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Boy will be boys: sex differences in wild infant chimpanzee social interactions

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Abstract

Sex differences in the behaviour of human children are a hotly debated and often controversial topic. However, several recent studies have documented a biological basis to key aspects of child social behaviour. To further explore the evolutionary basis of such differences, we investigated sex differences in sociability in wild chimpanzee, *Pan troglodytes schweinfurthii*, infants at Gombe National Park, Tanzania. We used a long-term data set on mother–infant behaviour to analyse the diversity of infant chimpanzee social partners from age 30 to 36 months. Male infants ($N = 12$) interacted with significantly more individuals than female infants did ($N = 8$), even when maternal sociability was controlled for. Furthermore, male infants interacted with significantly more adult males than female infants did. Our data indicate that the well-documented sex differences in adult chimpanzee social tendencies begin to appear quite early in development. Furthermore, these data suggest that the behavioural sex differences of human children are fundamentally rooted in our biological and evolutionary heritage.

Keywords

chimpanzee; mother–infant interaction; *Pan troglodytes schweinfurthii*; sex difference; social behaviour

Sex differences in the behaviour of human children are a hotly debated and often controversial topic (McIntyre & Edwards, 2009). In terms of sociability, evidence from a variety of studies suggests that girls outperform boys (higher rates of eye contact: Hall, 1985; social understanding: Hall, Carter, & Horgan, 2000; prosocial behaviour: Eisenberg,

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Fabes, & Spinrad, 2006). However, other studies have documented that boys play in larger groups, while girls tend to participate in more dyadic play (Fabes, Martin, & Hamish, 2003; Maccoby & Jaklin, 1987). One persistent assumption is that differential treatment of girls and boys by parents and teachers is a primary driver of sex-typical behaviour (Witt, 1997). However, several studies have also shown a biological basis in key aspects of social behaviour in human children. For example, in human neonates, female infants prefer looking at a face (a social object), while male infants prefer looking at a mobile (a mechanical object) (Connellan, Baron-Cohen, Wheelwright, Batkia, & Ahluwalia, 2000).

For further investigation into the evolutionary and biological bases of sex differences in behaviour, we can look to one of our closest living relatives, the chimpanzee, *Pan troglodytes*. Wild chimpanzees live in 'communities' (Goodall, 1968) that range in size from 20 to 180 individuals. These communities are multimale, multifemale and are characterized by a male dominance hierarchy in which philopatric males form the stable core of the community and defend a group territory (Goodall, 1986). Within these stable communities, grouping patterns represent a fission–fusion social system, wherein temporary subgroups form as a result of a combination of factors that may include food availability, sexual state of females and social relationships with other individuals (Goodall, 1986; Matsumoto-Oda, Hosaka, Huffman, & Kawanaka, 1998). Neighbouring chimpanzee communities are highly territorial and intercommunity interactions can have fatal results (Wilson & Wrangham, 2003).

In East African chimpanzees, *P. t. schweinfurthii*, adult females are less gregarious than adult males, spending much of their time accompanied only by their dependent offspring (Gombe: Murray, Sandeep, Pusey, 2007, Kanyawara: Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007, Mahale: Hasegawa, 1990). In addition, association indices between female–female dyads are weaker than those found for male–male dyads (Gilby & Wrangham, 2008). Females become more social when they are sexually receptive (Goodall, 1986, Williams, Liu, & Pusey, 2002) and less social when they are pregnant (Pusey, Murray, Wallauer, Wilson, & Wroblewski, 2008). In addition, mothers are less gregarious than nonmothers (Otaali & Gilchrist, 2006). Additional sex differences in behaviour observed in adult chimpanzees include differences in feeding and ranging patterns (Wrangham & Smuts, 1980), a female bias towards tool use (Boesch & Boesch, 1981; McGrew, 1979) and a male bias towards hunting of vertebrate prey (Gilby, Eberly, Pintea, & Pusey, 2006; McGrew, 1979) and territorial defence (Muller & Mitani, 2005).

Sex differences in the behaviour of young wild chimpanzees have also been reported, although much less data are available. The adult female bias for tool use is found in youngsters, with young female chimpanzees acquiring a skill known as 'termite fishing' up to 2 years earlier than young males (Lonsdorf, Pusey, & Eberly, 2004). During the developmental period of this skill, young females spend more time watching their mothers' tool use behaviour, while young males spend more time playing during tool use sessions (Lonsdorf, 2005). Similarly, young females spend more time 'ant dipping' and 'nest making' than young males (Hiraiwa-Hasegawa, 1989). Intriguingly, young females at one study site also perform 'stick carrying', in which a stick is cradled and carried in a form of play mothering, significantly more often than do young males (Kahlenberg & Wrangham, 2010).

For young chimpanzees, the mother–infant relationship is of paramount importance because young chimpanzees have a long period of nutritional and social dependency, and they lack direct paternal care (Goodall, 1967, 1986; but see Lehmann, Fickenscher, & Boesch, 2006). Physical contact between the mother and infant characterizes most of the first 2 years of life (Goodall, 1967), with offspring spending the majority of their time in physical contact or

within arm's reach of their mother until the age of 3 years (Gardner-Roberts, 1998). Offspring are nutritionally dependent on their mother through infancy until weaning between the ages of 3 and 5 years, but they remain behaviourally dependent (i.e. continually travelling and socializing with) through the juvenile years, until at least the age of 8 years (Pusey, 1990). Only after the age of 10 years do most chimpanzees start to spend the majority of time away from their mother (Pusey, 1983, 1990). Studies of infant sociality must therefore tease apart maternal effects of sociality from infant social behaviour.

Socioecological theory predicts that, given the differing correlates of reproductive success, adult female chimpanzees should be primarily motivated by maximizing feeding efficiency, while adult males should be primarily motivated by establishing themselves socially so that they have access to females, either via high rank in the dominance hierarchy or through alliances (Muller & Mitani, 2005; Wragham & Smuts, 1980). Therefore, it is perhaps not surprising that female-biased sex differences in youngsters have been found that centre on food-finding techniques and caretaking behaviours. Similarly, it is not surprising that sex differences in association patterns among subadult chimpanzees have been found, wherein adolescent male chimpanzees leave their mothers sooner (Hayaki, 1988) and, thus, are more gregarious than adolescent females (Pusey, 1983). However, investigations of sex differences in the social behaviour of chimpanzee infants have been more limited. Goodall (1967) first outlined the typical stages of behavioural and social development of wild infant chimpanzees using a sample of four individuals through the first 6 months of life. Later stages of development were also described, although with smaller sample sizes representing each stage. Subsequently, Plooi (1984) and Rijt-Plooi and Plooi (1987) focused on a cohort of six mother–infant pairs up to the age of 30 months, but their ability to test for sex differences was limited due to small sample sizes. Brent, Bramblett, Bard, Bloomsmith, & Blangero (1997) investigated the effect of siblings on social relationships in infant chimpanzees from birth to 24 months and found suggestive, but nonsignificant, differences in social behaviours such that males were slightly more social than females.

In this study, we examined sex differences in infant chimpanzee sociability at Gombe National Park, Tanzania. Given that young chimpanzees of both sexes are constrained to their mothers' social group, we used a long-term data set of detailed mother–infant behavioural data to investigate direct infant social interactions (grooming, play, physical contact) rather than associations measured as presence in the same social group. Unlike previous studies focusing on younger individuals, we focused on the age class from 30 to 36 months, which corresponds to the period when infants begin spending the majority of their time out of maternal contact and represents their first independent forays into their social group. In particular, we were interested in whether the number and type of social partners differ between male and female chimpanzee infants outside of the expected and frequent interactions with maternal relatives.

METHODS

Study Site

Gombe National Park is a small (35 km²) park, located on the western border of Tanzania and is home to three communities of chimpanzees. Our study focused on the Kasekela community, which ranges in the centre of the park and has been studied continuously since 1960. These chimpanzees are habituated to human observers and easily recognized, and matrilineal kinship is known for as many as four generations. Historically, the Kasekela community has ranged in size from 38 to 62 individuals, with age–sex classes composed of 6–14 adult males, 12–25 adult females, 6–14 subadult (<12 years of age) females and 7–15 subadult males.

Behavioural Data Collection and Study Subjects

Detailed mother–infant behavioural data have been systematically collected on members of the Kasekela community since 1970. Researchers record data on each mother, her youngest offspring and (when possible) visible older siblings during 1 min point-samples, which include information on behaviour, proximity, locomotion, vocalizations, play, aggression and interactions with other chimpanzees. The mother–infant dyad is the focal unit. In addition, researchers collect group composition data (individuals present) every 5 min during the focal period. For this analysis, we included only those infants that had at least 10 h of digitized data during the age range of 30–36 months (mean = 34.7 h, range 10.4–59.9 h), from at least 5 separate days of observation. Applying these criteria, we included data from 20 infants ($N = 8$ females, $N = 12$ males) from 10 different mothers. These data were collected during 1978–2012. The observational protocol adhered to all welfare and legal requirements of the host country (Tanzania) and was approved and permitted through the Tanzania Wildlife Research Institute, Tanzania National Parks, and Tanzania's Commission on Science and Technology.

Variables

Our response variable of interest was the number of social partners with whom an infant chimpanzee had direct (contact) interactions. As such, we counted the number and type of individuals that an infant had either groomed, played with or physically contacted within the period of interest. These individuals were further categorized as (1) immediate family (mothers and nonadult siblings), (2) maternal family (matrilineally related individuals: adult siblings, grandmother, cousins, etc.), or (3) other (nonmaternally related individuals). Social partners were also designated by sex (M, F) and age class (infant: <6 years; juvenile/adolescent: 6–12 years; adult: >12 years). We were particularly interested in infant interactions outside the immediate family and wanted to avoid biasing results due to variation in family size (e.g. number of other young siblings), so the main response variable in our models was the number of infant social partners that were not immediate family.

In recognition of the importance of the maternal relationship for young chimpanzees, we also investigated and controlled for mothers' number of social partners. To remove any biases of variability in the number of offspring a mother had, we counted the number of nonoffspring social partners for each mother.

Because larger amounts of observation time may lead to more opportunities to observe social interactions, we also included a term in all statistical models to control for duration (in hours) of data collected. In addition, because the data included were collected over a long period (1978–2012), we included a 'year' term to investigate the effects of anomalous years, anomalous data collectors, or long-term temporal patterns.

We also wanted to investigate and/or control for various factors known to impact chimpanzee sociality. As such, we investigated the following variables.

1. Season: chimpanzee party sizes are known to vary seasonally (Wrangham, 1977). We investigated the effect of the month at which the 6-month interval began for each infant.
2. Community size: the total number of chimpanzees (i.e. potential social partners) in the Kasekela community during the period of data collection.
3. Total individuals encountered: the total number of unique individuals that were present at least once during the follows collected within the 6-month interval.

4. Average group size per follow: the average number of other individuals present across the analysed follows.
5. Median group size per follow: the median group size across the analysed follows.

Statistical Analyses

We used SAS version 9.2 for all statistical analyses. Because there were multiple offspring from the same mother in the data set, we used linear regression using a mixed model format (PROC MIXED) to include a random effect for mother. We first conducted bivariate regression to identify those covariates demonstrating a significant relationship with the outcome. We used forward selection to find the best-fit model, using likelihood ratio tests, and we examined significant covariates for interaction.

RESULTS

There were significant sex differences in the number and type of social partners for infant chimpanzees ($N = 8$ females, 12 males). Figure 1 shows the mean number of social partners in each of three categories for male versus female infants, with male infants interacting with more individuals overall. The best-fit model for predicting offspring number of social partners was one that included a term for mothers' number of (nonoffspring) social partners ($F_{8,1} = 8.00$, $P = 0.022$) and the interaction between mothers' number of social partners and offspring sex ($F_{8,1} = 5.52$, $P = 0.047$). Figure 2 illustrates the interaction term; both male and female infants interacted with more individuals than did their mothers, but male infants did so significantly more than female infants. Variables that could confound results (year, season, duration of observation, community size, total individuals encountered, average and median group size across analysed follows) were not significant. Despite the length and depth of the data set, there were only three mothers for whom we had data as the mother of both a male and a female offspring (Fig. 3). The single significant predictor of mothers' number of social partners was offspring sex ($F_{7,1} = 9.35$, $P = 0.018$).

We also investigated interactions with different age–sex classes. There were no significant differences between male and female infants for the number of nonadult social partners (infants, juveniles, adolescents). However, infant sex did significantly predict the number of adult social partners ($F_{9,1} = 13.36$, $P = 0.005$), with female infants interacting with significantly fewer adults than male infants. To further investigate this effect, we analysed infant interactions with adult males and adult females separately. There was no significant difference between the sexes in the number of adult female social partners. However, infant sex was a significant predictor of the number of adult male social partners. As above, the best-fit model for predicting offspring number of adult male social partners was one that included a term for mothers' number of adult male social partners ($F_{8,1} = 7.11$, $P = 0.029$) and the interaction between a mother's number of adult male social partners and offspring sex ($F_{8,1} = 9.91$, $P = 0.014$). Figure 4 illustrates the interaction term; in this case, female infants interacted with significantly fewer adult males than their mothers did, whereas male infants did not differ from their mothers. Importantly, mothers of male offspring did not differ statistically from mothers of female offspring in the number of adult males they interacted with (see Fig. 4).

To ensure that our results did not merely reflect maternal gregariousness or grouping preferences, we investigated whether offspring sex predicted the following variables: total individuals present during any of the analysed follows and the average and median number of individuals present over all group compositions taken during analysed follows. None of these variables were predicted by offspring sex.

DISCUSSION

Our results demonstrate that sex-specific differentiation in the social behaviour of male and female infant chimpanzees is present from the very earliest forays into their social group. Young male chimpanzees interacted with more individuals overall (Figs 1, 2) even when their mothers' number of social partners and measures of group size were controlled for. Importantly, this result was not driven by differences in family size because interactions with siblings and dependent offspring were removed for infants and mothers, respectively, in all statistical analyses.

Given that mother and infant chimpanzees typically remain in each other's presence constantly during the first 5 years of life, it is difficult to disentangle whether the mother or the infant is responsible for the differences in diversity of social partners we found. When considered over the 6-month period of interest, infant sex alone was not a significant predictor of maternal sociality (total, average, median number of individuals), suggesting that sex differences in the number of infant social partners cannot be explained by maternal grouping patterns. However, in the three cases for which we had data for male and female infants with the same mother, mothers of male infants directly interacted with more individuals than did mothers of female infants (Fig. 3). How can we explain these seemingly conflicting results? One possibility is that when a male infant interacts with a more diverse group of individuals, the mother is drawn to that social interaction to maintain proximity to her infant and thus engages in more social contacts. In contrast, because female offspring interact with fewer individuals, their mothers interact with fewer individuals as well. Another and more intriguing possibility is that mothers 'grease the social wheels' for their sons by initiating social interactions.

In our study, male infants interacted with significantly more adult males than did female infants (Fig. 4). Following on from our argument above, we might predict that mothers of females would then also interact with fewer adult males than mothers of males. However, this was not the case; the number of adult males that a mother interacted with did not differ according to infant sex. This suggests that infant females may actually be avoiding interactions with adult males while infant males do not. In adulthood, stable male–female social bonds are rare in chimpanzees owing to the promiscuous mating system, while strong male–male bonds can be enduring (Mitani, 2009) and lead to increases in dominance rank and reproductive success (Gilby et al., 2013). Taken together, our results demonstrate that even at the very young age of 30–36 months, young chimpanzees show patterns of social behaviour that match adult sex-specific social roles.

Our results complement those of other primate studies showing distinct sex differences in the behaviour of youngsters that correspond to differing sex roles in adulthood. For example, in the matrilineal social system of baboons, Cheney (1978) found that immature male and female baboons (*Papio ursinus*) interact with the adults of their community in ways that would predict increased fitness at adulthood. Immature females interact more with adult females carrying infants, while immature males interact with adult females at lower rates overall and more frequently when the females are cycling. Similarly, sex differences in the development of grooming behaviour has been extensively studied in rhesus macaques, *Macaca mulatta* (reviewed in Roney & Maestripieri, 2003), which also show a matrilineal social structure based around stable groups of related females. In these monkeys, young females groom others at higher rates through the first year of life than do young males and this grooming is targeted at female kin. A male bias in rough-and-tumble play has been documented in multiple species, including patas monkeys, *Erythrocebus patas*, Japanese macaques, *Macaca fuscata*, and olive baboons, *Papio anubis* (reviewed in Brown & Dixon, 2000) and is theorized to be related to male–male competition in adulthood. Similarly, a

female bias in play parenting has been found in multiple species (e.g. macaques: Lovejoy & Wallen, 1988; chimpanzees: Kahlenberg & Wrangham, 2010) and is presumed to relate to the development of maternal behaviours. Taken as a whole, these consistent and accumulating reports of sex differences in the behavioural development of nonhuman primates suggest that while gender socialization in humans may play a role in magnifying the differences between young males and females, these behavioural sex differences are fundamentally rooted in our biological and evolutionary heritage.

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Highlights

- We examined sex differences in the social behaviour of chimpanzee infants.
- Male chimpanzee infants were more social overall than female chimpanzee infants.
- Male infants socialized with adult males significantly more than female infants did.
- Chimpanzee sex-specific social roles were present at a very young age.

Figure 1.

Diversity of social partners for male and female chimpanzee infants aged 30–36 months ($N = 8$ females, 12 males). Values are means $\pm$ SE.

Figure 2.

Mean $\pm$ SE number of social partners for male and female chimpanzee infants ($N = 8$ females, 12 males) and their mothers ($N = 10$).

Figure 3. Mean $\pm$ SE number of social partners for three mothers when they had female versus male offspring. Numbers above bars represent the numbers of offspring in each category.

Figure 4. Mean $\pm$ SE number of adult male social partners for male ($N = 12$) and female ($N = 8$) chimpanzee infants and their mothers ($N = 10$).