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Early Social Exposure in Wild Chimpanzees: Mothers with Sons are More Gregarious than Mothers with Daughters

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ABSTRACT

In many mammals, early social experience is critical to developing species appropriate adult behaviors. While mother-infant interactions play an undeniably significant role in social development, other individuals in the social milieu may also influence infant outcomes. Additionally, the social skills necessary for adult success may differ between the sexes. In chimpanzees (*Pan troglodytes*), adult males are more gregarious than females and rely on a suite of competitive and cooperative relationships to obtain access to females. In fission-fusion species, including humans and chimpanzees, subgroup composition is labile and individuals can vary the number of individuals with whom they associate. Thus, mothers in these species have a variety of social options. In this study, we investigated whether wild chimpanzee maternal subgrouping patterns differed based on infant sex. Our results show that mothers of sons were more gregarious than mothers of daughters; differences were especially pronounced during the first six months of life when infant behavior is unlikely to influence maternal subgrouping. Furthermore, mothers with sons spent significantly more time in parties containing males during the first six months. These early differences foreshadow the well-documented sex differences in adult social behavior and maternal gregariousness may provide sons with important observational learning experiences and social exposure early in life. The presence of these patterns in chimpanzees raises questions concerning the evolutionary history of differential social exposure and its role in shaping gender-typical behavior in humans.

SIGNIFICANCE STATEMENT

Early social experience is critical to developing appropriate adult behavior. Mothers are particularly important social partners but may also facilitate or restrict access to others. Studies investigating human parental facilitation are limited and confounded by culture. Comparative studies therefore provide invaluable insight into how parents provide social opportunities for offspring. We investigated maternal subgrouping patterns by infant sex in one of our closest relatives, chimpanzees, and found that mothers with sons were more gregarious. Infants themselves may influence patterns later in infancy, but differences were apparent early in life when mothers and infants are in almost constant contact. Furthermore, mothers with sons associated more with adult males, potential behavioral models, early in life. These differences foreshadow sex-typical adult social behavior.

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INTRODUCTION

Early socialization is critical to developing social competency later in life. In mammals, mothers have enormous influence on their offspring's early social experience with implications for adult social behavior. In humans, the relative contribution of parental and others' social influence on the development of sex typical behavior receives considerable attention and is often debated (1-4). Comparative research provides insight into the origins and development of sex differences in the absence of human cultural gender socialization. Decades of research in rodent and primate models have demonstrated that social deprivation curtails the development of species-appropriate behaviors (5-8) and cognition (9-10). Primate mothers are critical for the normal social development of their infants (11-13) with classic studies demonstrating that maternal deprivation is associated with intense anxiety (14), inappropriate aggression (15), and an inability to form social relationships (16). The mother-infant relationship is therefore critical to proper social development; however, research also demonstrates the importance of the larger social milieu (17-20). For example, a recent study in mice found that early interactions with mothers and peers independently shape adult behavior (21). Likewise, some negative impacts of maternal-deprivation are attenuated in macaques that are raised in peer groups (22).

Most primates rear their offspring in a stable social group in which mothers can influence infant interactions with conspecifics. Restrictive or protective mothering styles have been observed in some Old World monkey species and style correlates with maternal rank, parity, offspring sex, and perceived risk to the infant (23-25). These patterns demonstrate maternal influence on the early social experiences of infants in species that live in cohesive groups. However, much less is known about how mothers influence infant social opportunities in species that live in fission-fusion social groups. Fission-fusion species, particularly those that have high fission-fusion dynamics such as humans and chimpanzees (26), are an excellent paradigm in

which to consider individual differences in infant social exposure since subgroup size and composition varies over time. This dynamic social system allows flexibility in the amount of social exposure that infants experience.

Here, we examine how maternal gregariousness varies by infant sex in wild chimpanzees (*Pan troglodytes*). Chimpanzees live in permanent communities or unit groups with multiple males and females. Temporary subgroups, or parties, form within the community and often change composition over the course of the day. Studies have demonstrated that party size is related to food availability and the presence of fertile females (27-29). The social flexibility characteristic of chimpanzees may allow mothers and infants to associate in parties of different sizes depending upon the optimal strategy for infant development.

Given well-documented differences between adult males and females, particularly regarding social behavior, it seems possible that maternal subgrouping patterns vary by infant sex in a manner that foreshadows adult sex-specific behavioral strategies. Adult male east African chimpanzees (*P.t. schweinfurthii*) are more gregarious and aggressive than females as they compete for high dominance rank, which affords greater access to estrous females (28, 30). Males also cooperate with each other to form coalitions for dominance rank acquisition, community defense, and communal hunting (31) with some male-male relationships enduring for years (32). While inter-site variation exists (e.g. 33-34), east African female chimpanzees are generally less gregarious than males (35) and at Gombe National Park, Tanzania, Kasekela community females spend approximately 40-70% of their time alone or with adult daughters and dependents (36-38). Females also exhibit comparatively low levels of physical aggression (28, 39-41). Emerging evidence suggests that sex differences in social behavior appear early in life. For example, male infants have significantly more social partners than their female counterparts when they first spend the majority of time out of reach from their mother (30-36

months) (42). Specifically, males in this age class interact more with unrelated individuals, particularly adult males, than do females. Yet, it is unclear to what extent mothers mediate social exposure based on infant sex. Differences in maternal gregariousness may predispose male and female infants to different levels of independence and sociability very early in life, which may influence development. In chimpanzees and other fission-fusion species, mothers may join or leave parties, thereby affording or restricting social exposure. Once infants are able to travel without being carried by their mother, they may also influence maternal patterns by leading mothers to join or remain in parties (43).

As in most other primates, the chimpanzee mother-infant relationship is primary in early life. Infants are in almost constant contact with their mothers for the first 4-6 months of life (28) when they have low levels of social interactions with non-mothers (this study). Mothers with infants later form nursery groups that contain several mothers (44-47). Infants only begin traveling under their own power more than they are carried by their mother around the age of 3.5 years old (48). Infants begin eating solid foods by six months of age (49), yet remain nutritionally-dependent upon their mother until they are weaned between 4-5 years old (50-51).

In this study, we investigated differences in maternal subgrouping patterns based on infant sex. We hypothesized that maternal gregariousness varies in ways that would foster sex-appropriate social development. Since male offspring will need to integrate into the adult male hierarchy and rely more on social skills and bonds for success as adults, while females will ultimately spend more of their time alone with dependent offspring, we predicted that mothers with male offspring would be more gregarious than mothers with female offspring. We tested this prediction with 37 years of data on maternal subgrouping among the wild chimpanzees at Gombe National Park, Tanzania. We considered three measures of gregariousness for mothers who were observed with both sons and daughters. The first measure was the time spent with

another adult who is not an immediate female family member (mother or adult daughter). This measure allowed mother-adult daughter pairs to count as non-social time given that some study females do not emigrate and frequently associate with their mothers; excluding their time together allows us to address the question of infant exposure to the larger social milieu. Secondly, we examined average party size and composition. Specifically, we examined the average adult party size, as well as the average number of maternal kin (individual adults related through the matriline) and maternal non-kin (individual adults not related through the matriline) present in a mother's party over the course of a day. Thirdly, we investigated subgrouping preferences by comparing the proportion of time mothers spent in mixed-sex (at least one adult male in the party) and female-only parties (at least one additional adult female, but no adult males, in the party). The second and third measures of gregariousness include mothers and adult daughters in the count of adults present in order to yield the actual adult party size and composition. We compared each of our metrics by infant sex during two time periods: the first six months of life, and from six months to 3.5 years of age. Infants are in nearly constant contact with their mother during the first six months of life such that they are unlikely to directly influence their mother's subgrouping patterns, while patterns at older ages may reflect both maternal and infant social preferences and interactions. The first six months postpartum is also distinct in that it corresponds to the period when mothers experience the highest metabolic costs of lactation (52), which may influence behavior. Females with infants less than 3.5 years of age in our study very rarely exhibited sexual swellings, which are known to influence female gregariousness (53). Finally, we investigated infant interactions with non-mothers across the entire infancy (infants aged ≤ 3.5 years) using a complementary 24-year dataset on infant behavior to investigate how maternal gregariousness relates to infant social interactions.

RESULTS

All results on maternal subgrouping patterns are from analyses of data from well-sampled mothers who were observed with both sons and daughters as infants ($N = 9$ mothers with at least 10 follows during the first six months of the infant's life). This within-mother comparison allows for direct testing of our prediction; however, results based on a larger sample of mothers, including mothers that were just observed with offspring of one sex, are provided in the supporting information to demonstrate the generality of the patterns. Categorical maternal rank (high versus low) was also included as a fixed factor in all analyses of maternal subgrouping patterns since females of different ranks face different competitive pressures that may influence gregariousness. Rank results are included in Tables S1 and S2. Notably, in our dataset high-ranking females were no more likely than low-ranking females to have a son versus a daughter (chi-square with Yates correction:).

Maternal time spent with others. Infant sex was a significant predictor of the time spent with others beyond immediate female family members for both time periods (LMM: first six months: $F_{1,447} = 13.00$, $p = 0.0003$; late infancy: $F_{1,1824} = 9.90$, $p = 0.002$; Figure 1) (first six months: 459 follows on 9 mothers with 25 sons and 18 daughters; late infancy: 1836 follows on 9 mothers with 27 sons and 19 daughters). A post-hoc test revealed within-female differences based on the sex of her offspring. The estimated least square mean proportion of time each mother spent with others when with her son(s) versus when with her daughter(s) was significantly different during the first six months (Paired T-test: $T(9) = 3.23$, $p = 0.01$; Figure S1) and tended to be different over late infancy ($T(9) = 2.00$, $p = 0.08$). In each period, mothers were more gregarious when they had sons than daughters.

Maternal party size and composition. Infant sex significantly predicted the daily average party size in both periods (LMM: first six months: $F_{1,400} = 8.47$, $p = 0.004$; late infancy: $F_{1,1750}$

= 8.64, $p = 0.003$). The average party size in each period was higher for sons than for daughters (Table 1).

Infant sex predicted the daily average number of maternal kin (the average number of a mother's maternal kin present in a mother's party or parties per day) in both periods (LMM: first six months: $F_{1,400} = 12.41$, $p = 0.0005$; late infancy: $F_{1,1750} = 24.92$, $p < 0.0001$). Mothers with sons associated with a significantly higher average number of maternal kin than mothers with daughters (Table 1). It is important to note that there is no difference in the number of maternal kin available to mothers with sons versus mothers with daughters. There was also a significant difference by infant sex in the daily average number of maternal non-kin in the first six months and late infancy (LMM: first six months: $F_{1,400} = 6.36$, $p = 0.01$; late infancy: $F_{1,1750} = 5.45$, $p = 0.02$). Mothers with sons associated with a higher number of maternal non-kin on average than mothers with daughters (Table 1).

Mothers with sons spent significantly more time in mixed-sex parties than mothers with daughters during the first six months ($F_{1,447} = 15.16$, $p = 0.0001$) but there was no difference during late infancy ($F_{1,1824} = 2.39$, $p = 0.12$; Figure 2a). Infant sex also predicted the proportion of time spent in female-only parties in late infancy ($F_{1,1824} = 26.42$, $p < 0.0001$), but not during the first six months ($F_{1,447} = 0.13$, $p = 0.72$; Figure 2b). During late infancy, mothers spent a significantly higher proportion of their time in female-only parties with sons than with daughters.

Maternal gregariousness and infant social interactions. Infants first interacted (groomed or played) with non-mothers (including siblings) at 0.43 ± 0.06 years old (mean \pm SD; $N=14$ infants with ≥ 10 hours of observation before first interaction). The average proportion of minutes during a follow that an infant was observed interacting with non-mothers during the

first six months of life was $0.0006 (\pm 0.0027 \text{ SD})$ and increased to peak during the infancy period at a proportion of $0.176 (\pm 0.124 \text{ SD})$ at age 27-30 months. The number of non-mothers an infant interacted with per day (hereafter referred to as social partners) significantly increased with both increasing infant age ($\beta = 0.0006$) and average daily party size including all age classes ($\beta = 0.176$). While there was a main effect of infant sex with males having significantly more social partners than females ($\beta = 0.124$), there was also a significant interaction between infant sex and average daily party size ($\beta = 0.0027$), with the number of social partners increasing with party size more for male infants than female infants (662 follows on 21 mothers, 29 male infants, and 17 female infants; Figure S2).

DISCUSSION

Mothers in species with a fission-fusion social structure can influence their offspring's social environment through selective subgrouping. Since the social associates of infant chimpanzees are restricted to those individuals with whom the mother spends time, chimpanzee mothers are able to influence their offspring's social experience to an even greater extent than females of fission-fusion species with more physically precocious infants (e.g. bottlenose dolphins: 54). In this study, we found that mothers with sons were more gregarious than mothers with daughters; they spent more time with others and had larger average party sizes with a higher number of both maternal kin and non-kin present on average throughout the day. The percent difference in time spent with individuals beyond immediate female family members reported here translates to ~2 more hours per day for male infants during early infancy, a substantial ~25% increase in social exposure time.

It is noteworthy that mothers with daughters did not associate as much with maternal kin as mothers with sons, despite the fact that family parties should be safe social environments. This result suggests the intriguing possibility that social exposure in general is not as critical for females, which is in accord with the lower gregariousness observed in adult females compared to

adult males. Association with others may carry costs in terms of increased competition, heightened risk of infanticide, and higher stress. Females, particularly those with low ranks, experience increased social stress in larger parties (55). Interestingly, mothers with infant daughters were likely opting out of a competitive and stressful context while mothers with sons incur these costs. Additionally, compared to mothers with daughters mothers with sons spent more time with adult males during the first six months, indicating preference for association with males early in their infant's life. Although mothers with sons did not spend more time in female-only parties than mothers with daughters in the early months, they did so during late infancy. This pattern suggests that once males began interacting with others at appreciable levels, their mothers started spending more time in nursery groups comprised of females and dependent offspring; this pattern may have been driven in part by the infant males themselves.

In a previous study, we demonstrated that males had more social partners during the 30-36 month age window when they first spent the majority of time out of reach from the mother, but we did not detect differences in maternal party size (42). Here, our investigation over a broader range of infant ages revealed that mothers with sons were more gregarious than mothers with daughters, particularly early in the infant's life. Additionally, our results here indicate that as offspring get older and begin moving farther from their mothers (48) they appear to make use of these social opportunities since the number of social partners per day increased with offspring age. Compared to female infants, male infants also made greater use of the social opportunities provided them by interacting with more conspecifics as average party size increased. These results suggest both maternal facilitation and infant sociability are at play in the increased social interactions by young males.

Interestingly, even in the first 6 months of life when an infant is primarily in contact with the mother and cannot reasonably be expected to direct maternal subgrouping, mothers with sons

were far more gregarious than mothers with daughters. During this first 6 months of life, very low levels of infant interaction with non-mothers begin to occur, but are insufficient to drive the observed differences in maternal subgrouping. These early ages, however, may serve as an important period of social exposure and observational learning. Indeed, the greater gregariousness of mothers with sons compared to daughters may provide these young males with more of an opportunity to observe, and eventually interact with, members of the broader social milieu. Most intriguing is the possibility that the opportunity to observe adult models facilitates development of social skills important for success as an adult, particularly for males. Indeed, a previous study of the same population found a tendency for sons of mothers who more frequently associated with adult males during their son's immaturity to achieve higher rank as adults (37). Theory and empirical research predict that individuals will exhibit biases in which models they choose to observe in order to avoid unreliable information and maximize the transfer of useful information (56-58). Importantly, there is evidence that young male chimpanzees attend to same-sex models and sex-typical behavior. For example, juvenile and early adolescent males often watch their adult counterparts during copulations and displays, even following and imitating the behavior (59-60). Thus, the opportunity to observe adult male behavior, particularly early in infancy, may influence social development in male infant chimpanzees and provide a future competitive advantage.

While our results are consistent with our hypothesis that maternal subgrouping patterns provide infants with social exposure that fosters sex-appropriate social development, an alternative hypothesis is that mothers associate with adult males early in infancy to garner protection against aggression or infanticide (61-62, 28). In terms of intercommunity aggression, killings occur more frequently when the victim's party is greatly outnumbered (63), thus the presence of males may provide some safety in numbers. However, Kasekela female core areas tend to be well within community boundaries (64) and evidence from the Kanyawara community in Uganda

indicates females use boundary areas less than males (65). Thus, seeking protection from attacks by foreign males is unlikely to drive mothers to regularly associate more with adult males. There is evidence of adult males intervening in intracommunity female conflicts and attempting to prevent infanticide (e.g. 61, 66-67). However, in this case the male protection hypothesis also seems unlikely to drive the observed patterns since adult males themselves may present a risk to infants. There are documented cases of infanticide committed by community males (63), thus association with adult males in general may be considered a risk to infant safety. The surest way to avoid intracommunity infanticide should be to avoid parties, which Kasekela mothers appear to do by spending up to 70% of their time alone or with close female kin (37-38). A Kanyawara study found that mothers were less gregarious than non-mothers and less likely to group with adult males, which the authors suggest avoids the risk of injury to their infants by aggressive adult males (68). However, given the number of females who do not emigrate, future studies of the Kasekela community should investigate if natal mothers associate more with male relatives, which may allow them to expose infants to groups while mitigating risks.

Another possibility is that the sex-biased differences in maternal gregariousness are driven by others. Attraction to infants by conspecifics is well documented in a number of primate species (e.g. 69-71). Community members may be more attracted to male infants than female infants, thereby remaining in the company of mothers with sons for longer periods. Young males will eventually integrate into the community, while young females may emigrate at adolescence. Attraction by others could also explain the general increase in time spent in female-only parties as peers may draw mothers together as they play. Though attraction by others is an intriguing possibility, it should be noted that in the chimpanzee fission-fusion social system mothers have the option to leave and must at least acquiesce to remaining in a party.

If we are correct that the patterns we describe result largely from the mother's behavior, our results raise questions concerning the proximate mechanisms driving differences in maternal subgrouping patterns based on infant sex, particularly at early ages. An intriguing possibility concerns the role of maternal androgens. Despite mixed results, some studies in both humans and non-human primates have found higher levels of circulating androgens in mothers carrying a male rather than a female fetus, particularly in the second half of pregnancy (reviewed in 72). Elevated maternal testosterone may influence the propensity to group since studies have demonstrated a positive correlation between female testosterone and female aggression or competition (humans: 73-74). Chimpanzee mothers may be more likely to remain in parties, where levels of competition are higher, if their testosterone levels are high. Prenatal testosterone might also predispose male chimpanzee infants to greater physical activity levels than females as has been observed in humans (reviewed in 75-76). This greater activity by males may prompt mothers to provide more external stimuli for their young male infants.

Given the close evolutionary relationship between chimpanzees and humans, how do these results compare to patterns observed in humans? The human literature provides some examples of differential parental behavior toward infants based on sex. For example, mothers communicate in a way that encourages risk-taking by boys and vulnerability perception by girls (77) and parents participate in more strenuous play with boys (78). However, evidence for sex differences in parental facilitation of social situations is surprisingly scant, despite a few studies that have reported no sex difference in parents arranging peer contacts (79-80). Nevertheless, children of parents that initiate more social contacts have more consistent companionship and more play partners, while boys with more parent-initiated interactions have greater peer acceptance and lower levels of rejection; however this advantage is not true for girls (80).

In humans, females are often considered more prosocial than males (e.g. 81-85); however boys are reported to play in larger same-sex groups than girls and recent research found greater social tolerance among males as predicted by the evolutionary need for male-male cooperation (e.g. 86-88). Likewise, east African adult male chimpanzees navigate a complicated social landscape involving both competition and cooperation (31). While important differences in social structure exist (e.g. pair-bonding in humans: 89), both humans and chimpanzees exhibit a fission-fusion social system, which affords mothers of both species the opportunity to influence their offspring's social development by controlling exposure to potential models and social partners. Our results indicate that among the chimpanzees of Gombe, maternal gregariousness differs by infant sex in a manner that foreshadows sex differences in adult behavior. Future studies by our group will relate variation in maternal sociality to adult behavior and outcomes in general; however the greater gregariousness of mothers with sons compared to daughters in particular may provide young males with the exposure to social behavior and skills important for success as an adult. Given early sex differences in behavior in chimpanzees and the persistent role of male cooperative hunting and defense in chimpanzees and humans, the question remains whether differential maternal grouping patterns based on infant sex were present during human evolution and contributed to the development of gender-typical behaviors.

MATERIALS AND METHODS

Data were collected on the wild chimpanzees of Gombe National Park, Tanzania. The central Kasekela community has been under continuous study since 1960. We used two different datasets for these analyses: one focused on adults; the other focused on mothers and their offspring. Further detail on these datasets can be found in SI Material and Methods. Briefly, both datasets contain detailed behavioral data collected using standard quantitative sampling techniques. For analyses of maternal subgrouping patterns, we analyzed data from 1974 to 2011

resulting from daily focal follows of individual adults. Notably, party composition scans were recorded every 15 minutes with all adult community members indicated as present or absent (see SI Materials and Methods for more details). All maternal subgrouping by infant sex analyses were run during two different periods: the first six months of life and late infancy (6 months – 3.5 years of age). We also accounted for covariates of maternal gregariousness including maternal rank and season (see SI Materials and Methods). We also tested for a main effect of infant age on maternal subgrouping patterns over the entire period of infancy; however as infant age was not a significant predictor it was removed from all analyses except the analysis of infant social partners (see below).

We calculated the daily proportion of time spent with others as the number of party composition scans during which the mother was with other adult individuals, divided by the total number of party composition scans for the day. Because 50% of females in the Kasekela community remain in their natal community and associate at high levels with their mothers, we scored a mother associating with only her adult daughter (or vice versa) and their dependent offspring as alone.

We fit linear mixed models (LMMs) (PROC MIXED, SAS 9.3) that included maternal rank, infant sex, mother ID, and the interaction between infant sex and mother ID as fixed effects. Season was included as a random effect to control for temporal variation in food availability and subgrouping patterns. We then performed a post-hoc test on the sex by mother id interaction to compare each mother's mean time spent with others by her infant's sex after controlling for covariates. Specifically, we tested for significant within-female differences between the amounts of time spent with others with sons versus daughters with a paired t-test. We also investigated whether the sex of the next oldest sibling influenced results using a larger sample of mothers (see SI Materials and Methods). Sibling sex was not a significant predictor of time spent with others and those results are included in SI Results.

To investigate differences in party size and composition, we first calculated the daily average party size as the sum of the number adults (adult age ≥ 12 years) present at each party composition scan, divided by the number of party composition scans that day. Thus, this measure of association incorporates both the number of individuals as well as the amount of time spent with them. We also examined the average number of adult maternal kin (individuals related through the mother; calculated as the sum of the number of maternal kin present during each party composition scan divided by the number of party composition scans that day), and the average number of adult non-maternal kin (individuals not related through the mother) present in the mother's party over the course of a day. A mother's maternal kin included both males and females of all generations.

We further compared the daily proportion of time spent in female-only and mixed-sex parties by infant sex. Each party composition scan was scored based on the sex of all adults present. In this analysis, unlike the analysis of time spent in parties, adult daughters or mothers were counted. Thus, females were considered to be in female-only parties rather than alone when associating with just their mother or adult daughter. Mixed-sex parties contained the mother and at least one adult male (including adult sons). All daily proportions were calculated as the number of party composition scans in the party type, divided by the total number of party composition scans. All measures of maternal subgrouping patterns were analyzed using LMMs with maternal rank and infant sex as fixed effects and mother id as a random effect. The proportion of time by party type model also included season as a random effect, while the average party size and composition models included season nested in year to control for community size changes.

To examine the relationship between maternal gregariousness and infant social interactions, we used a separate behavioral dataset focused on mothers and their offspring (see SI Materials and

Methods). Specifically, we fit a generalized linear mixed model (GLMM) with poisson error distribution and logit link function. Fixed effects included infant sex, infant age in days, average daily party size (including individuals of all ages), and the interaction of sex and daily average party size. Random effects included season nested within year and infant ID nested within mother ID to control for repeated, uneven sampling of infants, and mothers with more than one infant in the dataset. We determined the significance of each fixed effect by using likelihood ratio tests to compare the full model to those that did not contain the variable of interest (90). GLMM analysis was conducted using the lme4 package (91) in R (version 3.0.1, R Core Development Team 2013).

This study was completely observational in nature; the subjects are well-habituated to human observation. Our research has approval from the Tanzanian governing bodies, including Tanzania National Parks, the Tanzanian Wildlife Research Institute, and the Tanzanian Commission for Science and Technology.

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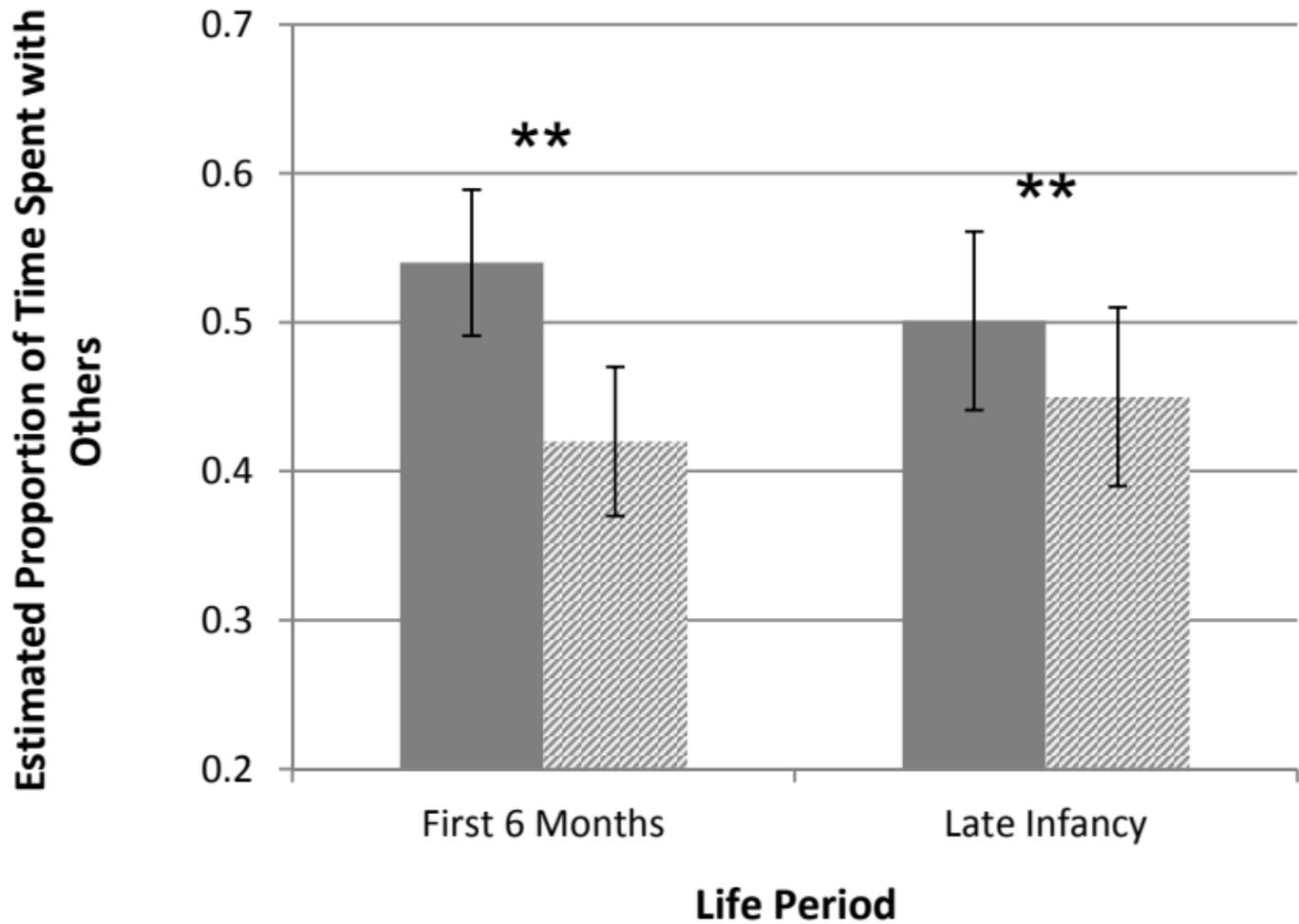
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FIGURE CAPTIONS

Figure 1. Least square means for the time mothers spent with others were estimated from the LMM on well-sampled mothers observed with sons and daughters. First six months: 459 follows on 9 mothers with 25 sons and 18 daughters. Late infancy (6 mos – 3.5 yrs): 1836 follows on 9 mothers with 27 sons and 19 daughters. Error bars represent standard errors. ** $p < 0.005$

Figure 2. Least square means for the proportion of time mother spent in a) mixed-sex and b) female-only parties were estimated from the LMM on mothers observed with sons and daughters. Error bars represent standard errors. ** $p < 0.005$



■ Sons
▨ Daughters

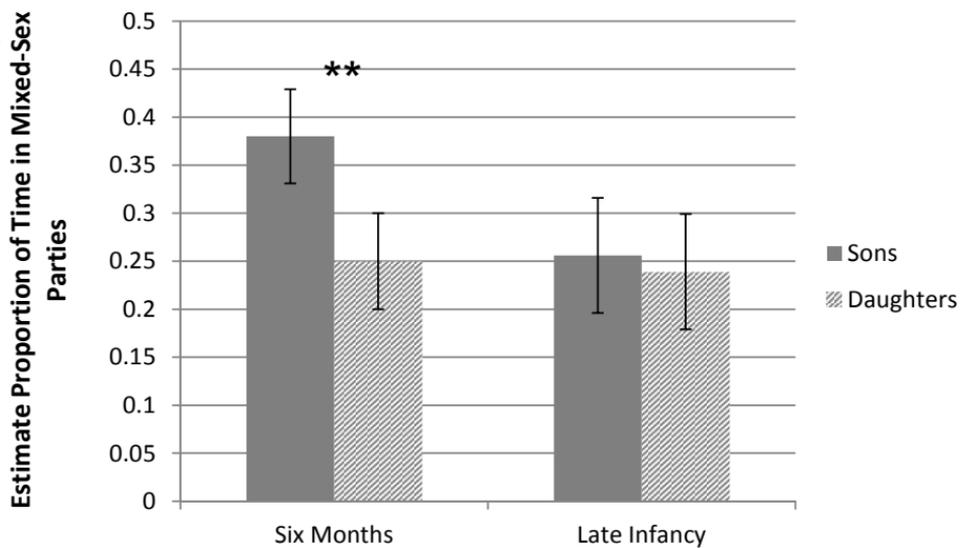
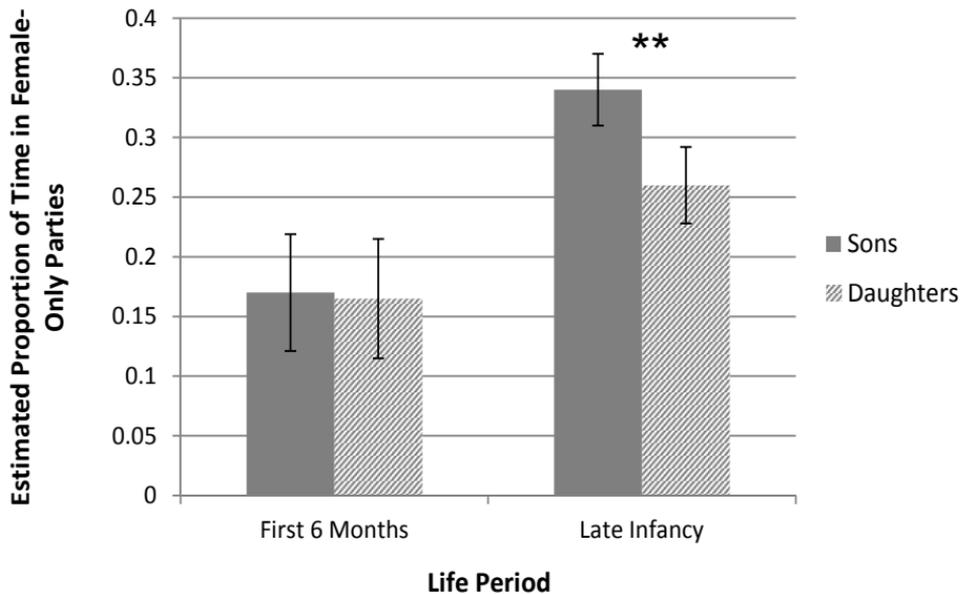
A**B**

Table 1. Estimated Daily Average Party Size and Kin Composition

		Party Size	Maternal Kin	Maternal Non-Kin
First 6 Months	Sons	7.49	1.30	5.89
	Daughters	5.34	0.91	4.19
Late Infancy	Sons	5.11	0.96	4.15
	Daughters	4.21	0.70	3.51

Least square means were generated from a model that included maternal rank and year nested in season. All comparisons between mothers with sons and mothers with daughters were significant ($p < 0.05$).

SUPPORTING INFORMATION

Below we present additional information on methods, results from a larger sample of mothers, and supporting tables and figures.

SI MATERIALS AND METHODS

Behavioral data sets. We investigated grouping patterns of mothers and their infants (aged ≤ 3.5 years) over a 37-year period (1974-2012) during which the study community contained between 31-62 individuals with 12-25 adult females and 6-14 adult males (adult age ≥ 12 years).

For analyses of maternal grouping patterns, we analyzed data from daily focal follows of individual adults that were collected between 1974 and 2011. A team of (usually two) research staff follow one adult chimpanzee each day (usually from night nest-to-night nest). They collect continuous data on the feeding and social interactions of the target of the follow, and party composition at regular intervals. A party is defined as a subgroup of individuals that travel, forage, and/or rest together. The team visually confirms the identity of any new arrivals and then tracks party membership at 15-minute intervals through visual observation or short-range vocalizations. A party member leaves when they travel away from the target of the follow or vice versa. Research staff rotate through adult members of the community with the goal of collecting one follow on each adult per month. In the unusual case of a mother with twin infants, these data were counted once to avoid pseudoreplication.

To examine the relationship between maternal gregariousness and infant social interactions, we used a behavioral dataset focused on mothers and their offspring. Data are collected on the focal mother, youngest dependent offspring, and next oldest offspring at 1-minute point samples during these family follows. The targeted follow length varied over the years of the study from 6-hours to night nest-to-night nest. Behaviors recorded include those such as traveling, resting,

feeding, and social interactions including grooming and play. We focused on the 24-year period (1988-2012) when party composition scans were regularly conducted as described above (5-minute intervals until 2011 and every 15 minutes thereafter). In the unusual case of a mother with twin infants, these data were not included in these analyses.

Covariates of maternal sociality. Maternal rank was calculated by the direction of pant-grunts (a vocalization that functions as a formal indicator of dominance) in two-year periods over the study duration (e.g. 1974-1975, 1976-1977, 1978 -1979). We assigned binary dominance rank (high or low) based on the Modified David's Score (MDS) (1); high-ranking individuals were at least $\frac{1}{2}$ standard deviation above the mean MDS (2). Season was based on rainfall data and following the precedence of other studies that demonstrate seasonal differences in weight and gregariousness; groups are smaller and individuals weigh less during the dry season (e.g. 3-5). Each follow was assigned a season based on the month in which it took place: wet (November-April) or dry (May-October).

Additional analyses on larger sample of mothers. All maternal sociality by infant sex results in the main text are from analyses run using data on mothers that had sufficient follows with both sons and daughters. Below, we describe analyses using data from a larger sample of mothers, including mothers that were just observed with offspring of one sex or the other. This dataset included 662 follows on 32 mothers with 42 sons and 30 daughters for the first six months of life and 2496 follows on 31 mothers with 45 sons and 32 daughters for late infancy. All analyses on the larger sample of mothers were analogous to those in the main text with the addition of mother ID as a random factor to control for uneven sampling on different mothers.

Maternal time spent with others by sibling sex. We also extend our analysis of this larger sample of mothers to investigate the potential confound of older siblings by investigating how

the time spent in groups relates to sibling sex over the entire infancy (0-3.5 years old). In order to investigate how the presence of older siblings influenced maternal gregariousness, we tested the relationship of sibling sex and age on maternal time with others in a model analogous to our infant-based analyses. Each follow was scored as containing a sibling if the mother had another dependent offspring < 8 years old. Older siblings generally continue to associate at high rates with their mothers until they reach puberty at 8-10 years of age (6). In the infrequent cases where two dependent older siblings were present, we considered the youngest. For this analysis, we used a LMM that included infant sex, older sibling sex, older sibling age, and maternal rank as fixed effects, and season and mother as random effects.

Maternal gregariousness and infant social interactions. We investigated how infant social interactions relate to age, and how the number of social partners varied by infant sex, age, and party size using a dataset focused on mothers and offspring. The proportion of time infants spent in social interactions was calculated as the number of 1-minute point samples at which the infant was observed interacting (grooming or playing) with a non-mother, divided by the total number of 1-minute point samples for that infant on a given day. The number of infant social partners per day was calculated as the number of unique individuals of all ages (excluding their mother) that an infant was observed interacting with during a given day. Daily average party size was calculated as the sum of the number of individuals of all age classes present at each party composition scan, divided by the number of party composition scans that day. We set a minimum inclusion criterion of four hours of good observation time per follow in order to exclude shorter follows where social interactions were unlikely to be captured. Minutes on which the behavior was uncertain because of lost or obscured view were excluded. The resulting dataset included 662 follows on 21 mothers, 29 male infants, and 17 female infants ranging in age from 3 days to ≤ 3.48 years.

SI RESULTS

Maternal gregariousness by maternal rank from data on well-sampled mothers. Results of LMMs using data on well-sampled mothers described in the main text are provided in Tables S1 and S2. In late infancy, low-ranking female social patterns follow expectations based on their lower competitive ability as they spend more time alone, have smaller groups, and spend less time with adult males. Avoidance of males is likely related to higher social stress for low-ranking females in mixed-sex groups (2). The results regarding early infancy female-only association patterns are surprising since high-ranking females appear to adjust their grouping patterns to avoid female-only parties. Future work should investigate the specific female individuals mothers group with during the first 6 months of their infant's life to consider how these associations relate to infant socialization and the mitigation of competition and infant risk.

Additional analyses on larger sample of mothers. In the text below we present results from the additional analyses run on the larger sample of mothers described in the SI Materials and Methods above.

Maternal time spent with others by infant sex. Our results for the larger sample of mothers demonstrate similar patterns as those reported in the main text for females observed with infants of each sex. Mothers with sons spent significantly more time with others during late infancy than mothers with daughters ($F_{1,2462} = 5.43$, $p = 0.02$; mothers with sons least squares mean = 0.61 ± 0.04 SE, mothers with daughters least squares mean = 0.57 ± 0.04 SE). Compared to mothers with daughters, mothers with sons also tended to be more gregarious during the first six months of life ($F_{1,627} = 2.65$, $p = 0.10$; mothers with sons least squares mean = 0.56 ± 0.06 SE, mothers with daughters least squares mean = 0.50 ± 0.06 SE). Maternal rank significantly predicted the amount of time spent with others during late infancy ($F_{1,2462} = 4.08$,

$p = 0.04$) as low-ranking mothers spent more time with others than high-ranking mothers (low-ranking estimate: 0.61 ± 0.04 ; high-ranking estimate: 0.56 ± 0.05 SE).

Maternal time spent with others by sibling sex. Sibling sex did not significantly predict maternal time spent with others ($F_{1, 1877} = 2.03$, $p = 0.15$), but infant sex remained significant ($F_{1, 1877} = 4.11$, $p = 0.04$). Time spent with others varied by sibling age ($F_{1, 1877} = 8.33$, $p = 0.004$) as the time spent with others increased with sibling age. Maternal rank did not significantly predict maternal time spent with others ($F_{1, 1877} = 1.56$, $p = 0.21$).

Maternal party size and composition by infant sex. Our results for the larger set of females again demonstrate the same patterns reported in the main text. Infant sex significantly predicted the average daily party size in both periods (first six months: $F_{1, 567} = 4.30$, $p = 0.04$; late infancy: $F_{1, 2388} = 7.49$, $p = 0.006$). The average daily party size in each time period was higher for sons than for daughters (Table S3). Maternal rank did not significantly predict the average party size at any stage.

Infant sex also predicted the average daily number of maternal kin present in the first six months and late infancy (first six months: $F_{1, 567} = 10.31$, $p = 0.001$; late infancy: $F_{1, 2388} = 32.74$, $p < 0.0001$). Mothers with sons had a significantly higher number of maternal kin present on average than mothers with daughters (Table S3).

There was a significant difference by infant sex on the daily average number of non-kin during late infancy and a tendency during the first six months (first six months: $F_{1, 567} = 3.31$, $p = 0.07$; late infancy: $F_{1, 2388} = 4.16$, $p = 0.04$). Mothers with sons had a higher average number of non-kin present than mothers with daughters (Table S3). Maternal rank did not significantly predict the average number of non-kin present in the party.

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SUPPORTING TABLE AND FIGURE CAPTIONS

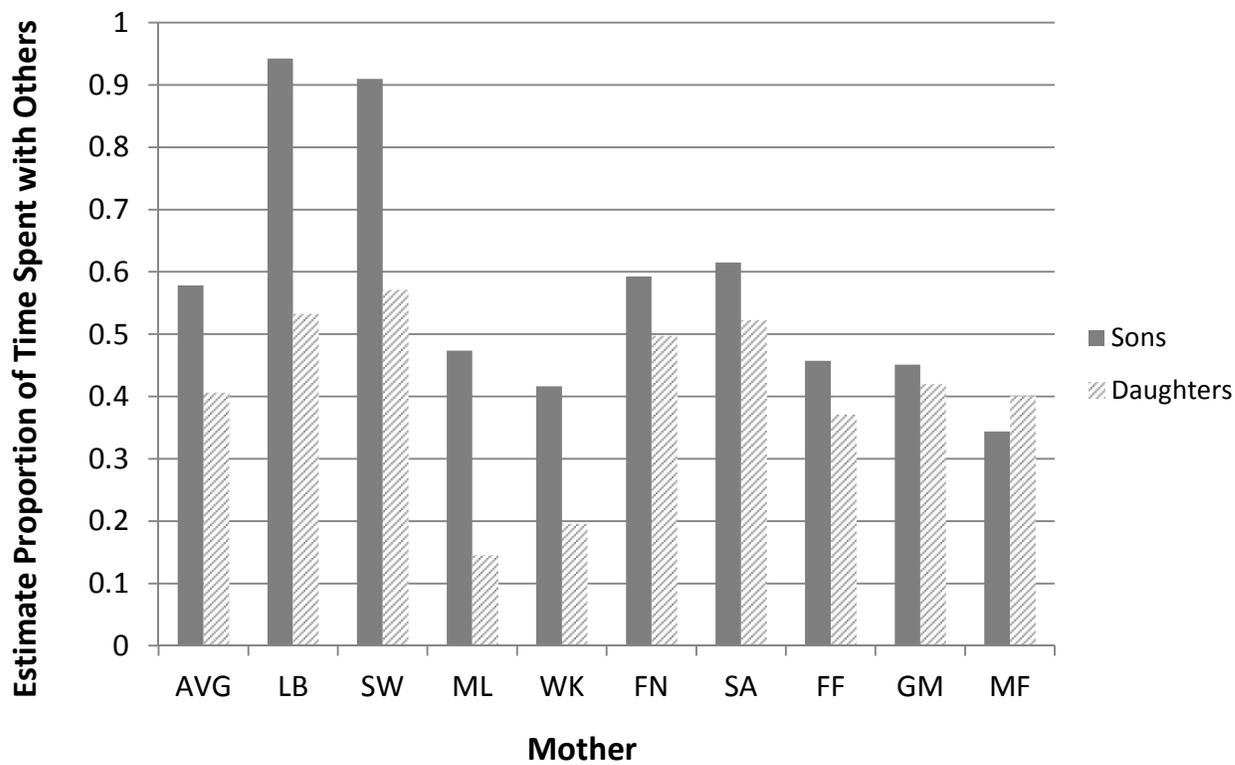
Table S1. Fixed Effects Results From LMMs on Data from Well-Sampled Mothers. Estimated averages for each measure of gregariousness in each life period by mother's rank are provided in Table S2. Estimated averages by infant sex are presented in Figures 1 and 2 and Table 1 in the main text.

Table S2. Estimated Average Measures of Gregariousness by Mother's Rank from Data on Well-Sampled Mothers. Estimated least square means (standard error) were generated from LMMs from data on well-sampled females that included infant sex and maternal rank as fixed effects, and year nested in season as random effects. **Indicates comparison between high and low ranking mothers was significant ($p < 0.05$). *Indicates tendency ($p = 0.053$). Statistics are presented in Table S1.

Table S3. Estimated Average Party Size and Kin Composition from Data on Larger Sample of Mothers. Estimated least square means were generated from a LMM that included maternal rank as a fixed effect and mother ID and season as random effects. All comparisons between mothers with sons and mothers with daughters were significant ($p < 0.05$) except for a tendency for more non-kin adult associates with sons during the first six months of life ^a.

Figure S1. Time Spent with Others for Well-Sampled Mothers during the First Six Months of Life. Least square means for each mother with an infant of each sex were generated from the mother ID by infant sex interaction term in a LMM that also included maternal rank as a fixed effect and season as a random effect. Includes data from 459 follows on 9 mothers with 25 sons and 18 daughters

Figure S2. Infant Social Interactions by Party Size. Predicted number of daily non-mother infant social partners for each sex given the partial effect of average daily party size (including individuals of all age classes) from the GLMM. Each point represents an individual follow day (N = 662 follow days; 14.4 ± 13.2 mean \pm sd follows per infant; 46 infants). The interaction between infant sex and average daily party size was significant (). See main text for more detailed results.



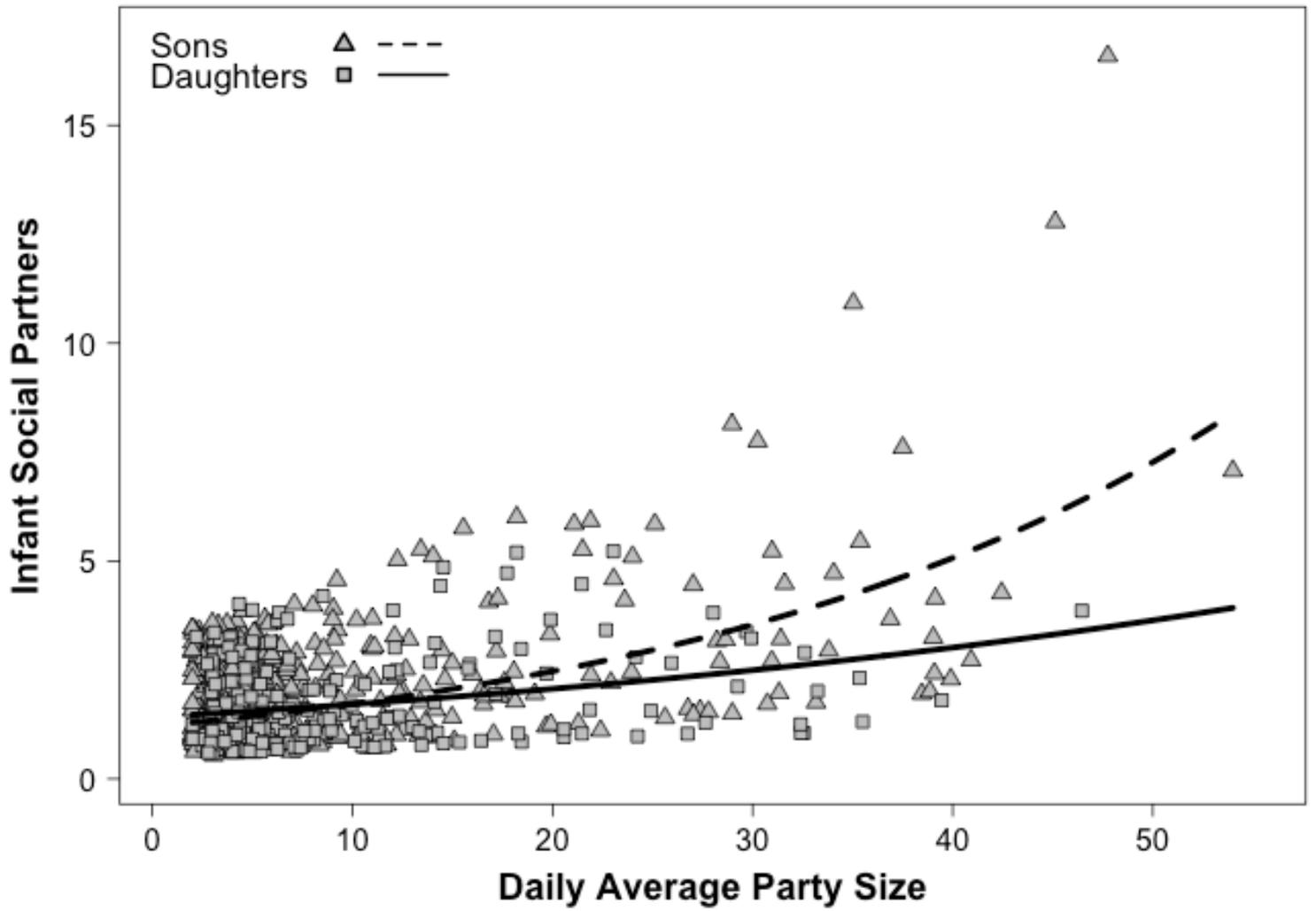


Table S1. Fixed Effects Results From LMMs on Data from Well-Sampled Mothers

Response Variable	Life Period	Explanatory Variable	Numerator d.f.	Denominator d.f.	F	p
Time with Others	First 6 Months	Infant Sex	1	447	13.00	0.0003
		Mother's Rank	1	447	1.12	0.2898
	Late Infancy	Infant Sex	1	1824	9.90	0.0017
		Mother's Rank	1	1824	5.57	0.0184
Party Size	First 6 Months	Infant Sex	1	400	8.47	0.0038
		Mother's Rank	1	400	2.34	0.1272
	Late Infancy	Infant Sex	1	1750	8.64	0.0033
		Mother's Rank	1	1750	3.74	0.0532
Maternal Kin	First 6 Months	Infant Sex	1	400	12.14	0.0005
		Mother's Rank	1	400	0.03	0.8646
	Late Infancy	Infant Sex	1	1750	24.92	<0.0001
		Mother's Rank	1	1750	2.46	0.1170
Maternal Non-Kin	First 6 Months	Infant Sex	1	400	6.36	0.0121
		Mother's Rank	1	400	1.27	0.2614
	Late Infancy	Infant Sex	1	1750	5.45	0.0196

		Mother's Rank	1	1750	2.52	0.1123
Mixed-Sex Parties	First 6 Months	Infant Sex	1	447	15.16	0.0001
		Mother's Rank	1	447	1.13	0.2881
	Late Infancy	Infant Sex	1	1824	2.39	0.1221
		Mother's Rank	1	1824	7.70	0.0056
Female-Only Parties	First 6 Months	Infant Sex	1	447	0.13	0.7188
		Mother's Rank	1	447	7.02	0.0083
	Late Infancy	Infant Sex	1	1824	26.42	<0.0001
		Mother's Rank	1	1824	1.54	0.2147

Estimated averages for each measure of gregariousness in each life period by mother's rank are provided in Table S2. Estimated averages by infant sex are presented in Figures 1 and 2 and Table 1 in the main text.

Table S2. Estimated Average Measures of Gregariousness by Mother's Rank from Data on Well-Sampled Mothers.

Response Variable	Life Period	Mother's Binary Rank	
		High	Low
Time with Others	First 6 Months	0.55(0.07)	0.50(0.06)
	Late infancy**	0.56(0.05)	0.50(0.05)
Party Size	First 6 Months	7.4(1.3)	5.4(1.1)
	Late infancy*	5.2(0.69)	4.2(0.60)
Maternal Kin	First 6 Months	1.1(0.27)	1.1(0.22)
	Late infancy	0.91(0.16)	0.75(0.15)
Maternal Non-Kin	First 6 Months	5.6(0.95)	4.5(0.84)
	Late infancy	4.2(0.55)	3.5(0.47)
Mixed-Sex Parties	First 6 Months	0.33(0.07)	0.28(0.06)
	Late infancy**	0.27(0.05)	0.20(0.05)
Female-Only Parties	First 6 Months**	0.12(0.04)	0.22(0.03)
	Late infancy	0.31(0.04)	0.28(0.04)

Estimated least square means (standard error) were generated from LMMs from data on well-sampled females that included infant sex and maternal rank as fixed effects, and year nested in season as random effects. **Indicates comparison between high and low ranking mothers was significant ($p < 0.05$). *Indicates tendency ($p = 0.053$). Results presented in Table S1.

Table S3. Estimated Average Party Size and Kin Composition from Data on Larger Sample of Mothers.

		Party Size	Maternal Kin	Maternal Non-Kin
First 6 Months	Sons	6.40	0.87	5.61 ^a
	Daughters	5.29	0.61	4.64 ^a
Late Infancy	Sons	5.88	0.58	5.41
	Daughters	5.15	0.35	4.90

Estimated least square means were generated from a LMM that included maternal rank as a fixed effect and mother ID and season as random effects. All comparisons between mothers with sons and mothers with daughters were significant ($p < 0.05$) except for a tendency for more non-kin adult associates with sons during the first six months of life^a.