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Female chimpanzee associations with male kin: trade-offs between inbreeding avoidance and infanticide protection

Kaitlin R. Wellens [a, *], Sean M. Lee [b], Jack C. Winans [c], Anne E. Pusey [d], Carson M. Murray [b]

[a] Department of Biology, Trinity Washington University, Washington, D.C., U.S.A.
[b] Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, D.C., U.S.A.
[c] Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, NY, U.S.A.
[d] Department of Evolutionary Anthropology, Duke University, Durham, NC, U.S.A.

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A large body of literature demonstrates the adaptive benefits of social relationships between kin, including fitness and survival. Given that most social mammals are characterized by male-biased dispersal, the majority of research on kin selection and associated advantages focuses on social relationships between female kin. Meanwhile, research on social relationships between adult male and female kin has primarily focused on inbreeding avoidance or the benefit to adult sons, with less attention on potential advantages these social relationships may provide females. The general pattern of male dominance over females in most mammal species suggests that females may benefit from protective associations with adult male kin. Using 43 years of behavioural data on the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania, we examined association patterns between females and their adult maternal male kin. We specifically focused on how these associations may represent a trade-off between inbreeding avoidance and protection for females, particularly against infanticide. In accordance with inbreeding avoidance, we predicted that females' association with adult kin would decrease when they were maximally tumescent, signalling sexual receptivity. To determine whether female–male kin associations provide protection to females, we examined female associations with adult male kin during their first year postpartum when infants are most vulnerable to infanticide. We predicted that during this first year postpartum, females would have a higher association with male kin than with unrelated males. We found that females associated more with adult sons and brothers than with unrelated males when they did not have a sexual swelling. Female association increased with all males across tumescence but females associated less with their brothers than they did with their sons and unrelated males when they were maximally tumescent, providing equivocal support for the inbreeding avoidance hypothesis. Furthermore, females associated more with both sons and brothers than with unrelated males in the first 6 months of the postpartum period. Higher association with brothers, relative to unrelated males, persisted throughout the first year postpartum. Together, these results speak to the cost–benefit trade-off in female and adult male kin associations, highlighting the potential protective advantage for females, especially during the postpartum period.

Kin selection plays a fundamental role in the evolution of social organization and behaviour across the animal kingdom (Hamilton, 1964; K. R. Foster et al., 2006; Silk, 2007; Silk et al., 2009). The importance of kinship to affiliative social behaviour has been well documented in taxa ranging from insects (Bourke, 1997; Lukasiewicz et al., 2017), spiders (Anthony, 2003) and birds (Downing et al., 2020; Ju & Lee, 2016; Krakauer, 2005) to long-lived mammals, such as primates (De Moor et al., 2020; reviewed in Silk et al., 2009), elephants (Archie et al., 2006) and cetaceans (Baird & Whitehead, 2000; Diaz-Aguirre et al., 2020; Frère et al., 2010). Given that the majority of mammal species are characterized by female philopatry and male-biased dispersal (Clutton-Brock & Lukas, 2012; Greenwood, 1980; Lawson Handley & Perrin, 2007; Lukas & Clutton-Brock, 2011; Pusey, 1987), research on social relationships among kin has primarily focused on the adaptive value of associations between related females. As predicted, a growing

* Corresponding author.
E-mail address: WellensK@Trinitydc.edu (K. R. Wellens).

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body of literature in group-living species demonstrates that maternal female relatives often associate at high levels and that these social relationships provide several benefits (house mice, *Mus musculus*: König, 1994; horses: Heitor et al., 2006; degus, *Octodon degus*: Ebensperger et al., 2004; meerkats, *Suricata suricatta*: Russell et al., 2002; rhesus macaques, *Macaca mulatta*: Sade, 1965; baboons: Silk et al., 2010; Colombian ground squirrels, *Urocitellus columbianus*: Dobson et al., 2012; Viblanc et al., 2010; fox squirrels *Sciurus niger*, and grey squirrels, *Sciurus carolinensis*: Kopowski, 1996).

Studies have demonstrated that close associations between female kin are correlated with shorter interbirth intervals (mice: König, 1994), increased likelihood of reproduction (elephants: Lynch et al., 2019), reduced predation risk (bison, *Bison bison*: Brookshier & Fairbanks, 2003) and increased offspring survival (vervet monkeys, *Chlorocebus pygerythrus*: Fairbanks & McGuire, 1986; Japanese macaques, *Macaca fuscata*: Pavelka et al., 2002; baboons: Silk et al., 2009). Notably, in baboons, this benefit is bidirectional, as both members of mother–daughter dyads that form stronger relationships have higher offspring survival rates than dyads that form weaker bonds (Silk et al., 2009).

The mechanisms through which fitness is enhanced via social relationships among female kin include protection and support in competitive contexts. For example, related female baboons protect each other from aggression and demonstrate coalitionary behaviour (Silk et al., 2004). Similarly, female vervet monkeys with mothers alive in the group are less likely to receive aggression, more likely to be defended during aggressive events and more likely to challenge other females than females without a mother (Fairbanks & McGuire, 1986). In macaques, maternal half-sisters support one another significantly more than paternal half-sisters or nonkin in aggressive interactions (Widdig et al., 2006). Such support among female relatives can result in matrilineal rank inheritance as daughters acquire their rank from their mothers via both direct rank inheritance (hyaenas: Engh et al., 2000; baboons: Hausfater et al., 1982) and coalitionary support (baboons: Chapais, 2004). Rank, in turn, affects females' health (Koenig, 2002; Sapolsky, 2005) and reproductive success (Silk et al., 2003).

Studies on the adaptive function of intersexual social relationships among kin have often focused on inbreeding avoidance, which is a key driver of sex-biased dispersal (Pusey, 1987; but see de Boer et al., 2021). The prevailing pattern in social mammals is male-biased dispersal (reviewed in Lawson Handley & Perrin, 2007) such that adult females rarely reside with adult male relatives, other than the potential for co-residence with fathers in long-lived species. However, several mammal species, including white-lined bats, *Saccopteryx bilineata*, plateau pika, *Ochotona curzoniae*, mountain gorillas, *Gorilla beringei beringei*, and western gorillas, *Gorilla gorilla*, and spider monkeys (summarized in Greenwood, 1980; gorillas: Harcourt, 1978; Parnell, 2002; Manguette et al., 2020; spider monkeys: Aureli & Schaffner, 2008) are typically characterized by male philopatry. Existing research has focused on female dispersal as an inbreeding avoidance strategy: a meta-analysis showed that female dispersal occurs in species wherein male breeding tenure exceeds female age at first reproduction (Lukas & Clutton-Brock, 2011). For example, western gorilla groups predominantly comprise a single breeding male, and females exhibit unconditional dispersal presumably to avoid breeding with their silverback fathers (Manguette et al., 2020). However, in mountain gorilla groups comprising multiple breeding males, up to half of females remain in their natal groups and successfully avoid breeding with their fathers (Vigilant et al., 2015), indicating that dispersal is not the only avoidance mechanism. Similarly, breeding groups of feral horses, *Equus ferus*, overlap spatially, yet females disperse among groups and avoid inbreeding when encountering male kin (Duncan et al., 1996; Linklater & Cameron, 2009). In Indo-Pacific dolphins, *Tursiops aduncus*, and chimpanzees, *Pan troglodytes*, lower association rates between mothers and sons once sons reach weaning (chimpanzees: Pusey, 1983; dolphins: Tsai & Mann, 2013) and sexual maturity (chimpanzees: Pusey, 1983; dolphins: Gibson & Mann, 2008) may mitigate inbreeding risk. Additionally, mother–adult son associations may be particularly low when mothers are cycling (dolphins: Wallen et al., 2017). Behavioural mechanisms to maintain intersexual relationships between kin while minimizing inbreeding risk may be adaptive if such relationships confer benefits to either party or both parties.

Indeed, research suggests that sons can benefit from maternal presence during development and adulthood. For example, research in chimpanzees and bonobos, *Pan paniscus*, demonstrates that maternal rank can impact the outcome of immature aggressive interactions (chimpanzees: Markham et al., 2014) and adult male mating success (bonobos: Surbeck et al., 2011). In a number of species, maternal presence impacts sons' survival and reproductive success. Research in ungulates has shown that orphaned male red deer, *Cervus elaphus*, are more likely to die of natural causes and less likely to grow antlers by 16 months of age, ultimately impacting fitness, than males who are not orphaned (Andres et al., 2013). In chimpanzees, males orphaned anytime up to 15 years of age face significantly lower survival than males who are not orphaned (Nakamura et al., 2014; Stanton et al., 2020). Similarly, male chimpanzees whose mothers die after weaning but prior to maturity, sire their first offspring at older ages and have a lower probability of siring offspring than nonorphaned males (Crockford et al., 2020). Additionally, a series of studies on killer whales, *Orcinus orca*, documents how mothers assist their sons in foraging efforts (Brent et al., 2015; E. A. Foster et al., 2012; Wright et al., 2016), including directly provisioning their sons (Wright et al., 2016). Adult sons are also significantly more likely to follow their mothers than are adult daughters (Brent et al., 2015). For killer whale males, the ecological support provided by mothers relates to their survival, as adult males experience a significant increase in mortality risk in the first year after their mother dies (E. A. Foster et al., 2012).

Despite numerous examples of the benefits for males from intersexual relationships between kin, few studies have investigated the benefits of intersexual social relationships in male-philopatric species from the female perspective. However, based on a general pattern of male dominance over females in most mammal species, there are strong reasons to expect females may also experience direct benefits from co-residency with adult male kin. Our study investigated the associations between mothers and adult maternal male kin (henceforth, male kin) in wild chimpanzees at Gombe National Park, Tanzania. Chimpanzees are one of only a few mammal species characterized by female-biased dispersal with adult males remaining in their natal community with their mothers (Greenwood, 1980; Pusey, 1987). The chimpanzees of Gombe present a particularly interesting system in which to test for potential benefits of co-residence with male kin because some adult females in this population do not leave their natal community (Goodall, 1986). Therefore, we can examine female social relationships with both adult sons and maternal brothers.

Chimpanzees are characterized by fission–fusion social systems, in which party size changes over the course of a day (Goodall, 1986), allowing a high degree of flexibility in female association patterns. Studies have demonstrated that maternal rank predicts the outcome of immature aggressive interactions during development. For example, sons with relatively higher-ranking mothers are significantly more likely to win aggressive interactions between peers with lower-ranking mothers (Markham et al., 2014). This

immature period may be one of the few times a mother can afford social protection to her son since adult males outrank all females (Goodall, 1986). As adults, sons may benefit from their mothers by inheriting their ranging patterns, which has been suggested to increase sons' foraging efficiency (Murray et al., 2008) and affect which females they reproduce with (Langergraber et al., 2013). Much less is known about adult female–maternal brother associations aside from evidence of decreased association when the female reaches reproductive age (Pusey, 1980). It remains an open question whether females benefit from co-residing with maternal male relatives. Because of the intersexual dominance hierarchy, adult males can theoretically act as a social buffer for related females.

Using 43 years of behavioural data on the wild chimpanzees at Gombe National Park, we investigated patterns of association between females and their adult male maternal relatives with particular focus on how such associations might reflect trade-offs between inbreeding avoidance and potential protection against infanticide. First, we compared female associations with male kin to their associations with other males as a function of sexual receptivity. The risk of inbreeding with adult sons and brothers will be higher when females are ovulating, as indicated by maximal tumescence of sexual swellings (Deschner et al., 2003; Emery Thompson, 2005). Accordingly, we predicted that female associations with male kin would be lower than with nonkin when the females were maximally tumescent. Alternatively, there may be no difference in female association based on relatedness and sexual receptivity if females can avoid inbreeding through other mechanisms and male relatives provide protective services. Second, we examined how female associations with male kin and other males vary across the female's first year postpartum. The risk of infant injury from aggressive interactions may be higher for clinging infants, as the majority of infanticides happen within the first 6 months of infancy (Bronikowski et al., 2016; Wilson et al., 2014). Notably, a number of within-community infanticides are instigated by female attackers (Goodall, 1986; Lowe et al., 2020; Pusey et al., 2008; Walker et al., 2021; Wilson et al., 2014). Since previous work has demonstrated that aggression between females is lower in the presence of males (Kahlenberg et al., 2008), association with adult male maternal kin could provide a critical protective service to infants. Therefore, we predicted that females' association with male kin would be higher than their association with nonmale kin during the first year after giving birth.

METHODS

Study Site and Subjects

Our study took place in the Kasekela community of Gombe National Park, Tanzania. Gombe is a small park (35 km^2) located on the eastern shore of Lake Tanganyika. The Kasekela community has been studied continuously since 1960 and data collection methods have been consistent since 1973. Each day, teams of researchers and Tanzanian field staff collect systematic and detailed behavioural data during full-day (from night nest to night nest) focal follows of one individual with the goal of conducting one monthly follow on each adult. These data include a continuous record of focal feeding and ad hoc data collection on social behaviours, including grooming, mating and aggression. Changes in party composition are collected continuously throughout the day and the reproductive states of all females are recorded. Female chimpanzees exhibit sexual swellings of the anogenital region during menstrual cycles; these swellings vary in size but are maximally tumescent for 10–12 days during the 35-day cycle (Wallis, 1997; Emery Thompson et al., 2005). In our population, the size of swellings are scored on a quarter scale ranging from 0 to 1:0 (detumescent), 0.25, 0.50, 0.75 and 1 (maximally tumescent). Females are most receptive and more likely to conceive when maximally tumescent (Wallis, 1997; Emery Thompson et al., 2005). In this study, we analysed available data from 1974 to 2017. During this time, the study community contained 31–63 individuals, 12–26 adult females (>12 years) and 6–14 adult males (>15 years).

Analysis 1: Female Association with Maternal Male Kin as a Function of Swelling Status

Our unit of analysis was a focal follow on an adult female that either had an adult son or an adult brother alive in the community. We only included follows that were at least 6 h in duration to ensure that we had sufficient data to characterize daily female associations with adult sons, maternal brothers and nonmaternally related males (hereon, unrelated males). Association was calculated as the number of minutes that females were in the same party as males during a focal follow. We only considered adult male associates, which we defined as males aged 15 years and older.

To test our prediction that female association with male kin is inversely related to the probability of conception as assayed by swelling size, we fitted a generalized linear mixed model (GLMM) using a negative binomial error structure in R v.4.1.0 (R Core Team, 2021). We parameterized our response variable as the daily number of minutes that females spent associating with a given male and included an offset term for the total daily focal female follow duration. We fitted our model using the 'glmer' function in package 'lme4' v.1.1–27 (Bates et al., 2015). We passed the negative binomial family from package 'MASS' (Ripley et al., 2013) to the 'family' argument in our model, providing a dispersion parameter to accommodate observed variance in our data exceeding the model predicted mean. We confirmed that model assumptions were satisfied and that our model did not suffer from overdispersion using the 'simulateResiduals' and 'testDispersion' functions in package 'DHARMa' (Hartig & Hartig, 2017).

Our predictor variables included the relatedness category (son, brother or unrelated males as defined above) between females and their male associates, the swelling size of the focal female (0, 0.25, 0.5, 0.75 or 1) and the interaction between these two predictors. We also included control predictors for season and year to account for ecological variation that could impact association patterns. We characterized wet and dry seasons according to rainfall patterns: the dry season at Gombe spans May–October and the wet season spans November–April. We scaled our year predictor to facilitate model convergence. Our model also included a random effect for female identity (ID) since individual females appeared as the focal multiple times throughout the study period ($N = 1690$ female focal follows, mean follows per female = 130, range 6–854 follows per female). Finally, we also included a random slope for the social relationships between females and their male associates, which allows the effect of social relationship to randomly vary among different focal females. Our analyses included all females that met the above criteria, resulting in 12 unique female–son pairs ($N = 9$ females), 8 unique female–maternal brother pairs ($N = 7$ females) and 161 unique female–unrelated male pairs ($N = 13$ females).

As an initial test of significance, we conducted a likelihood ratio test to compare the full model, which included all predictors and random effects, against its null model, which only included control predictors and random effects (Forstmeier & Schielzeth, 2011), using the 'Anova' function in base R. On the condition that the full model was a significantly better fit than the null model, we conducted Wald tests with type III sums of squares to determine the significance ($\alpha = 0.05$) of predictor variables in our full model using the 'Anova' function (case sensitive) in package 'car' v.3.0–11 (Fox &

Weisberg, 2019). On the condition that the interaction term had a significant effect in our full model, we conducted pairwise post hoc comparisons of least-squares means generated from the full model using the 'lsmeans' function from package 'lsmeans' v.2.30 (Lenth, 2020) in order to compare daily association time between male associate categories for each swelling size. We plotted model predicted values using the 'interact_plot' function and 95% confidence intervals in package 'jtools' v.2.1.0 (Long & Long, 2017).

Analysis 2: Female Association with Maternal Male Kin Following Parturition

To test our hypothesis that mothers associate more with male kin when their infants are most vulnerable to infanticide, we fitted a GLMM with a Gaussian error structure to analyse how mother–adult male association rates changed with infant age. We specifically focused on the first year of infancy as a critical period of infant survivorship. Additionally, older infants interact more with conspecifics and may begin to partially drive association patterns. We aggregated the data into 3-month bins with the first bin beginning at the infant's birth date to discern more precisely how female–male associations change with infant age. Here, we used a dyadic association index, a common method in fission–fusion species, to estimate the proportion of time two individuals spent together during the 3-month bin. Our measure of time together was on based the simple ratio index (SRI) (Cairns & Schwager, 1987) calculated for each pair in each period: $P_{AB}/(P_A + P_B - P_{AB})$, where P_{AB} is the total observation time that both A and B are in the same party, P_A is the total observation time that A is in the party and P_B is the total observation time that B is in the party (Gilby et al., 2008; Schel et al., 2013). Our measure did not include a term for days on which A and B were located in separate parties since we almost always only had one focal follow per day.

To be included in the sample, females had to have an infant alive for the entire 3-month bin. Given that bins were based on infant birth dates rather than the start and end of seasons, we could not classify bins by season. Thus, we *z*-transformed SRIs in each 3-month period using the mean across all male–female dyads in that same period to control for temporal variation in association patterns that could be associated with ecological variables, maternal characteristics or demographic factors that could impact association. Therefore, the reported dyadic association measures reflected differences in standard deviations from the mean of each period. Specific dyads appeared multiple times in the data set since SRIs for that dyad were calculated and transformed in each 3-month period during which both were alive throughout.

We included all female–male dyads in which (1) both members were alive at the beginning and end of the bin and (2) females that were observed for at least 30 h during the 3-month bin. These inclusion criteria resulted in 7 unique female–adult son dyads ($N = 6$ females), 10 unique female–adult maternal brother dyads ($N = 6$ females) and 112 unique female–other adult male dyads ($N = 10$ females). The average observation time for females that were included in our analyses was 199.7 h (range 37.0–423.5).

The response variable in our LMM was the *z*-transformed SRI and our predictor variables included relatedness between females and their male associates, infant age and the interaction between these two predictors. We included control predictors for infant sex and scaled year. We included a random effect of unique dyad to account for repeat measures and uneven sampling. We again included a random slope for social relationships. We followed the same steps as in Analysis 1 to conduct an initial test of significance, evaluate significance of predictors, perform pairwise post hoc comparisons if necessary and plot model predicted values using 95% confidence intervals.

Statement of Research Ethics

All data collection in this research was observational in nature and approved by the relevant Tanzanian governing bodies, including the Tanzania Commission for Science and Technology, the Tanzania Wildlife Research Institute and Tanzania National Parks.

RESULTS

Analysis 1: Female Association with Male Kin as a Function of Swelling Status

Our full model for female–male association was a significantly better fit than the null model: $\chi^2_5 = 4421$, $P < 0.001$. The interaction effect between females' social relationships with male associates and focal female swelling status was significant in our full model: $\chi^2_2 = 64.376$, $P < 0.001$ (see Table 1 for full model summary). Our post hoc analysis showed that females (1) associated more with all males when they had larger sexual swellings, (2) associated significantly more with their sons than with unrelated males and tended to associate with their sons more than with their brothers during low swelling stages (i.e. swelling status = 0 and 0.25) and (3) associated with unrelated males as much as they associated with their sons during higher swelling stages (i.e. swelling sizes = 0.5, 0.75 and 1) (Fig. 1, Table 2).

Analysis 2: Female Association with Maternal Male Kin Following Parturition

Neither infant sex nor scaled year was significant in our full model, so we removed these control predictors from both our full and null models. Our full model was a significantly better fit than the null model ($\chi^2_5 = 21.025$, $P < 0.001$). The interaction between females' social relationships with male associates and the age of their infants had a significant effect in our full model ($\chi^2_2 = 7.884$, $P = 0.019$; see Table 1 for full model summary). Our post hoc analysis showed that females associated with their adult sons more than with other males early during their infants' first year, but this

Table 1
Model summaries for Analyses 1 and 2

	Estimate	SE	*z*	*P*
Analysis 1: Association time ~ season + year + swelling status*male social relationship				
Intercept	−2.041	0.131	−10.310	–
Swelling status*son	−0.050	0.152	−0.327	0.744
Swelling status*unrelated	0.554	0.132	4.182	<0.001
Analysis 2: Z-transformed DAI ~ infant age*male social relationship				
Intercept	−0.091	0.074	−1.244	–
Infant age*son	0.001	0.070	0.015	0.988
Infant age*unrelated	−0.336	0.116	−2.896	0.004

DAI: dyadic association index. Reference group for male associate category is brother. Control predictors omitted.

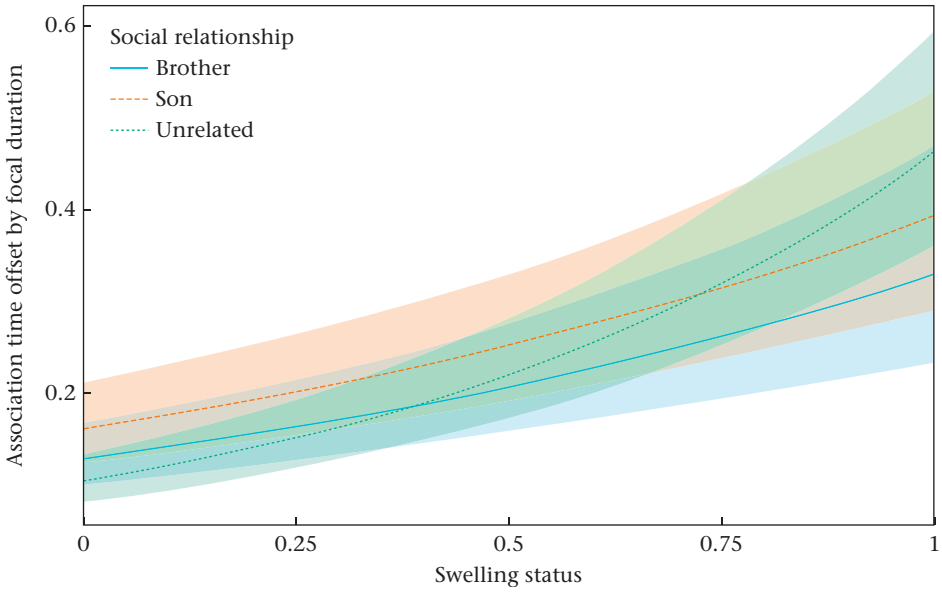

Figure 1. Model predicted values for female–male association time as a function of female swelling status with 95% confidence intervals.

Table 2
Pairwise post hoc comparison of least-squares means for female–male association based on female swelling status

Swelling status	Contrast	Estimate	SE	*z*	*P*
0	Son – Unrelated	0.437	0.086	5.076	<0.001
	Brother – Son	−0.219	0.122	−1.800	0.170
	Brother – Unrelated	0.218	0.053	4.104	<0.001
0.25	Son – Unrelated	0.286	0.086	3.319	0.003
	Brother – Son	−0.207	0.124	−1.668	0.212
	Brother – Unrelated	0.079	0.0582	1.358	0.363
0.5	Son – Unrelated	0.135	0.091	1.480	0.301
	Brother – Son	−0.194	0.137	−1.417	0.332
	Brother – Unrelated	−0.059	0.079	−0.755	0.731
0.75	Son – Unrelated	−0.016	0.101	−0.156	0.987
	Brother – Son	−0.182	0.158	−1.148	0.484
	Brother – Unrelated	−0.198	0.106	−1.874	0.146
1	Son – Unrelated	−0.167	0.113	−1.470	0.305
	Brother – Son	−0.170	0.185	−0.915	0.631
	Brother – Unrelated	−0.336	0.135	−2.485	0.035

Results are averaged over levels of season. Asymptotic degrees of freedom method and Tukey method *P* value adjustment for comparing a family of three estimates.

association decreased to levels comparable to their associations with other males later during their infants' first year. Female–brother associations were either significantly higher or tended to be significantly higher than female associations with unrelated males throughout the first year postpartum (Fig. 2, Table 3).

DISCUSSION

Prosocial relationships among kin are pervasive in social species, and benefits associated with intrasexual relationships with kin are well studied (males: lions, *Panthera leo*: Chakrabarti et al., 2020; macaques: De Moor et al., 2020; dolphins: Diaz-Aguirre et al., 2020; chimpanzees: Sandel 2017; Bray & Gilby, 2020; females: elephants: Lynch et al., 2019; wild boar, *Sus scrofa*: Podgórski et al., 2014; spotted hyaenas, *Crocuta crocuta*: Vullioud et al., 2019). Studies on intersexual relationships among adult kin have predominantly focused on costs, typically those associated with inbreeding. When the benefits of intersexual relationships among adult kin have been studied, they have often focused on benefits to males (see Introduction). Here, we investigated intersexual associations between female chimpanzees and their adult male maternal kin with a particular interest in how these associations might reflect trade-offs between potential protective benefits to females and inbreeding avoidance.

Inbreeding avoidance can occur through several different mechanisms, including sex-biased dispersal (review in Pusey & Wolf, 1996; black grouse, *Tetrao tetrix*: Lebigre et al., 2010; chimpanzees: Pusey, 1980; gorillas: Manguette et al., 2020) and mating avoidance (threespine sticklebacks, *Gasterosteus aculeatus*: Frommen & Bakker, 2006; German cockroaches, *Blattella germanica*: Lihoreau & Rivault, 2010; great tit, *Parus major*: Szulkin et al., 2009; gorillas: Vigilant et al., 2015; but see de Boer et al., 2021). Previous research has demonstrated that chimpanzees rarely breed with close relatives (Walker et al., 2017) and there are very few instances of offspring sired by sons or brothers (Constable et al., 2001; Inoue et al., 2008; Matsumoto et al., 2021; Walker et al., 2017). Research further demonstrates that females avoid mating with male relatives by resisting their mating attempts (Goodall, 1986; Pusey, 1980; Tutin, 1979) and reducing association at sexual maturation (Pusey, 1980).

Our results provide mixed support for reduced association as a mechanism through which female chimpanzees avoid mating with adult brothers (Pusey, 1980). Females' associations with unrelated males and, contrary to our prediction, with sons and brothers, increased with female swelling size, but females' associations with adult brothers was significantly lower than their associations with adult sons and unrelated males when the female was maximally tumescent. This suggests that when a female is ovulating and therefore most likely to conceive (Deschner et al., 2003; Emery Thompson, 2005), inbreeding risk between brothers and sisters is potentially reduced through less pronounced increases in association. However, this result provides equivocal support for reduced association as inbreeding avoidance since adult brothers still increased their association with sisters during tumescence. Note, however, that the lower association with adult brothers was not an artefact of decreased male sociality with age (Rosati et al., 2020); there was no difference in the average age between maternal brothers and unrelated males.

Why do mothers and adult sons continue to associate at high levels, even when they have a higher probability of conception?

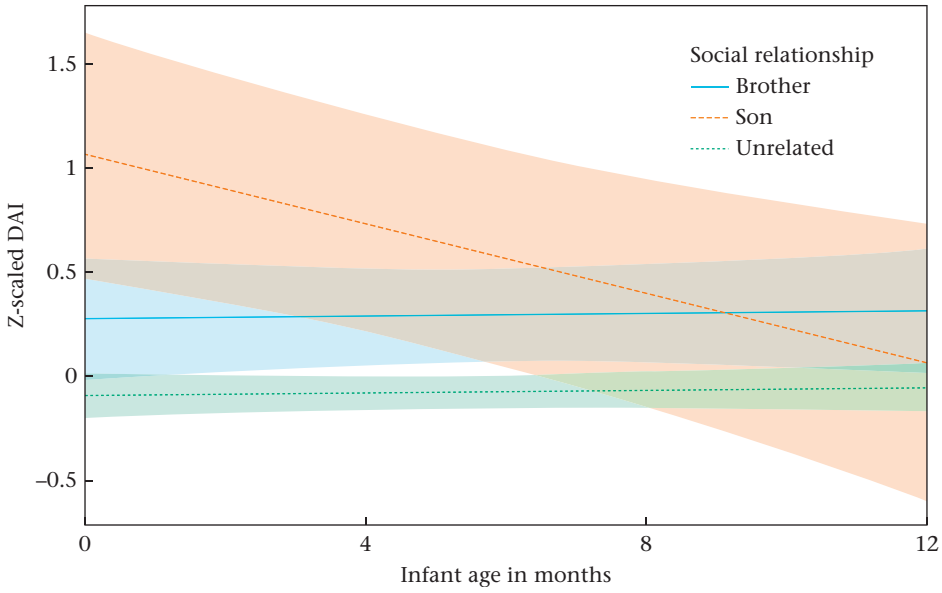

Figure 2. Model predicted values for *z*-scaled female–male dyadic association index (DAI) as a function of infant age with 95% confidence intervals.

Previous research has noted that most sons have no interest in mating with mothers (Goodall, 1986; Tutin, 1979) while brothers may actively pursue mating with sisters (Matsumoto et al., 2021; Robertson et al., 2020). The presence of receptive females also increases party size in wild chimpanzees (Goodall, 1986; Matsumoto et al., 2021; Pepper et al., 1999), which may provide sons and brothers with an increased opportunity to socialize with other community members. In any case, it appears that inbreeding risk from increased association with adult male kin while receptive may be outweighed by other benefits accrued through that association. One potential benefit, which should be investigated in the future, is whether the presence of adult sons reduces sexual coercion; numerous studies have demonstrated that males are often aggressive towards receptive females (Feldblum et al., 2014; Muller et al., 2007, 2011). This could also explain why adult brothers increase their association with sisters during tumescence.

Indeed, work in other species demonstrates that social relationships among kin can serve the important functions of social buffering and support in agonistic contexts (reviewed in Mattison et al., 2019). On a broad level, kinship often plays a strong role in coalition and alliance formation, which can have a protective function (white-nosed coatis, *Nasua narica*: Gompper et al., 1997; dolphins: Möller et al., 2001; African wild dogs, *Lycaon pictus*: de Villiers et al., 2003; greylag geese, *Anser anser*: Scheiber et al., 2005). Furthermore, studies have demonstrated that individuals are more likely to intervene during conflict when kin are involved (e.g. ravens, *Corvus corax*: Fraser & Bugnyar, 2012; white-lipped peccaries, *Tayassu pecari*: Leonardo et al., 2021).

In chimpanzees, females most often receive aggression from sexually coercive males (as above) but also from other females in several contexts, including extreme aggression towards female immigrants (Goodall, 1986; Pusey et al., 2008; reviewed in Pusey & Schroepfer-Walker, 2013) and female-led infanticide (Lowe et al., 2020; Walker et al., 2021; Wilson et al., 2014). The risk of infanticide, in particular, shapes female postpartum association patterns. Mothers take 'maternity leave' and avoid associating with high-risk conspecifics directly before and after birth (Lowe et al., 2019; Nishida et al., 1990; Nishie & Nakamura, 2018; Pusey et al., 2008). Maternity leaves can last from several days to weeks after birth (Matsumoto & Hayaki, 2015; Pusey et al., 2008) and are thought to prevent infanticide (Pusey et al., 2008; Nishie & Nakamura, 2018). However, a recent study suggested that mothers may also bias association with males according to the risk they pose during the postnatal period. For example, Lowe et al. (2019) found that females with newborns reduced their association with rank-rising males, i.e. those males that were ascending the social dominance hierarchy after birth, suggesting those males represented a higher infanticide risk to newborn infants as predicted by sexual selection (Hrdy, 2009).

Here, we predicted that females would bias association towards adult brothers and sons in the postnatal period as a potential counter-infanticide strategy, because males often intervene in intrasexual aggression and female aggression rates are lower when males are present (Kahlenberg et al., 2008). Thus, female-led infanticide should be less likely in groups with adult males. Male kin, especially those with high rank, may also be able to protect the female against potential infanticidal males (Wilson et al., 2014). Our results demonstrate that females associated significantly more with their sons than with unrelated males for the first 3 months of the postnatal period. This pattern shifted to a tendency during months 3–6 postpartum. Females also tended to associate more with brothers than with unrelated males during the first 3 months of the postnatal period, but the biased association tended to be less pronounced than with sons during this period. Given that most within-community infanticides occur within the first 6 months of life

Table 3
Pairwise post hoc comparison of least-squares means for z-transformed dyadic association index during each infant age bin

Infant age	Contrast	Estimate	SE	t	*P*
0 < 3 months	Son – Unrelated	1.160	0.310	3.734	0.010
	Brother – Son	−0.792	0.345	−2.298	0.088
	Brother – Unrelated	0.367	0.165	2.225	0.081
3 < 6 months	Son – Unrelated	0.815	0.275	2.965	0.060
	Brother – Son	−0.448	0.300	−1.491	0.347
	Brother – Unrelated	0.367	0.129	2.838	0.037
6 < 9 months	Son – Unrelated	0.470	0.293	1.607	0.306
	Brother – Son	−0.103	0.317	−0.326	0.943
	Brother – Unrelated	0.367	0.131	2.800	0.039
9 < 12 months	Son – Unrelated	0.125	0.356	0.352	0.934
	Brother – Son	0.241	0.387	0.623	0.809
	Brother – Unrelated	0.366	0.169	2.169	0.091

Results were averaged over levels of season. Asymptotic degrees of freedom method and Tukey method *P* value adjustment for comparing a family of three estimates.

(reviewed in Walker et al., 2021; Wilson et al., 2014), our results suggest that association with maternal kin may act as one of many potential counter-infanticide strategies adopted by female chimpanzees. Higher association with sons dissipated after 6 months postpartum, after which there was no difference in association between mothers and sons or unrelated males, but the pattern of biased association between mothers and brothers persisted for the entire first year of an infant's life (as either a tendency or significant result). Note, however, that the increased association with brothers was specific to the first year of life. Females did not associate more with brothers in general during the rest of the lactation period, which varies between 4 and 7 years (reviewed in Lonsdorf et al., 2020).

Recent work demonstrates that continued maternal presence and care after weaning impact male offspring survival (Nakamura et al., 2014; Stanton et al., 2020) and reproductive success (Crockford et al., 2020). By comparison, we know very little about how adult male kin benefit female chimpanzees or females in other systems characterized by male philopatry. Our results demonstrate that while females generally associated at high levels with their adult sons, these associations were particularly pronounced in comparison to their associations with brothers and unrelated males in the early postnatal period. Similarly, females associated with adult brothers more than with unrelated males throughout the first year of the postnatal period. These patterns point towards a potential adaptive value for female association with adult male relatives in male-philopatric species. Future studies should incorporate more detailed analyses on protection and finer-scale spatial data to help examine the mechanisms through which these social relationships benefit females and their offspring. Future studies should also examine how the presence of maternal male kin impact female health and reproductive success.

Author Contributions

K.R.W., A.E.P., J.C.W. and C.M.M. conceived of the study. A.E.P. and C.M.M. curated long-term behavioural data. K.R.W., S.M.L. and J.C.W. conducted analyses. Funding to support relevant long-term data and analyses was acquired by A.E.P., C.M.M. and K.R.W. K.R.W. and C.M.M. drafted the original manuscript, and all authors were involved editing and revising the manuscript.

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Declarations of Interest

None.

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