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Wild female baboons bias their social behaviour towards paternal half-sisters

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Adult female cercopithecines have long been known to bias their social behaviour towards close maternal kin. However, much less is understood about the behaviour of paternal kin, especially in wild populations. Here, we show that wild adult female baboons bias their affiliative behaviour towards their adult paternal half-sisters in the same manner and to the same extent that they bias their behaviour towards adult maternal half-sisters. Females appear to rely heavily on social familiarity as a means of biasing their behaviour towards paternal half-sisters, but may use phenotype matching as well.

Keywords: kin biasing; paternal half-sisters; paternal relatedness; kin recognition

1. INTRODUCTION

The tendency to bias beneficial behaviour towards kin and detrimental behaviour away from kin will evolve through kin selection whenever the inclusive fitness benefits of doing so outweigh the costs (Hamilton 1963, 1964; West-Eberhard 1975). Indeed, kin-biased behaviour has been observed in many taxa, including both invertebrates (e.g. Getz & Smith 1983; Ryan & Gamboa 1986; Breden & Wade 1987) and vertebrates (e.g. Beecher *et al.* 1981; Blaustein & O'Hara 1982; Waldman 1985; Pfennig *et al.* 1993; Parr & de Waal 1999). The prevalence of such kin biasing in the natural world indicates that kin selection on behaviour can have strong and pervasive effects on the societies of species that exhibit kin biasing.

Baboon and other cercopithecine primate females have long been observed to bias their behaviour towards maternal kin. Maternally related adult females are more affiliative than unrelated females in a number of ways: they spend more time grooming, spend a greater proportion of their time in close proximity to each other and are more likely to aid each other in agonistic interactions (see review in Gouzoules & Gouzoules 1987).

Much less is understood about the distribution of behaviour among paternally related cercopithecine females. Because paternity in wild non-human primates can not be determined by observation alone, the few existing studies of paternal kinship have relied primarily on captive animals. Further, most have yielded negative or ambiguous results (Wu *et al.* 1980; Small & Smith 1981; Sackett & Frederickson 1987; Kuester *et al.* 1994; Erhart *et al.* 1997). By contrast, although only two studies of paternal kinship in wild primates (Pope 1990; Alberts 1999) and only one in semi-free-ranging ones (Widdig *et al.* 2001) have been published (to our knowledge), all indicate that, at least in some situations, individuals discriminate between paternal kin and non-kin. Among wild howler monkeys, father–son coalitions are more stable than coalitions made up of unrelated males (Pope 1990). Among wild savannah baboons, paternal half-siblings form sexual consortships that are less cohesive than those formed between unrelated pairs (Alberts 1999). Among provisioned rhesus macaques in an island colony, paternal half-sisters are more affiliative towards each other than unrelated females (Widdig *et al.* 2001).

Here, we describe patterns of behavioural biasing towards both paternal and maternal kin in wild baboons, and we test hypotheses about the mechanisms of biasing. The two commonly proposed mechanisms are phenotype matching and familiarity (Holmes & Sherman 1982; Hepper 1986). Phenotype matching requires no learning or prior experience with kin, and is based on shared reliable genetically based cues. The definition of 'familiarity' varies across studies, probably because relevant cues vary across taxa (for eusocial insects see Hepper & Cleland (1999); for vertebrates see Tang-Martinez (2001); for birds see Komdeur & Hatchwell (1999); for non-human primates see Bernstein (1991); and for humans see Wolf (1995)). Here, we propose a definition of familiarity relevant to cercopithecine primates, and outline hypotheses designed to test the contributions of different mechanisms to paternal-kin biasing.

(a) *Familiarity*

Under what circumstances will animal B be 'familiar' enough to animal A that A shows a behavioural bias towards B? We propose that familiarity in cercopithecines is two-tiered. The *first tier* depends on A and B sharing the same mother, who is present and interacting with them both during A's infancy and juvenile period. If this is the case, then B will be familiar to A. Ample evidence from the literature on captive and wild cercopithecines supports this notion. For instance, maternal half-siblings exhibit strong mutual avoidance of each other as sexual partners, *unless* they are separated during the early life of one,

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resulting in the loss of the crucial maternal connection (e.g. Kuester *et al.* 1994). This first tier can be termed 'maternal familiarity'. The *second tier* involves frequent social interactions, and can be termed 'social familiarity'. B will be 'familiar' to A if: (i) B is a relatively frequent social partner of A during A's infancy and juvenile period; (ii) B is a frequent social partner when A passes through key developmental stages (e.g. weaning, sexual maturity); and (iii) B is a constant part of A's social environment (i.e. is present from the time that A is born, or nearly so). Social familiarity is thus a graded phenomenon, rather than one with a threshold, and is not necessarily symmetrical: B may be more 'socially familiar' to A than A is to B. For instance, if B is several years older than A, then (i) B may be a frequent social partner of A during A's infancy while the reverse is not true; (ii) B may be a frequent social partner when A passes through key developmental stages while the reverse is not true; and (iii) B will be a constant part of A's social environment while the reverse is not true because B was alive for several years before A was born.

For paternal half-sisters, social familiarity is the only reliably available familiarity cue, as far as we know. If females use social familiarity as the basis for affiliative biasing, we would expect the strength of affiliative relationships between females to be a function of age proximity. This is because the components of social familiarity are more prevalent among age peers (e.g. Pereira 1988; Fairbanks 1993). This prediction was articulated and confirmed by Widdig *et al.* (2001). Rhesus macaques breed seasonally; age cohorts are well defined, each cohort is sired by only a few males, and the predominant sires change from one year to the next. Consequently, Widdig *et al.* (2001) predicted and found a clear threshold for paternal-kin biasing: females born in the same year were more affiliative towards each other than females born more than one year apart. By contrast, baboons are non-seasonal breeders, so we predict a graded change in the strength of relationships as age differences increase, rather than a threshold.

The alternative mechanism, if social familiarity does not explain affiliative biasing, is phenotype matching. If females use phenotype matching, we would expect the strength of affiliative relationships between females to be a function of kinship, independent of age proximity. Widdig *et al.* (2001) found some evidence for this. While age proximity explained much of the variation in affiliative relationships in their study, they also found that, among non-peers, paternal half-sisters were more affiliative than non-kin.

(b) *Goals*

The *first goal* of this study was to test the hypothesis that maternal half-sisters and paternal half-sisters are equally attractive partners for adult female baboons (because they are roughly equally related). For this purpose, we examined the extent to which females bias their affiliative behaviour towards paternal half-sisters and maternal half-sisters.

The *second goal* of the study was to identify potential mechanisms of paternal-kin biasing (familiarity versus phenotype matching). In baboons and other cercopithecines, most paternal half-siblings are members of the same age cohort, but not all members of a particular age cohort are related to each other (Altmann 1979; Altmann *et al.* 1996; Widdig *et al.* 2001). This is because, while high-ranking males sire a disproportionate number of offspring, males other than the highest-ranking male also sire offspring (for this population see Hausfater (1975); Altmann *et al.* (1996) and Alberts *et al.* (2003)). Hence, the adult females in an age cohort vary in their levels of relatedness to each other, but should have similar levels of social familiarity across the cohort.

Widdig *et al.* (2001) found evidence that female rhesus monkeys bias their affiliative behaviour based on age proximity (they are more affiliative towards peers than non-peers), but they also found evidence for phenotype matching. Females were significantly more affiliative towards paternal half-sisters than non-kin, both among peers and among non-peers (Widdig *et al.* 2001). Here, we follow a similar procedure to examine the effects of age proximity and of paternal kinship on affiliative behaviour. We predicted that females would have stronger relationships with same-aged females than with females much older or younger than themselves. We also predicted that, if social familiarity is the sole cue used to achieve this biasing, this would be true of both non-kin and paternal half-sisters. If phenotype matching occurs, then females should bias their behaviour towards paternal half-sisters irrespective of their age differences.

2. METHODS

(a) *Subjects, study site and behavioural data*

Twenty-nine wild adult female baboons, members of three distinct social groups living in the Amboseli basin, Kenya, were studied during 1996–1997. All study groups were unsupplemented by human food sources and free-ranging in their natural habitat. The subjects, along with other group members, are part of long-term ongoing research (e.g. Altmann 1980; Muruthi *et al.* 1991; Altmann 1998; Alberts 1999). Between 125 and 150 10 min focal-animal samples (Altmann 1974) were collected for each female giving an average of 23.3 h per female. Continuous data were collected on all occurrences of agonistic and affiliative interactions. Agonistic interactions were also collected *ad libitum*, and were used to assign relative dominance ranks to each female. Affiliative interactions included solicit groom, lipsmack, present, directed cohesion grunt, follow, muzzle-to-muzzle greeting, embrace and approach. Point-sample data were collected at 1 min intervals on activity (feed, rest, move, groom, be groomed, other social) and on the focal female's closest adult female neighbour, regardless of distance.

(b) *Identifying kin and non-kin*

Our analysis focused on social relationships of females in three kin categories: true non-kin, paternal half-sisters and maternal half-sisters. We excluded other kin categories from the analysis in order to control for degree of relatedness. Twelve focal females had one or two paternal half-sisters (hereafter simply called paternal sisters), six focal females had one, two or three maternal half-sisters (hereafter called maternal sisters) and 27 focal females had three to seven true non-kin available as social partners.

Maternal sisters were identified using matrilineal genealogies and records of pregnancies and births, which are monitored on a near-daily basis as part of our ongoing population monitoring;

maternal sisters were identified without error. However, all females were adult at the onset of the behavioural study, and most were conceived before 1989, when we began collecting samples for DNA analysis in this population. Hence, we had no DNA for most of their potential fathers, precluding a standard paternity analysis. Instead, paternal sisters were identified by patterns of allele sharing at five X-chromosome microsatellite loci, using a combination of blood- and faeces-derived DNA (Smith 2000; Smith *et al.* 2000). Microsatellite markers on the X chromosome are more powerful for excluding paternal sisters than are autosomal markers. Males are haploid for the X chromosome, so all of a male's daughters inherit his single X chromosome and hence share one identical allele at every X-linked locus. In addition to genetic analyses, we used demographic data to exclude as paternal kin pairs of females who did not share at least one 'demographic potential father' (adult or sub-adult male in the group when they were conceived). Assignment of genotypes was complicated by the fact that most of the genotyping was done from faecal DNA; genotypes obtained from faecal DNA are subject to allelic dropout and occasionally produce spurious bands (see review in Smith *et al.* 2000). Hence, we accepted a heterozygote genotype as final only after at least three identical replicates were produced, and we accepted a homozygous genotype as final only after 16 replicates were produced (see Smith *et al.* (2000) for more details). We then applied a stringent set of criteria in identifying paternal sisters. For instance, even when females shared potential paternal alleles at all loci, we discounted the match if we were unable to obtain the requisite number of replicates from each female. As a result, our inclusions were conservative; it is likely that some paternal-sister pairs were excluded from the analysis because they did not meet our criteria. The paternal sisters were identified in this manner before any behavioural data were analysed.

Kin categories excluded from this analysis included mother–daughter ($n = 9$ pairs), 'other' maternal relatives (e.g. grandmother–grand-daughter, aunt–niece, etc., $n = 6$), 'other' paternal relatives (aunt–niece, $n = 3$) and 'unknown' ($n = 36$). Unknown pairs were those who were not maternally related and for which paternal relatedness could not be resolved, because of difficulties in genotyping one member of the pair. The excluded pairs represented an unbiased sample of social relationships; the distribution of 'affiliation indices' (see § 2d) did not change when they were excluded from the sample ($t = 0.715$, $p = 0.48$) and the means were nearly identical (all pairs, mean ± s.e. = 1.29 ± 0.04; after exclusions, mean ± s.e. = 1.24 ± 0.06).

(c) *Identifying age-cohort members (same-aged versus differently aged females)*

All females in this analysis were known from birth, and their birth dates were known to within a few days, as a result of near-daily monitoring of the study groups. Baboons are non-seasonal breeders and so age cohorts are not definable as those animals sharing a common birth season. Because there was no obvious threshold for identifying pairs of 'same-aged' and 'differently aged' females, we used an arbitrary cut-off. Six out of the nine paternal-sister dyads in our analysis were born within 1 year of each other. However, males reside in each social group for an average of 2 years (Alberts & Altmann 1995). Thus, 1 year and 2 years are both biologically reasonable cut-offs. Where possible, we tested hypotheses defining age cohorts both as females born within 1 year of each other, and as females born within 2 years of each other.

(d) *Data analysis*

For all comparisons, we used two-tailed Mann–Whitney *U*-tests. We calculated five measures of affiliation for each focal female towards each of her social partners: (i) rate of affiliative interactions directed by focal female towards partner; (ii) proportion of time focal female spent grooming partner; (iii) proportion of focal female's total time that partner was her nearest neighbour; (iv) proportion of focal female's resting time that partner was her nearest neighbour; and (v) proportion of focal female's feeding time that partner was her nearest neighbour. Analysing each of these separately is inappropriate: the multiple tests required would increase the risk of type-I error, and the behaviours are not independent of each other.

We therefore calculated, for each dyad (each focal female towards each social partner), a single cumulative measure of affiliation, the 'affiliation index' (AI), as follows:

$$\mathrm{AI} = \frac{\sum_{i=1}^{5} \frac{x_i}{\mathrm{median}}}{5},$$

where x_i represents the five measures of affiliation and median is the global median. This index is a measure of the extent to which each female's affiliative behaviour towards each partner is, on average, above or below the global median across all behaviours. High values represent strongly affiliative relationships (see also Sapolsky *et al.* 1997; Alberts 1999; Widdig *et al.* 2001). Note that the AI for any focal female x towards partner y was always different from the corresponding AI for focal female y towards x. The rate at which x directs affiliative behaviours towards y is not necessarily correlated with the reverse rate, and similarly x may be y's nearest neighbour without the reverse being true.

Mean AIs were then calculated for each female for each category (maternal sisters, paternal sisters, non-kin; table 1). That is, we used each focal female as the unit of analysis, and examined her average behaviour towards different kin categories. Thus, for instance, female VIN had a mean AI towards her maternal sisters of 1.043, a mean AI towards her paternal sisters of 1.544 and a mean AI towards true non-kin of 0.805.

For some analyses, however, we had to use pairs of females, rather than each focal female, as the unit of analysis. This resulted in sample sizes different from the previous analysis. For instance, while 12 females had paternal sisters, so that $n = 12$ in figure 1, those 12 females resolved into nine pairs in figure 2, because some paternal sibships consisted of three females (i.e. one set of six females resulted in six dyads, while the remaining six females resulted in three dyads). We took the AI for each pair of females x and y as the mean of the two AIs (AI for focal x towards partner y and AI for focal y towards partner x).

(e) *Power analyses*

The nature of our study—taking advantage of natural experiments in a wild population—meant that in some cases important results were derived from small sample sizes, resulting in low power. In these cases, we performed retrospective power analyses using JMP v. 3.2.1 (SAS Institute 1997), and we present these below (see § 3b). We have presented the results, despite low power in some tests, because they are to our knowledge the first tests of crucial hypotheses. As such they may be important for future studies.

Table 1. Mean affiliation indices for each focal female for each kin category.

focal female	true non-kin	paternal half-sisters	maternal half-sisters	social group
ASH	0.941	0.956	—	Dotty's
DOT	1.064	—	—	Dotty's
DOV	0.567	4.317	—	Dotty's
ECH	0.952	1.857	—	Dotty's
KAT	1.975	1.445	—	Linda's
KEL	1.364	2.652	—	Weaver's
LAR	1.276	2.123	—	Linda's
LAS	0.491	—	—	Weaver's
LAZ	1.012	—	—	Weaver's
LIM	—	2.445	—	Weaver's
LIN	1.086	1.510	—	Linda's
LUN	1.119	—	—	Weaver's
MYS	1.060	—	—	Linda's
NIG	1.859	—	—	Linda's
NIX	1.290	1.462	—	Linda's
NYO	1.459	1.122	—	Linda's
OCH	0.749	—	—	Dotty's
OMO	0.958	—	—	Dotty's
PRU	1.213	—	—	Weaver's
VEL	0.845	—	1.533	Dotty's
VIN	0.805	1.544	1.043	Dotty's
VIV	0.656	—	1.316	Dotty's
VIX	0.622	—	—	Dotty's
VOR	0.521	—	1.911	Dotty's
WAG	1.040	—	1.765	Weaver's
WAS	1.134	—	—	Linda's
WEA	—	—	1.787	Weaver's
WEM	1.767	—	—	Linda's
WEN	1.192	1.472	—	Weaver's

3. RESULTS

(a) *Females biased their behaviour towards paternal and maternal sisters*

Adult females were significantly more affiliative towards both maternal and paternal half-sisters than towards true non-kin (figure 1; maternal sisters versus true non-kin: $p = 0.014$; paternal sisters versus true non-kin: $p = 0.0004$). Levels of affiliation did not differ between maternal and paternal sisters ($p = 0.67$). These findings are consistent with predictions based on kin-selection theory. Table 2 gives values for each affiliative behaviour individually, pooled within kin categories, to illustrate that all the affiliative measures varied in the same direction.

The strong affiliative relationships of paternal sisters were not caused by patterns of rank difference or rank proximity among them. Dominance rank is strongly influenced by maternal lineage in cercopithecine primates (Melnick & Pearl 1987) but not by paternal lineage as far as we can tell. That is, females were not consistent in how closely ranked they were to their paternal sisters; some paternal-sister pairs were close in rank (one pair was adjacent, in rank positions six and seven) and others were quite far apart in rank (the greatest rank difference was seven, in a pair ranked three and 10, respectively; the mean rank difference for paternal sisters was 3.7 ranks apart). Further, AIs for maternal sisters and paternal sisters had very similar ranges and distributions (figure 1) in spite of the fact that maternal sisters were always adjacent in rank or nearly so, while paternal sisters were quite variable in their rank distances.

(b) *Affiliative relationships with same-aged and differently aged social partners, and with paternal kin*

AIs decreased as age differences between pairs of females increased (figure 2; table 1; $r^2_{\text{adj.}} = 0.193$, $p = 0.0001$). This pattern held true even when we excluded paternal sisters and examined non-kin alone ($p = 0.03$ for a 1 year cut-off and $p = 0.05$ for a 2 year cut-off). This confirms the prediction that females use social familiarity as a basis for affiliative biasing.

However, females were equally affiliative with differently aged and with same-aged paternal sisters ($p = 0.59$). In particular, five females had paternal sisters more than 1 year apart, with mean AI ± s.e. = 2.23 ± 0.43, and nine females had paternal sisters within 1 year, with mean AI ± s.e. = 1.87 ± 0.32, a non-significant difference. (Two out of our 12 females with paternal sisters had one sister in each category, resulting in a sample of 14 for this test.) The small sample prevented us from doing this test with both 1 year and 2 years as the threshold.

Why did females apparently not differentiate between same-aged and differently aged paternal sisters? It may be because of our small sample size: a power analysis indicates that a difference of the magnitude seen for non-kin would require at least $n = 18$ to achieve significance and there were only 14 in our sample. However, our data do not even show a trend in the predicted direction. These results, like the results of Widdig *et al.* (2001), raise the possibility that female cercopithecines use phenotype matching instead of or in addition to social familiarity to bias behaviour towards paternal kin.

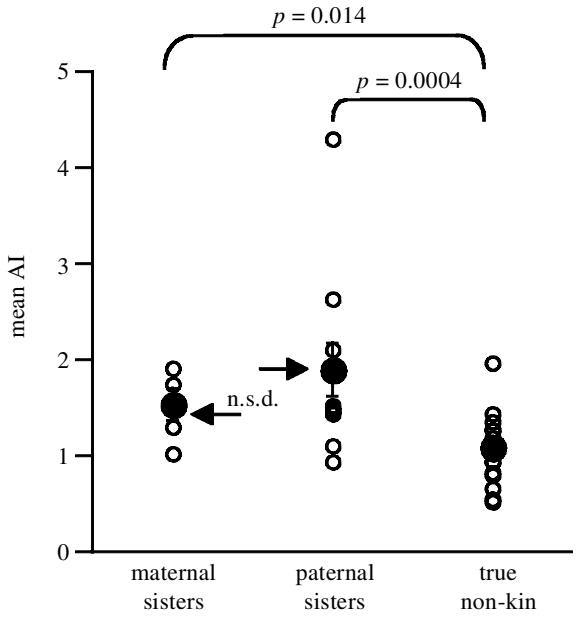

Figure 1. Females are more affiliative towards their paternal and maternal sisters than they are towards non-kin. Each open circle represents the mean AI of one female towards all other females within the given kin category; closed circles are means (with s.e.). There is no significant difference (n.s.d.) in the AI between paternal and maternal sisters. See § 3a for details.

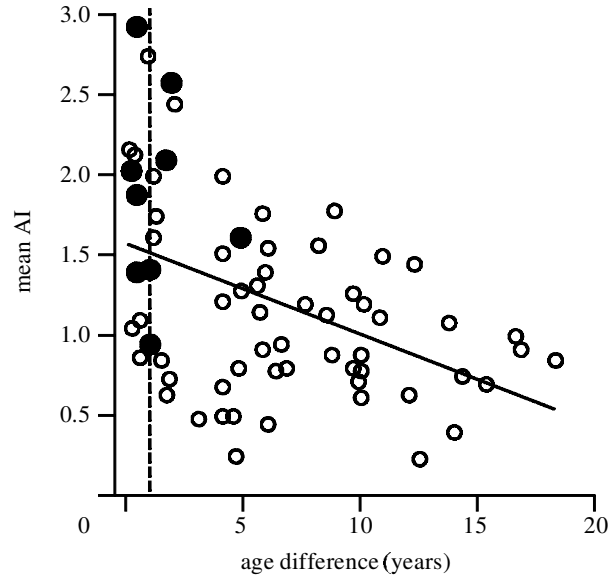

Figure 2. Age proximity predicts the strength of affiliative relationships. Each point represents the mean AI for one pair of females. Open circles represent pairs of true non-kin; closed circles represent pairs of paternal sisters. Note that 12 females had paternal sisters, but this resulted in nine paternal-sister dyads in this analysis (because some females had two paternal sisters). Twenty-seven females had true non-kin in the group, resulting in 58 pairs of non-kin in this analysis. The vertical dashed line delineates females born within one year of each other. ($r^2_{adj.} = 0.193$, $p = 0.0001$.)

One way to test this would be to compare pairs of paternal sisters with pairs of non-kin, controlling for age difference. That is, to compare pairs of paternal sisters with pairs of non-kin that had the same age differences as the paternal sisters. To do this we treated each pair of paternal sisters as the unit of analysis, and then selected from among pairs of non-kin those nine pairs with age differences that were closest to the age differences that we observed among paternal sisters. The result was a set of nine paternal-sister dyads and a comparable set of nine non-kin dyads that had the same distribution of age differences as the paternal-kin dyads. We then compared these two sets of female pairs. Paternal sisters showed a non-significant tendency to be more affiliative than unrelated females matched for similar age differences (mean AI ± s.e. = 1.88 ± 0.20 and 1.36 ± 0.26, respectively, $p = 0.1451$). However, our small sample size limited the power of this test to $\beta = 0.74$.

4. DISCUSSION

Adult female baboons biased their social behaviour towards paternal sisters as much as they did towards maternal sisters. This startling result is somewhat different from that reported by Widdig *et al.* (2001). Like us, they found that females were more affiliative towards paternal sisters than towards non-kin. However, in their study, maternal sisters had much stronger relationships than did paternal sisters. Maternal kinship is virtually always identified as a key factor explaining variance in the relationships of cercopithecines. Our data indicate that paternal kinship probably also explains a significant amount of variance.

Why did paternal sisters in our study exhibit stronger relationships than those described by Widdig *et al.* (2001)? Widdig *et al.* studied a large provisioned island population, with high birth rates and survival. In that population matrilines grow very large and females typically have many close maternal relatives; they may also have many paternal sisters. Females will experience constraints on how many close relationships they can have, so that they simply have to choose between different types of kin. Females should choose maternal sisters over paternal sisters if, as is probably the case, they are less likely to misidentify maternal sisters. In wild populations such as that in Amboseli, which are stable or increasing only slightly, females usually do not have a large set of kin among which to choose. The combination of long interbirth intervals and high infant mortality (Altmann *et al.* 1988; Alberts & Altmann 2003) means that both matrilines and paternal sibships may be small. These demographic considerations mean that a paternal sister may be the only, or one of the only, sisters available as partners for wild cercopithecine females, a situation very different from that experienced by most females in large provisioned populations. This illustrates both the strength and the weakness of wild studies: many females in our study lacked adult sisters of either kind (table 1), resulting in an unbalanced 'experimental' design but representing a very common demographic situation, almost certainly the one in which the behaviours described here evolved.

(a) *Why do females bias their behaviour towards paternal sisters?*

One might argue that the observed tendency for age-mates to have strong relationships is simply a by-product of cercopithecine social structure, rather than a kin-selected behaviour (Chapais 2001). That is, in closed social

Table 2. Behaviours used to calculate the AI, with mean values for all pairs of maternal siblings, all pairs of paternal siblings and all pairs of true non-kin.

behaviour	paternal siblings	maternal siblings	true non-kin	difference 1[a]	difference 2[a]
rate of affiliative interactions directed by focal female towards partner	0.042	0.027	0.018	−0.009	−0.024
proportion of time focal female spent grooming partner	0.189	0.126	0.101	−0.025	−0.088
proportion of focal female's total time that partner was her nearest neighbour	0.14	0.132	0.101	−0.031	−0.039
proportion of focal female's resting time that partner was her nearest neighbour	0.137	0.125	0.101	−0.024	−0.036
proportion of focal female's feeding time that partner was her nearest neighbour	0.126	0.142	0.101	−0.041	−0.025

[a] Difference 1 is (true non-kin − maternal siblings) and difference 2 is (true non-kin − paternal siblings). Note that all differences are negative, indicating that both maternal and paternal siblings scored higher on all measures of affiliation than true non-kin.

groups with multiple juveniles of different ages, juveniles will become familiar with age-mates simply because they play together frequently. This could result in social preferences for same-aged partners during adulthood, irrespective of kinship. In this scenario, the fact that same-aged partners are often paternal kin (see figure 2) is incidental.

We view this scenario as unlikely, and argue that the tendency to bias affiliative behaviour towards age-mates probably results from kin selection, for two reasons. First, relationships among paternal kin should experience selection pressures similar to those experienced by relationships among maternal kin, and available evidence clearly supports the hypothesis that kin selection has shaped relationships among maternal kin in cercopithecines (see review in Chapais (2001)). Second, while females are more affiliative with female age-mates than with differently aged partners, opposite-sex age-mates show exactly the opposite tendency: males and females born into the same group at the same time are significantly less likely to mate upon reaching adulthood than those born far apart in time (Alberts 1999). An 'incidental' hypothesis is difficult to support in this case.

In fact, in cercopithecine groups paternal-kin relationships may respond to kin selection more readily than maternal-kin relationships, because paternal half-sisters will usually be more closely related than maternal half-sisters. That is, $r > 0.25$ for paternal half-sisters in these societies. This is because adult females in a cercopithecine group are more closely related to each other than are the adult males (e.g. Altmann *et al.* 1996; de Ruiter & Geffen 1998). Thus, paternal sisters share alleles not only through their common father, but also through their different mothers. The kinship coefficients of paternal sisters are also slightly elevated because they inherit identical X chromosomes from their father.

Thus, even if the tendency to associate with age-mates arose fortuitously, we would expect kin selection to reinforce it wherever age-mates are likely to be paternal siblings. A test of this would involve comparing societies in which paternal siblings tend to be age-mates (e.g. many cercopithecines) with those in which age-mates are not more likely than differently aged partners to be paternal siblings (e.g. plains zebras, mountain gorillas, hamadryas baboons, callitrichids).

(b) *What mechanisms do females use to bias their behaviour towards maternal and paternal sisters?*

Age proximity, which modulates social familiarity, has a large impact on social relationships among adult females that are not maternal sisters. The consequence is that females are likely to develop strong affiliative preferences for paternal sisters. Further, both our data and those of Widdig *et al.* (2001) indicate that paternal sisters are more affiliative than non-kin when age differences are controlled for: that is, both datasets indicate that adult female cercopithecines may use phenotype matching to identify paternal sisters. These results, combined with other reports that wild primates discriminate paternal kin (Pope 1990; Alberts 1999), indicate the need for further studies.

What mechanisms might females use for phenotype matching? One possible mechanism is visual matching. Parr & de Waal (1999) found that captive chimpanzees, looking at photographs of unfamiliar conspecifics, tended accurately to match photographs of mothers with their sons. Very little work has been done on visual recognition of this sort in non-human primates (see also Dasser 1988). A second possible mechanism is olfactory matching. While primates are generally considered to have poorly developed olfactory capabilities relative to other mammals, humans at least appear to be sensitive to odour differences correlated with genetic differences in the major histocompatibility complex (MHC) (Wedekind *et al.* 1995; Wedekind & Furi 1996; Jacob *et al.* 2002). The MHC is a good candidate for a phenotype matching system. It is highly genetically variable and appears to affect mate-choice decisions in mice (Egid & Brown 1989; Potts *et al.* 1991) and humans (Ober *et al.* 1997; but see Hedrick & Black 1997). MHC variation in natural populations, and its effect on behaviour, remain understudied (see reviews in Alberts & Ober 1993; Brown & Eklund 1994; Penn & Potts 1999).

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REFERENCES

Alberts, S. C. 1999 Paternal kin discrimination in wild baboons. *Proc. R. Soc. Lond.* B **266**, 1501–1506. (DOI 10.1098/rspb.1999.0807.)

Alberts, S. C. & Altmann, J. 1995 Dispersal in male baboons: balancing costs and opportunities. *Am. Nat.* **145**, 279–306.

Alberts, S. C. & Altmann, J. 2003 Matrix models for primate life-history analysis. In *Primate life histories and socioecology* (ed. P. M. Kappeler & M. E. Pereira), pp. 66–102. University of Chicago Press.

Alberts, S. C. & Ober, C. 1993 Genetic variability in the major histocompatibility complex: a review of non-pathogen-mediated selective mechanisms. *Yearbook Phys. Anthropol.* **36**, 71–89.

Alberts, S. C., Watts, H. E. & Altmann, J. 2003 Queuing and queue-jumping: long term patterns of reproductive skew among male savannah baboons. *Anim. Behav.* (In the press.)

Altmann, J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267.

Altmann, J. 1979 Age cohorts as paternal sibships. *Behav. Ecol. Sociobiol.* **6**, 161–164.

Altmann, J. 1980 *Baboon mothers and infants*. Cambridge, MA: Harvard University Press.

Altmann, S. A. 1998 *Foraging for survival*. University of Chicago Press.

Altmann, J., Altmann, S. & Hausfater, G. 1988 Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 403–418. University of Chicago Press.

Altmann, J. (and 12 others) 1996 Behavior predicts genetic structure in a wild primate group. *Proc. Natl Acad. Sci. USA* **93**, 5797–5801.

Beecher, M. D., Beecher, I. M. & Hahn, S. 1981 Parent–offspring recognition in bank swallows (*Riparia riparia*). II. Development and acoustic basis. *Anim. Behav.* **29**, 95–101.

Bernstein, I. S. 1991 The correlation between kinship and behavior in non-human primates. In *Kin recognition* (ed. P. G. Hepper), pp. 6–29. Cambridge University Press.

Blaustein, A. R. & O'Hara, R. K. 1982 Kin recognition in *Rana cascadae* tadpoles: maternal and paternal effects. *Anim. Behav.* **30**, 1151–1157.

Breden, F. & Wade, M. J. 1987 An experimental study of the effect of group size on larval growth and survivorship in the imported willow leaf beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae). *Environ. Entomol.* **16**, 1082–1086.

Brown, J. L. & Eklund, A. 1994 Kin recognition and the major histocompatibility complex: an integrative review. *Am. Nat.* **143**, 435–461.

Chapais, B. 2001 Primate nepotism: what is the explanatory value of kin selection? *Int. J. Primatol.* **22**, 203–229.

Dasser, V. 1988 A social concept in Java monkeys. *Anim. Behav.* **36**, 225–230.

de Ruiter, J. & Geffen, E. 1998 Relatedness of matrilines, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proc. R. Soc. Lond.* B **265**, 79–87. (DOI 10.1098/rspb.1998.0267.)

Egid, K. & Brown, J. 1989 The major histocompatibility complex and female mating preferences in mice. *Anim. Behav.* **38**, 548–549.

Erhart, E., Coelho, A. & Bramblett, C. 1997 Kin recognition by paternal half-siblings in captive *Papio cynocephalus*. *Am. J. Primatol.* **43**, 147–157.

Fairbanks, L. A. 1993 Juvenile vervet monkeys: establishing relationships and practising skills for the future. In *Juvenile primates: life history, development, and behavior* (ed. M. E. Pereira & L. A. Fairbanks), pp. 211–227. Oxford University Press.

Getz, W. M. & Smith, K. B. 1983 Genetic kin recognition: honeybees discriminate between full and half sisters. *Nature* **302**, 147–148.

Gouzoules, S. & Gouzoules, H. 1987 Kinship. In *Primate societies* (ed. B. B. Smuts, D. L. Cheney, R. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 299–305. University of Chicago Press.

Hamilton, W. D. 1963 The evolution of altruistic behavior. *Am. Nat.* **97**, 354–356.

Hamilton, W. D. 1964 The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7**, 1–52.

Hausfater, G. 1975 *Dominance and reproduction in baboons (Papio cynocephalus)*. Basel, Switzerland: Karger.

Hedrick, P. W. & Black, F. L. 1997 HLA and mate selection: no evidence in south Amerindians. *Am. J. Hum. Genet.* **61**, 505–511.

Hepper, P. G. 1986 Kin recognition: functions and mechanisms, a review. *Biol. Rev.* **61**, 63–93.

Hepper, P. G. & Cleland, J. 1999 Developmental aspects of kin recognition. *Genetica* **104**, 199–205.

Holmes, W. G. & Sherman, P. W. 1982 Kin recognition in animals. *Am. Scient.* **71**, 46–55.

Jacob, S., McClintock, M. K., Zelano, B. & Ober, C. 2002 Paternally inherited HLA alleles are associated with women's choice of male odours. *Nature Genet.* **30**, 175–179.

Komdeur, J. & Hatchwell, B. J. 1999 Kin recognition: function and mechanism in avian societies. *Trends Ecol. Evol.* **14**, 237–241.

Kuester, J., Paul, A. & Arnemann, J. 1994 Kinship, familiarity and mating avoidance in Barbary macaques, *Macaca sylvanus*. *Anim. Behav.* **48**, 1183–1194.

Melnick, D. J. & Pearl, M. C. 1987 Cercopithecines in multimale groups: genetic diversity and population structure. In *Primate societies* (ed. B. B. Smuts, D. L. Cheney, R. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 121–134. University of Chicago Press.

Muruthi, P., Altmann, J. & Altmann, S. A. 1991 Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* **87**, 467–472.

Ober, C., Weitkamp, L. R., Cox, N., Dytch, H., Kostyu, D. & Elias, S. 1997 HLA and mate choice in humans. *Am. J. Hum. Genet.* **61**, 497–504.

Parr, L. A. & de Waal, F. B. M. 1999 Visual kin recognition in chimpanzees. *Nature* **399**, 647–648.

Penn, D. J. & Potts, W. K. 1999 The evolution of mating preferences and major histocompatibility complex genes. *Am. Nat.* **153**, 145–164.

Pereira, M. E. 1988 Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons (*Papio cynocephalus cynocephalus*). *Anim. Behav.* **36**, 184–204.

Pfennig, D. W., Reeve, H. K. & Sherman, P. W. 1993 Kin recognition and cannibalism in spadefoot toad tadpoles. *Anim. Behav.* **46**, 87–94.

Pope, T. R. 1990 The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* **27**, 439–446.

Potts, W. K., Manning, C. J. & Wakeland, E. K. 1991 Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature* **352**, 619–621.

Ryan, R. E. & Gamboa, G. J. 1986 Nestmate recognition in social wasps: the origin and acquisition of recognition odours. *Anim. Behav.* **34**, 685–695.

Sackett, G. P. & Frederickson, W. T. 1987 Social preferences by pigtailed macaques: familiarity versus degree and type of kinship. *Anim. Behav.* **35**, 603–606.

Sapolsky, R. M., Alberts, S. C. & Altmann, J. 1997 Hypercortisolism associated with social subordinance or social isolation among wild baboons. *Arch. Gen. Psychiatry* **54**, 1137–1143.

SAS Institute, Inc. 1997 *JMP statistics and graphics guide, v. 3.* Cary, NC: SAS Institute.

Small, M. F. & Smith, D. G. 1981 Interactions with infants by full siblings, paternal half-siblings, and non-relatives in a captive group of rhesus macaques (*Macaca mulatta*). *Am. J. Primatol.* **1**, 91–94.

Smith, K. L. 2000 Paternal kin matter: the distribution of social behavior among wild, adult female baboons. PhD thesis, University of Chicago, Chicago IL.

Smith, K. L., Alberts, S. C., Bayes, M. K., Bruford, M. W., Altmann, J. & Ober, C. 2000 Cross-species amplification, non-invasive genotyping, and non-Mendelian inheritance of human STRPs in savannah baboons. *Am. J. Primatol.* **51**, 219–227.

Tang-Martinez, Z. 2001 The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behav. Processes* **53**, 21–40.

Waldman, B. 1985 Olfactory basis for kin recognition in toad tadpoles. *J. Comp. Physiol.* A **156**, 565–577.

Wedekind, C. & Furi, S. 1996 Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proc. R. Soc. Lond.* B **264**, 1471–1479.

Wedekind, C., Seebeck, T., Bettens, F. & Paepke, A. J. 1995 MHC-dependent mate preferences in humans. *Proc. R. Soc. Lond.* B **260**, 245–249.

West-Eberhard, M. J. 1975 The evolution of social behavior by kin selection. *Q. Rev. Biol.* **50**, 1–33.

Widdig, A., Nürnberg, P., Krawczak, M. & Bercovitch, F. B. 2001 Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proc. Natl Acad. Sci. USA* **98**, 13 769–13 773.

Wolf, A. P. 1995 *Sexual attraction and childhood association: a Chinese brief for Edward Westermarck*. Stanford University Press.

Wu, H. M. H., Holmes, W. G., Medina, S. R. & Sackett, G. P. 1980 Kin preference in infant *Macaca nemestrina*. *Nature* **285**, 225–227.

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