

Kin biased investment in wild chimpanzees

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Summary

Kin selection theory predicts that recognition and preferences for kin can be highly beneficial. However, evidence of recognition of offspring by fathers in mammals has accumulated very slowly. Especially, in multi-male groups with a promiscuous mating system, like the chimpanzee, where offspring survival does not seem to depend on paternal care, paternal kin recognition has not yet been observed. In this study, we examined whether adult males of a wild chimpanzee community show recognition of their offspring (as determined genetically) and whether infants prefer to interact with kin rather than with unrelated peers. Our analysis utilises up to 14 years of observational data to investigate if adult males associate more frequently and behave less aggressively with females that carry their offspring. Furthermore, we use grooming and play behaviour to establish whether adult males and youngsters show preferences for kin versus non-kin. We found that, adult males did not associate preferentially with females with which they had offspring, but they were generally less aggressive towards any given female when she had a new born infant. Interestingly, however, fathers maintained these low rates of aggression long after the aggression rates of the non-sires had returned to their basal levels. Furthermore, fathers spent significantly more time playing with their own offspring. Thus, our data show for the first time that wild chimpanzee males can recognise their own offspring. Infants preferred to groom and tended to play more with their maternal siblings, but showed only a weak preference for playing with their paternal siblings when given the choice between similarly aged related and unrelated interaction partners. Despite the fact that paternal care does not play an obvious role in chimpanzee survival, kin recognition is observed in different aspects of the life of adult males and youngsters.

Keywords: chimpanzee, paternal care, kin recognition, kin preference, play.

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Introduction

Kin selection theory predicts that under many conditions it is beneficial to favour related individuals over non-related ones (Hamilton, 1964). Central to the theory is the ability to recognise kin which in turn should be highly adaptive. More specifically, one would predict that in species where youngsters need parental care, not only mothers, but also fathers, should recognise and favour their own offspring over other, non-related young. Indeed, in many taxa some forms of paternal investment have been observed, e.g., in arthropods (e.g., Tallamy, 2000), fish (e.g., Forsgren, 1997), birds (e.g., Møller, 2000; Møller & Cuervo, 2000), rodents (e.g., Schradin & Pillay, 2003, 2005) and primates (Borries et al., 1999; Buchan et al., 2003). However, in most of these cases, male-female pairs stay together for extended periods of time and paternity is relatively certain and easy to infer by the prospective father (with some exceptions in birds, Møller, 2000). In promiscuously mating species, paternity inference is less easy and until now, there is little proof that fathers can recognise their own offspring. In addition, it may be beneficial for females to confuse paternity to minimise the risk of infanticide by males and to reduce the costs of male harassment (Andersson, 1994; Eberhart, 1996). If paternity confusion is effective, males will not be able to easily infer paternity based on mating behaviour, making infanticide less likely as it would then be prone to errors (van Schaik, 2000). These conflicting inter-sexual strategies lead to an arms race in which we expect a strong selective pressure on females to confuse paternity certainty when infanticide risk exists, while there would be pressure on males to attempt to establish paternity.

The study of paternal investment in promiscuously mating species was, until recently, nearly impossible in wild mammal populations, as researchers could rarely be certain about the sire of any given young. Now, with recently developed genetic tools, paternity can be established in wild animal populations using non-invasive samples (see e.g., Vigilant, 2001), providing the opportunity to investigate to what extent males selectively support their own offspring. If males behave differentially towards their own offspring when compared to unrelated young, this is usually interpreted as an indication of paternity recognition. In primates, paternal care is common and can take many forms, such as grooming, carrying the offspring, protection against aggression by other group members, protection against predators, play or food sharing (Clutton-Brock, 1991; Dixson, 1998). Furthermore, if infants

are closely associated with their mother, most of the above mentioned behaviours could also be directed towards the mother, which could then be interpreted as an indirect form of paternal care. Although these behaviours could also be interpreted as investment into future mating success with the same female, we would then not expect males to bias their efforts solely towards those females with whom they already have an offspring, but also to invest into future reproductive opportunities with all other females. In promiscuously mating primates, only a few studies have shown that males can recognise their own offspring: In langurs and yellow baboons, males have been observed to selectively support their own infants when the infants are engaged in aggressive interactions with other, non-related individuals (Borries et al., 1999; Buchan et al., 2003). Additional evidence for the ability to recognize paternal kin in promiscuously mating primates comes from rhesus macaques, where adult females have been shown to prefer the company of paternal siblings over that of non-related individuals (Widdig et al., 2001). Although the mechanism by which fathers recognise their offspring is still unclear, it has been suggested previously that the amount of time a male spends in proximity to a fertile female might be a strong predictor of paternity and could be used as such by males (Alberts et al., 2003; Buchan et al., 2003). Paternal sibling recognition is even more problematic although phenotypic matching could make sibling recognition possible; it is however, not clear how it could serve to distinguish between paternal and maternal siblings (Parr & de Waal, 1999) in the absence of familiarity.

In this study we used data on wild chimpanzees to investigate whether chimpanzee males selectively support their own offspring and whether juveniles prefer paternal siblings over unrelated individuals. Chimpanzees live in a very fluid, fission-fusion society where association time between males and females is not expected to be a valuable predictor of paternity. Males mate promiscuously with many females and have not been observed to show paternal care. Infants stay in close proximity to their mother for the first 8 years of their lives and interact only occasionally with adult males. Although male-infant interactions are rare, males have been observed to occasionally groom and play with infants. Furthermore, since infants and mothers stay in close proximity, males may show some indirect form of paternal care by behaving differentially towards those females that carry their offspring. We used 14 years of behavioural data on wild chimpanzees (*Pan troglodytes verus*) of

the Taï National Park, Côte d'Ivoire, to investigate the following four questions: (1) Can paternity be predicted based on copulation rates or association time around conception? (2) Do adult chimpanzee males show indirect paternal care by associating more with, or exhibiting less aggression towards, those females that carry their offspring? (3) Do adult chimpanzee males play and groom preferentially with their own infants? (4) Do young chimpanzees play and groom preferentially with paternal half-sibs rather than their unrelated peers?

Methods

Study site and data collection

The Taï National Park, Côte d'Ivoire, comprises an area of approximately 4540 km² and consists of evergreen lowland rainforest (for detailed description of the study site see Boesch & Boesch-Achermann, 2000). Data presented in this study were derived from three communities; the North, Middle and South Communities which were habituated in 1979, 1995 and 1993, respectively. With the help of field assistants, all communities have been continuously observed since their habituation. Data presented here for the analysis of father-offspring and father-mother interactions, encompass the period from Jan 1992 to Dec 2002 for the North community and 1999-2002 for the Middle and South communities. Data on sibling interactions encompass the time from 1989-2002. Community sizes varied between 1-7 adult males (aged >15 years), 7-25 adult females (aged >13 years), 7-19 subadults (aged between 5-15 for males and 5-13 years for females) and 4-16 dependent offspring (aged 0-4 years). Data were collected using daily focal animal follows (Altmann, 1974) and data on social interactions were collected systematically on checksheets by field assistants throughout the years. Targets were usually followed from nest to nest or as long as possible (mean observation time: 9.7 h \pm 2.1). The present study is based on a total of 515 follows on males (father-offspring and father-mother interactions), 1447 follows on females (father-mother interactions) and 480 follows on offspring and juveniles (sibling interactions). All behavioural data were entered either into the Taï-Chimp-BehaveBase, our large chimpanzee behaviour database, or in a mother-offspring database using Microsoft Access 1997. All paternity relationships were established genetically with exclusion probabilities

of >0.99% (see Vigilant et al., 2001; Boesch et al., 2006 for more details). The present study uses known paternity relations for 38 infants and 12 adult males.

Inference of paternity

Based on recent findings from Deschner et al. (2004) it is most likely that males can infer the time of likely conception from the sexual swelling size of the females. If this is indeed the case, males could know when a copulation may be fertile and infer paternity from this. However, the data in our longterm database are not detailed enough to test this hypothesis directly. Thus, in this study we test two different, simpler hypotheses, namely that chimpanzees can infer paternity from copulation frequencies and from association patterns.

Copulation rates around conception

To determine if males could derive paternity based on copulation frequencies, we calculated copulation rates (number of copulations per 100 association minutes) for all adult males and females during their most likely time of conception. The most likely time of conception was defined as the 8th month before a birth plus/minus one month. Two comparisons were made: for males we compared their copulation rates with females which whom they sired an offspring to their copulation rates with unconceiving females at the same time periods (within male comparison). For females, we compared their copulation rates with sires to those of all other males that were observed to copulate with the females during her most likely time of conception (within female comparison). These two analyses allow us to consider individual knowledge of males ('have copulated x time with female a and x times with female b') and females ('have copulated more frequently with male a than with male b'), respectively.

Male-female association around conception

To determine if males can infer paternity from simply using association times with the female in question, we calculated the sociable dyadic association index (sDAI) for all adult males and females around the time of conception. Contrary to other indices, this index excludes times when individuals were observed alone and only uses 'social time', i.e., time spent in the company of

at least one other adult group member. The sDAI measures the proportion of time that individual A and B spent together in the same party as compared to the time they spent apart, but in company of other individuals (see Nishida, 1968; Boesch & Boesch-Achermann, 2000) and was calculated as follows:

$$\text{sDAI} = \frac{\text{social time}_{A+B \text{ together}}}{\text{social time}_{A \text{ without } B} + \text{social time}_{B \text{ without } A} + \text{social time}_{A+B \text{ together}}}$$

Association indices were calculated using only the days of the three oestrus cycles of the most likely time of conception. We then compared the association index of the sire to the highest index of any of the non-sires.

Indirect paternal care: male-female interactions

Because fathers could show indirect paternal care by being protective towards the females that carry their offspring, we analysed male-female interactions. Young chimpanzees under the age of 8 years are still associated with their mother for about 75-95% of the time, so that association or aggression towards mothers can be assumed to affect the infant as well. During the first year of their life baby chimpanzees are almost always in body contact with their mothers. Also during their second year of life infants do not range far from their mother. At about 3 years of age weaning takes place, however, infants remain dependent on their mother until they are about 5 years old. At this time the mother starts cycling again (inter-birth-interval around 5.5 years, Boesch & Boesch-Achermann, 2000). Five to 10 year old chimpanzees are usually referred to as juveniles (Goodall, 1986; Boesch & Boesch-Achermann, 2000).

Dyadic association

To test if males associate more with the mothers of their offspring than with other females, we calculated the sDAI for all males and females with infants across three different time periods: 6 months before the birth of a new baby (t1), up to 6 months after birth (t2) and 7-12 months after birth (t3). This allowed us to compare sDAIs within males over time as well as between males (fathers and non-fathers). We further wanted to test, if males had an overall tendency to associate with females with related offspring as compared to all other females (irrespective of the presence or absence of infants). For this we calculated sDAIs for all other male-female associations, including females without or with older infants.

Aggression

The following male behaviour elements were considered to be aggressive and potentially harmful to females: displaying, chasing, attacking, pushing, beating, and biting. To test if males display different levels of aggression toward females depending on whether they carry an offspring related to the male or not, we calculated the rate of aggressive interactions (number of aggressive interactions/association time) towards mothers during two time periods after the birth of a new infant: 0-6 months after birth of an infant (t2) and 7-12 months after birth (t3). This allowed us to compare aggression rates of individual males at different time points as well as between different males (fathers and non-fathers). These aggression rates were compared to a baseline aggression rate, which was based on the rate with which males behaved aggressive towards females with 2-3 years old infants. This comparison was chosen to minimise the influence of confounding factors, such as the arrival of a new infant in the group or the presence of females with sexual swellings. Females with infants 2-3 years of age neither carry a dependent infant nor do they have regular sexual swellings, and thereby constitute an appropriate control group. Additionally, we also calculated the aggression rates of males towards all other adult females (irrespective of whether or not they had an offspring) in the community during the same time periods as above. This analysis served two purposes: firstly, it allowed us to determine if males indeed distinguish between females carrying their own offspring and other females, and secondly to exclude the hypothesis that these males were simply less aggressive during those times.

Direct paternal care: male-offspring interactions

In order to analyse if males interact primarily with their own offspring, we analysed play and grooming interactions between adult males and infants/juveniles up to 10 years of age. Aggression towards young infants and interventions when infants are fighting are rare in chimpanzees and could therefore not be used as an indicator for paternity recognition.

Paternal play

To test if fathers played more with their offspring than with unrelated infants, we analysed all instances of male-offspring play that took place when males had the choice between playing with a related or unrelated infant of

similar age. We calculated number and duration (in minutes) for all independent play events between adult males and infants/juveniles. A play event was considered to be independent if it was separated from previous play by either an interaction with a different individual or by at least 1 hour of no play. To control for the null hypothesis that males play at random with whoever is present, both frequency and duration of play were corrected for the number of infants present in the community during a given month, as the probability with which a father would choose his own infant by chance depends on the number of infants present in the community. For this correction we transformed observed frequencies or durations into a 'score' that corrected the observed value according to infant availability, using an inverse probability correction procedure (Thompson, 2002). The observed value was multiplied by $c = 1/(2 \times p)$, with p being the probability that the infant was chosen by chance. This factor corrects a choice of the rarest category of infants for its lower probability to be chosen by chance (so that the corrected frequency is above one) and a choice of the more frequent category of infants for its higher probability to be chosen by chance (leading to a corrected frequency below one). For example, if in a given month a male had the choice between two of his own offspring and 5 unrelated young between 0-2 years of age, play events with his own offspring would be multiplied by $c = 1/(2 \times (2/7)) = 1.75$ while play events with each unrelated young by $c = 1/(2 \times (5/7)) = 0.7$. If he had chosen randomly seven times, he would have played two times with his own offspring and five times with non-offspring, in which case c would be 3.5 for both categories (2×1.75 for play with own offspring and 5×0.7 for non-offspring). Although chimpanzees live in a fission-fusion system and not all infants may be present in a party at any given time, we based our calculations on the number of related/non-related infants present within the community rather than within a party because we assumed that adult males (which are dominant over females) can choose with which individuals they would like to associate. This implies that a male could choose from any of the community members and not only between members of the same party. Transformed play scores were then averaged for each male to account for differences in observation time for each male.

Infant chimpanzees have been observed to play in different ways and with different frequencies according to their age (Goodall, 1968, 1986; Boesch, pers. obs.). Therefore, in our analysis we only considered choices

between play partners of similar age. Three age categories were defined: 0-2 years (cat1), 2-5 years (cat2) and 5-10 years (cat3). These categories respond roughly to physical development of chimpanzee infants (see Goodall, 1986; Boesch & Boesch-Achermann, 2000), i.e., dependent babies carried by their mother (0-2 years), infants with an increasing degree of independence (2-5 years) and juveniles (5-10 years). Statistical analyses were based on weighted mean play frequency and duration of play by individual males with related and unrelated young.

Paternal grooming

Grooming data were analysed in the same way as data on play events.

Paternal sibling recognition: infant interactions

Play

In contrast to males, infants are always associated with their mothers, and are therefore not free to choose with which individuals they associate. To account for this, we restricted our analyses on infant play to those situations in which infants had the choice between playing with unrelated and related individuals of similar age within the same party. The number of independent play events and the duration of play were recorded for each occurrence of play. Presence of others was obtained from scan samples which were carried out every 15 minutes during observation. Possible play partners were categorised into the same age classes as previously stated, as playing with individuals of certain ages might be preferred. The kinship classes used were, maternal half-sibs, paternal half-sibs and unrelated individuals. Play events were categorised into choices between (1) maternal siblings and unrelated playmates within the same age class and (2) paternal half-siblings and unrelated playmates within the same age class. The few cases in which infants had the choice between maternal, paternal and unrelated individuals were included into the above mentioned categories. Data were corrected for the number of possible play partners present within each age and kinship class in the party to account for chance events. Corrections were the same as for the paternal-offspring play, i.e., $c = 1/(2 \times p)$, with p being the probability that the infant within this category was chosen by chance. Two questions were addressed: (i) do infants prefer paternal siblings over unrelated play partners of similar ages and (ii) do infants prefer maternal siblings (which

are always considerably older due to the long chimpanzee inter-birth interval) to unrelated similarly aged play partners?

Grooming

Grooming data were analysed in the same way as play data. However, we pooled data across the different age categories, because only very few age-matched dyads showed grooming behaviour after taking choice situations and age classes into account. Therefore, we analysed grooming behaviour across the three age classes, still including only those situations in which infants/juveniles had the choice between partners of the same age-class.

Statistical analyses

Whenever possible, comparisons were made on individual level, i.e., activities were averaged across individuals and statistical tests were done on individual level, so that n equals the number of individual chimpanzees in the analysis. This counterbalances for differences in observation time between individuals. Data on paternal play, paternal grooming, dyadic association, copulation rates and infant interactions were analysed using either Student's t -test, Student's t -test for related samples or Friedman test for comparing more than two groups across time. Data on male-female aggressive interactions were analysed using 1-sample t -tests, comparing the observed values to a fixed baseline value. Adjusted p -values for multiple testing with the improved Bonferroni-Hochberg method (Hochberg, 1988) were used when more than three comparisons were made. Since we had clear directional predictions for all analyses, we used 1-tailed statistics with $p = 0.05$ as the significance level.

Results

Inference of paternity

Copulation rates around conception

During the likely time of conception, fathers did not copulate more frequently with females with which they sired an offspring than with other females (male perspective; paired sample t -test: $t = -1.57$, $N = 13$, $p > 0.92$). Thus, males are not expected to infer paternity from copulation

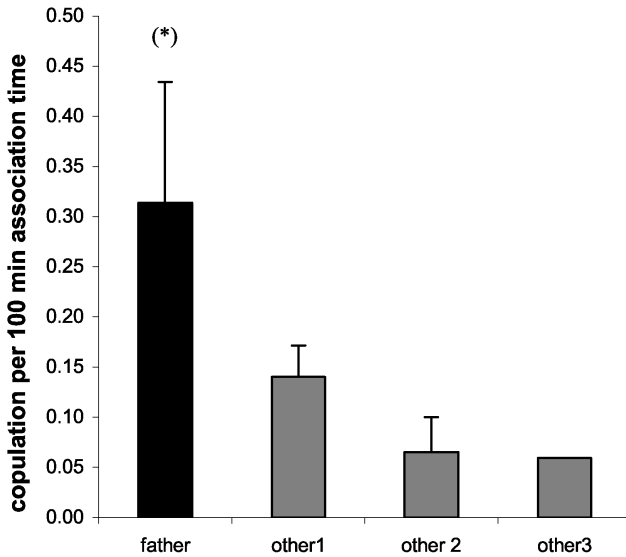


Figure 1. Copulation rate (number of copulations during 100 minutes of association time) + SE during the conception period between females and fathers (black bar) versus other males (grey bars). For all figures, ** indicates significant differences values $p < 0.01$, * indicates significant differences values $p < 0.05$, (*) indicates tendencies with values $p < 0.10$.

frequencies alone. However, females tended to copulate more often with the male which sired their current offspring than with other males in the community that did not sire the infant (paired sample t -test: $t = 1.76$, $N = 13$, $p < 0.054$, Figure 1). Thus, contrary to males, females might be able to use copulation frequencies to infer paternity likelihood.

Male-female association around conception

During the most likely time of conception, sDAIs of females and the father of their offspring were not significantly higher than sDAIs of the same females with other males in the community (paired samples t -test: $t = 0.61$, $N = 14$, $p > 0.27$).

Indirect paternal care: male-female interactions

Dyadic association

Overall, association indices were not affected by either the birth of an infant or by paternity. The sDAIs of males with females with newly born infants

were not influenced by paternity (Student's t -test: $t = 0.34$, $N = 11$, $p > 0.35$ (t1), $t = -0.21$, $N = 10$, $p > 0.42$ (t2), $t = 0.53$, $N = 8$, $p > 0.3$ (t3)). Furthermore, fathers showed similar association tendencies towards all females in the community before and after the birth of the infant, irrespective of whether or not they had fathered the offspring (paired sample t -test: $t = 1.12$, $N = 11$, $p > 0.14$ (t1), $t = -0.4$, $N = 10$, $p > 0.35$ (t2), $t = -0.52$, $N = 8$, $p > 0.31$ (t3)), indicating that males do not have a general tendency to associate with or avoid small infants. Finally, fathers did not change their association patterns with the mother of their offspring when comparing 6 months before birth, 6 months after or 12 months after birth (Friedman test: $\chi^2 = 1$, $N = 8$, $p > 0.3$), indicating that chimpanzee males do not use association patterns as an indirect form of paternal care.

Aggression

As can be seen in Figure 2a, all males showed significantly reduced aggression rates towards females with young infants compared to the baseline level (1-sample t -test: fathers: $t = -5.155$, $N = 10$, $p < 0.001$, adj. $p_{\text{limit}} = 0.006$; non-fathers: $t = -5.762$, $N = 10$, $p < 0.001$, adj. $p_{\text{limit}} = 0.006$). However, after the first 6 months, fathers showed significantly reduced (as compared to baseline) aggression rates towards those females, with which they had sired an infant (1-sample t -test: $t = -5.48$, $N = 8$, $p < 0.001$, adj. $p_{\text{limit}} = 0.006$), while aggression rates of all other males (non-sires) towards the same females were undistinguishable from baseline levels (1-sample t -test: $t = -0.402$, $N = 9$, $p > 0.34$). When we compared the aggression rates of males towards females without young infants during the same time periods as used above, we did not find any differentiation from baseline values, indicating that our baseline measure correctly reflects aggression rates between the sexes (1-sample t -test: fathers t1: $t = -0.22$, $N = 10$, $p > 0.41$; fathers t2: $t = -0.14$, $N = 8$, $p > 0.44$; non-fathers t1: $t = -1.1$, $N = 10$, $p > 0.15$; non-fathers t2: $t = -0.19$, $N = 9$, $p > 0.42$). This demonstrates, that males were selectively less aggressive towards the mothers of their offspring while maintaining normal aggression rates towards all other females within the community during the same time periods (paired sample t -test between sires/non-sires & mothers and sires/non-sires & other females: sires t1: $t = -1.8$, $N = 10$, $p < 0.06$, sires t2: $t = -2.6$, $N = 8$, $p < 0.002$; non-sires t1: $t = -1.9$, $N = 10$, $p < 0.05$, non-sires t2: $t = -0.5$, $N = 9$, $p > 0.3$; Figure 2a, b).

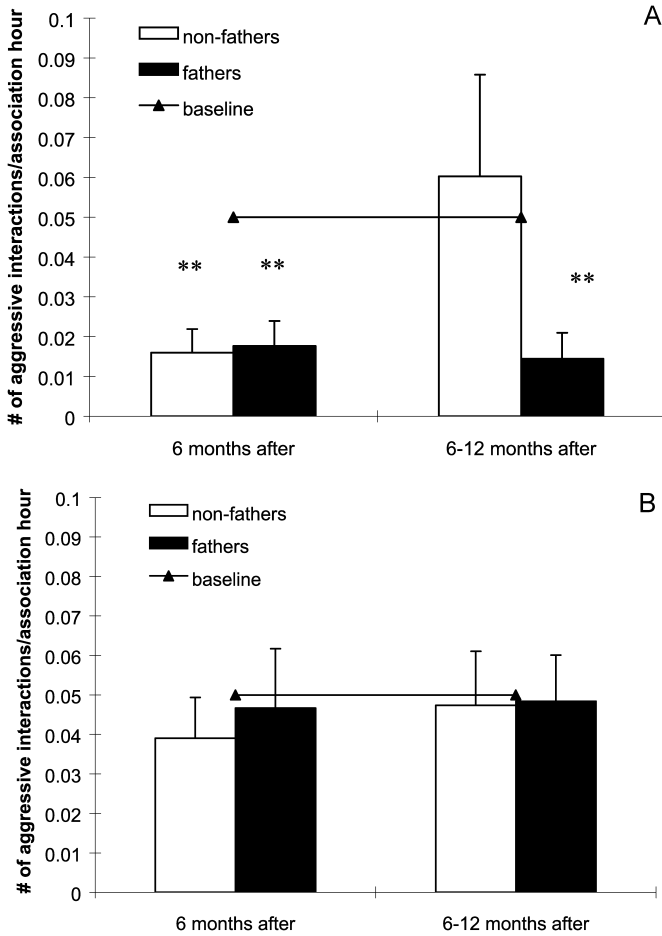


Figure 2. (a) Mean (+SE) male aggression rates towards females after the birth of an infant. The line indicates the baseline level of aggression during the study period. Asterisks indicate significant differences compared to baseline. (b) Mean (+SE) male aggression rates towards all other adult females (irrespective of whether or not they had infants) within in the community during the same time periods as in Figure 2a.

Direct paternal care: male-offspring interactions

Play

During the study period, 301 play events between 8 adult males and 50 infants were recorded (age cat1: 48, age cat2: 117, age cat3: 136). The average duration of a play bout between an adult male and a juvenile/infant was

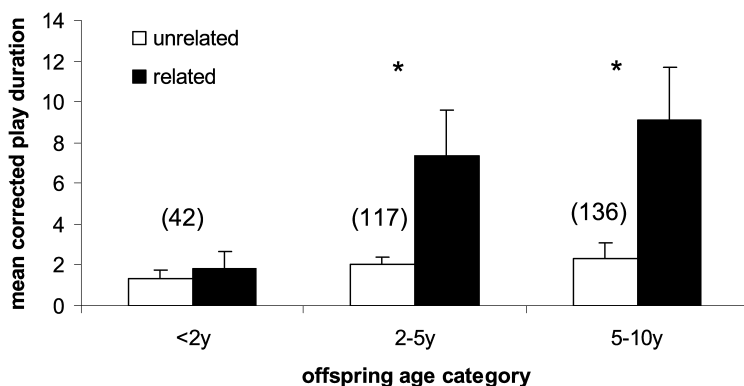


Figure 3. Mean (+SE) duration of play bouts between males and offspring of different ages. Values are corrected values (see text). For all figures, values in parentheses indicate the number of observed play events per category.

3.06 minutes. Fathers played significantly longer with their own offspring than with unrelated infants between 2-5 years of age (paired sample t -test: $t = -2.6$, $N = 6$, $p < 0.03$) and youngsters between 5-10 years of age (paired sample t -test: $t = -2.2$, $N = 6$, $p < 0.04$; see Figure 3). There was, however, no significant effect for 0-2 year old infants (paired sample t -test: $t = -0.4$, $N = 6$, $p > 0.35$; see Figure 3). No significant difference was found in the number of play occurrences between fathers and related or unrelated young (paired sample t -tests: 0-2y: $t = -0.4$, $N = 6$, $p > 0.33$; 2-5y: $t = -1.3$, $N = 6$, $p > 0.12$; 5-10y: $t = -0.8$, $N = 6$, $p > 0.21$).

Grooming

All together 198 grooming events between 6 adult males and 26 infants were recorded. The average duration of a grooming bout between an adult male and a juvenile/infant was 4.5 minutes. Almost all grooming events took place between males and youngsters older than 5 years (age cat1: 9 grooming bouts (3 males), age cat2: 1 grooming bout, age cat3: 188 grooming bouts (6 males)). As there was too few data for age classes 1 and 2, statistical tests were only carried out for cat3. There was a tendency of fathers to groom their own offspring longer than unrelated youngsters (paired sample t -test: $t = -1.59$, $N = 6$, $p < 0.09$ (cat 3), see Figure 4). No significant effect of relatedness on grooming frequency was found (paired sample t -test: $t = 0.35$, $N = 6$, $p > 0.37$).

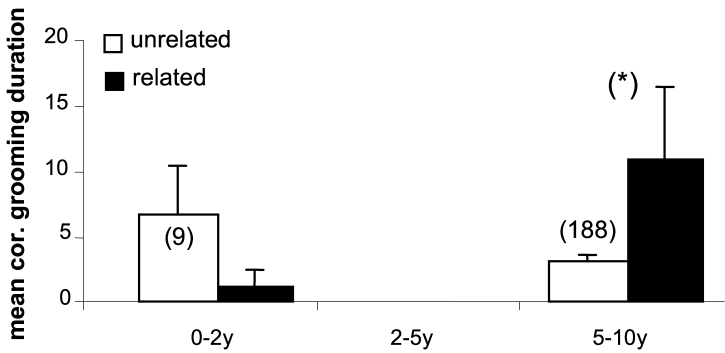


Figure 4. Mean (+SE) duration of grooming bouts between males and offspring of different ages. Values are corrected values (see text). Only one grooming event was recorded for 2-5 year old infants, and as no mean could be calculated, it is not displayed.

Paternal sibling recognition: infant interactions

Play

Overall, we recorded 57 play events (i.e., play situations where both, related and unrelated playmates of a given age category were present) for 0-2 year old chimpanzees, 186 for 2-5 year old and 81 for 5-10 year old chimpanzees. Average play duration was 3.9 minutes and data were derived from 10 different infants. Two to 5 year old infants had a tendency to play longer with paternal half-siblings than with unrelated play mates (paired sample *t*-test: $t = 1.59$, $N = 9$, $p < 0.08$; Figure 5). All other comparisons in play duration (paired sample *t*-test: 0-2y: $t = -0.7$, $N = 4$, $p > 0.25$; 5-10y: $t = 0.34$, $N = 5$, $p > 0.37$) or play frequency (paired sample *t*-test: 0-2y: $t = 0.88$, $N = 4$, $p > 0.22$; 2-5y: $t = 0.7$, $N = 9$, $p > 0.25$; 5-10y: $t = 1.28$, $N = 5$, $p > 0.13$) were non significant. For maternal half-sibs, 2-5 year old infants played significantly more often and tended to do so for longer duration, with maternal half-sibs than with unrelated playmates (paired sample *t*-test: Frequency: $t = 2.47$, $N = 4$, $p < 0.05$; Duration: $t = 2.3$, $N = 4$, $p < 0.06$; Figure 6a, b). No difference was found in any of the other age categories (paired sample *t*-tests: Duration: 0-2y: $t = 0.43$, $N = 4$, $p > 0.34$; 5-10y: $t = -0.13$, $N = 2$, $p > 0.45$; Frequency: 0-2y: $t = 1.62$, $N = 4$, $p > 0.1$; 5-10y: $t = 35$, $N = 2$, $p > 0.39$).

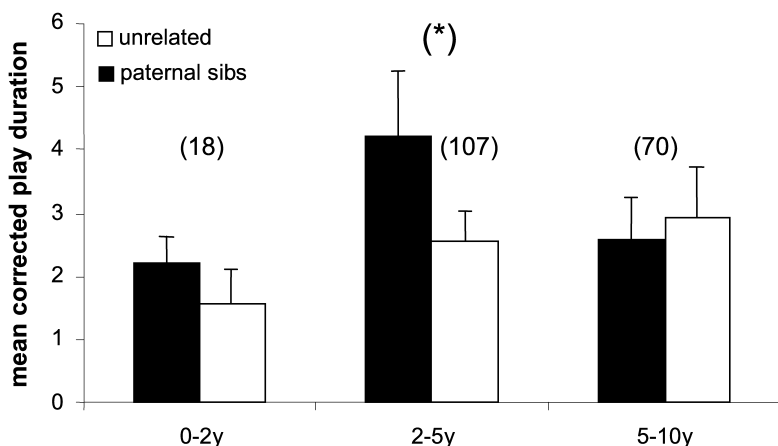


Figure 5. Mean play duration (+SE) of chimpanzees when given the choice between similar-aged paternal half-siblings and unrelated playmates. Values are corrected values (see text).

Grooming

Overall, we recorded 42 grooming events in which individuals could choose between related and unrelated grooming partners of the same age (16 for 0-2 year old, 16 for 2-5 year old and 10 for 5-10 year old chimpanzees). However, these 42 grooming events were derived from only 4 different individuals. As such, we combined the data across the age classes rather than analysing each age class separately. Grooming bouts lasted on average 3.2 minutes. Maternal half-siblings groomed significantly more often (paired sample *t*-test: $t = 6.11$, $N = 4$, $p < 0.005$) and tended to groom longer (paired sample *t*-test: $t = 2.19$, $N = 4$, $p < 0.06$) than unrelated partners (Figure 7). No significant difference was found between paternal half-siblings and unrelated individuals for either grooming frequency (paired sample *t*-test: $t = 1.39$, $N = 4$, $p > 0.12$) or duration (paired sample *t*-test: $t = 1.18$, $N = 4$, $p > 0.16$).

Discussion

Although paternal behaviour was not found in all contexts analysed in this study, our data show for the first time that chimpanzee males can indeed recognise their own offspring. They significantly reduce aggression towards

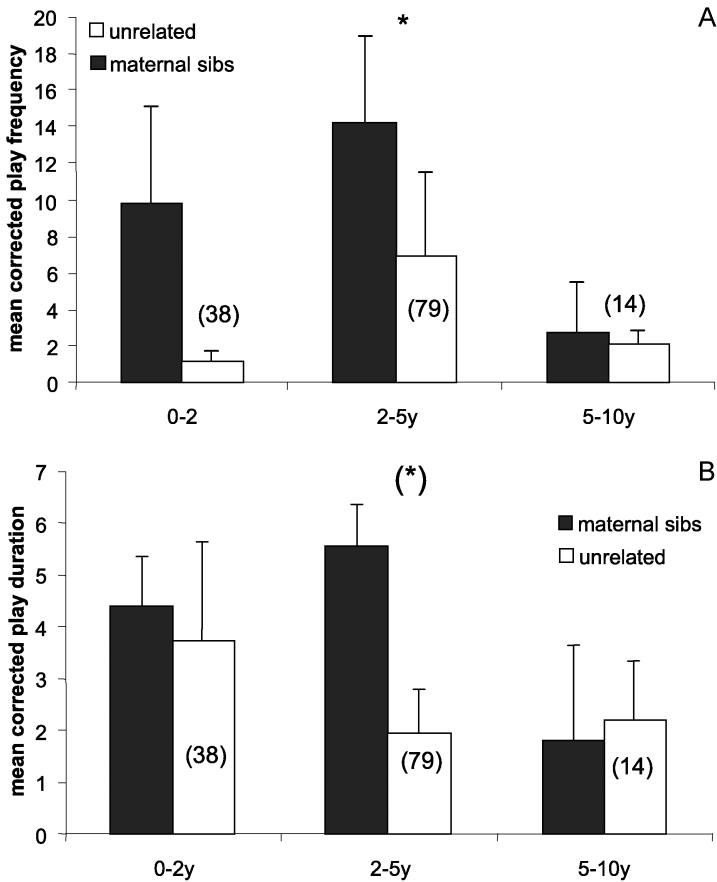


Figure 6. (a) Mean play frequencies (+SE) of infants when given the choice between same aged maternal and unrelated individuals. Values are corrected values (see text). (b) Mean play duration (+SE) of chimpanzees when given the choice between similar aged maternal half-siblings and unrelated playmates. Values are corrected values (see text).

females that carry an infant they have sired and they play significantly longer with their own offspring than with unrelated infants. Males also showed a tendency to groom their own young longer than unrelated individuals. No paternal behaviour was observed in association preferences and in play and grooming frequencies. In our sample, females but not males might have inferred paternity from copulation frequencies around time of conception. Males, however, may use other indicators, such as the timing of copulation (see Deschner et al., 2004) to infer their likelihood of paternity. Infants, when given a choice, clearly preferred to interact with maternal kin over unrelated

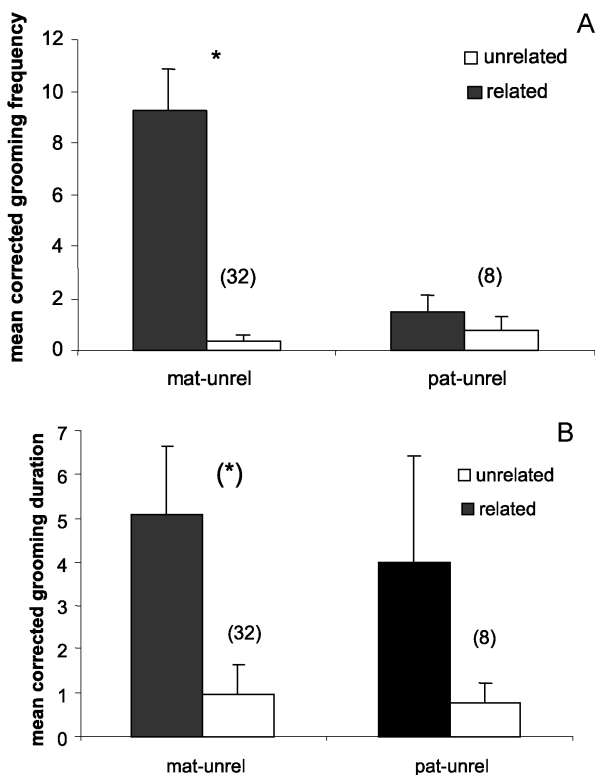


Figure 7. (a) Mean grooming frequencies (+SE) of chimpanzees when given the choice between similar-aged maternal (mat)/paternal (pat) half-siblings and unrelated (unrel) individuals. Values are corrected values (see text). (b) Mean grooming duration (+SE) of chimpanzees when given the choice between similar-aged maternal (mat)/paternal (pat) half-siblings and unrelated (unrel) playmates. Values are corrected values (see text).

youngsters, and showed a tendency to prefer paternal siblings over unrelated peers for playing.

Our result of paternal kin recognition in chimpanzees adds to the body of knowledge on paternity ascertainment in multi-male groups, as was found in yellow baboons. This result is remarkable given that in some human societies paternity certainty is very inconsistent and traditional knowledge about reproduction often does not match with the biological reality (Hill & Hurtado, 1996; Strassman, 1996). Although it seems easy to understand the mechanism of paternity recognition in one male groups such as in langurs (Borries et al., 1999), males living in multi-male groups have to consider clues other than direct presence, to infer paternity. Alberts et al. (2003) have

proposed that in baboons association patterns of males with females during the estrous period are very reliable predictors of paternity. However, in the present study, we showed that in chimpanzees association patterns do not allow males to predict paternity. Paternity recognition in chimpanzees is further complicated by the fact that they do not live in stable social groups like baboons or langurs but in a fission-fusion society where the community splits into frequently-changing, smaller subgroups (parties). Average party size represents only 11% to 22% of the actual community size and changes in party composition occur about every 25 minutes in Taï chimpanzees (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004). Therefore, males have more difficulties in monitoring the behaviour of a given female to ascertain paternity. Our finding of paternity recognition, however, is in line with recent reports from hyenas (*Crocuta crocuta*) (Van Horn et al., 2004). Hyenas, like chimpanzees, live in multi-male fission-fusion societies and paternity recognition is difficult to achieve. Nevertheless, hyena males associate more closely with daughters than with sons or non-kin. Similarly, hyena cubs were found to behave less aggressive towards fathers than to other males, indicating that also cubs recognize their fathers. However, like chimpanzees, hyena males did not exhibit costly nepotistic behaviour (Van Horn et al., 2004).

The suggested mechanism for paternity recognition in hyenas is phenotype matching (Van Horn et al., 2004). In chimpanzees it might be possible that males infer the likelihood of conception from the size of a female's sexual swelling (Deschner et al., 2004) and can therefore time their mating efforts accordingly. Although we did not have the data to test this hypothesis, this scenario would explain why copulation frequencies within males did not predict paternity. It has been suggested previously that good timing rather than frequency increases the likelihood of fathering an offspring (see also Dixson, 1998; Constable et al., 2001). However, in Taï chimpanzees, successful sires tended to mate more frequently with a particular female at her most fertile moment, resulting in mating frequency being a reliable indicator of paternity for females but not for males. Contrary to females, males (in a fission-fusion society) will not be able to assess their own mating effort in comparison to that of other males because females will be frequently out of sight. Although females could potentially infer paternity from copulation frequencies (Figure 1), it seems unlikely that a bias in female behaviour is responsible for the finding that fathers spend more time playing with kin

than with non-kin. If females used their inference of paternity to increase tolerance specifically with inferred fathers, we would expect to observe an increased frequency of father-offspring play. However, what we observe is a kin-biased increase in play duration rather than frequency. In addition, association patterns were not kin biased and we therefore believe that our findings are an indication of male recognition of their offspring. Thus, whatever the mechanism, it is important to note that even in a flexible fission-fusion society with a promiscuous mating system, like that of chimpanzees, it remains possible for males to ascertain their paternity. By this, one of the central tenets of kin selection theory is supported, despite doubts that have arisen regarding the likelihood of the emergence of a proximate mechanism permitting kin recognition in large social groups (Kummer et al., 1997).

Tai male chimpanzees did not show kin preference in all the analysed contexts. Fathers played longer with their offspring, but did not groom them preferentially. Similarly, fathers were less aggressive towards females carrying their very young offspring but did not associate with them more often. Traditionally, it has been proposed that only mothers, and not fathers, invest in their offspring for many years and sometimes past their weaning time (Goodall, 1986; Boesch & Boesch-Achermann, 2000). Males, on the other hand, are thought to focus their attention on sexual competition, which in such a multi-male society is very high (Goodall, 1986; Boesch et al., 2006). Thus, rather than investing a lot of time into paternal care, males living in polygynous groups with no clear reproductive season and long inter-birth intervals, such as chimpanzees, are expected to secure future reproductive success by mating with other fertile females. This study reveals that males at the same time also invest in paternal care, but do so only in some contexts. To maximise their fitness males should invest differentially in own offspring as well as in future reproductive success. This trade-off will be reflected in the way males distribute their time between females with whom they have already sired an infant and sexually reproductive females with whom they want to sire an offspring. The fact that male Tai chimpanzees do not associate or groom preferentially with their own infants (or their mothers) might be a consequence of this time constraint, as both behaviours are potentially important components of a strategy aimed at gaining more mating opportunities with sexually active females. Furthermore, grooming as well as playing with infants may be used not only in the context of paternal care but also

as a means to gain access to fertile females, which could explain why frequencies of grooming and play behaviour do not differ between related and unrelated pairs. However, when males are already associated with their own offspring, they spend significantly more time playing with their own infants than with unrelated young, suggesting kin recognition. By doing so, they potentially enhance their infants future social skills, without investing into costly behaviours or loosing future reproductive opportunities.

Another low-cost form of paternal care is the reduction of aggressive behaviours towards those females with whom they have an infant. This behaviour, during a phase where females and infants are clearly quite vulnerable, might have a direct benefit for the infant. Although all males show a significantly reduced aggression rate towards females with new-born babies, fathers maintain this behaviour long after other males have resumed baseline aggression rates, thereby selectively protecting these females and their offspring.

Given that chimpanzees live in a fluid fission-fusion social system it will be almost impossible to distinguish between true paternal care and indirect paternal care as a means to enhance future reproductive success. However, this study is the first indication of paternity recognition in chimpanzees and further work will be needed to investigate the benefits males and infants gain from these behaviours. More costly, but very rarely occurring behaviours, such as support during aggressive interactions and meat sharing will probably help to answer some of these questions, but unfortunately our data did not allow us to analyse this. However, the fact that we did observe paternal behaviour for less costly but more frequent interactions suggests that fathers in Tai chimpanzees could also intervene in more costly and important circumstances for their offspring. In addition, paternal investment in chimpanzees may pay only in certain domains when taking into account lifetime reproductive strategies. Therefore males might prefer to invest in play with their offspring which benefits their long-term social development and in their early survivorship by reducing their aggression towards the mother of their young, rather than investing in grooming or being a passive presence near the mother (association).

The fact that male chimpanzees recognise their own offspring, rises the question whether paternity confusion as a female strategy to reduce the risk of infanticide really does work. Given that paternity recognition might not

be perfect and males could make mistakes (Keller, 1997), paternity confusion might still be a partly effective strategy because males that mated with a particular female at some point during her conceptive cycle might still assume a certain probability of having sired an offspring. This male inference of paternity might limit infanticide occurrences, although within community infanticides by males have been observed in only one chimpanzee population (e.g., Hamai et al., 1992). In addition, chimpanzee females may still benefit from mating with multiple males by reducing male harassment, which is potentially costly to females. Thus, paternity recognition and paternity confusion might be maintained in a population in a co-evolutionary process as long as either mechanism is not perfect.

Sibling recognition of both maternal and paternal siblings has recently been demonstrated in adult female macaques (Widdig et al., 2001), in female baboons (Smith et al., 2003) and in hyenas (Wahaj et al., 2004). Since adult chimpanzees have been able to correctly identify mother-son relationships based on face recognition tests (Parr & de Waal, 1999), we hypothesised that chimpanzees might be able to use phenotype matching to identify paternal and maternal siblings. However, our data provide only weak evidence that youngsters prefer paternal kin over unrelated peers. Furthermore, we found only weak support for maternal sibling preferences. Why is that so? Obviously, the small sample size and the rarity of the behaviours that we used as potential indicators of such recognition, would make the detection of such an effect only possible if it was very strong. Maternal siblings are usually considerably older as the inter-birth interval is on average 5 years in Taï chimpanzees (Boesch & Boesch-Achermann, 2000) and youngsters, when having a choice, prefer to play with same age peers rather than with older maternal siblings (Goodall, 1986). However, maternal siblings remain associated 80 to 100% of the time through their mother and are therefore very familiar with each other, which may explain why maternal siblings prefer one another for grooming, an activity for which age seems less relevant and for which a preference for similar aged partners has not yet been reported. Paternal kin recognition, on the other side, might be more complex in a multi-male society like that of chimpanzees. Recognition of paternal siblings, which spend less time together and are usually less familiar with each other, is more difficult to explain. Phenotype matching has been suggested as a mechanism by which paternal kin can be recognized in e.g. macaques (Widdig et al., 2001), baboons (Smith et al., 2003) and hyenas (Wahaj et al., 2004). Furthermore, if

age-similarity is used as a proxy for paternal kin recognition (Alberts, 1999), chimpanzees are expected to play with all similar aged peers to the same extent. Additionally, it may be important for young chimpanzees to socialize and familiarise themselves with all other youngsters in the community, thus, play and grooming should involve all individuals. This may also explain why we only found a weak preference for kin in young chimpanzees. For chimpanzees, our data provide only limited evidence for the existence of paternal kin recognition and more data are needed to assess its relevance.

Taken together, our findings indicate that chimpanzee males are able to identify their own offspring, and these are preferred over unrelated young in certain contexts. The growing body of evidence of kin recognition in species showing very little overt paternal investment adds strength to the basic assumption made by kin selection theory. Kin recognition could possibly be a general ability in social animals despite the fact that the proximate mechanism making such recognition possible, still needs to be elucidate. This study along with other recent publications, stress the fact that male chimpanzees have an astute awareness of reproductive processes, as they seem to be able to detect the likelihood of conception from the size of female sexual swellings and adapt their mating behaviour to that knowledge (Deschner et al., 2004), and that male mating initiatives reflect female preference for certain males (Stumpf & Boesch, 2005, in prep.). Thus, males seem to be able to monitor several aspects concerning their reproduction and it should therefore not be too surprising that males can also recognise their offspring. We should expect such recognition to be quite widely present in the social species.

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