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

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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.

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, 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,

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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 (Otali & 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 period, 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; Wrangham & 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 samples sizes representing each stage. Subsequently, Plooij (1984) and Rijt-Plooij and Plooij (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, and 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 km^2) 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