Behavioral Ecology and Sociobiology (2018) 72: 117
https://doi.org/10.1007/s00265-018-2531-5

ORIGINAL ARTICLE

Sex differences in maternal sibling-infant interactions in wild chimpanzees

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Received: 28 December 2017 / Revised: 10 June 2018 / Accepted: 14 June 2018 / Published online: 26 June 2018

Abstract

Apart from the crucial bonds between mothers and offspring, siblings are an important first social partner in most primate species. Socioecological theory predicts that sibling-infant interactions may differ depending on whether the older immature sibling is male or female. Here, we used 24 years of long-term data from wild chimpanzees in Gombe National Park, Tanzania, to characterize maternal sibling-infant relationships and investigate sex differences therein. Since young female primates typically exhibit higher rates of interest in infants, we hypothesized that older sisters would be more likely than older brothers to groom, play with, and carry infant siblings. Alternatively, due to male-biased philopatry in this species, older brothers may be equally or more likely to interact with these potential future allies. We also examined whether sibling-infant interactions differed according to sibling age and sex of the infant. For both play and grooming, we found a significant interaction between sibling age and sibling sex. Older brothers had increased likelihood of playing and grooming with infant siblings as they themselves aged. Additionally, male-male siblings played significantly more than any other dyad type. Older sisters had decreased likelihood of playing with age and maintained relatively consistent likelihood of grooming; they also spent more time with their infant siblings at later ages. Instances of carrying young infants were exceedingly rare and did not differ by sibling sex. Thus, the sex combination of sibling-infant dyads may have substantial consequences for the social development of both individuals, which we argue is an important focus of future research.

Significance statement

The role of siblings in nonhuman primate social development is relatively understudied, and socioecological theory predicts that male and female siblings may interact differently with infants. We conducted the most detailed investigation to date of sibling relationships in wild chimpanzees and found distinct differences in how immature brothers and sisters interact with infant siblings. Older brothers have an increased likelihood of playing and grooming with infant siblings as they themselves age. We also found that male-male siblings played more than all other dyad types, which may have consequences for fostering alliances in adulthood. Older sisters show decreased likelihood of playing with age and maintain relatively consistent likelihood of grooming; they also spend more time with their infant siblings at later ages. We argue that a renewed focus on understanding the importance of siblings on primate social development is warranted.

Keywords Chimpanzees · Siblings · Sex differences · Apes · Social development

Introduction

Nonhuman primates have a relatively prolonged period of pre-reproductive dependency compared to other mammals. While the ultimate function of this immature post-weaning life stage is still debated, there is general consensus that it is likely an important time for learning social, foraging, and other skills (e.g., Pagel and Harvey 1993; Lonsdorf and Ross 2012). With regard to social development, the significance of the mother-infant relationship for acquisition of social skills has been

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Communicated by A. Widdig

This article is a contribution to the Topical Collection An evolutionary perspective on the development of primate sociality - Guest Editors: Federica Amici and Anja Widdig

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recognized since the 1960s (Harlow et al. 1965). However, mothers and infants do not exist in a vacuum and other members of the social group may frequently interact with immatures. Interactions between non-mothers and infants have been studied across the primate order (Hrdy 1976; Mitani and Watts 1997; Ross and MacLarnon 2000), including in humans (*Homo sapiens*, e.g., Maestripieri and Pelka 2002), where both interest in infants and performance of caretaking behaviors are significantly more frequent in younger, less experienced females. Thus, many have theorized that such behaviors are evolutionarily rooted in "learning to mother" (Lancaster 1971; Fairbanks 1990; Tardif et al. 1993) and represent practice for later mothering in immature females. Alternatively, Silk (1999) and others (e.g., Paul and Kuester 1996) argue that in some species (e.g., bonnet macaques (*Macaca radiata*), Barbary macaques (*Macaca sylvanus*) interest in infants does not attenuate substantially at adulthood, and thus, female-biased interest in infants is simply a "by-product" of selection for appropriate maternal care. Other commonly proposed functional hypotheses regarding interest in infants include kin-selected cooperative rearing or a form of harassment/competition (reviewed in Hrdy 1976; Paul and Kuester 1996). Given the long lifespan and complex social dynamics of many primates, and the need for long-term data to test ultimate functions, distinguishing between these proposed explanations is challenging in wild settings. However, Meredith (2015) recently used a nested Bayesian Markov chain Monte Carlo modeling approach to determine whether sex-biased patterns of infant interest and adult patterns of care showed correlated evolution, which would support the "learning to parent" or "by-product" hypotheses. If not, then alternative hypotheses such as cooperative rearing or harassment would be more strongly supported. Using data on juvenile interest in infants and adult patterns of care in 34 primate species, Meredith (2015) found support for both the "learning to parent" and the "by-product of selection for adult infant care" hypotheses, and argued that sex differences in interest in infants may serve different functions at different life stages.

Given that the majority of primates examined exhibit sex differences in immature interest in infants, it is reasonable to predict that such differences would also occur within maternal kin groups if older siblings have prolonged association with mothers and younger siblings. Primates are one of the few mammalian taxa that are not typically born in litters in which siblings have an extended period of association during development. Indeed, close maternal kin, particularly siblings, are often the first non-mother social partners and these relationships may persist throughout life depending on species-specific patterns of dispersal. Most of our knowledge about nonhuman primate sibling relationships during maturation come from female philopatric Old World monkey species with matrilineal dominance hierarchies (e.g., macaques (*Macaca* spp.): Amici et al. 2018; Maestripieri 2018, both in topical collection on An evolutionary perspective on the development of primate sociality), savannah baboons (*Papio cynocephalus*), and vervets (*Cercopithecus aethiops*): reviewed in Silk 2002) or cooperatively breeding species in which older siblings of both sexes remain in the group to help rear younger offspring (e.g., cotton-top tamarins, *Saguinus oedipus*: Cleveland and Snowdon 1984). For example, vervet monkey maternal siblings (< 4 years of age) exhibit higher levels of grooming and support during agonistic encounters when compared to non-siblings. In addition, female-female sibling dyads that are close in age tend to spend relatively more time in proximity compared to other dyad types (Lee 1987). Amici et al. (2018, topical collection on An evolutionary perspective on the development of primate sociality) report multiple findings regarding kin relationships from a study of free-ranging rhesus macaques and document sex differences that reflect sex biases in adult patterns of behavior. For example, immatures preferentially interact with same-sex kin compared to opposite-sex unrelated group members. However, whether or not male and female immatures interact differently with infant siblings was not reported.

Compared to other taxa, much less has been described regarding interactions between immatures and infants in wild apes despite their protracted developmental period relative to other primates (Watts and Pusey 1993). Indeed, the abovementioned comparative analysis of juvenile interest in infants across the primate order (Meredith 2015) did not include data from any ape taxa. In chimpanzees, prior investigations of sex-biased behavior toward infants have reported inconsistent patterns and have been limited by small sample sizes. At Mahale Mountains National Park, Nishida (1983) conducted a 12-month field study of alloparenting behavior directed by all age-sex classes to a cohort of six infants ($n = 5$ males, 1 female) under 2 years of age. Consistent with the female-biased pattern described above, nulliparous females showed more and longer interaction bouts than other age-sex classes. However, in chimpanzees at Gombe National Park, Tanzania, Pusey (1990) investigated immature interactions ($n = 7$ males, 5 females) with all infants age 0–3.5 years, and found no sex differences in interactions. When sibling-infant interactions were examined specifically, Pusey (1990) found that older sisters ($n = 2$) tended to interact more with infant siblings than older brothers ($n = 3$), but was limited by small sample sizes. Also at Gombe, Brent et al. (1997) compared the social development of infants with and without older siblings, but were unable to examine whether there were differences according to the sex of older sibling due to insufficient sample size. In a study of social partner preference, Lehman et al. (2006) found that immature chimpanzees preferred to play and groom with maternal siblings, but sex differences were not examined. In two of the few studies of adult sibling relationships in chimpanzees, maternal brothers (but not paternal brothers) were found to preferentially affiliate and cooperate with each other (Langergraber et al. 2007) and form longer-lasting social bonds when compared to non-kin (Mitani 2009). Due to male-biased philopatry in chimpanzees, brothers may be particularly important social partners, but the development of these relationships has not been described. Given that wild chimpanzees are one of our closest living relatives, and that sibling relationships remain a persistent interest in human child development (e.g., Whiteman et al. 2011), the paucity of data on sibling relationships is surprising and merits further investigation. Therefore, in this contribution, we use a long-term dataset to examine social interactions between maternal siblings in wild chimpanzees at Gombe National Park, Tanzania, in the context of the widespread sex differences in infant attraction reported in other primates.

Wild chimpanzees live in communities (Goodall 1968) that range in size from 20 to 180 individuals. These communities are multimale, multifemale, and characterized by a male dominance hierarchy in which philopatric males form the stable core of the community, hunt cooperatively, and defend a group territory (Goodall 1986). Within these communities, subgrouping patterns are characterized as fission-fusion, wherein temporary subgroups or “parties” 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 et al. 1998). In East African chimpanzees, *P. t. schweinfurthii*, adult females are typically less gregarious than adult males, spending much of their time accompanied only by their dependent offspring (Gombe: Wrangham and Smuts 1980; Murray et al. 2007, Kanyawara: Emery Thompson et al. 2007; Mahale: Hasegawa 1990; but see Wakefield 2008 for Ngogo). Physical contact between the mother and infant characterizes most of the first 2 years of life (Goodall 1967). Offspring are nutritionally dependent on their mother through infancy until weaning between the ages of 3 and 5 years (Pusey 1983), but they remain behaviorally dependent (i.e., continually traveling 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). As a result, chimpanzee mothers are usually traveling with more than one offspring at a time, and most chimpanzee infants will spend lengthy portions of their development in the presence of older siblings. Given that eastern chimpanzee mothers are relatively less gregarious than other community members (e.g., Otali and Gilchrist 2006), siblings are second only to the mother in terms of a source of social interaction for an infant (Goodall 1968; Brent et al. 1997).

Prior studies of immature chimpanzees have characterized social behavior at different life stages and sex differences therein. Male infants show accelerated social development when compared to female infants, including earlier peaks in social play and spatial independence from their mothers (Lonsdorf et al. 2014a) and a larger number of social partners in infancy (Lonsdorf et al. 2014b). Post-weaning, male juveniles and adolescents spend more time at far distances (> 15 m) from their mothers and also spent greater amounts of time “leading” their mothers during travel (Pusey 1983, 1990). The grooming patterns of weaned individuals also differs by sex; males spend a higher percentage of time grooming outside of the family unit (mothers and maternal siblings) than females, and this difference is particularly strong with regard to grooming adult males (Pusey 1990).

In this study, we analyzed the largest available dataset of wild chimpanzee maternal kin relationships to characterize the frequency of social interactions between siblings, and to investigate whether there are sex differences in the behavior of immatures toward their infant maternal siblings (hereafter “infant siblings”). Specifically, we analyzed three affiliative social behaviors that include direct contact: grooming, play, and carrying of infants. Following the theoretical framework and empirical evidence that juvenile interest in infants is related to adult patterns of care in primates, we predicted that older sisters would engage in all three affiliative behaviors significantly more than older brothers. An alternate, non-mutually exclusive hypothesis is that older brothers would affiliate with male infant siblings at equal or higher rates than sisters because these interactions may foster adult male-male social bonds. Finally, as older siblings are becoming more independent from their maternal family and may therefore interact less with infant siblings, we also examined the effect of sibling age in all analyses. We focus on the perspective of the older sibling since they are interacting down the age structure, and are more likely to be actively allocating their time among different social partners, as opposed to infants who are not yet independent from their mothers.

Methods

Study site

Gombe National Park is a small protected area (land area ~ 35 km^2) in western Tanzania and is currently home to three communities of chimpanzees. Our study focused on the Kasekela community, which ranges in the center of the park and has been studied continuously since 1960. These chimpanzees are habituated to human observers, are individually recognized, and matrilineal kinship is known for as many as four generations. Historically, the Kasekela community has ranged in size from 38 to 64 individuals, with age-sex classes ranging from 6 to 14 mature males, 12 to 25 mature females, 6 to 14 immature (< 12 years of age) females, and 7 to 15 immature males. Following Foerster et al. (2015), we use 12 years as age of maturity in this population; 12 years is the earliest recorded age that a male at Gombe has fathered offspring (Wroblewski et al. 2009) and mean age at sexual maturity for females is 11.47 years (Walker et al. 2018).

Behavioral data collection and study subjects

Detailed data on maternal family relationships have been collected on members of the Kasekela community since 1970. We focused our analyses on the time period from 1989 to 2013, wherein both sibling behavioral data and party composition were collected. To collect these data, focal follows on families (mothers and the two youngest immature offspring) are conducted by two researchers who work in a team to record 1-min instantaneous point samples on behavior of the mother, her youngest offspring, and the next oldest sibling (see Lonsdorf et al. 2014a for a more detailed ethogram). It was not possible to record data blind because our study required observation of individually identified animals. Party composition scans are also conducted at regular intervals during each follow (5-min intervals until 2011 and 15-min intervals thereafter). Follow duration has varied over the course of the study from 6 to 12 h; however, some follows were less than 6 h and durations were unequal due to time spent searching for and losing sight of focal individuals. When a focal individual (either mother, infant, or sibling) was out of sight on the scan, they were marked as "bad observation." As such, we instituted a criterion of at least 2 h of good observation on the sibling for a follow to be included in our analyses. We selected this cutoff after inspection of the occurrence of our target behaviors changed dramatically (i.e., more than a 10% change in frequency of occurrence of the target behaviors) for follows less than 2 h when compared to those that were longer.

The unit of analysis was a focal follow, which was included in the dataset when the older sibling was observable for a minimum of 120 min and was still immature (< 12 years of age; see above). Following previous investigations of sibling behavior and alloparenting in wild chimpanzees (Nishida 1983; Brent et al. 1997), we specifically focused on older sibling interactions with infants under 2 years of age. Infants in this age class are within 1 m of their mothers on average and travel on their own (i.e., not riding ventrally or dorsally) less than 2% of observation time (Goodall 1967; Lonsdorf et al. 2014a), so are unlikely to be the primary initiator of interactions. Using these criteria, our dataset contained 382 follows (mean minutes of observation time on siblings per follow = 298, SD = 126, range 120–744 min) on 24 siblings (14 female, mean age = 6.01 years, SD = 1.6, range 4.06–11.78; 10 male, mean age = 5.84 years, SD = 0.96, range 4.01–7.73) of 26 infants (11 female, mean age = 0.97 years, SD = 0.59, range 0.008 to 1.99; 15 male, mean age = 0.99 years, SD = 0.54, range 0.005 to 0.54) from 11 mothers (see Table 1). Mean observation time per focal sibling was 72.9 h (SD = 62.6, range 5.7 to 196.1). While infant age was always under 2 years, sibling age varied and was therefore controlled for in all analyses (see below).

Response variables

To quantify older sibling behavior toward infants, we calculated the percent of observation time spent engaged in affiliative social interactions with infant siblings per follow day. We focused on social play, grooming, and carrying, as defined by the Gombe chimpanzee glossary (the Jane Goodall Institute, unpublished records; Lonsdorf et al. 2014a):

> *Social play*: Non-aggressive interaction between two or more individuals that include one or more of the following: tickling, wrestling, chasing, kicking, rubbing, thrusting, biting, or pulling. May incorporate an object (e.g., tugging of sticks back and forth).
> *Social groom*: Parting of another individual's hair with hands, fingers and/or lips, and removal of debris or ectoparasites.
> *Carry*: Encompasses both dorsal riding (when an infant sits or lies on the back of another) and ventral riding (when an infant clings to another's belly).

Predictor variables

Our main predictors of interest were sibling sex and sibling age. In addition, we included several variables in our statistical models that may be expected to affect either the occurrence or observation of social interactions.

> *Sibling age*: We included sibling age (in days) as a continuous variable to account for changes in behavior as the sibling matures. We also included an interaction term between sibling age and sibling sex to account for age-related changes that may differ according to sex during the juvenile and adolescent periods (Pusey 1983, 1990).
> *Average party size*: From the sibling's perspective, the number of potential other social partners increases with party size and may therefore affect the probability that an older sibling interacts with his/her infant sibling. In addition, immature male chimpanzees interact with more nonfamily social partners as compared to immature females (Pusey 1990; Lonsdorf et al. 2014b; Murray et al. 2014), so party size may affect sibling-infant interactions differently for older brothers versus other sisters. We therefore included a term in each model for average party size during the follow (the mean of all party composition point samples for the day) and an interaction term for average party size and sibling sex.
> *Infant sex*: There are distinct developmental differences between male and female chimpanzees that occur during

Table 1 Demographic and sample size information for mothers, older siblings, and infants. Age range, number of follows, and total observation time is given for each focal sibling-infant pair

Mother ID	Sibling ID	Sibling sex	Infant ID	Infant sex	Age range (years)	No. of follows	Total observation time (hours)
CD	CF	F	CN	F	8.3–8.4	2	6.6
FF	FLI	F	FUR	F	4.3–6.0	37	196.1
FN	FAM	F	FAD	F	4.1–5.5	26	127.3
PI	TT	F	TG	F	5.4–6.4	2	5.7
TG	TAB	F	TAR	F	6.1–6.8	18	125.0
CD	CN	F	CAD	M	8.9–8.9	2	7.2
DL	DIA	F	DUK	M	5.7–7.6	25	192.3
FF	FS	F	FO	M	4.3–6.0	13	41.7
FN	FAD	F	FFT	M	4.1–4.8	15	101.5
PI	TG	F	TN	M	6.1–6.5	4	11.0
SA	SAM	F	SIR	M	5.5–7.3	9	43.9
SA	SR	F	SN	M	6.2–7.2	8	23.3
SW	SI	F	SDB	M	10.4–11.8	10	45.7
SW	SI	F	SU	M	6.1–6.8	3	12.7
TZ	ZEL	F	ZIN	M	6.4–7.5	8	40.5
BAH	BRZ	M	BAS	F	4.9–4.9	1	7.7
FF	FE	M	FLI	F	6.0–7.7	23	84.8
FN	FND	M	FAM	F	4.1–5.8	21	105.0
GM	GD	M	GA	F	4.9–5.6	5	12.7
SA	SN	M	SAM	F	5.2–7.0	29	152.0
TG	TOM	M	TAB	F	5.5–7.5	13	74.8
FF	FE	M	FI	M	4.3–4.8	10	40.3
FF	FO	M	FE	M	4.0–4.5	4	12.0
FN	FU	M	FND	M	4.0–5.4	27	117.9
GM	GIM	M	GIZ	M	5.6–7.5	30	163.5
PI	TN	M	TZN	M	5.4–7.2	37	143.4

the first 2 years of life, especially with regard to mode of travel (riding ventrally or dorsally) and percent of time spent playing. These differences are less pronounced for traveling independently and proximity to mother under the age of two (Lonsdorf et al. 2014a). As such, we included infant sex in all models, as well as an interaction term for infant sex and sibling sex to account for the fact that dyads may interact differently according to sex combination (male-male, male-female, female-female).

Sibling observation time: Given that the length of each daily follow varied and that the likelihood of observing any specific behavior increases with observation time, we included a continuous variable to control for the total minutes of good observation on the sibling in each follow.

Statistical analyses

We fit separate generalized linear mixed models (GLMMs) to examine playing, grooming, and carrying infant siblings. Since the percentages of time spent performing all three behaviors were low and included a high proportion of true zeros (see "Results" section), we converted all percentages to a binary 1/0 response variable to represent whether or not the behavior occurred during a given follow (1 if the behavior occurred, 0 if the behavior did not occur) and fit GLMMs with a binomial error distribution and a logit link function in R version 3.4.3 using the glmer function from the lme4 package (Bates et al. 2015). Dichotomizing the response variables does result in coarser measures of sibling-infant interactions; however, when we attempted to fit GLMMs without this conversion using a negative binomial error distribution, the models failed to converge.

All models included a random intercept of sibling nested within mother to account for multiple and unbalanced days of observation on each sibling and inclusion of multiple siblings from a single mother. For each behavior, we fit a full model with all of the variables described above as well as random slopes for sibling age and average party size. However, in order to balance the risk of Type 1 error against the loss of statistical power, we compared these random slope and intercept models to intercept-only models using likelihood ratio tests (LRTs) (see Matushek et al. 2017). If random slopes did not significantly improve the model fit, we selected the intercept-only model. After fitting full models for each behavior, we removed non-significant fixed effect interaction terms to produce a final, reduced model. Significance of fixed effects was based on the wald Z statistic with alpha = 0.05, though we discuss interaction terms with alpha < 0.10. All models including fixed effects were significantly better than null models that included random effects only based on LRTs. We used the "anova" function in the car package (Fox and Weisberg 2011) to conduct model comparisons, and the lsmeans package (Lenth 2016) to conduct Tukey's post hoc tests of significant interactions. We calculated variance inflation factors (VIFs) for each final model using the vif.mer function, which is available online at https://github.com/aufrank/R-hacks/blob/master/mer-utils.R. No VIF was greater than 3.5 indicating that collinearity was not an issue. Dispersion parameters were 0.866 for the grooming model and 1.06 for the playing model. Model stability was assessed by comparing estimates derived from models with a level of the random effects (sibling ID) dropped one at a time. This assessment revealed no influential levels.

Data availability statement The datasets generated and analyzed for the current study are available from the corresponding author on reasonable request.

Results

The first pattern to emerge is that older brothers were not present in follows for sufficient amounts of time to be included in the dataset after the age of 8 years. This was not due to the death or disappearance of these individuals; instead, it reflects the fact that male juveniles and adolescents begin to travel in parties without their mothers and therefore, infant siblings, earlier than female immatures (Pusey 1983, 1990). In contrast, older sisters continue to spend significant time with their maternal family group (i.e., at least 2 h per follow) and appear in the dataset until almost 12 years of age.

The average percent of time that older siblings spent playing with infant siblings was 3.6% of follow time (SD = 5.4%, range 0 to 31%) and play occurred during 58% of follows. When we fit the full model, the interaction between average party size and sibling sex was not significant and was thus excluded from the model. Incorporation of a random slope for sibling age significantly improved model fit ($\chi^2 = 11.78$, $df = 4$, $p = 0.019$) and was thus retained in the model, while incorporation of a random slope for average party size did not ($\chi^2 = 0.87$, $df = 4$, $p = 0.928$), and was removed. Parameter estimates and associated p values for the model with all single variable fixed effects and significant interactions are reported in Table 2. We found a significant interaction between sibling age and sibling sex, indicating different patterns of play with age (Fig. 1). Older sisters continued to play with young siblings at older ages, albeit with decreasing likelihood. In contrast, older brothers had an increased likelihood of playing with their infant siblings up to 8 years of age. We also found different patterns of play according to the sex combination of the dyad (Fig. 2). We confirmed that inclusion of this interaction term significantly improved model fit using LRT ($\chi^2 = 6.98$, $df = 1$, $p = 0.008$). We then used post hoc Tukey's tests adjusted for multiple comparisons to compare dyad types (Table 3), and found that male-male sibling dyads are more likely to play than any other sex combination. The likelihood of playing with infant siblings did not change with increasing average party size.

The average percent of time that older siblings spent grooming infant siblings was 0.6% of follow time (SD = 1.5%, range 0 to 11%) and grooming occurred during 30% of follows. When we fit the full model, the interaction between average party size and sibling sex was not significant and was thus excluded from the model. We retained the interaction of infant sex × sibling sex, which was marginally significant at the $p < 0.10$ level, for the purposes of comparison to the play model. Incorporation of random slopes for sibling age ($\chi^2 = 3.90$, $df = 4$, $p = 0.419$) and average party size ($\chi^2 = 0.01$, $df = 4$, $p = 1$) did not significantly improve model fit and were removed. Parameter estimates and associated p values for the model with all single variable fixed effects and interactions significant at the $p < 0.10$ level are reported in Table 2. We found a significant interaction between sibling age and sibling sex, indicating different patterns of grooming with age (Fig. 3). Older sisters continued to groom young siblings relatively consistently at older ages, while older brothers had an increased likelihood of grooming their infant siblings up to 8 years of age. While there was a tendency for grooming to differ among different dyad types, no pairwise comparisons were significant. All older siblings were less likely to groom infant siblings as average party size increased.

Carrying of infants by siblings was exceedingly rare, only occurring on 25 follows (6.5%) with a mean percentage value of 0.06% (SD = 0.3%) and a range of 0 to 3%. None of our variables of interest predicted carrying behavior.

Discussion

In this contribution, we analyzed 24 years of behavioral data on wild chimpanzee siblings to conduct the most detailed investigation to date of maternal sibling-infant interactions in any wild great ape. Contrary to our prediction that interest in infants would be female-biased, older sisters were not more likely to play, groom, or carry infant siblings than older brothers. Instead, we found that sibling-infant interactions

Table 2 Results of generalized linear mixed models examining the relationship between elder sibling sex and interactions with infant siblings

Term	Play				Groom			
	Estimate	SE	Z	P	Estimate	SE	Z	P
Intercept	− 2.205	1.006	− 2.191	–	− 1.213	0.563	− 2.155	–
Sibling age	1.792	0.701	2.558	–	0.198	0.215	0.921	–
Sibling sex	0.494	0.789	0.626	–	− 0.775	0.581	− 1.336	–
Infant sex	1.764	0.694	2.541	–	− 0.263	0.596	− 0.441	–
Sibling observation minutes	0.784	0.201	3.899	*< 0.001*	0.655	0.154	4.244	*< 0.001*
Average party size	− 0.050	0.162	− 0.309	0.758	− 0.564	0.186	− 3.037	*0.002*
Infant sex*sibling sex	2.835	1.044	2.714	*0.006*	1.514	0.795	1.903	0.057
Sibling age × sibling sex	2.842	0.686	4.144	*< 0.001*	0.976	0.381	2.564	*0.010*

Significance ($p < 0.05$) is indicated in italics. The reference category for all sex-based variables is female. (−) Indicates the value is not shown because it does not have a meaningful interpretation

changed with age differently depending on sibling sex. Older sisters continued to spend significant time with the maternal family group during maturation and thus had more sustained opportunities for interacting with their infant siblings, while older male siblings did not spend significant amounts of time with the maternal family group after 8 years of age. However, older brothers showed increased rates of both playing and grooming up until that point. Furthermore, male-male sibling dyads were significantly more likely to play than other dyad types. Both older brothers and older sisters were less likely to groom infant siblings as average party size increased, but this was not the case for play. Carrying of infants under 2 years of age was exceedingly rare and its likelihood was not predicted by any of our variables of interest.

Our analyses of play with infant siblings revealed two important interactions. Figure 1 illustrates how the likelihood of play changed with age; older brothers had increased likelihood of playing between 4 and 8 years of age, while older sisters showed decreased likelihood of playing between 4 and 12 years of age. Secondly, Fig. 2 shows that male-male dyads were significantly more likely to play than any other dyad type. Infant male chimpanzees play more than infant females at younger ages (Lonsdorf et al. 2014b) and in many primates, juvenile males show higher overall rates of play (especially rough-and-tumble play) than juvenile females (reviewed in Meredith 2013; Lonsdorf 2017). While we are unable to distinguish play types in our analyses, high rates of play between brothers may reflect both increased likelihood of play in both partners and similarity in play types. We controlled for average party size in our analyses because prior research suggested that the presence of alternative social partners could affect male and female siblings differently. However, average party size had no effect on the likelihood of sibling-infant play. An interesting possibility for future

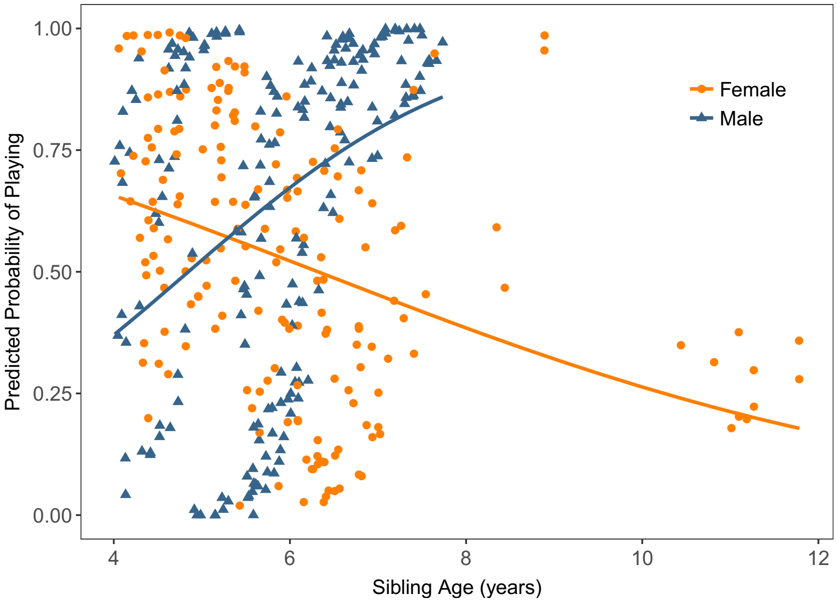

Fig. 1 Model predicted probabilities of play occurring between older siblings and infant siblings according to sibling age. Each point represents an individual follow ($n = 382$), which are separated by sex of the sibling and displayed with the best fit line

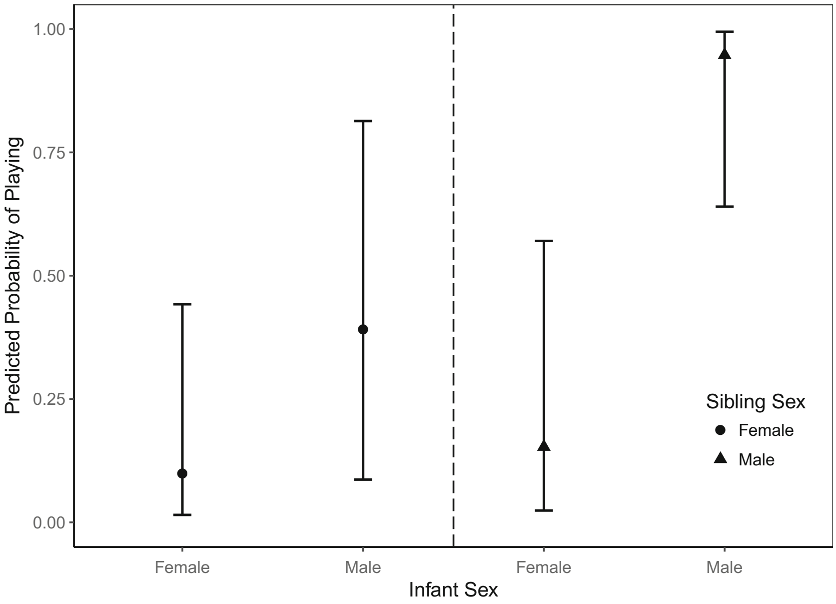

Fig. 2 Model predicted probabilities of play by sex composition of the dyad. Infant sex is displayed in the *x*-axis separately by sibling sex. Symbols indicate model estimated means. Lines represent 95% confidence intervals for each dyad type

investigation is whether additional partners join the sibling-infant play dyad, which may provide the infant opportunities for exposure to the larger social group while in the presence of a relatively "safe" play partner.

Sibling grooming showed an age pattern similar to play in terms of males being increasingly likely to groom younger siblings between 4 and 8 years of age. Older sisters were more consistent in their likelihood to groom infant siblings between 4 and 12 years of age. The interaction between infant sex and sibling sex was marginally significant, suggesting that grooming may differ among dyad types, but no pairwise comparisons were significant. This may be due to a lack of statistical power given that grooming was rarer than playing (occurring on 30 versus 58% of follows), and this pattern warrants further examination as more data accumulate from the ongoing study. In contrast to play, all siblings were less likely to groom infant siblings in larger parties. One possible interpretation is that grooming may be an important social tool for immatures to employ with all age-sex classes as they mature and start to develop social bonds outside the maternal family group. Thus, older siblings may decrease grooming with infant siblings and allocate their grooming effort to others in larger parties. In contrast, play is a social behavior that is typically only performed with other immatures and so may not be subject to the same reallocation.

Table 3 Differences in play according to sex composition of the dyad. Post hoc Tukey's tests adjusted for multiple comparisons, comparing dyad type 1 to dyad type 2. Dyads are ordered by sibling sex (S) followed by infant sex (I)

Dyad 1 (S-I)	Dyad 2 (S-I)	Estimate	SE	Z	Adjusted *P*
M-F	M-M	− 0.556	0.204	− 2.729	*0.032*
F-M	M-M	− 0.794	0.106	− 7.474	*< 0.001*
F-F	M-M	− 0.848	0.079	− 10.692	*< 0.001*
F-F	M-F	− 0.292	0.175	− 1.671	0.339
F-F	F-M	− 0.054	0.095	− 0.567	0.942
M-F	F-M	0.239	0.181	1.320	0.550

Significance ($p < 0.05$) is indicated in italics

Carrying of infant siblings was observed on less than 6% of follows and was not predicted by any of our proposed variables. This may represent a lack of maternal permissiveness for this behavior as mothers are subject to intragroup infanticide attempts from both males (reviewed in Wilson et al. 2014) and other females (Pusey et al. 2008). Alternatively, given that the presence of juveniles has been shown to restrict maternal day range (presumably due to their small size: Pontzer and Wrangham 2006), the energetic burden of carrying infants may simply be too great for immatures.

The results above clearly demonstrate that older brothers and older sisters have significantly different interactions with their infant siblings. Female siblings spend more time in the maternal family group (Pusey 1983, 1990; this study) and are thus are more likely to interact with their infant siblings later into maturation. Whether older sisters are staying and interacting because of attraction to infant siblings, a lack of investment outside of the kin group given most females disperse at sexual maturity, or whether these interactions are a by-product of female immatures' delayed independence is impossible to know. Regardless, this relatively prolonged association may afford immature females opportunities for "learning to parent" that they would not have with non-maternally related infants, given that mothers are typically not permissive of unrelated nulliparous females' attempts to interact with their infants (Nishida 1983). An obvious next question is

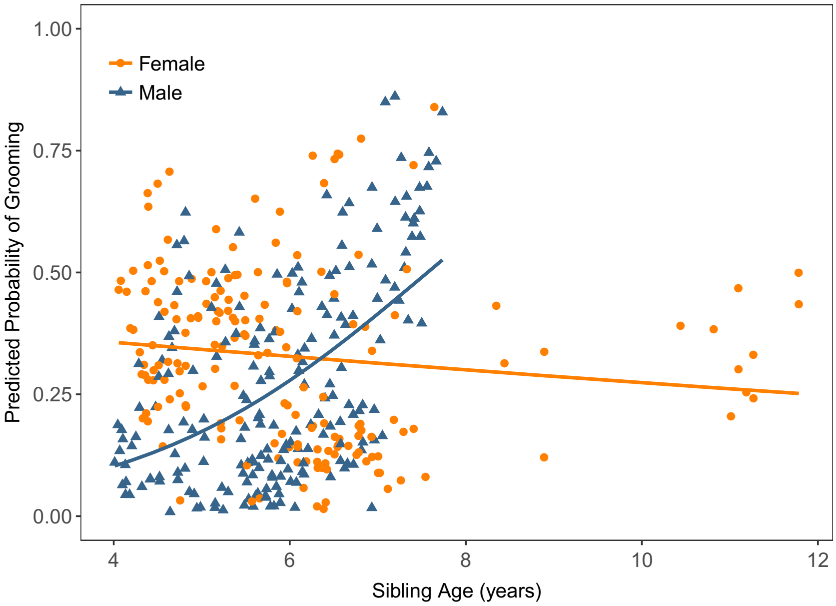

Fig. 3 Model predicted probabilities of grooming occurring between older siblings and infant siblings according to sibling age. Each point represents an individual follow ($n = 382$), which are separated by sex of the sibling and displayed with the best fit line

whether the opportunity to interact with younger siblings is beneficial for older sisters as they become mothers themselves, which would provide additional support for the "learning to parent" hypothesis of interest in infants. A positive relationship between infant experience and firstborn breeding success has been documented in several species, (e.g., Florida scrub jays, *Aphelicoma coerulescens* (Woolfenden and Fitzpatrick 1984); Mongolian gerbils, *Meriones unguiculatus* (Salo and French 1989); cotton-top tamarins (Tardif et al. 1993)). Unfortunately, this is exceedingly difficult to test in wild chimpanzees due to aspects of their life history. Ideally, one would investigate whether lastborn daughters (who do not have such opportunities for practice) are less successful at raising their own firstborn offspring when compared to earlier-born daughters. However, chimpanzee mothers show little evidence of menopause and therefore often have a nursing infant up until their own death (Alberts et al. 2013). On average, there is a 50% chance that a lastborn infant is female, and if that infant is still nursing when the mother dies, it does not survive (Goodall 1986). As such, there is low likelihood for lastborn offspring to survive and be female. Coupled with the slow mean generation time of chimpanzees, there is simply a paucity of data available to test this question. Even at Gombe, the longest-running wild chimpanzee field site, there are only three lastborn females who survived to reproduce themselves; two of the three lost their firstborn offspring in the first 2 years of life, while one successfully weaned her firstborn. Thus, while we cannot directly compare whether lastborn females have lower first-offspring survival compared to earlier-born females, future studies will investigate the relationship between the degree of infant attraction shown by immature females and more detailed aspects of subsequent quality of maternal care.

Our finding that male-male sibling dyads are significantly more likely to play than other dyad types concurs with research across the primate order regarding the importance of play for male immatures (reviewed in Meredith 2013; Lonsdorf 2017). For chimpanzees, multiple lines of convergent evidence suggest that male-male play is likely to be critical for male social development. Mature male chimpanzees stay in their natal community and male-male social bonds are important for both achieving higher dominance rank and fathering offspring (e.g., Wroblewski et al. 2009; Newton-Fisher et al. 2010; Gilby et al. 2013). The sex differences that have been documented during development are consistent with the idea that male-male interactions during maturation may foreshadow the importance of these relationships and physical interactions in adulthood. Male infants have a more diverse set of social partners and interact with adult males significantly more than female infants (Lonsdorf et al. 2014a), and peak in their rates of play at younger ages (Lonsdorf et al. 2014b). Moreover, Heintz et al. (2017) found that play during infancy is correlated with achieving both social (spatial independence from mother) and physical milestones (riding dorsally and traveling independently). Additionally, amount of social play was correlated with a younger age of first mating attempt for males (Heintz et al. 2017). Thus, the higher likelihood of play between brothers may prove beneficial in adulthood for both the infant and the older sibling, potentially as "practice" for future dominance-related interactions, and in terms of developing social bonds. However, the inconsistency of patterns between playing and grooming undermines the male social bond formation hypothesis since grooming is the primary mode of adult male social interactions and we found no bias for brothers to groom more with male infant siblings. Nonetheless, future studies on how affiliation during development relates to adult bonds are sorely needed.

Our analyses focused on characterizing and examining interactions between maternal siblings given that female chimpanzees are relatively solitary, and thus, maternal siblings are the most frequent social partners. However, interactions and relationships between paternal siblings are relatively understudied and also warrant investigation. In adult male chimpanzees at Ngogo, maternal brothers (but not paternal brothers) were found to preferentially affiliate and cooperate with each other (Langergraber et al. 2007). In the only investigation of relationships among immature paternal siblings (Lehmann et al. 2006) found only a weak preference for playing with paternal siblings when other unrelated individuals were available. Thus, the role and importance of paternal siblings remains unknown. Degree of relatedness (half versus full siblings) will also be important to investigate as sufficient genetic data matched to behavioral data become available.

An additional set of questions for future study is whether there are more generalized long-term effects of being in a same- or mixed-sex sibling dyad as well as the effects of birth order and number of older siblings. Our current behavioral data collection protocol specifically targets the mother, the infant, and the next oldest sibling. Additional older siblings often associate with their mother and may also interact with infant siblings, but our dataset does not consistently capture these interactions, so we are limited to demographic analyses. In the first of these, Stanton et al. (2014) found no difference between first- and later-born offspring on the probability of survival in the Gombe chimpanzees, although offspring who had an older immature sibling alive, regardless of firstborn status, were more likely to survive than those who did not (Stanton et al. 2017). However, specific birth order and sibling sex interactions have not yet been investigated. In addition, other adult outcomes such as rank status or reproductive success have yet to be examined. In the human child development literature, there is conflicting evidence regarding differences in behavior between same-sex and mixed-sex sibling dyads. Cross-culturally, a consistent pattern of more positive behavioral interactions between same-sex dyads and more negative behavioral interactions between mixed-sex dyads has been reported (Whiting and Whiting 1975; Dunn and Kendrick 1981). However, Abramovitch et al. (1986) conducted naturalistic observations of interactions between siblings and found that birth order was more predictive of interaction rates than sex composition of the dyad. With regard to gendered behavior, Rust et al. (2000) found that in two-children families, same-sexed siblings were more sex-typed than mixed-sex dyads (i.e., dyads comprised of two girls showed more female-typical behavior than dyads comprised of a boy and a girl). Furthermore, they found that having an older brother influenced younger siblings toward both more masculine and less feminine behaviors, while having an older sister did not reduce masculine behaviors or increase feminine behaviors in younger siblings. However, it was not possible to tease apart social and cultural gender socialization from these results, because, as the authors point out, it is typically more socially acceptable for girls to behave like boys than vice versa.

In summary, we argue that investigation of sibling relationships and their downstream effects in chimpanzees and other primates is an important focus of future study for several reasons. Given the slow life history of many primates, and especially the great apes, we know very little about the impacts of these relationships for either the younger or older sibling with regard to adult outcomes. Moreover, nonhuman primates provide an opportunity to examine whether and how the sex combination of the dyad affects development and adult outcomes in the absence of the overt gender socialization present in humans. As more long-term data becomes available from multiple study sites and species, we will be better able to understand the varied influences on primate social development and the subsequent consequences for fitness in adulthood.

Acknowledgments We are grateful to Federica Amici and Anja Widdig for their invitation to the topical collection “An evolutionary perspective on the development of primate sociality.” The authors thank the Jane Goodall Institute and Tanzania National Parks (TANAPA) for initiating and continuing the over 57-year research tradition at Gombe. Special thanks are due to Jane Goodall and Anne Pusey for their initiation and preservation of the family follow dataset, respectively. We are extremely grateful to the Gombe Stream Research Centre staff, the Government of Tanzania, Tanzania National Parks, Tanzania Commission for Science and Technology, and Tanzania Wildlife Research Institute for continued support of this research. Thanks are also due to Karen Anderson, Victoria Fiorentino, and Sophia Reji for data management, and to the numerous assistants who participated in long-term data entry. We also thank Anne Pusey, Sean Lee, Kaitlin Wellens, and three anonymous reviewers for helpful comments on earlier versions of this manuscript. This work was supported by grants from the Leo S. Guthman Foundation, the National Geographic Society, and the National Institutes of Health (5R00HD057992).

Funding This study was supported by grants from the Leo S. Guthman Foundation, the National Geographic Society, and the National Institutes of Health (5R00HD057992); the long-term data collection is supported by the Jane Goodall Institute.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval This study was completely observational in nature and the chimpanzees were well-habituated to human observation. Permission to conduct behavioral data collection at Gombe National Park was granted and approved by the relevant governing bodies in Tanzania: Tanzania National Parks, the Tanzanian Wildlife Research Institute, and the Tanzanian Commission for Science and Technology.

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