Paternal kin discrimination in wild baboons

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Mammals commonly avoid mating with maternal kin, probably as a result of selection for inbreeding avoidance. Mating with paternal kin should be selected against for the same reason. However, identifying paternal kin may be more difficult than identifying maternal kin in species where the mother mates with more than one male. Selection should nonetheless favour a mechanism of paternal kin recognition that allows the same level of discrimination among paternal as among maternal kin, but the hypothesis that paternal kin avoid each other as mates is largely untested in large mammals such as primates. Here I report that among wild baboons, *Papio cynocephalus*, paternal siblings exhibited lower levels of affiliative and sexual behaviour during sexual consortships than non-kin, although paternal siblings were not significantly less likely to consort than non-kin. I also examined age proximity as a possible social cue of paternal relatedness, because age cohorts are likely to be paternal sibships. Pairs born within two years of each other were less likely to engage in sexual consortships than pairs born at greater intervals, and were less affiliative and sexual when they did consort. Age proximity may thus be an important social cue for paternal relatedness, and phenotype matching based on shared paternal traits may play a role as well.

Keywords: kin recognition; inbreeding avoidance; paternal relatedness

1. INTRODUCTION

The costs of inbreeding may be substantial (Charlesworth & Charlesworth 1987), and consequently many animals avoid relatives as mates. Sex-biased dispersal, common among mammals and birds, separates opposite-sex relatives and thus reduces the risk of close inbreeding (Pusey & Wolf 1996). However, the extent of dispersal varies among and within species, so that close relatives do sometimes encounter each other as potential mates. Apparently this occurs frequently enough that the risk of inbreeding depression leads to recognition and avoidance of relatives as mates: even species characterized by nearly complete sex-biased dispersal typically show strong aversion to mating with close relatives (Pusey 1990; Pusey & Wolf 1996).

In most species of large mammal, such kin avoidance is documented only among maternal relatives. This is because paternity is difficult to establish in species in which females mate with more than one male, so that observers can only assign paternity reliably with molecular analysis. Selection should favour a mechanism that allows the same level of discrimination among paternal kin as is observed among maternal kin, but the hypothesis that paternal kin avoid each other as mates is largely untested in large mammals.

For baboons, as for other animals, two possible mechanisms of paternal kin recognition exist (Holmes & Sherman 1983). The first is phenotype matching, in which individuals compare phenotypic traits of potential kin, such as odour, to their own traits and assess kinship on that basis (Holmes & Sherman 1983). Phenotype matching is common in small mammals but has not yet been established in large mammals (Blaustein *et al.* 1987; Walters 1987; Bernstein 1991; Halpin 1991). One laboratory study presented evidence that isolated juvenile macaques in a laboratory setting may prefer to sit near unfamiliar paternal half siblings rather than unfamiliar non-kin (Wu *et al.* 1980). Attempts to replicate this finding have been unsuccessful (Sackett & Frederickson 1987; Erhart *et al.* 1997), and in any case the biological relevance of these tests is unclear (Walters 1987). The second possible mechanism of paternal kin recognition involves social cues, such as persistent affiliative associations. These are strongly implicated in maternal kin recognition (Walters 1987; Bernstein 1991), but have yet to be investigated as mechanisms for paternal kin recognition. A likely social cue for paternal relatedness in baboons is age proximity, because age cohorts are likely to represent paternal sibships (Altmann 1979). The current study represents the first empirical test of the hypothesis that paternal siblings are able to use age proximity as an indicator of paternal relatedness.

Baboon populations are composed of stable social groups of 10–200 individuals, and usually include multiple adults of both sexes (Melnick & Pearl 1987). Females remain in their group of birth throughout their lives, and associate closely with maternal relatives in relationships defined by mutual grooming, proximity, and support during social conflicts (Melnick & Pearl 1987; Walters 1987). Males transfer between groups, first when they near adulthood and then repeatedly throughout their lives (Packer 1979; Pusey & Packer 1987; Alberts & Altmann 1995a). Adult males typically have no close relatives other than offspring in the groups where they reside.

Female baboons are sexually receptive only during the follicular phase of their sexual cycle, when they exhibit the sexual swelling typical of many primate species. Mating occurs in the context of mate-guarding episodes, or sexual consortships, characterized by close proximity and following of the female by the male, as well as by sexual behaviour (Hausfater 1975; Packer 1979). The

majority of copulations occur during consortships (Altmann *et al.* 1996).

Because of the species-typical pattern of male dispersal and female matrilocality, opportunities to mate with relatives are limited for baboons. However, dispersal is not always complete before adulthood, and in the study population nearly 50% of males remain in their natal group long enough to mate there (Alberts & Altmann 1995*a*). In this situation, baboons, like many other mammals, show strong avoidance of maternal relatives as mates (Alberts & Altmann 1995*a*; Pusey & Wolf 1996). This, together with the observation that offspring of non-dispersing males show reduced viability in the study population and elsewhere, supports the prediction that baboons experience selection to avoid close inbreeding (Packer 1979; Alberts & Altmann 1995*a*; but also see Bulger & Hamilton 1988). However, it raises the question of whether they avoid paternal as well as maternal relatives.

2. METHODS

As a test of the hypothesis that paternal kin discriminate against each other as mates, I examined sexual consortships among adult males and females of a well-studied baboon group in Amboseli National Park, Kenya. This group (Lodge Group) was monitored continually, beginning in 1984 as part of the long-term monitoring of the Amboseli baboon population, with observers spending several days each week with the group collecting demographic, reproductive and general behavioural data (see, for example, Muruthi *et al.* 1991; Altmann *et al.* 1996). The group experienced rapid growth after it began to feed for part of the time on a refuse dump associated with a tourist lodge. As a result of its enhanced nutrition and frequent contact with humans, patterns of male dispersal in Lodge Group were altered during this period of food enhancement. In particular, male transfer into the group ceased for a time and male transfer out of the group was reduced. Consequently, a natural experiment developed in which a high proportion of adults in the group were maternal or paternal relatives.

(a) *Consortship occurrence among paternal siblings*

Sixteen natal males engaged in 2384 h of sexual consortships with 29 natal females in Lodge Group between March 1989 and December 1995. All of these consortships occurred after the natal males had attained adulthood, i.e. had experienced the pattern of rapidly rising dominance rank and subsequent high levels of sexual activity that signals adulthood in this species (Alberts & Altmann 1995*b*; see also Hamilton & Bulger 1990). Paternity for these subjects was determined based on cumulative inclusion across ten microsatellite loci and two blood proteins (see Altmann *et al.* (1996) for details). Fathers were identified for 18 out of the 29 females (i.e. for all but two of the females that were born after the observations on Lodge Group began in 1984) and for 13 of the 16 natal males.

Of these 13 males, 12 had both known paternal half-sisters and known non-relatives available as potential mates among the females that were sexually active during this period. Animals were defined as unrelated if they were known to have different fathers, and if they had no known matrilineal relatives in common (this, in most cases, meant that they could not be closer than maternal second cousins). The total number of female consort hours potentially available to each male were summed for two classes of female: (i) females

which were unrelated to the male (mean available female consort hours per male = 699), and (ii) females which were the male's paternal half-sisters (mean available female consort hours per male = 357). The proportions that each male obtained of those two classes of available consort hours were then computed. The result was two measures for each male: the proportion of paternal sisters' consort time that he obtained, and the proportion of non-relatives' consort time that he obtained. These values were compared by using a Wilcoxon signed-ranks test.

(b) *Consortship cohesiveness of paternal siblings*

As part of a larger study on mating behaviour, I collected 80 h of detailed data on behaviour of paternal siblings and unrelated pairs during sexual consortships. Consortship data were collected for nine different females (born between 1975 and 1989) and six different males (born between 1983 and 1987) comprising 14 mating pairs. To control for possible effects of male natality on mating preferences of females, only pairs in which the male was born in Lodge Group were included in this analysis. The timing of sexual consortships relative to the phase of female sexual cycle did not differ between paternal siblings and unrelated pairs (range on which consortships occurred relative to the onset of deturgescence of the sex skin was from 1 to 15 days in both cases; means were 5.91 days and 5.96 days before deturgescence, respectively).

Data were collected on all affiliative, sexual and agonistic behaviours performed by the pair, during 40 min focal samples of females in each pair (Altmann 1974). Agonistic interactions were included in the analysis because in baboons and macaques they tend to reflect overall levels of interaction; that is, they tend to be positively rather than negatively correlated with proximity and affiliation (Massey 1977; Walters 1987). Data on the proximity of the male partner (whether or not he was within 3 m of the female) were collected every 2 min during the focal sample. A set of 12 measures (table 1) deemed to encompass the range of behaviours relevant to mate-guarding effectiveness and sexual activity were extracted from these data: (i) rate of genital inspection; (ii) rate of herding (in which the male nips, nudges or butts the female in an apparent effort to control her direction of movement); (iii) rate of sexual mounts with and without ejaculation; (iv) rate of lips-macking; (v) rate at which one partner waits for the other during group movement; (vi) rate at which grooming is solicited by one partner or the other; (vii) rate of agonistic interactions; (viii) rate of perineal presents by the female to the male; (ix) proportion of perineal presents followed by sexual behaviour on the part of the male; (x) proportion of time in which the male was within 3 m of the female; (xi) proportion of times one partner followed the other after the other left a 3 m radius around the first; (xii) proportion of time spent grooming with the partner.

Initially, the differences between mean values of each behaviour for unrelated and related pairs were taken, and these differences were compared with a sign test (table 1). However, probable lack of independence among behaviours makes this comparison of behaviours, rather than of pairs, unsuitable for establishing statistically significant differences between paternal siblings and unrelated pairs. Instead, a cumulative measure of 'cohesiveness' of each pair was calculated as the pair's deviation from the median for each of these 12 behaviours:

$$\frac{\sum_{i=1}^{12} \dfrac{x_i}{\text{median}}}{12}.$$

Table 1. *Mean values for behaviours within sexual consortships, for related and unrelated pairs*

(A negative value in the difference column indicates that pairs consisting of paternal siblings showed lower rates or proportions than pairs consisting of unrelated animals.)

behaviour	paternal siblings (mean)	unrelated pairs (mean)	difference
'present' rate	0.63	0.72	−0.00
'inspection' rate	1.80	1.92	−0.12
'herding' rate	0.54	2.38	−1.84
mounting rate (with and without ejaculation)	1.60	3.19	−1.59
'lipsmacking' rate	1.60	1.52	+0.08
'waiting for' rate	0.19	1.27	−1.08
'solicit grooming' rate	0.89	1.85	−0.96
agonism rate	0.82	1.95	−1.13
proportion of female 'presents' followed by male sexual behaviour	0.25	0.27	−0.02
proportion of time male is within 3 m of female	0.65	0.78	−0.13
proportion of 'leaves' followed by 'follows' by partner	0.37	0.47	−0.10
proportion of time spent grooming with partner	0.22	0.21	+0.01

The result was an index of consortship cohesiveness for each pair, reflecting whether the pair was, on average, above or below the median value for consortship cohesiveness (see also Sapolsky *et al.* 1997). Paternal siblings and unrelated pairs were compared with a Mann–Whitney *U*-test.

It was not possible with the available data to distinguish between the effects of female and male behaviour on consortship cohesiveness. Preferences may be expressed in a complex manner within a pair, with each partner's behaviour depending to some extent on the behaviour of the other. This, combined with heterogeneity in the small sample available, made it impracticable to perform a fine-grained analysis of sex-specific contributions to consortship cohesiveness with these data.

(c) *Consortship occurrence among age-cohort members*

Next I examined the extent to which age-cohort members avoid each other as mates. I chose two years as the biologically relevant measure of age proximity because two factors suggest that the average pair of paternal siblings will be born at most two years apart. First, the mean duration of stay in groups is two years for adult males in Amboseli (Alberts & Altmann 1995a). Second, high-ranking males father most of the offspring in the population (Hausfater 1975; Altmann *et al.* 1996) but males maintain high rank (ranks 1 or 2) for an average of just 14 months, after which they steadily drop in rank (S. Alberts and J. Altmann, unpublished data). Thus, even if they remain in groups longer than two years the number of offspring they produce will usually decrease dramatically.

Twelve out of 16 males and 20 out of 29 females in the sample (see § 2(a)) were born after observations began in 1984. Age estimates were accurate to within a few days for these animals (i.e. animals were typically seen within a few days after parturition). Four males and four females in the sample were juveniles when observations began, and in these cases ages were assigned based on size and patterns of growth. Five females were multiparous in 1984 and were considered to have no age-cohort members among the 16 natal males in the sample.

Males were included in the analysis only after they had experienced the pattern of rapidly rising dominance rank and subsequently high levels of sexual activity that signal adulthood in this species (Alberts & Altmann 1995b). Each of the 16 adult natal males had both age-cohort members (females born within two years of the male) and members of different age cohorts

available as mates. The total number of female consort hours potentially available to each male was summed for two classes of female: (i) females who were members of the male's age cohort (mean available female consort hours per male = 320); and (ii) females who were not members of the cohort (mean available female consort hours per male = 783). The proportions that each male obtained of these two classes of available consort hours were then compared by using a Wilcoxon signed-ranks test. Note that among members of other age cohorts, males were as likely to consort with older females as with younger females (mean proportion of consort hours obtained with older females = 0.133; mean proportion of consort hours obtained with younger females = 0.178; Mann–Whitney *U*-test, $p = 0.34$).

(d) *Consortship cohesiveness of age-cohort members*

Among the 14 pairs for which within-consortship behavioural data were available (see § 2(b)), four pairs were members of the same age cohort (three pairs of paternal sibs and one unrelated pair) and ten were members of different age cohorts (two pairs of paternal sibs and eight unrelated pairs). The timing of sexual consortships relative to phase of the female sexual cycle did not differ between members of the same and different age cohorts (range of days on which consortships occurred relative to the onset of deturgescence of the sex skin was from 1 to 15 days in both cases; means were 5.84 days and 5.96 days before deturgescence, respectively). Consortship cohesiveness between members of the same and different age cohorts were compared by using a Mann–Whitney *U*-test. Mean values of each behaviour for members of the same and different age cohorts were also compared (table 2). However, as with paternal siblings and unrelated pairs, probable lack of independence among behaviours makes this comparison of behaviours, rather than of pairs, unsuitable for establishing statistically significant differences between members of the same and different age cohorts.

3. RESULTS

Paternal half-siblings did not show significant avoidance of each other as consort partners. The proportion of paternal sisters' consort time that each male obtained was not significantly different from the proportion of non-relatives' consort time that he obtained (Wilcoxon signed-ranks test, one-tailed test, $t_S = 23$, $n = 2$, $p = 0.12$; figure 1).

Table 2. *Mean values for behaviours within sexual consortships, for members of the same and different age cohorts*

(A negative value in the difference column indicates that pairs consisting of members of the same age cohort showed lower rates or proportions than pairs consisting of members of different age cohorts.)

behaviour	same cohort (mean)	different cohort (mean)	difference
'present' rate	0.46	0.78	−0.32
'inspection' rate	0.58	2.40	−1.82
'herding' rate	0.60	2.18	−1.58
mounting rate (with and without ejaculation)	1.28	3.16	−1.88
'lipsmacking' rate	1.32	1.64	−0.32
'waiting for' rate	0.39	1.09	−0.70
'solicit grooming' rate	0.46	1.93	−1.47
agonism rate	0.70	1.89	−1.19
proportion of female 'presents' followed by male sexual behaviour	0.31	0.24	+0.07
proportion of time male is within 3 m of female	0.53	0.81	−0.28
proportion of 'leaves' followed by 'follows' by partner	0.36	0.47	−0.11
proportion of time spent grooming with partner	0.14	0.24	−0.10

However, paternal half-sibs exhibited significantly lower cohesiveness within consortships than non-relatives, consistent with a discrimination against paternal half-siblings within consortships (Mann–Whitney U-test, $n_1 = 9$, $n_2 = 5$, $U = 39$, $p < 0.025$; figure 2). Because nine out of the 12 behaviours, including rate of sexual mounts, showed lower mean values when pooled across related compared to unrelated pairs (table 1), this discrimination was likely to translate into reduced rates of conception for related pairs. Data on actual rates of conception are not available for comparison between unrelated and related pairs. Females in this group have several non-conceptive cycles for every conceptive one, and several consort partners per cycle (S. Alberts and J. Altmann, unpublished data). Thus, it will take some time to accumulate data on reproductive outcomes of mating between paternal siblings.

Males obtained significantly less of the consort time of members of their own age cohort compared with members of other age cohorts. In particular, 13 out of 16 males obtained a smaller proportion of the consortships of their age-cohort members than they did of members of other age cohorts (Wilcoxon signed-ranks test, one-tailed test, $t_S = 42$, $n = 16$, $p = 0.014$; figure 3). Consortships between members of the same age cohort were also significantly less cohesive than were consortships between members of different age cohorts (Mann–Whitney U-test, $n_1 = 10$, $n_2 = 4$, $U = 40$, $p < 0.001$; figure 2). Again, this discrimination was likely to translate into reduced rates of conception for pairs belonging to the same age cohort (table 2).

Note that the three pairs with the lowest cohesiveness scores were paternal siblings which were also members of the same age cohort (figure 2). Further, the one pair of animals that were both unrelated and born within two years of each other scored the lowest among unrelated pairs and the highest among age-cohort members. These patterns suggest that both age-cohort membership and relatedness through the paternal line may affect consortship cohesiveness.

4. DISCUSSION

These data indicate that baboons employ a simple rule to avoid paternal relatives, namely 'discriminate against natal members of your age cohort,' and that they may also use phenotype matching to discriminate against
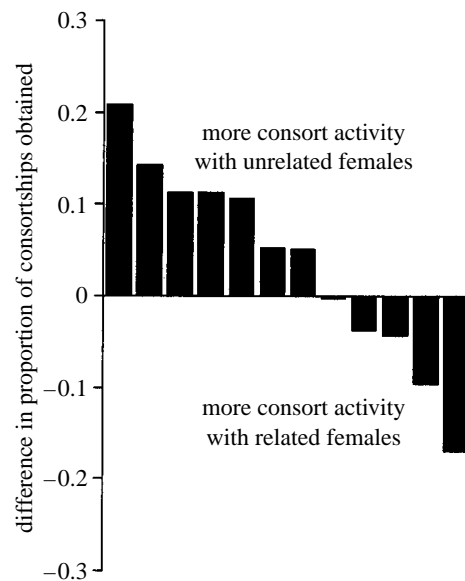

Figure 1. Difference, for each male, between consort activity with unrelated females and with paternal half-sisters. Each bar represents the value, for one male, of $(U - R)$, where U is the proportion obtained by the male of the consort time of unrelated females and R is the proportion obtained by the male of the consort time of paternal half-sibs. Bars are rank ordered. Bars above the expected value of zero represent males that consorted more with unrelated females; bars below the expected value of zero represent males that consorted more with paternal half-sibs. Males did not consort significantly less with paternal half-sibs than with unrelated females (Wilcoxon signed-ranks test, $p = 0.12$).

paternal kin as mates. Discrimination against age-cohort members will indeed prevent mating with paternal relatives, but will prevent mating with some non-relatives as well. Further, although the average pair of paternal siblings will be born within two years of each other, paternal relatives will sometimes occur in other age cohorts, as in the current study. Age-cohort membership thus varies in quality as a cue of paternal relatedness, because it is neither a necessary nor a sufficient predictor of paternal relatedness. Similarly, the effectiveness of phenotype matching for identifying relatives will depend on the variability of the phenotype in question and on
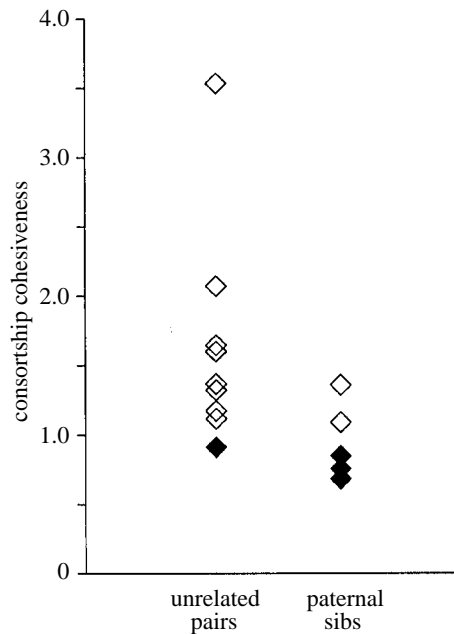
Figure 2. Consortship cohesiveness for unrelated pairs and paternal half-siblings. Paternal half-sibs scored significantly lower (Mann–Whitney U-test, $p < 0.025$). Open diamonds represent pairs in which the male and female belong to different age cohorts; closed diamonds represent pairs in which the male and female belong to the same age cohort. Note that the three pairs with the lowest cohesiveness scores were paternal siblings which were also members of the same age cohort, and that the one pair of animals that was both unrelated and born within two years of each other scored the lowest among unrelated pairs and the highest among age-cohort members.
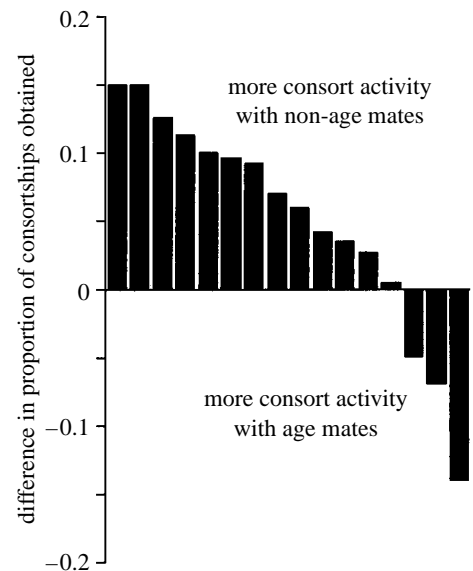

Figure 3. Difference, for each male, between consort activity with females of the same age cohort and with females of different age cohorts. Each bar represents the value, for one male, of $(D-S)$, where D is the proportion obtained by the male of the consort time of females born more than two years before or after him and S is the proportion obtained by the male of the consort time of females born within two years of him. Bars are rank ordered. Bars above the expected value of zero represent males that consorted more with females of different age cohorts; bars below the expected value of zero represent males that consorted more with members of the same age cohort. Males consorted significantly more with females of different age cohorts (Wilcoxon signed-ranks test, $p = 0.014$).

how specific it is to a group of relatives. Some combination of phenotype matching and age proximity will usually be the best means of identifying which animals to discriminate against as mates; the relative value of each will vary with the demographic and genetic structure of the group.

The opportunity costs of producing an inbred offspring are substantially lower for males than for females (Clutton-Brock & Harvey 1976; Waser *et al.* 1986). Females are therefore likely to be under stronger selection to avoid inbred matings than are males; data from other primate species indicate that virtually all sexual contact between maternal relatives is initiated by males (Enomoto 1978; Tutin 1979; Pusey 1980; Goodall 1986; Chapais & Mignault 1991; Manson & Perry 1993; reviewed in Pusey 1990). Indeed, males may be selected to obscure their genetic identity whenever possible, to increase the likelihood of successfully copulating with sisters. For maternal relatives, concealing the relationship from group members is difficult, because the mother–offspring relationship is such an enduring one. For paternal relatives, where social indicators of paternity are more equivocal, the opportunity for concealment is greater.

In this study, it was not possible to distinguish the effects of females versus males on consortship formation or cohesiveness. However, female mating preferences in baboons are largely expressed through levels of cooperation within consortships (Strum 1982; Smuts 1985;

Rasmussen 1983). Because male baboons are nearly twice the size of females, females have little influence on whether a particular male consorts with them (Bercovitch 1987), although they can influence consortship duration to some extent (Bercovitch 1987) and they can increase the probability that a consortship with a preferred male will form (Smuts 1985). The fact that females are known to contribute more to the cohesiveness of consortships than to whether a consortship occurs suggests that aversion on the part of females may be responsible for the lower levels of cohesiveness seen in consortships between paternal relatives and between age-cohort members.

What remains to be explained is the difference in the strength of mating avoidance between maternal and paternal relatives, and between age-cohort members and actual paternal relatives. First-order maternal relatives virtually never mate (Alberts & Altmann 1995a; Pusey & Wolf 1996). In this study, members of the same age cohort consorted with reduced probability relative to members of different age cohorts, and consortships between paternal half-sibs were not significantly less likely than consortships between non-relatives. The strength and accuracy of relatedness cues doubtless play a role in these differences. Animals should avoid maternal and paternal relatives to the same degree, because inbreeding costs should be the same for mating with both types of relative. However, whereas social cues of maternal relatedness are strong and unambiguous, social cues of paternal relatedness are

approximate, and phenotypic cues of both maternal and paternal relatedness in males may be subject to selection for ambiguity. The current study indicates that baboons use social cues to avoid paternal relatives and may use phenotypic cues as well. The social cues, involving age proximity, are likely to stem from close association during the juvenile period, but further work will be needed to illuminate the mechanisms by which differentiation among juveniles of different ages develops. Illumination of the mechanisms by which phenotypic cues might work will require further study as well.

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