to help the other. This translates into the amount of time a given female would have to wait in order for her aid to be reciprocated by the other if females were to prove reluctant to become involved while they were pregnant or had a young infant (referred to as 'wait time').

Looked at in this way, it is apparent that the length of time when both females within a partnership were potentially available to act as coalition partners was quite variable, but in most cases was fairly short. On average, both females were available for only 20% of the total time (Table 2). Rather more promisingly, at least one female would be free to come to her partner's aid just over 50% of the time on average. However, this involved a mean wait time of almost six and half months before her partner would be free to reciprocate.

All these primary pairs were close in rank. It is possible that distantly ranked dyads could show different patterns, and that low ranking females may be able to reap rewards from grooming partners who are relatively free

TABLE 2. *Availability of partners through time for 'primary partner' dyads for period Jan 1997–June 2001*

Dyad	Rank distance ¹⁾	Both partners available (%)	One partner available (%)	Mean 'wait time' (months) ²⁾
JU-AL	2.0	22.2	59.3	8.0
SA-AL	1.0	7.4	64.8	7.0
BE-EM	1.5	20.4	64.8	7.0
GI-SA	2.0	12.9	37.0	4.0
AI-EM	2.0	29.6	27.8	3.0
DE-BE	3.5	29.6	66.6	12.0
DE-EM	2.0	20.4	44.4	4.8
JU-SA	1.0	14.8	48.1	5.2
Mean	1.9	19.7	51.6	6.4

¹⁾ Mean rank distance over four year period. Rank distance changed due to the death of 3 females during April 1998.

²⁾ Mean amount of time that only one partner was available as a potential coalition partner for the other.

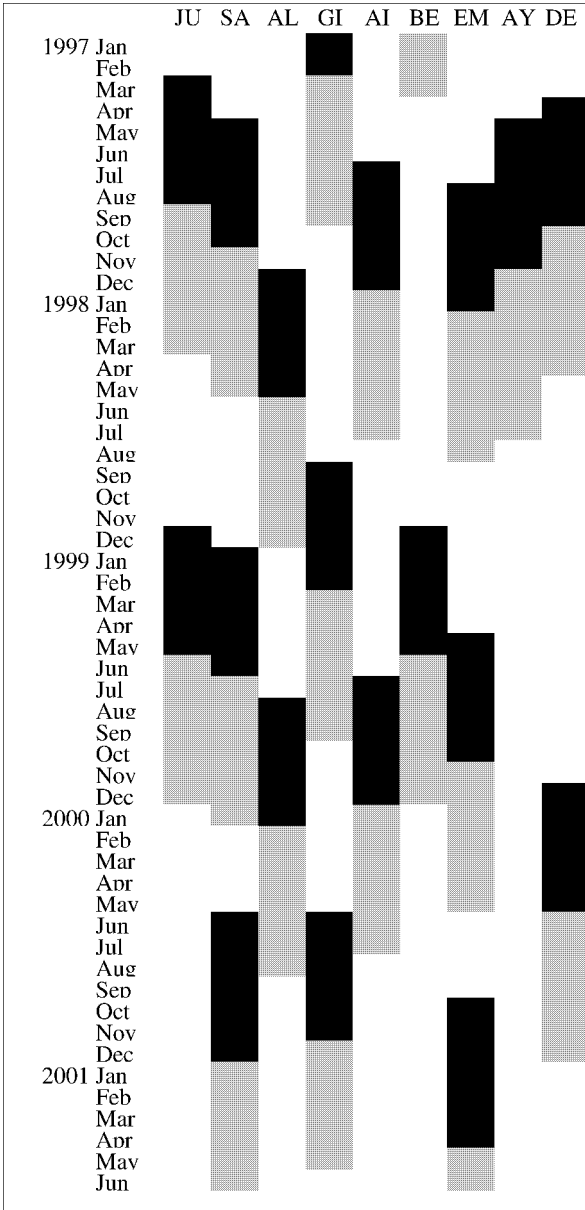


Fig. 4. Reproductive histories for nine adult females between January 1997 and June 2001 inclusive. Black bars represent gestation periods and grey stippled bars represent the month of birth and the first 6 months of the lactational period.

TABLE 3. *Partner availability through time for distantly ranked dyads during the period Jan 1997–Jun 2001*

Dyad	Rank distance ¹⁾	Both partners available (%)	One partner available (%)	Higher or lower available for longer?	Mean wait (months)
EM-JU	8.0	16.7	53.7	H	5.8
DE-JU	10.0	22.2	51.9	=	7.0
EM-SA	7.0	14.8	33.3	L	3.6
DE-SA	9.0	20.4	38.9	L	7.0
Mean	8.5	18.5	44.4		5.9

¹⁾ mean rank distance over four year period. Rank distance changed due to the death of 3 females during April 1998.

to come to their aid. However, data from four dyads of distantly ranked females shows a similar pattern (Table 3). Both females were available for less than 20% of the time on average and, in two out of the four cases, it was the lower ranking female that showed higher availability across time.

Given these findings, we suggest that coalition formation may be more likely in seasonal breeders, like vervet monkeys and the macaque species, where females are all out of action at the same time, and the period of low partner availability/unreliability is short and predictable. Small body size may also interact with seasonality to increase the likelihood of coalition formation since smaller animals develop at faster rates, so that the overall length of time that a potential coalition partner is unavailable will be significantly shorter than for larger bodied animals. We are currently examining patterns of coalition formation across species in relation to factors like body size and seasonality in order to determine whether any consistent patterns exist.

Finally, the size of the female cohort within a group may also partly determine the likelihood of coalition formation, since an animal could overcome a lack of partner reliability through time by increasing its number of potential coalition partners. Small cohort sizes will limit coalition formation, since there will be fewer females available to choose from in the first place, and females will thus be unable to make use of such a 'bet-hedging' strategy. According to this hypothesis, chacma females, who do not form coalitions, should live in smaller cohorts on average than females in coalition-forming populations of olive and yellow baboons. To test this, we compare data from 11 populations of baboons (6 non-chacma and 5 chacma) across Africa,

where long-term studies can confirm the presence or absence of behaviour patterns. As predicted, cohort sizes were significantly smaller in chacmas than in olive/yellow baboons (Table 4: median cohort size: chacma = 12.7, non-chacma = 19.8. Mann-Whitney U -test: $U = 0.500$, $m = 6$, $n = 5$,

TABLE 4. *Comparison of cohort size between chacma and non-chacma (olive and yellow) baboons*

Locality	Sub-species	Coalitions?	Mean female cohort size	Source
De Hoop, South Africa	Chacma	No	9.5	pers. obs.
Okavango Delta, Botswana	Chacma	No	12.7	Bulger & Hamilton, 1987; Silk <i>et al.</i> , 1999
Mkuzi, South Africa	Chacma	No	17.0	pers. obs.
Drakensberg, South Africa	Chacma	No	6.9	Henzi & Lycett, 1995
Cape Point, South Africa	Chacma	No	14.0	Hall, 1963; D. Gaynor, pers. comm.
Tana River, Kenya	Yellow	Yes	19.0	Bentley-Condit, & Smith, 1997; Bentley-Condit, pers. comm.
Amboseli, Kenya	Yellow	Yes	17.5	Noë & Sluitjer, 1995; Samuels, <i>et al.</i> , 1987
Mikumi, Tanzania	Yellow	Yes	30.0	D. Rasmussen, 1981; K. Rasmussen, 1985; G. Norton, pers. comm.
Laikipia, Kenya	Olive	Yes	17.0	Kenyatta, 1995; S. Strum, pers. comm.
Gombe, Tanzania	Olive	Yes	20.5	Ransom, 1981; A. Collins, pers. comm.
Gilgil, Kenya	Olive	Yes	24.0	Bercovitch, 1988; S. Strum, pers. comm.

$p = 0.004$), suggesting that chacma females have significantly fewer potential coalition partners available to them, reducing their ability to compensate for any potential differences in partner reliability across time.

While these data identify some of the potential constraints on coalition formation, the key question that needs to be answered in this context is the level to which partner reliability can drop before the system collapses. Investing in a relationship with a coalition partner that is available for only a fraction of the time may not pay in the long-term, and the inherent uncertainty in such a system would leave it very vulnerable to cheating. In order to clarify this, formal modeling is required to establish the acceptable level of partner uncertainty within an evolutionarily stable system. This is beyond the scope of this paper, but it is clear that a state-dependent modeling approach could provide some valuable pointers to the relative importance of factors like partner reliability, body size and female cohort size in determining the frequency of coalition formation.

General discussion

The data presented in this paper are intended to be illustrative and suggestive, not conclusive. However, they are sufficient to cast doubt on some of the assumptions made about the relationships of female primates and to suggest directions for future research.

First, the finding that grooming does not necessarily form a reliable index of a relationship between two animals is important and needs to be taken seriously. In particular, females were significantly more likely to groom their primary partners when there was a young infant present than when there was not, suggesting that an animal's immediate concerns have a major impact on patterns of grooming between individuals.

This concurs with our other findings, which showed that the immediate returns to be gained from grooming for own hygienic/hedonistic benefits may be sufficient to explain patterns of grooming reciprocity both within and between groups (Barrett *et al.*, 1999). Kapsalis & Berman (1996), using long-term data from the Cayo Santiago rhesus macaques, also show that patterns of grooming rank are labile over time, and argue that this may be a response to changes with social and environmental circumstances. Relying on grooming alone to characterise 'relationships' may therefore be

misleading. Instead, it may be more profitable to make a separation between patterns of affiliation and any exchange of grooming as a commodity within the 'biological market' of the group. Measures of proximity and aggression can be used to index overall levels of affiliation, while grooming, in the first instance, can be considered as something that females barter for short-term advantage, rather than as an indicator of a social bond. Decoupling affiliation from grooming would make the analysis of the adaptive value of affiliation more tractable, since it would allow the separation of an animal's short-term concerns — which are most likely to involve the exchange of grooming — from the long-term consequences of maintaining affiliative long-term relationships with particular animals (if the latter exist).

In other words, we believe it is crucial to recognize that grooming may not have the single function of promoting long-term affiliation between animals, but can also be used for short-term gain. Our personal view at present is that all social decision-making is governed by short-term concerns and that long-term 'relationships' are artefacts of how we analyse and interpret data. However, this is not to say that these decisions do not have long-term consequences; females who make judicious decisions in the short-term are likely to show higher fitness returns in the long run as well. Nor do we rule out the possibility that long-term affiliation does occur between certain females (*e.g.* kin). Rather we question the notion that females have these long-term goals *in mind* when they make decisions on a daily basis.

This brings us to the second aspect of primate sociality that we query: the role of coalitions. At present, our main argument that female monkeys are unable to plan strategically in the long-term requires experimental confirmation; we are currently beginning to work on these issues and hope that, by highlighting the untested assumptions concerning the skills required for social decision-making, we will also prompt others to attempt the relevant experiments. Notwithstanding this lack of specific data, current experimental evidence from the cognitive literature suggests that female-female coalition formation is most likely governed by a simple evolutionary rule-of-thumb. This does not mean, however, that the resulting behavioural patterns shown will be simple; Hemelrijk (1996a, b; 1998) has demonstrated in a number of theoretical papers how simple decision rules can lead to complex patterns occurring as an emergent property. One empirical example of how simple rules can lead to complex patterns of social engagement is provided by Hill (1999; Hill & Okayasu, 1995, 1996), who suggests that the 'youngest

ascendancy' form of matrilineal inheritance seen in Japanese macaques (where the youngest daughter in a matiline outranks her older sisters) occurs as the result of an interaction between food provisioning, aggression levels and a rule of thumb that leads adult females to protect their most vulnerable offspring. Hill (1999) points out that provisioning results both in large matriline sizes and a concomitant increase in food-related aggression. He further suggests that females have been selected to protect vulnerable offspring against aggression and so inevitably find themselves frequently defending their youngest daughters against other females, including her own siblings. Over time, this reinforces the dominance of the youngest daughter to such an extent that, eventually, she is able to outrank her older sisters. Hill (1999) predicted that in smaller non-provisioned groups, where levels of aggression were lower, mothers would not be required to intervene so frequently on behalf of their youngsters and youngest ascendancy would not occur. In line with this, females living on islands that have never received artificial provisioning showed no evidence of youngest ascendancy.

Findings like these suggest that demographic constraints on partner availability need to be considered in much greater detail since it is likely that they will ultimately explain patterns of coalition formation. While birth and death rates within a population will be key determinants of the overall availability of partners, we also suggest that reproductive scheduling may impose a temporal constraint on those partners that are available. Our data on female baboons suggest that, if females were to avoid conflict during reproductively vulnerable periods, then partner reliability through time is likely to be low and that, if they are to overcome this, females must have a large number of potential coalition partners available to them. The fact that chacma baboon cohorts are significantly smaller than those of baboons living in east Africa (see also Henzi *et al.*, 1999, which shows that group sizes overall are smaller among chacma baboons), suggests the possibility that a lack of reliability exacerbated by low overall partner availability renders coalition formation non-viable among these southern baboons.

Phylogenetic history may also partly account for these patterns. We have suggested elsewhere that differences between male baboons in their tendency to form coalitions can be traced back to ecological conditions at the time that the baboon races were becoming differentiated (Henzi *et al.*, 1999). The extreme seasonal nature of chacma habitats in the Pleistocene predict group sizes smaller than those of the more equatorial olive and yellow baboons

(and also those of present day chacmas). We suggested that under these conditions most chacma groups would contain only one male and that, as a consequence, the ability to form coalitions with other males could not have been selected for. Thus, the chacmas of today do not form coalitions, even though multi-male groups are now common, due to the absence of a selection pressure in the recent past and a consequent evolutionary lag. A similar argument can be advanced for females; the small cohort sizes (and low partner reliability) of chacma groups during recent evolutionary time meant that coalitionary behaviour was not selected for, so that, even though some populations today have female cohort sizes comparable, or even larger, than east African populations (*e.g.* Moremi, Botswana), females lack the capacity to engage in this behaviour.

These arguments raise a number of interesting issues that future research should tackle. First, a more detailed examination of coalition formation among yellow and olive baboons is needed. Data on the frequency of coalition formation, with whom coalitions are formed and who they are directed against, and how these patterns vary with female reproductive state over time and between females with different reproductive histories, would allow a comprehensive examination of both the constraints on coalition formation and may also shed light on their adaptive value. Second, such an analysis would also be able to answer interesting questions regarding the impact of market forces on partner choice: are coalitions consistent and stable through time, or do they reflect the operation of short-term market effects whereby coalitionary aid is 'sold' to the highest bidder present? Third and finally, a more detailed examination of chacma baboon competitive interactions is needed in order to determine the tactics used by females in the absence of coalition formation. That is, to investigate whether the lack of coalitions in chacma baboons represents a sub-optimal strategy due to evolutionary lag compared to their East African counter-parts, or whether the available alternatives are equally efficient at alleviating the negative effects of competition (and therefore maybe equally adaptive). We are currently collecting such data (Payne *et al.*, in prep.; Escherria-Lozano *et al.*, in prep.) and look forward to seeing comparative data from other baboon sub-species.

Lastly, we wish to reiterate the importance of determining process, as well as outcomes, when examining individual behaviour. The dynamics of inter-individual interaction provide valuable information that is lost when these inherently noisy patterns are smoothed out into 'relationships'. The

analogy is similar to the mean-variance trade-off often seen in studies of animal behaviour. Animals not only make decisions in response to the mean availability of resources in the environment, but they also respond to the variance in resource availability. The level of risk and uncertainty associated with a particular resource often provides a much stronger predictor of behaviour than mean values alone. In a similar manner, the variability in social interactions across time may be more meaningful to an individual female monkey (and indeed to a human observer) than the overall mean level of interaction with a particular individual.

In conclusion, we suggest that in order to answer the question: 'what are friends for?' we must first tackle questions concerning the process of individual interaction, the impact of stochastic changes in demographic structure and the limits of species' cognitive abilities.

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