Fedurek, P, Girard-Buttoz, C, Tkaczynski, PJ, Hobaiter, C, Zuberbühler, K, Wittig, RM and Crockford, C

Maternal gregariousness and female audience effects mediate mother–infant proximity in wild chimpanzees

http://researchonline.ljmu.ac.uk/id/eprint/26065/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Fedurek, P, Girard-Buttoz, C, Tkaczynski, PJ, Hobaiter, C, Zuberbühler, K, Wittig, RM and Crockford, C (2025) Maternal gregariousness and female audience effects mediate mother–infant proximity in wild chimpanzees. Animal Behaviour. 223. ISSN 0003-3472

Animal Behaviour 223 (2025) 123156

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Maternal gregariousness and female audience effects mediate mother–infant proximity in wild chimpanzees

Pawel Fedurek [a], [b], [*], [1], Cédric Girard-Buttoz [c], [d], [e], [f], [*], [1], Patrick J. Tkaczynski [e], [f], [g], Catherine Hobaiter [b], [h], Klaus Zuberbühler [b], [h], [i], Roman M. Wittig [d], [e], [f], Catherine Crockford [d], [e], [f]

[a] *Division of Psychology, Faculty of Natural Sciences, University of Stirling, Stirling, U.K.*
[b] *Budongo Conservation Field Station, Masindi, Uganda*
[c] *ENES Bioacoustics Research Laboratory, Centre de Recherche en Neurosciences de Lyon, CNRS, Inserm, University of Saint-Etienne, Saint-Etienne, France*
[d] *The Ape Social Mind Lab, Institut des Sciences Cognitives Marc Jeannerod, CNRS, Lyon, France*
[e] *Department of Human Behavior, Ecology & Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[f] *Taï Chimpanzee Project, CSRS, Abidjan, the Republic of Côte d'Ivoire*
[g] *Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, U.K.*
[h] *School of Psychology and Neuroscience, University of St Andrews, St Andrews, U.K.*
[i] *University of Neuchâtel, Department of Comparative Cognition, Neuchâtel, Switzerland*

ARTICLE INFO

Article history:
Received 11 July 2023
Initial acceptance 15 December 2023
Final acceptance 13 January 2025
Available online xxx
MS. number: 23-00371R

Keywords:
audience effects
eastern chimpanzee
female–female competition
gregariousness
infanticide
mother–offspring bond
Pan troglodytes schweinfurthii
Pan troglodytes verus
western chimpanzee

In animal species with parental care, maintaining offspring–carer proximity is an important adaptation protecting offspring from threats such as predation and conspecific aggression, but doing so may limit other social opportunities. Investigating factors impacting mother–infant proximity can, therefore, provide insights into the evolution of maternal responses towards multidimensional threats. Here, we examine the social factors impacting mother–offspring proximity in two populations of wild chimpanzees with differing levels of infanticidal threats, eastern chimpanzees, *Pan troglodytes schweinfurthii*, in Budongo Forest, Uganda and western chimpanzees, *P. t. verus*, in Taï Forest, Ivory Coast. We assessed whether (1) the number of males and females in fission–fusion subgroups predicts proximity levels between mothers and their youngest infants, (2) whether it is mediated by maternal gregariousness and (3) whether this relationship differs in the two populations. In both populations and independent of maternal gregariousness, we found no clear relationship between mother–infant proximity and the number of males in the party. However, in Budongo, where an infanticidal threat is high, mother–infant proximity was mediated by both maternal gregariousness and the number of other females present. Less gregarious mothers were closer to their youngest offspring in parties with large numbers of females, while the opposite pattern applied to highly gregarious mothers. In Taï, more gregarious females were more often in proximity with their offspring. Our results demonstrate that the immediate social environment, maternal social phenotype and overall community-specific threats can all influence maternal response to varying exposure to threats. The consequences of exposure to this environment on offspring's social development merit further investigation.

Maintaining proximity to offspring is an important part of maternal protectiveness in species showing maternal care, allowing mothers to shield offspring from threats such as predators and aggressive conspecifics (Davies et al., 2012; Palombit, 1999). Investigating factors affecting mother–infant proximity can therefore shed light on the evolution of maternal responses towards multidimensional threats. For example, the risk of aggression posed by conspecifics impacts maternal strategies, with mothers facing a higher risk of aggression displaying more restrictive maternal styles towards their offspring, as shown in

---

[*] Corresponding authors.
E-mail addresses: pawel.fedurek@stir.ac.uk (P. Fedurek), cedric.girard-buttoz@cnrs.fr (C. Girard-Buttoz).
[1] Shared first authorship.

https://doi.org/10.1016/j.anbehav.2025.123156

yellow baboons (Altmann, 1980). Infanticide is a particularly extreme example of a threat posed by adults towards infants (Agrell et al., 1998; Ebensperger, 1998; Palombit, 1999) and it can impact the time mothers spend with adult conspecifics (Lowe, Hobaiter, & Newton-Fisher, 2019; Lukas & Huchard, 2014). Therefore, maintaining mother–infant proximity can be especially relevant in mammalian species where infanticide, typically by males, is a common occurrence (Agrell et al., 1998; Ebensperger, 1998; Weingrill, 2000). Indeed, there is evidence from a handful of mammal species that mothers and their offspring adjust their proximity to each other in the presence of potentially aggressive or infanticidal individuals. For example, in eastern chimpanzees, *Pan troglodytes schweinfurthii*, mother–offspring proximity decreased with the number of males, but not females, present in the party (Otali & Gilchrist, 2006). Similarly, in Bornean orang-utans, *Pongo pygmaeus wurmbii*, mothers were closer to their infants when in proximity to adult males (Scott et al., 2023). Mares in feral horses, *Equus caballus,* were more protective, showing higher rates of suckling and approaches towards their foals, when males were nearby (Cameron et al., 2003). Infanticide has also been proposed as one of the factors mediating mother–infant proximity maintenance in toothed whales (Odontoceti; Mann, 2019).

Another factor that can impact the level of a mother's protectiveness is maternal gregariousness. The gregariousness of female mammals varies considerably across species (Aureli et al., 2008; Davies et al., 2012). This variation has been attributed to individuals balancing the costs of competition with group members when in proximity to them and the costs of being exposed to predators when isolated from the group (Dunbar, 1988; Krause & Ruxton, 2002). This variation has also been linked to interindividual variability in terms of exposure to competition with conspecific males and females, and therefore to the aggression risk posed by them (Sterck et al., 1997; Wrangham, 1980). Importantly, the level of female gregariousness as a function of social competition and risk of aggression can also vary between and within populations (Aureli et al., 2008; Langergraber et al., 2009). Maternal gregariousness affects their offspring's exposure to group members and, therefore, to any threat of aggression they pose. Therefore, maternal gregariousness could also influence maternal protectiveness, a trait that should be evident in the closeness between the mother and the infant. However, whereas the costs and benefits of group living and gregariousness have been well studied (Ward & Webster, 2016), whether and how gregariousness impacts the safeguarding of offspring in species with prolonged dependency has received little attention. Similarly, it is unknown whether and how mothers' general pattern of gregariousness (e.g. Tkaczynski, Mielke, et al., 2020) mediates the relationship between mother–infant proximity and the number of conspecifics of each sex to which the offspring are exposed. These are important questions, as maintaining mother–infant proximity has protective benefits but could also impose costs on an offspring's opportunities for socialization and social development (Murray et al., 2014).

Species that form societies with a high degree of fission–fusion dynamics (Aureli et al., 2008) provide an ideal opportunity for testing hypotheses that consider how the presence of conspecifics and maternal gregariousness influences mother–infant proximity. In such societies, individuals experience regular temporal changes in terms of whom they interact with within the group, and thus gregariousness can vary substantially across females within the same community. In some species that form societies with a high degree of fission–fusion dynamics, such as bottlenose dolphins, *Tursiops* sp., the rate of an offspring's interactions with other group members depends on group size (Gibson & Mann, 2008). Yet, no studies have looked in detail at how mother–infant proximity is mediated by mothers' general level of gregariousness.

Chimpanzees are a good study system to examine how maternal gregariousness might be related to mother–infant proximity dynamics. They show highly flexible societies where subgroup (hereafter: 'party') size and composition can change frequently, with individuals of both sexes often joining and leaving different parties repeatedly within a single day (Chapman et al., 1995; Sugiyama, 1968). Infanticide is relatively common in chimpanzees (Lowe, Hobaiter, Asiimwe, et al., 2019; Wilson et al., 2014). However, while infanticides by in-group members have been consistently recorded in all populations of eastern chimpanzees under long-term observation, no such case of within-group infanticide has ever been recorded in western chimpanzees, *Pan troglodytes verus,* even in populations studied for over 40 years (Lowe, Hobaiter, Asiimwe, et al., 2019; Wilson et al., 2014). Infanticide in chimpanzees is frequently, but not exclusively, committed by males and often targets young infants below 1 year of age (Lowe, Hobaiter, Asiimwe, et al., 2019; Wilson et al., 2014). However, female chimpanzees also compete with each other for space and food and can be aggressive towards each other and infants (Emery Thompson et al., 2007; Kahlenberg, Emery Thompson, Muller, & Wrangham, 2008; Kahlenberg, Emery Thompson, Muller, & Wrangham, 2008; Pusey et al., 2008), with female-led infanticide not uncommon (Goodall, 1977; Lowe, Hobaiter, Asiimwe, et al., 2019; Pusey et al., 2008; Townsend et al., 2007).

Considering that in-group infanticide has been observed in eastern chimpanzees but not in western chimpanzees, it is likely that eastern mothers are more protective of their dependent offspring concerning other community members than western mothers. Indeed, in the Kanyawara community of chimpanzees, mother–infant proximity increased in the presence of adult males in the party (Otali & Gilchrist, 2006). A recent study showed that during times of social instability and elevated levels of male aggression, mothers in the Sonso community of chimpanzees avoided parties containing males competing for social rank, and possibly sought out males more likely to offer protection (Lowe, Hobaiter, & Newton-Fisher, 2019). However, the risk of infanticide from out-group chimpanzees (Lowe, Hobaiter, Asiimwe, et al., 2019; Wilson et al., 2014) may be increased by avoiding in-group members, for example, by spending more time in peripheral areas of the community range. Such differences in protectiveness should be reflected in how mothers from both subspecies adjust proximity to their offspring (e.g. Lee et al., 2020) in response to variations in the number of male and female conspecifics present.

Furthermore, whereas interindividual differences in gregariousness are found in eastern and western female chimpanzees (Lemoine et al., 2019; Thompson González et al., 2021; Tkaczynski, Mielke, et al., 2020), these differences appear more marked for Eastern chimpanzees. Some 'core' females regularly spend time in large parties with other adult individuals of both sexes, while other 'peripheral' females are much more solitary, spending a considerable amount of time on their own, with their offspring, or one or two other adult females (Emery Thompson et al., 2007; Emery Thompson & Wrangham, 2006; Murray et al., 2006; Pusey et al., 1997). Interestingly, within-individual levels of association patterns appear stable across years in adult females, irrespective of the reproductive state or age of the youngest offspring (Thompson González et al., 2021; Tkaczynski, Mielke, et al., 2020). The reason behind the higher variation in gregariousness in eastern chimpanzee females could be related to female–female competition and/or to a relaxed predation pressure as compared to western chimpanzees (Boesch & Boesch-Achermann, 2000) as well as, on the proximate level, to between-individual differences in personality (Tkaczynski, Mielke, et al., 2020). However, it is also possible that less gregarious females limit their frequency of association with conspecifics as a strategy to limit their offspring's exposure to potentially risky adult individuals. After giving birth, young mothers, especially in eastern chimpanzees, can be reclusive, avoiding contact with other group members presumably to avoid aggression and infanticide (Nishie & Nakamura, 2018; Otali & Gilchrist, 2006; Pusey et al., 2008; Wrangham, 2000), a pattern found in other species where infanticide by in-group members is common, such as spotted hyaenas, *Crocuta crocuta,* (Smith et al., 2008). Females with a low level of gregariousness might be less familiar to, and have weaker social ties with, other community members (Gilby & Wrangham, 2008; Sandel & Watts, 2021), and be less likely to receive support from them during aggressive interactions, potentially making them and their offspring more vulnerable to aggression. It is therefore possible that less gregarious females are more protective towards their offspring than more gregarious females when they are in parties with other adult individuals, especially in populations with a high risk of infanticide. Alternatively, considering the scarcer opportunities for nongregarious mothers' offspring to socialise with other community members, which can impact their social development (Murray et al., 2014), nongregarious mothers may be less protective or restrictive in terms of their offspring's interactions with others: an aspect that has not yet been investigated.

In this study, we examined how mother–infant proximity, which reflects maternal protectiveness, is impacted by factors that increase apparent risk to offspring. Mother–infant proximity is relatively easily controlled and can be adjusted rapidly in response to very short-term changes in the composition and proximity of other individuals in the social party. We hypothesized that mother - infant proximity is flexibly adjusted depending on the level of threat the infant is exposed to. We considered several components of this threat in two populations and subspecies of chimpanzees with contrasting degrees of infant-directed severe aggression, including infanticide: eastern chimpanzees in Budongo Forest, Uganda and western chimpanzees in Taï Forest, Ivory Coast. The first component was the immediate social environment and risk reflected by the number of mature males or females in a party. The second component was maternal social phenotype, specifically mother gregariousness. The last component was the broader social setting reflected by the risk of lethal aggression in the two study populations, with the risk being considerably higher in Budongo than in Taï. We formulated a set of predictions deriving from this hypothesis that we illustrate in Fig. 1. First, we predicted a positive relationship between the number of sexually mature males and females in the party and the probability of mothers and their infants being within 1 m proximity (hereafter: mother–infant proximity; Fig. 1). Considering that, in general, chimpanzee males pose a considerably higher threat of aggression to infants than females (Wilson et al., 2014), we predicted that, in both populations, the relationship between the number of males in the party and mother–infant proximity would be stronger compared with that between the number of females in the party and mother–infant proximity (e.g. Otali & Gilchrist, 2006). Alternatively, since chimpanzee female–female social bonds can be relatively weak (Gilby & Wrangham, 2008) and between-female competition in this species is well documented (Emery Thompson, 2013; Townsend et al., 2007), the presence of other females rather than males may affect mother–infant proximity. We also predicted that the effect of the number of males and females in the party on mother–infant proximity would be stronger for mothers with low gregariousness due to their lower level of familiarity with other community members compared with more gregarious females (Fig. 1). Alternatively, being in larger parties might be an opportunity for the offspring of the less gregarious females to socialise with other individuals, in which case we expect a positive relationship between the number of adult individuals in the party and mother–infant distance for mothers with low gregariousness. The within-group risk of infanticide is considerably elevated in the eastern chimpanzees of Budongo relative to the western chimpanzees of Taï (Lowe, Hobaiter, Asiimwe, et al., 2019; Wilson et al., 2014), including our three study communities in Taï (where within-group infanticide has never been documented). Consequently, in evaluating interpopulation effects, we anticipated that all the aforementioned effects would manifest more prominently in Budongo than in Taï (Fig. 1).

METHODS

Study Site and Study Populations

For this study, we collected behavioural data from five communities of wild chimpanzees from two subspecies: *P. t. verus* in Taï National Park, Ivory Coast and *P. t. schweinfurthii* in the Budongo

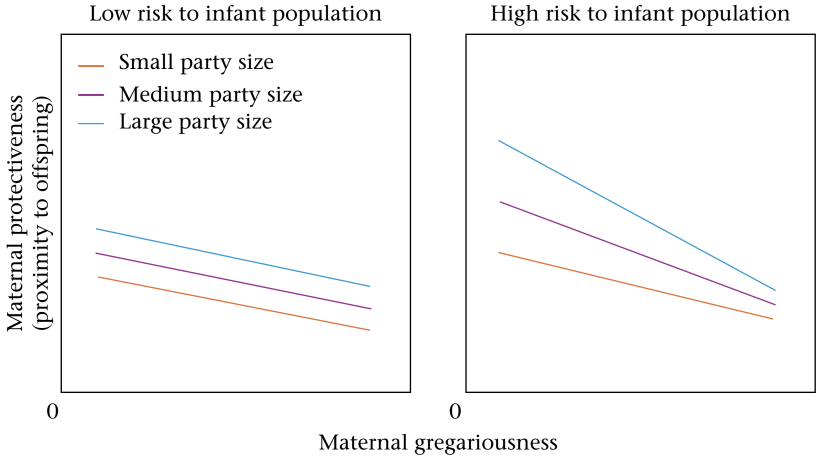

Figure 1. Factors that may lead to variation in maternal protectiveness (reflected by mother–infant proximity). Here, in larger parties, especially those with more males, higher protectiveness is anticipated, and more gregarious mothers are expected to be less protective due to stronger social ties within the community (both panels). In populations with 'low-risk' from conspecifics to infants (left panel), females are expected to respond to changes in party size in a similar way regardless of their gregariousness. In contrast, in 'high-risk' populations (right panel) less gregarious mothers are expected to show greater sensitivity to changes in the immediate social environment (party size and composition) than more gregarious mothers. 0 = low level of mother–infant proximity (*Y* axis) and maternal gregariousness (*X* axis).

Forest, Uganda. In Budongo, one author and one field assistant collected data on the Waibira (January 2017–January 2018) and Sonso (January 2018–November 2018) communities. The Sonso community has been studied since 1990 (Newton-Fisher, 1999; Reynolds, 2005) and, at the time of the study, comprised 75 individuals (Table 1). The Waibira community has been studied since 2011 (Samuni et al., 2014) and during the study, this community comprised 95 named individuals, with a small number of highly peripheral individuals not formally named (Table 1).

In Taï, one author and three field assistants collected data on the East, North and South communities between December 2016 and June 2018. During the study period, the East, North and South communities comprised 32–34, 19–20 and 41–42 individuals, respectively (Table 1). All communities in Taï are fully habituated to human presence, with the North, South and East communities being regularly observed since 1982, 1993 and 2000, respectively (Boesch & Boesch-Achermann, 2000; Wittig, 2018).

Ethical Note

The study was approved by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology in Uganda, and the Ministere de l'Enseignement superieur et de la Recherche Scientifique, the Ministere des Eaux et Forets and the Office Ivoirien des Parcs et Reserves in Cote d'Ivoire. Fieldwork at both study sites was purely observational and did not interfere with chimpanzee behaviour. We followed all disease transmission prevention protocols established by the Budongo Conservation Field Station and the Taï Chimpanzee Project. We complied with all the relevant international, national and institutional guidelines for the care and use of animals.

Data Collection

Chimpanzees have a protracted development, and mothers can have several immature offspring at the same time. In our data set, 21 of 43 mothers (48.8%) had more than one immature offspring. We focused our behavioural data collection on adult females and their youngest immature offspring, given that they are the most vulnerable to infanticide ($N = 43$ mother–infant dyads in total, Table 1). For this study, we considered only the youngest offspring of each female that was not older than six years old (Budongo $N = 20$ mother–infant dyads; Taï $N = 23$ dyads; Table 1). We applied this cutoff to the data because, in chimpanzees, weaning occurs between 4 and 6 years old, and 6 years is therefore the upper age at which young chimpanzees are usually carried (Boesch & Boesch-Achermann, 2000; Goodall, 1986). As such, 6 years old represents the maximum age of clear maternal dependence. Thereafter, until around 10 years old, offspring remain associated with their mothers during the majority of the day but move and feed independently (Goodall, 1986; Tkaczynski, Behringer, et al., 2020; Wittig & Boesch, 2019). As infants below 6 years old are particularly reliant on their mothers, including maternal support with locomotion, mother–offspring proximity before offspring reach 6 years old most likely reliably reflects maternal protectiveness.

Each day of data collection, we randomly selected one female with offspring and followed either the mother or one of her offspring for half a day (5–6 h). Every 10 min, we recorded a scan sample (Altmann, 1974) to collect the following data: (1) whether or not (0/1) the youngest offspring was within 1 m of the mother (if the mother was the focal individual), or whether the mother was within 1 m of the youngest offspring (if the infant was the focal individual) and (2) the identity of all the adult and subadult males (aged ≥13 years) and females (aged ≥11 years) in the party (hereafter mature individuals).

Definitions

Mothers and their youngest offspring were in 'proximity' when they were within 1 m of each other.

We defined a 'party' as all individuals present within the visual range of the focal animal (typically around 35 m; Newton-Fisher, 1999).

The 'gregariousness' of an individual reflects the probability of finding this individual in a party with other chimpanzees. 'Maternal gregariousness' was established by calculating the proportion of 10 min scans recorded during the study period in which the female was recorded in the party when she was not the focal animal when taking the scan sample (Emery Thompson & Wrangham, 2006; Table 1). Excluding the focal data from the analysis was important because at Budongo, and in other eastern chimpanzee populations, nongregarious or 'peripheral', females can be difficult to locate and follow by researchers and, when they become available for observations, they are often found in large parties (Emery Thompson & Wrangham, 2006; Reynolds, 2005). Consequently, focusing on focal data to establish the gregariousness of these peripheral females would considerably overestimate their gregariousness level. In contrast, the proportion of party composition scans where a given female was recorded in a party when focal-following any

Table 1
Sample distributions showing mean ± SD and range (respectively) of the variables included in the study, and the total number of infants and their mothers included in the study, per community

Community	Budongo		Taï	
	Proportion of scans		Proportion of scans	
Mother and infant within 1 month	0.48		0.54	
Presence of a maximally tumescent female	0.12		0.24	
	Mean ± SD	Range	Mean ± SD	Range
Mother's age (Years)	30.70 ± 9.06	19–43	26.50 ± 10.26	14–47
Infant's age (Years)	2.463 ± 1.47	0–5	2.621 ± 1.64	0–5
No. of dependent offspring	1.60 ± 0.60	1–3	1.52 ± 0.68	1–3
Mother's gregariousness	0.13 ± 0.07	0.04–0.30	0.30 ± 0.08	0.18–0.46
No. of males in the party	1.61 ± 2.75	0–15	1.13 ± 1.57	0–6
No. of females in the party	3.12 ± 2.57	0–14	3.54 ± 2.33	0–16
	Total no.		Total no.	
No. of mothers in the study	20		23	
No. of male infants in the study	12		12	
No. of female infants in the study	8		11	

other female in the community reliably reflects the gregariousness level of that female and mitigates the issue of unbalanced sampling effort across individuals. Gregariousness data for each female incorporated in the study are in Table A1.

Data Processing

Before running our statistical model, we assigned each 10 min proximity scan between the mother and her youngest offspring to a 'scan cluster', with each cluster comprising the same number and identity of mature males and females. For example, if there was a change in the number of mature males and/or females between two consecutive 10 min scans, this was the start of a new scan cluster. This process was conducted to account for the nonindependence of consecutive scans recorded under the same social condition (that is, when the identity and number of mature males and females in the party did not vary). In total, 5757 (Budongo $N = 1645$, Taï $N = 4112$) 10 min scans were thereby assigned to 2377 scan clusters (Budongo $N = 560$, Taï $N = 1817$). Scan clusters comprised varying numbers of 10 min scans (Mean = 2.42 scans, SD = 2.96, range 1–30).

Interobserver Reliability

We conducted interobserver reliability tests between individuals who collected the data to ensure that the data were collected systematically. Interobserver reliability tests using intraclass coefficient tests (ICC; Shrout & Fleiss, 1979) were initially conducted between P.J.T. and P.F. at Budongo and Taï, with the frequency and duration of variables recorded by each significantly correlated ($ICC > 0.80$). Research assistants started collecting behavioural data only once they had recorded two consecutive tests with variables such as proximity and party composition data significantly correlated with those recorded by the authors ($ICC > 0.80$).

Statistical Analysis

To assess the effect of maternal gregariousness and the number of mature males and females in the party on the proximity between mothers and their youngest offspring, we used Bayesian estimation and a generalized linear mixed model with a binomial error distribution on the full dataset (model 1). Each scan constituted a data point and the response variable was whether the mother and her youngest offspring were in proximity (1) or not (0) for each scan. We ran this model in R 4.1.2 (R Core Team, 2014) using the function 'brm' from the package brms (Bürkner, 2018).

We used as test predictors (1) maternal gregariousness, (2) the number of mature males (i.e. aged ≥13 years; Goodall, 1986) in the party and (3) the number of mature females (i.e. aged ≥11 years) in the party. To specifically test our hypothesis that the relationship between mother–infant proximity and the number of mature individuals present in the party is mediated by the mother's gregariousness and that this relationship is likely to be stronger in Budongo than in Taï, we included two three-way interactions: (1) between the mother's gregariousness, number of mature females in the party and population (0-Budongo, 1-Taï) and (2) between mother's gregariousness, the number of males in the party, and the population. We expected less gregarious females to be more at risk in larger parties than more gregarious females and therefore to be more responsive to changes in male and female numbers than more gregarious females. We also expected these phenomena to be stronger in Budongo, where the risk of infanticide is higher than in Taï (Fig. 1b). In addition, we included the following control variables since they might influence the proximity of a mother to her youngest offspring (e.g. Lonsdorf, Anderson, et al., 2014; Lonsdorf, Anderson, et al., 2014): (4) mother's age, (5) youngest offspring's age, (6) youngest offspring's sex and (7) the total current number of immature offspring (males aged ≤12 years; females aged ≤10 years) of the mother. As the presence of maximally tumescent females is associated with elevated male aggression (Muller & Wrangham, 2004; Watts, 1998), we included whether a maximally tumescent female was present in the party or not (0, no maximally tumescent female present in the party; 1, a maximally tumescent female present in the party) as another control variable. Note that the focal female could be fully tumescent. In addition to the fixed effects, we included the following random effects: mother–offspring dyad ID, date and scan cluster ID to account for multiple scans being recorded on the same mother–offspring dyad, on the same day, and under the same social conditions. We also included the number of mature males and females in the party as random slopes within mother–offspring dyad ID and date, to reduce type I error rate and to account for the potential nonuniform variation of our predictor variables within the random effects (Barr et al., 2013).

Before running the model, we z-transformed the values of all quantitative variables into a mean of 0 and a standard deviation of 1 to improve model convergence and interpretation of the model estimates. We also tested for collinearity issues by quantifying variance inflation factors for our predictor variables using the function 'vif' from the package 'car' (Fox & Weisberg, 2011). Collinearity was not an issue (all variance inflation factor value < 2).

The presence of adult kin individuals in the party may provide mothers with social support and influence the proximity they maintain with their offspring, therefore potentially influencing our results. However, we do not have kinship data for the Waibira community. To account for the possible influence of kinship, we reran a model (model 2a) using the same fixed and random effect structure as in model 1 but adding the test predictor 'presence of mature maternal kin in the party at the time of the scan Y/N' on a subset of data excluding the Waibira community (that is, comprising four study communities, one in Budongo, the Sonso community and three in Taï, East, North and South). Since the level of statistical support for a given effect can be influenced also by the mere reduction in sample size from model 1 to model 2a rather than by the addition of the predictor 'kin presence', we ran a third model (model 2b) on the same dataset as the one used for model 2a but without the parameter 'kin presence' (that is, with an identical structure to model 1).

Likewise, the presence of individuals particularly aggressive towards infants, especially males and females that committed in-group infanticide, can influence mother–offspring proximity. Since no in-group infanticide has ever been reported in Taï in over 40 years and since we did not have enough data before the onset of the current project in Waibira to accurately identify all infanticidal males and females, we focused on the Sonso community in Budongo for a third analysis. In this analysis, we aimed to assess if controlling for the presence of infanticidal individuals in the party affected our results. To this end, we ran a model only on Sonso data (model 3a), including the same single predictors as in model 1 with the addition of 'presence of nonkin infanticidal individuals Y/N' (that is, individuals that were involved in attacking the mother during infanticides during the study period, $N = 9$ males and $N = 2$ females), and the two-way interactions between maternal gregariousness and the number of males in the party and maternal gregariousness and the number of females in the party. As for models 2a and 2b, we aimed to assess if the potential change in the results compared with model 1 was truly resulting from the inclusion of the parameter 'presence of infanticidal individuals' or if it was simply a by-product of the reduction in sample size. We ran, therefore, model 3b on Sonso-only data, but excluding the parameter 'presence of infanticidal individuals'.

We ran 6000 iterations (4000 for warmup) on 16 chains. We used weakly regularizing priors for the fixed effects (normal [0,1]) and the priors given by default by the function ‘get_prior’ of the package ‘brms’ for the random effects (i.e. student t [3, 0, 2.5] for the random intercepts and slopes). We chose weakly regularising priors for the fixed effects since they give less weight to outlier data points and help constrain model predictions to biologically meaningful estimates and credible intervals (CIs; N. Lemoine, 2019). We then extracted the 95% and 89% CI for each fixed effect from the posterior distribution of the model.

Sampling diagnostics (Rhat = 1 for all predictors in all models) and trace plots confirmed chain convergence for all models. Effective sample sizes (all > 8300) confirmed no issues with autocorrelation of sampling for all models. Note that the effective sample size is a measure of autocorrelation and does not correspond to the number of data points that were used for the model. We provide the posterior predictive check of each model in Figs A1–A5.

RESULTS

Table 1 shows a summary of the data collected. Mothers in both populations spent approximately half of their time within 1m of their offspring (Table 1).

Full Model (Model 1)

In our full statistical model, model 1 ($N = 2377$ scan clusters and 43 mother–infant dyads), we found no support for the three-way interaction between the number of males in the party, mother gregariousness and population (the 89% CI was centred around 0 with no discernible direction of the estimate for the effect of the interaction, Table 2). In contrast, we found support for a consistent effect of the interaction between the mother’s gregariousness, the number of females in the party, and the population (Table 2). The 89% CI for this interaction did not comprise 0 (0.02–0.93, Table 2), and it was supported by 95.2% of the posterior.

This indicates that the mother’s gregariousness mediated the relationship between mother–infant time in proximity and the number of females in the party and that this effect differed between the Taï and Budongo populations. In Budongo, for the less gregarious mothers, an increase in the number of females in the party was associated with a higher likelihood for the mother and her youngest infant to be within 1 m of each other, while the opposite association was found for highly gregarious mothers (Fig. 2a). However, we did not find this pattern in Taï chimpanzees. Instead, more gregarious mothers in Taï were overall more likely to be close to their youngest offspring than less gregarious mothers (Fig. 2b). In parties with large numbers of females, this relationship was weaker but still positive (Fig. 2b).

There was a consistent negative relationship between infant age and the probability of being within 1 m of their mother (supported by 100% of the posterior distribution, Table 2, Fig. 3). We also found that mothers were consistently more likely to be in proximity to their youngest offspring when a maximally tumescent female was present in the party (supported by 98.7% of the posterior distribution, Table 2). There was no consistent relationship between mother–infant proximity and the mother’s age, infant’s sex or the number of dependent offspring (all 89% CI overlapped 0, and all of these effects were supported by less than 80% of the posterior distribution, Table 2). The proportion of variance in the response explained by the fixed and the random effects (conditional R^2) and the fixed effect only (marginal R^2) was 0.91 and 0.69, respectively.

Controlling for Maternal Kin Presence (Models 2a and b)

We used a subset of data for which we had maternal kinship information (that is, removing the data from the Waibira community) to evaluate whether the results of model 1 were driven by kin presence (model 2a). The results were very similar in model 2a and model 1 (Table 2 and Table A2), and we did not find support for kin presence influencing mother–offspring proximity (only 71% posterior support and 89% CI largely overlapped 0, Table A2). In model 2a, we still found relatively strong support for the three-way interaction between maternal gregariousness, number of females in the party, and population, albeit with less posterior support (90.1% in model 2a versus 95.2% in model 1; Table 2 and Table A2). Yet, rerunning model 2a without kinship as a predictor (that is, with an identical model structure to model 1) but with the same subset of data (model 2b), we found very similar support for this three-way interaction (90.9%, Table A3). This indicates that the loss of support is linked to a loss of power and shows that not controlling for kin in the full model probably did not alter the results.

Table 2
Effect of population, maternal gregariousness and number of male and female party members on mother–infant proximity (results from the full model 1)

Predictor	Estimate	SE	95% CI low	95% CI high	89% CI low	89% CI high	% Posterior in support
Intercept	−0.24	0.67					
No. of dependent offspring	−0.16	0.18	−0.51	0.19	−0.45	0.13	80.60
Mother’s age (Years)	−0.13	0.22	−0.56	0.3	−0.48	0.22	72.80
Infant age (Years)	−0.87	0.16	*−1.17*	*−0.54*	*−1.12*	*−0.6*	100.00
Infant sex (Male)	0.33	0.39	−0.42	1.09	−0.28	0.94	81.20
Maximally tumescent female in the party (Yes)	0.37	0.16	*0.05*	*0.69*	*0.11*	*0.63*	98.70
Mother’s gregariousness	−0.12	0.4	−0.9	0.67	−0.75	0.52	61.90%
No. of males in the party	0.46	0.42	−0.41	1.25	−0.22	1.09	87.10
Population (Taï)	0.18	0.65	−1.13	1.42	−0.86	1.19	61.70
No. of females in the party	−0.65	0.37	−1.35	0.09	*−1.22*	*−0.06*	96.00
Mother gregariousness * no. of males	0.32	0.26	−0.19	0.84	−0.09	0.74	89.40
Mother gregariousness * population (Taï)	0.37	0.54	−0.68	1.43	−0.48	1.23	75.50
No. of males * population (Taï)	−0.54	0.48	−1.45	0.47	−1.28	0.23	88.20
Mother gregariousness * no. of females	−0.6	0.24	*−1.08*	*−0.12*	*−0.98*	*−0.21*	99.30
No. of females * population (Taï)	0.46	0.4	−0.35	1.21	−0.18	1.08	88.30
No. of males * population (Taï) * Mother gregariousness	−0.05	0.36	−0.73	0.67	−0.61	0.53	56.00
No. of females * population (Taï) * mother gregariousness	0.47	0.29	−0.09	1.04	*0.02*	*0.93*	95.20

The coded level for each categorical predictor is indicated in parentheses. Control predictors are italicized. The 95% credible interval (CI) low and 95% CI high indicate the lower and upper limits of the 95% CI. Likewise, the 89% CI low and 89% CI high indicate the lower and upper limits of the 89% credible interval. ‘% posterior in support’ indicates the% of the posterior distribution supporting a given effect. The 95% and 89% CI not overlapping 0 are italicized.

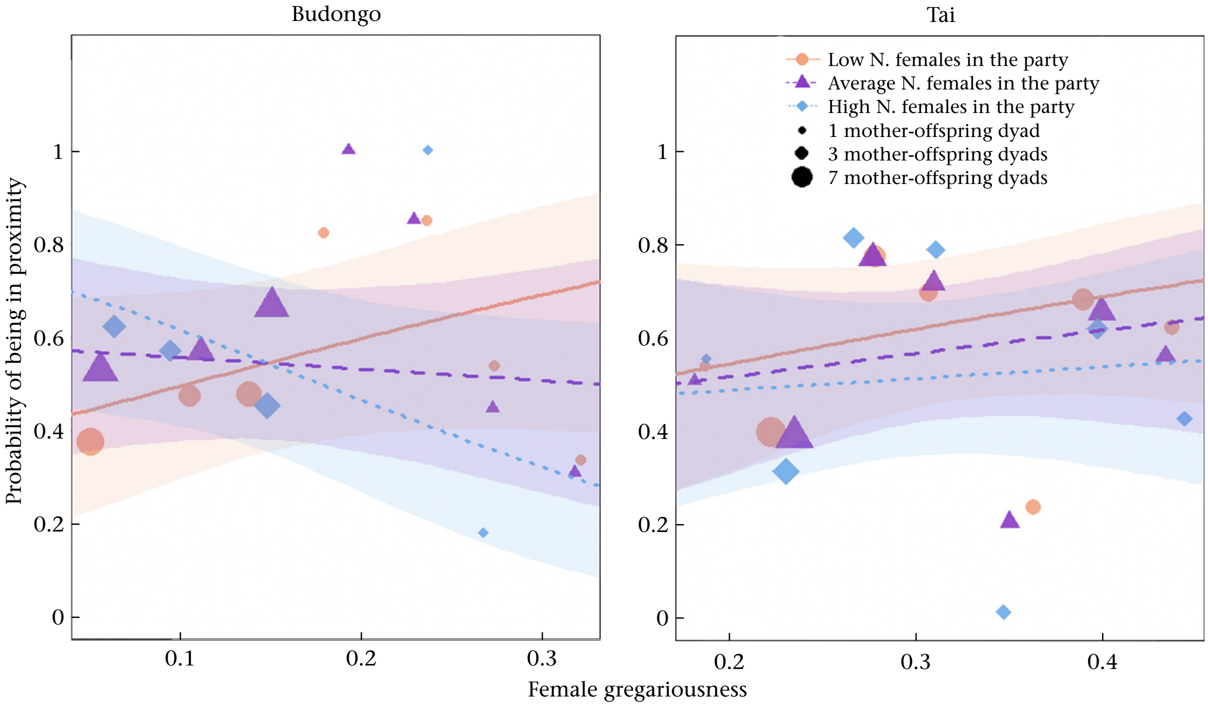

Figure 2. Relationship between mother–infant proximity and a mother's gregariousness as a function of the number of females in the party at (a) Budongo and (b) Taï. The lines indicate the mean prediction of the statistical model (model 1), and the coloured area is the 89% credible interval (CI) extracted from the posterior distribution of model 1. Each dot represents binned data across all females with certain gregariousness levels when exposed to a high, average and low number of females in the party. The size of the dot is proportional to the number of mother–offspring dyads that contributed to each dot.

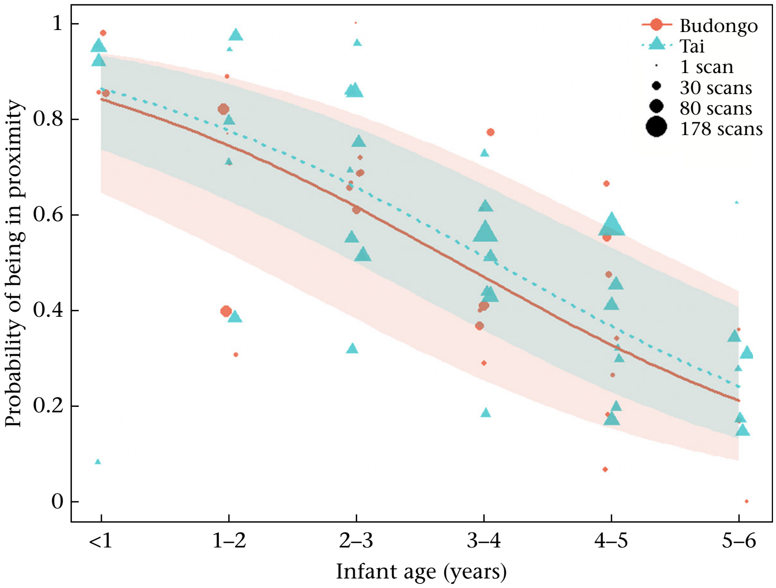

Figure 3. Relationship between the infant's age and mother–infant proximity in the two study populations. The lines indicate the mean prediction of the statistical model (model 1), and the coloured area is an 89% credible interval (CI) extracted from the posterior distribution of model 1. Each dot is binned data for a given individual within a given age interval. Note that the same individual can appear in two age classes and thus can be represented by two different dots. Dot size is proportional to the number of scans that were recorded for a particular mother–offspring dyad.

Controlling for the Presence of Infanticidal Males (Models 3a and b)

We used a further reduced subset of data focusing only on the Sonso community in Budongo to investigate the effect of the presence of infanticidal males on the proximity between mothers and their youngest offspring (model 3a). Again, the results were very similar to the full model (model 1, see Table A4) and we did not find support for the presence of infanticidal males having a consistent effect on mother–offspring proximity (only 66.1% of posterior support, Table A4). In model 3a, and despite the drastic reduction in the dataset size, we still found relatively good support for a two-way interaction between maternal gregariousness and the number of females in the party (93.6% posterior support, Table A4). We did not include the three-way interaction with the population since we only considered one community in this model). As above, rerunning model 3a without 'infanticidal male presence' as a predictor but with the same subset of data (model 3b) generated identical support for this two-way interaction (93.6%, Table A5). This indicates that the loss of support is linked to a loss of power and shows that not controlling for the presence of infanticidal males in the full model probably did not alter the results.

DISCUSSION

In many mammalian species, adult individuals pose a considerable threat to infants, with infanticide being a particularly extreme example (Agrell et al., 1998; Ebensperger, 1998; Palombit, 1999). The level of this threat should, therefore, impact the amount of time mothers and their infants spend close to each other. The purpose of this study was to test the hypothesis that time spent close between mothers and their youngest offspring varies with the number of mature males and females in the party (as a proxy for the relative threat from conspecific aggression directed towards mothers and offspring, including infanticide), contingent upon the gregariousness of the mother and the subspecies of chimpanzees that differ in infanticide risk. We found no support for the expected population-dependent joint effect of maternal gregariousness and the number of mature males in the party on the proximity between the mother and their youngest offspring. In contrast, we found a population-dependent joint effect of maternal gregariousness and the number of females in the party on mother–infant proximity. At Budongo, mother–infant proximity levels were mediated by both the gregariousness of the mother and the number of other females in the party: mothers who showed low gregariousness spent more time near their youngest offspring than highly gregarious mothers when there were many females present. The reverse pattern was evident when there were few females present. In Taï, our statistical model showed that a mother's gregariousness had a weak and uncertain positive effect on the proximity between her and her offspring. More specifically, there was no effect when the party size was big, but when the party size was small, gregarious mothers were more often near their offspring than in other social situations. Using additional models on subsets of data, we confirmed that our results were not driven by the presence of adult maternal kin or infanticidal individuals of both sexes in the party.

The lack of a clear effect of the number of males in the party on mother–infant proximity is surprising considering that in mammalian species where infanticide is present, including chimpanzees, males usually pose a considerably higher infanticide threat than females (Lowe, Hobaiter, Asiimwe, et al., 2019; Lukas & Huchard, 2014). Furthermore, in contrast to our study, a positive relationship between mother–infant proximity and the number of males in the party was found previously in the Kanyawara community of eastern chimpanzees (Otali & Gilchrist, 2006). Like at Kanyawara, (Muller et al., 2007), infanticide and coercive male-to-female aggression have both been frequently recorded in Budongo (Kaburu & Newton-Fisher, 2015). However, we did not find an effect of the number of males present or the presence of infanticidal males on mother–infant proximity, suggesting that the presence of infanticidal males is not a major factor in this respect in Budongo. Nor did we find an effect of maternal kin presence, which includes adult sons or brothers, who likely offer valuable social support to mothers against other community members, on mother–infant proximity. This result challenges the hypothesis that the presence of such males is responsible for the positive relationship between mother–infant proximity and the number of males in the party.

In contrast to the absence of a consistent effect of male party size, we found a consistent effect of the number of females in the party on mother–infant proximity levels modulated by population. More specifically, at Budongo, the distance between the mother and offspring was greater for gregarious females when the number of females in the party was high and was smaller for the less gregarious females in the same situation. We suggest two potential processes behind this pattern. First, in large female parties, less gregarious females are more protective of their offspring in response to the risk posed by other females. Indeed, although in chimpanzees the level of female–female competition is considerably less pronounced than competition among males, female chimpanzees do compete for space and food and can be aggressive towards each other (Emery Thompson et al., 2007; Kahlenberg, Emery Thompson, Muller, & Wrangham, 2008; Kahlenberg, Emery Thompson, Muller, & Wrangham, 2008; Valé et al., 2021). Similarly, chimpanzee mothers often intervene in conflicts involving their infants and offspring of other females, with less gregarious females potentially being less effective in such interventions than more gregarious ones due to perhaps having less social support and therefore maintaining closer proximity to their offspring to prevent conflicts. Furthermore, female-led infanticide, although rarer than infanticide committed by males, has also been regularly recorded in eastern chimpanzees (Goodall, 1977; Lowe, Hobaiter, Asiimwe, et al., 2019; Townsend et al., 2007), with infant mortality rates due to female-induced infanticide estimated to be responsible for up to 30% of all infanticides in Gombe chimpanzees (Pusey et al., 2008). Again, however, we did not find an effect of the presence of infanticidal individuals, including infanticidal females, on mother–infant proximity. Nevertheless, in chimpanzees, new mothers are often submissive towards other females and associate with adult males as if seeking protection against female aggression (Goodall, 1977, 1986; Lowe, Hobaiter, Asiimwe, et al., 2019). Less gregarious females may also be less familiar with and/or less closely bonded to other adult females, having had fewer opportunities to interact with them than more gregarious females, and as a result, they are more uncertain about the potential threat other females may represent. Indeed, mothers of infanticide victims are often younger females that recently immigrated (Lowe, Hobaiter, Asiimwe, et al., 2019), and had not yet fully integrated into the community. Similarly, peripheral females may have fewer opportunities to mate with many community males, a common paternity confusion reproductive strategy (Deschner & Boesch, 2007; Deschner et al., 2003, 2004), and are thus likely to face higher infanticide risk. Future studies should investigate how mother–infant proximity is modulated by the presence of other females in a range of species, including mammalian species where there is a high degree of female–female competition, such as mice, *Mus musculus,* and Syrian hamsters, *Mesocricetus auratus,* (Pandolfi et al., 2021). Such studies have the potential to illuminate, for example, the costs of mothering in species with a high level of female–female competition and maternal adaptations that mitigate the associated costs.

Second, being in large female parties might be an opportunity for infants to socialize with offspring of other females. This suggestion is supported by a previous study on the Kanyawara community of chimpanzees showing a negative relationship between mother–infant proximity and the number of females in the party (Otali & Gilchrist, 2006). In our study, however, mother–offspring proximity was a function of both female party size and maternal gregariousness, a combined effect that has not been investigated before. Interacting with peers facilitates infant social development in many mammalian species, including mice, *Mus musculus*, European rabbits, *Oryctolagus cuniculus*, rhesus monkeys, *Macaca mulatta*, and humans (Bautista et al., 2008; Bekoff, 1972; Branchi et al., 2013; Suomi, 2005; Vandell, 2000). In chimpanzees, the gregariousness of the mother during the early life of their offspring has important and long-lasting effects on the vocal development of the offspring (Bründl et al., 2022). Also, infants often engage in socializing activities, such as play, with the offspring of other females (Matsusaka, 2004; Shimada & Sueur, 2014). Being more familiar with other females from the community and their offspring, gregarious females may allow their offspring to move away at a greater distance to facilitate them socializing with the offspring of other females than nongregarious females.

Low levels of female gregariousness result in limited opportunities for offspring to socialize outside of immediate maternal kin. As in other mammalian species, limited socialization might have profound implications for social development (Bekoff, 1972; Branchi et al., 2013; Vandell, 2000). Less gregarious females spend considerably less time than more gregarious females in parties containing other community members, providing limited opportunities for their offspring to interact and to learn socially from others. Indeed, since gregariousness in chimpanzees has higher reproductive benefits for males than for females (Gilby & Wrangham, 2008), mothers adjust their ranging strategies depending on the sex of their offspring, with those having male infants being more gregarious than those with female infants (Murray et al., 2014). However, our study suggests that in Budongo, when less gregarious females are in parties with other females, they tend to spend more time near their infants. This maintenance of proximity is itself potentially an additional constraint on infant socialization that should receive attention from future research, for example, targeting mammalian species with protracted development living in societies with a high degree of fission–fusion dynamics and facing an infanticide threat, such as bottlenose dolphins, *Tursiops truncatus,* and harbour porpoises, *Phocoena phocoena* (Barbara, 1999; Dunn et al., 2002; Patterson et al., 1998). Focusing on such species would allow us to determine whether, indeed, these two factors favour trade-offs between maternal protection and offspring socializing opportunities in mammals generally.

Females that were more gregarious spent more time with their offspring in parties with fewer other females (Fig. 2). This happened in both Budongo and, to a lesser extent and with less certainty, in Taï. This is a noteworthy observation. It is possible that in large parties, highly gregarious mothers spend more time than less gregarious females socializing with other party members at the expense of spending time near their offspring. Similarly, offspring of more, rather than less, gregarious females may spend more time interacting with infants of other females when in large female parties. Therefore, when in small female parties, it is possible that more rather than less gregarious females and their offspring spend more time near each other to offset the compromised opportunities for doing so in larger female parties. Being near the mother might also provide the offspring with opportunities for social learning about important behaviours, such as tool use (Hobaiter et al., 2014; Lamon et al., 2017). Indeed, in bottlenose dolphins, calves adjust the level of their interactions with conspecifics depending on the mother's sociality, with sons seeking more contact with others when mothers are solitary (Gibson & Mann, 2008). More research, particularly focusing on mother and infant interactions with party members as a function of party size and composition, is needed to investigate this aspect. It is also important to note that while our results show that mother–infant proximity is modulated differently in the two populations by the number of females in the party (Fig. 2), the ontogeny of mother–infant proximity, shown as the probability of being within 1 m of each other as a function of the infant's age, is comparable in both populations (Fig. 3). Nevertheless, Taï mothers were closer on average to their infants than Budongo mothers (Fig. 3), possibly because predation pressure, including leopard attacks, in Taï is higher than in Budongo (Wittig & Boesch, 2003). Closer mother–offspring proximity in Taï might result in increased opportunities for infants to learn from the mother's complex behaviours that are present in Taï but not Budongo, such as nut cracking (Whiten et al., 1999).

Our findings show that the mother–infant proximity is affected by the immediate social environment (party size and composition), mother's social phenotype (maternal gregariousness) and larger social settings (population-dependent aggression risk). There is also a lot of variation within the communities we investigated in terms of when and how often mothers and offspring stay close. Our findings are relevant to our understanding of the selection pressures shaping maternal styles, with the three factors playing an important and synergistic role in this respect. The risk of conspecific aggression has been suggested to shape maternal styles in yellow baboons, with some mothers showing more restrictive and others more relaxed maternal strategies, depending on the risk of aggression (Altmann, 1980). Our results are consistent with these findings, showing that the presence of potentially aggressive individuals can shape maternal styles in chimpanzees. However, our results provide new insights into showing that maternal gregariousness influenced the response to such risks. In addition, higher predation pressure in one population than the other appeared to further heighten proximity maintenance. Our findings are relevant to the socioecological model, of which the original version focused on how group formation and structure results from ecological conditions, in particular food availability and predation risk, but also from the infanticidal threat posed by males (Wrangham 1980; van Schaik 1983; van Schaik & Kappeler 1997; Sterck et al. 1997). In our study, we addressed the latter, complementing this socioecological framework by showing that the risk of aggression and potential infanticidal threat by females may also impact individual social behaviour, such as mother–infant proximity maintenance, when considered as a function of maternal gregariousness.

Author Contributions

Catherine Crockford: Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition. **Pawel Fedurek:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cédric Girard-Buttoz:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Catherine Hobaiter:** Writing – review & editing, Resources, Data curation. **Patrick J. Tkaczynski:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Roman M. Wittig:** Writing – review & editing, Resources, Conceptualization. **Klaus Zuberbühler:** Writing – review & editing, Resources, Conceptualization.

Data Availability

The data set and R code used in the analyses are available via GitHub at https://github.com/MotherInfantProject/Mother-Infant-Project.

Declaration of Interest

The authors declare that they have no conflicts of interest to disclose.

Acknowledgments

We are grateful to the management and staff of the Budongo Conservation Field Station and the Taï Chimpanzee Project in Cote d'Ivoire. We thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology in Uganda, and the Ministere de l'Enseignement superieur et de la Recherche Scientifique, the Ministere des Eaux et Forets and the Office Ivoirien des Parcs et Reserves in Cote d'Ivoire for permission to conduct the study. We are grateful to the Centre Suisse de Recherches Scientifique en Cote d'Ivoire for their support. Core funding for the Taï Chimpanzee Project was provided by the Max Planck Society and for the Budongo Conservation Field Station by the Royal Zoological Society of Scotland. We are grateful to the editor Nick Newton-Fisher and an anonymous referee for helpful comments and suggestions on the draft of the paper. The study was funded by the European Research Council project grant (grant agreement number: 679787). We thank Lara Southern, Megan Draper, Tatiana Bortolato and Adrian Soldati for their contributions to data collection in the field.

References

Agrell, J., Wolff, J. O., & Ylönen, H. (1998). Counter-strategies to infanticide in mammals: Costs and consequences. *Oikos, 83*(3), 507–517. https://doi.org/10.2307/3546678

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3), 227–266. https://doi.org/10.1163/156853974x00534

Altmann, J. (1980). *Baboon mothers and infants*. University of Chicago Press.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I., & Henzi, S. P. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology, 49*(4), 627–654.

Bürkner, P. (2018). No title. Advanced Bayesian multilevel modeling with the R package brms. *R Journal, 10*(1), 395–411. https://doi.org/10.32614.

Barbara, J. M. (1999). Behavioral development in wild bottlenose dolphin newborns (Tursiops sp.). *Behaviour, 136*(5), 529–566. https://psycnet.apa.org/doi/10.1163/156853999501469.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bautista, A., Martínez-Gómez, M., & Hudson, R. (2008). Mother-young and within-litter relations in the European rabbit *Oryctolagus cuniculus*. In P. Celio, K. Alves, & K. Hackländer (Eds.), *Lagomorph biology: evolution, ecology, and conservation* (pp. 211–223). Springer.

Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *Quarterly Review of Biology, 47*(4), 412–434. http://www.jstor.org/stable/2820738.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press on Demand.

Bründl, A. C., Girard-Buttoz, C., Bortolato, T., Samuni, L., Grampp, M., Löhrich, T., Tkaczynski, P., Wittig, R. M., & Crockford, C. (2022). Maternal effects on the development of vocal communication in wild chimpanzees. *iScience, 25*(10), Article 105152. https://doi.org/10.1016/j.isci.2022.105152

Branchi, I., Curley, J. P., D'Andrea, I., Cirulli, F., Champagne, F. A., & Alleva, E. (2013). Early interactions with mother and peers independently build adult social skills and shape BDNF and oxytocin receptor brain levels. *Psychoneuroendocrinology, 38*(4), 522–532. https://doi.org/10.1016/j.psyneuen.2012.07.010

Cameron, E. Z., Linklater, W. L., Stafford, K. J., & Minot, E. O. (2003). Social grouping and maternal behaviour in feral horses (Equus caballus): The influence of males on maternal protectiveness. *Behavioral Ecology and Sociobiology, 53*, 92–101. https://doi.org/10.1007/s00265-002-0556-1

Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology, 36*(1), 59–70. https://doi.org/10.1007/BF00175729

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology*. J. Wiley.

Deschner, T., & Boesch, C. (2007). Can the patterns of sexual swelling cycles in female Taï chimpanzees be explained by the cost-of-sexual-attraction hypothesis? *International Journal of Primatology, 28*, 389–406. https://doi.org/10.1007/s10764-007-9120-1

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour, 66*(3), 551–560. https://doi.org/10.1006/anbe.2003.2210

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior, 46*(2), 204–215. https://doi.org/10.1016/j.yhbeh.2004.03.013

Dunbar, R. (1988). *Primate social systems*. Cornell University Press.

Dunn, D. G., Barco, S. G., Pabst, D. A., & McLellan, W. A. (2002). Evidence for infanticide in bottlenose dolphins of the western North Atlantic. *Journal of Wildlife Diseases, 38*(3), 505–510. https://doi.org/10.7589/0090-3558-38.3.505

Ebensperger, L. A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews, 73*(3), 321–346. https://doi.org/10.1017/S0006323198005209

Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology, 75*(3), 222–237. https://doi.org/10.1002/ajp.22084

Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour, 73*(3), 501–512. https://doi.org/10.1016/j.anbehav.2006.09.007

Emery Thompson, M., & Wrangham, R. W. (2006). Comparison of sex differences in gregariousness in fission-fusion species. In N. E. Newton-Fisher, H. Notman, V. Reynolds, & J. Paterson (Eds.), *Primates of western Uganda* (pp. 209–226). Springer.

Fox, J., & Weisberg, S. (2011). *Multivariate linear models in R. Thousand Oaks*.

Gibson, Q. A., & Mann, J. (2008). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour, 76*(2), 389–405. https://doi.org/10.1016/j.anbehav.2008.01.022

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology, 62*(11), 1831. https://doi.org/10.1007/s00265-008-0612-6

Goodall, J. (1977). Infant killing and cannibalism in free-living chimpanzees. *Folia Primatologica, 28*(4), 259–282. https://doi.org/10.1159/000155817

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Harvard University Press.

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology, 12*(9), Article e1001960. https://doi.org/10.1371/journal.pbio.1001960

Kaburu, S. S., & Newton-Fisher, N. E. (2015). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology, 69*(6), 1039–1052. https://doi.org/10.1007/s00265-015-1917-x

Kahlenberg, S. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2008). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour, 76*(5), 1497–1509. https://doi.org/10.1016/j.anbehav.2008.05.029

Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology, 29*(4), 931–947. https://doi.org/10.1007/s10764-008-9276-3

Krause, J., & Ruxton, G. (2002). *Living in groups*. Oxford, UK: Series in ecology and evolution. https://doi.org/10.1093/oso/9780198508175.001.0001.

Lamon, N., Neumann, C., Gruber, T., & Zuberbühler, K. (2017). Kin-based cultural transmission of tool use in wild chimpanzees. *Science Advances, 3*(4), Article e1602750. https://doi.org/10.1126/sciadv.1602750

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology: Official Journal of the American Society of Primatologists, 71*(10), 840–851. https://doi.org/10.1002/ajp.20711

Lee, S. M., Murray, C. M., Lonsdorf, E. V., Fruth, B., Stanton, M. A., Nichols, J., & Hohmann, G. (2020). Wild bonobo and chimpanzee females exhibit broadly similar patterns of behavioral maturation but some evidence for divergence. *American Journal of Physical Anthropology, 171*(1), 100–109. https://doi.org/10.1002/ajpa.23935

Lemoine, N. (2019). Moving beyond noninformative priors: Why and how to choose weakly informative priors in Bayesian analyses. In C. Boesch, & R. M. Wittig (Eds.), *Oikos* (pp. 912–928). Wiley Online Library. https://doi.org/10.1111/oik.05985.

Lemoine, S., Crockford, C., & Wittig, R. (2019). Spatial integration of unusually high numbers of immigrant females into the South Group: Further support for the bisexually bonded model in Taï chimpanzees. In R. M. Wittig, & C. Boesch (Eds.), *The chimpanzees of the Taï forest*. Cambridge University Press.

Lonsdorf, E. V., Anderson, K. E., Stanton, M. A., Shender, M., Heintz, M. R., Goodall, J., & Murray, C. M. (2014). Boys will be boys: Sex differences in wild infant chimpanzee social interactions. *Animal Behaviour, 88*, 79–83. https://doi.org/10.1016/j.anbehav.2013.11.015

Lonsdorf, E. V., Markham, A. C., Heintz, M. R., Anderson, K. E., Ciuk, D. J., Goodall, J., & Murray, C. M. (2014). Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS One, 9*(6), Article e99099. https://doi.org/10.1371/journal.pone.0099099

Lowe, A., Hobaiter, C., Asiimwe, C., Zuberbühler, K., & Newton-Fisher, N. E. (2019). Intra-community infanticide in wild, eastern chimpanzees: A 24-year review. *Primates, 61*(1), 1–14. https://doi.org/10.1007/s10329-019-00730-3

Lowe, A., Hobaiter, C., & Newton-Fisher, N. E. (2019). Countering infanticide: Chimpanzee mothers are sensitive to the relative risks posed by males on differing rank trajectories. *American Journal of Physical Anthropology, 168*(1), 3–9. https://doi.org/10.1002/ajpa.23723

Lukas, D., & Huchard, E. (2014). The evolution of infanticide by males in mammalian societies. *Science, 346*(6211), 841–844. https://doi.org/10.1126/science.1257226

Mann, J. (2019). Maternal care and offspring development in odontocetes. In B. Würsig (Ed.), *Ethology and behavioral ecology of odontocetes* (pp. 95–116). Springer.

Matsusaka, T. (2004). When does play panting occur during social play in wild chimpanzees? *Primates, 45*(4), 221–229. https://doi.org/10.1007/s10329-004-0090-z

Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 274*(1612), 1009–1014. https://doi.org/10.1098/rspb.2006.0206

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the 'challenge hypothesis'. *Animal Behaviour, 67*(1), 113–123. https://doi.org/10.1016/j.anbehav.2023.06.004

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology, 17*(6), 1020–1028. https://doi.org/10.1093/beheco/arl042

Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall, J., & Pusey, A. E. (2014). Early social exposure in wild chimpanzees: Mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences, 111*(51), 18189–18194. https://doi.org/10.1073/pnas.1409507111

Newton-Fisher, N. (1999). Association by male chimpanzees: A social tactic? *Behaviour, 136*(6), 705–730. https://www.jstor.org/stable/4535636.

Nishie, H., & Nakamura, M. (2018). A newborn infant chimpanzee snatched and cannibalized immediately after birth: Implications for "maternity leave" in wild chimpanzee. *American Journal of Physical Anthropology, 165*(1), 194–199. https://doi.org/10.1002/ajpa.23327

Otali, E., & Gilchrist, J. S. (2006). Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: The infant safety hypothesis. *Behavioral Ecology and Sociobiology, 59*(4), 561–570. https://www.jstor.org/stable/25063736.

Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology, 7*(4), 117–129. https://doi.org/10.1002/(SICI)1520-6505(1999)7:4%3C117::AID-EVAN2%3E3.0.CO;2-O

Pandolfi, M., Scaia, M. F., & Fernandez, M. P. (2021). Sexual dimorphism in aggression: Sex-specific fighting strategies across species. *Frontiers in Behavioral Neuroscience, 15*, Article 659615. https://doi.org/10.3389/fnbeh.2021.659615

Patterson, I., Reid, R. J., Wilson, B., Grellier, K., Ross, H. M., & Thompson, P. M. (1998). Evidence for infanticide in bottlenose dolphins: An explanation for violent interactions with harbour porpoises? *Proceedings of the Royal Society of London.Series B: Biological Sciences, 265*(1402), 1167–1170. https://doi.org/10.1098/rspb.1998.0414

Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology, 29*(4), 949–973. https://doi.org/10.1007/s10764-008-9281-6

Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science, 277*(5327), 828–831. https://doi.org/10.1126/science.277.5327.828

R Core Team. (2014). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing, 2013 https://www.R-project.org/.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation*. Oxford University Press.

Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition, 17*(4), 997–1005. https://doi.org/10.1007/s10071-014-0731-6

Sandel, A. A., & Watts, D. P. (2021). Lethal coalitionary aggression associated with a community fission in chimpanzees (*Pan troglodytes*) at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology, 42*(1), 26–48. https://doi.org/10.1007/s10764-020-00185-0

Scott, A. M., Susanto, T. W., Setia, T. M., & Knott, C. D. (2023). Mother-offspring proximity maintenance as an infanticide avoidance strategy in bornean orangutans (Pongo pygmaeus wurmbii). *American Journal of Primatology, 85*(6), Article e23482. https://doi.org/10.1002/ajp.23482

Shimada, M., & Sueur, C. (2014). The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *American Journal of Primatology, 76*(11), 1025–1036. https://doi.org/10.1002/ajp.22289

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin, 86*(2), 420–428. https://doi.org/10.1037//0033-2909.86.2.420

Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E., & Holekamp, K. E. (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour, 76*(3), 619–636. https://doi.org/10.1016/j.anbehav.2008.05.001

Sterck, E. H., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*(5), 291–309. https://www.jstor.org/stable/4601392.

Sugiyama, Y. (1968). Social organization of chimpanzees in the Budongo forest, Uganda. *Primates, 9*(3), 225–258. https://doi.org/10.1007/bf01730972

Suomi, S. J. (2005). Mother-infant attachment, peer relationships, and the development of social networks in rhesus monkeys. *Human Development, 48*(1–2), 67–79. https://doi.org/10.1159/000083216

Thompson González, N., Machanda, Z., Otali, E., Muller, M. N., Enigk, D. K., Wrangham, R., & Emery Thompson, M. (2021). Age-related change in adult chimpanzee social network integration. *Evolution, Medicine, and Public Health, 9*(1), 448–459. https://doi.org/10.1093/emph/eoab040

Tkaczynski, P. J., Behringer, V., Ackermann, C. Y., Fedurek, P., Fruth, B., Girard-Buttoz, C., Hobaiter, C., Lee, S. M., Löhrich, T., & Preis, A. (2020). Patterns of urinary cortisol levels during ontogeny appear population specific rather than species specific in wild chimpanzees and bonobos. *Journal of Human Evolution, 147*, Article 102869. https://doi.org/10.1016/j.jhevol.2020.102869

Tkaczynski, P. J., Mielke, A., Samuni, L., Preis, A., Wittig, R. M., & Crockford, C. (2020). Long-term repeatability in social behaviour suggests stable social phenotypes in wild chimpanzees. *Royal Society Open Science, 7*(8), Article 200454. https://doi.org/10.1098/rsos.200454

Townsend, S. W., Slocombe, K. E., Thompson, M. E., & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology, 17*(10), R355–R356. https://doi.org/10.1016/j.cub.2007.03.020

Valé, P. D., Béné, J. K., N'Guessan, A. K., Crockford, C., Deschner, T., Koné, I., Girard-Buttoz, C., & Wittig, R. M. (2021). Energetic management in wild chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire. *Behavioral Ecology and Sociobiology, 75*(1), 1–18. https://psycnet.apa.org/doi/10.1007/s00265-020-02935-9.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*, 120–144.

van Schaik, C. P., & Kappeler, P. M. (1997). Infanticide risk and the evolution of male–female association in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 264*(1388), 1687–1694. https://doi.org/10.1098/rspb.1997.0234

Vandell, D. L. (2000). Parents, peer groups, and other socializing influences. *Developmental Psychology, 36*(6), 699–710. https://psycnet.apa.org/doi/10.1037/0012-1649.36.6.699.

Ward, A., & Webster, M. (2016). *Sociality: The behaviour of group-living animals*. Springer International Publishing. https://doi.org/10.1007/978-3-319-28585-6

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology, 44*(1), 43–55. https://www.jstor.org/stable/4601544.

Weingrill, T. (2000). Infanticide and the value of male-female relationships in mountain chacma baboons. *Behaviour, 137*(3), 337–359. https://www.jstor.org/stable/4535709.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature, 399*(6737), 682–685. https://doi.org/10.1038/21415

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., Hobaiter, C. L., Hohmann, G., Itoh, N., & Koops, K. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature, 513*(7518), 414–417. https://doi.org/10.1038/nature13727

Wittig, R. M. (2018). Taï chimpanzees. In J. Vonk, & T. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1–7). Springer International Publishing.

Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology, 24*, 847–867. https://doi.org/10.1023/A:1024632923180

Wittig, R. M., & Boesch, C. (2019). Demography and life history of five chimpanzee communities in Taï National Park. In R. M. Wittig, & C. Boesch (Eds.), *The chimpanzees of the Taï forest: 40 years of research* (pp. 125–140). Cambridge University Press Cambridge.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*(3–4), 262–300.

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 248–258). Cambridge University Press.

Appendix

Table A1
Female gregariousness per community and population

ID	Population	Community	Gregariousness
MK	Budongo	Sonso	0.007
AN	Budongo	Sonso	0.039
JL	Budongo	Sonso	0.056
FL	Budongo	Sonso	0.058
GL	Budongo	Sonso	0.069
ML	Budongo	Sonso	0.112
KY	Budongo	Sonso	0.12
KG	Budongo	Sonso	0.122
KA	Budongo	Sonso	0.123
RS	Budongo	Sonso	0.131
KW	Budongo	Sonso	0.14
DL	Budongo	Sonso	0.147
KU	Budongo	Sonso	0.152
TJ	Budongo	Sonso	0.159
HT	Budongo	Sonso	0.174
JN	Budongo	Sonso	0.177
IN	Budongo	Sonso	0.21
OK	Budongo	Sonso	0.253
KL	Budongo	Sonso	0.304
SHY	Budongo	Waibira	0.028
KIP	Budongo	Waibira	0.048
NEV	Budongo	Waibira	0.061
LIR	Budongo	Waibira	0.063
KID	Budongo	Waibira	0.076
PEN	Budongo	Waibira	0.087
BAH	Budongo	Waibira	0.128
NOR	Budongo	Waibira	0.135
KET	Budongo	Waibira	0.15
LOT	Budongo	Waibira	0.181
ASA	Taï	South	0.221
HAV	Taï	South	0.284
ISH	Taï	South	0.266
JUL	Taï	South	0.184
KIN	Taï	South	0.295
LUC	Taï	South	0.214
OPA	Taï	South	0.262
PEM	Taï	South	0.228
SUM	Taï	South	0.278
TOU	Taï	South	0.217
UAP	Taï	South	0.234
XEL	Taï	South	0.214
BEL	Taï	North	0.406
MYS	Taï	North	0.36
NAO	Taï	North	0.402
NAR	Taï	North	0.383
PAN	Taï	North	0.46
PER	Taï	North	0.452
SUR	Taï	North	0.37
FAT	Taï	East	0.323
IND	Taï	East	0.409
POL	Taï	East	0.383
RWE	Taï	East	0.28
WAN	Taï	East	0.332
YEH	Taï	East	0.322
YED	Taï	East	0.216

Table A2

Results from model 2a control for the presence of maternal kin in the party on a subset of data not comprising the Waibira community

Predictor	Estimate	SE	95% CI low	95% CI high	89% CI low	89% CI high	% Posterior in support
Intercept	−0.41	0.88	−2.1	1.37	−1.77	1	
No. of dependent offspring	−0.14	0.2	−0.5	0.26	−0.46	0.18	75.7
Mother's age (Years)	−0.06	0.27	−0.6	0.46	−0.48	0.36	58.4
Infant age (Years)	−0.83	0.19	*−1.2*	*−0.46*	*−1.12*	*−0.53*	100.0
Infant sex (Male)	0.31	0.45	−0.6	1.19	−0.41	1.02	75.7
Maximally tumescent female in the party (Yes)	0.38	0.17	*0.05*	*0.72*	*0.11*	*0.66*	98.6
Kin present in the party (Y/N)	0.11	0.19	−0.3	0.49	−0.2	0.41	71.0
Mother's gregariousness	−0.17	0.41	−1	0.64	−0.82	0.48	66.2
No. of males in the party	0.34	0.48	−0.7	1.23	−0.46	1.06	78.7
Population (Taï)	0.3	0.76	−1.2	1.76	−0.93	1.48	65.9
No. of females in the party	−0.61	0.48	−1.5	0.43	−1.32	0.18	90.3
Mother gregariousness * no. of males	0.32	0.23	−0.1	0.77	−0.04	0.68	92.2
Mother gregariousness * population (Taï)	0.37	0.56	−0.7	1.47	−0.5	1.24	74.5
No. of males * population (Taï)	−0.39	0.52	−1.4	0.75	−1.16	0.48	80.0
Mother gregariousness * no. of females	−0.49	0.24	*−1*	*−0.03*	*−0.88*	*−0.11*	98.1
No. of females * population (Taï)	0.39	0.51	−0.7	1.32	−0.45	1.15	80.0
No. of males * population (Taï) * mother gregariousness	−0.06	0.3	−0.7	0.54	−0.54	0.42	58.5
No. of females * population (Taï) * mother gregariousness	0.36	0.29	−0.2	0.93	−0.09	0.81	90.1

The coded level for each categorical predictor is indicated in parentheses. Control predictors are italicized. The 95% credible interval (CI) low and 95% CI high indicate the lower and upper limits of the 95% CI. Likewise, the 89% CI low and 89% CI high indicate the lower and upper limits of the 89% credible interval. '% posterior in support' indicates the % of the posterior distribution supporting a given effect. The 95% and 89% CI not overlapping 0 are italicized.

Table A3

Results from model 2b is a control for model 2a, on the same subset of data not comprising the Waibira community but with the same structure as model 1 (without the factor presence of maternal kin in the party)

Predictor	Estimate	SE	95% CI low	95% CI high	89% CI low	89% CI high	% Posterior in support
Intercept	−0.4	0.87	−2	1.38	−1.71	1.02	
No. of dependent offspring	−0.13	0.2	−0.5	0.25	−0.46	0.18	75.1
Mother's age (Years)	−0.06	0.27	−0.6	0.47	−0.48	0.37	58.9
Infant age (Years)	−0.83	0.19	*−1.2*	*−0.45*	*−1.13*	*−0.53*	100.0
Infant sex (Male)	0.31	0.45	−0.6	1.19	−0.4	1.03	76.3
Maximally tumescent female in the party (Yes)	0.38	0.17	*0.05*	*0.72*	*0.11*	*0.66*	98.9
Mother's gregariousness	−0.18	0.41	−1	0.62	−0.84	0.47	67.5
No. of males in the party	0.33	0.49	−0.8	1.24	−0.47	1.06	78.3
Population (Taï)	0.32	0.76	−1.2	1.76	−0.92	1.49	67.3
No. of females in the party	−0.62	0.47	−1.5	0.37	−1.33	0.16	90.8
Mother gregariousness * no. of males	0.31	0.23	−0.1	0.77	−0.05	0.68	91.8
Mother gregariousness * population (Taï)	0.38	0.55	−0.7	1.45	−0.5	1.25	76.4
No. of males * population (Taï)	−0.38	0.53	−1.4	0.77	−1.18	0.5	78.7
Mother gregariousness * no. of females	−0.5	0.24	*−1*	*−0.02*	*−0.88*	*−0.11*	97.9
No. of females * population (Taï)	0.41	0.5	−0.7	1.3	−0.41	1.14	81.4
No. of males * population (Taï) * mother gregariousness	−0.06	0.31	−0.7	0.56	−0.54	0.43	58.0
No. of females * population (Taï) * mother gregariousness	0.38	0.29	−0.2	0.94	−0.09	0.83	90.9

The coded level for each categorical predictor is indicated in parentheses. Control predictors are italicized. A 95% credible interval (CI) low and 95% CI high indicate the lower and upper limits of the 95% credible interval. Likewise, the 89% CI low and 89% CI high indicate the lower and upper limits of the 89% CI. '% posterior in support' indicates the% of the posterior distribution supporting a given effect. The 95% and 89% CIs not overlapping 0 are italicized.

Table A4

Results from model 3a control for the presence of infanticidal individuals on a subset of data comprising only the Sonso community from Budongo

Predictor	Estimate	SE	95% CI low	95% CI high	89% CI low	89% CI high	% Posterior in support
Intercept	0.28	0.43	−0.56	1.14	−0.39	0.96	
No. of dependent offspring	0.21	0.33	−0.45	0.87	−0.32	0.74	0.741
Mother's age (Years)	−0.5	0.36	−1.23	0.23	−1.08	0.07	0.919
Infant age (Years)	−1.43	0.25	*−1.94*	*−0.95*	*−1.84*	*−1.04*	1
Infant sex (Male)	−0.68	0.45	−1.56	0.22	−1.4	0.03	0.939
Maximally tumescent female in the party (Yes)	1.31	0.55	*0.22*	*2.38*	*0.41*	*2.19*	0.99
Infanticidal individual in the party (Yes)	−0.14	0.34	−0.8	0.51	−0.68	0.39	0.661
Mother's gregariousness	−0.39	0.26	−0.91	0.12	−0.81	0.02	0.937
No. of males in the party	0.18	0.31	−0.45	0.8	−0.31	0.67	0.737
No. of females in the party	−0.23	0.33	−0.86	0.45	−0.75	0.31	0.765
Mother gregariousness * no. of males	0.46	0.32	−0.17	1.11	−0.03	0.98	0.933
Mother gregariousness * no. of females	−0.53	0.34	−1.17	0.19	−1.05	0.03	0.936

The coded level for each categorical predictor is indicated in parentheses. Control predictors are italicized. The 95% credible interval (CI) low and 95% CI high indicate the lower and upper limits of the 95% CI. Likewise, the 89% CI low and 89% CI high indicate the lower and upper limits of the 89% credible interval. '% posterior in support' indicates the% of the posterior distribution supporting a given effect. The 95% and 89% CI not overlapping 0 are italicized.

Table A5

Results from model 3b as a control model for model 3a also only on the Sonso community but without the predictor ‘presence of infanticidal male’

Predictor	Estimate	SE	95% CI low	95% CI high	89% CI low	89% CI high	% Posterior in support
Intercept	0.2	0.39	−0.55	0.99	−0.39	0.82	
No. of dependent offspring	0.2	0.33	−0.47	0.84	−0.33	0.72	0.737
Mother’s age (Years)	−0.5	0.36	−1.23	0.22	−1.08	0.07	0.901
Infant age (Years)	−1.42	0.25	*−1.92*	*−0.94*	*−1.83*	*−1.03*	1
Infant sex (Male)	−0.7	0.44	−1.54	0.19	−1.38	0.01	0.944
Maximally tumescent female in the party (Yes)	1.32	0.56	*0.23*	*2.42*	*0.43*	*2.22*	0.992
Mother’s gregariousness	−0.41	0.26	−0.92	0.11	*−0.82*	*−0.01*	0.93
No. of males in the party	0.14	0.3	−0.47	0.75	−0.33	0.62	0.7
No. of females in the party	−0.25	0.32	−0.88	0.41	−0.75	0.26	0.794
Mother gregariousness * no. of males	0.45	0.32	−0.18	1.09	−0.04	0.95	0.93
Mother gregariousness * no. of females	−0.54	0.34	−1.19	0.19	−1.07	0.03	0.938

The coded level for each categorical predictor is indicated in parentheses. Control predictors are italicized. The 95% credible interval (CI) low and 95% CI high indicate the lower and upper limits of the 95% CI. Likewise, the 89% CI low and 89% CI high indicate the lower and upper limits of the 89% credible interval. ‘% posterior in support’ indicates the% of the posterior distribution supporting a given effect. The 95% and 89% CI not overlapping 0 are italicized.

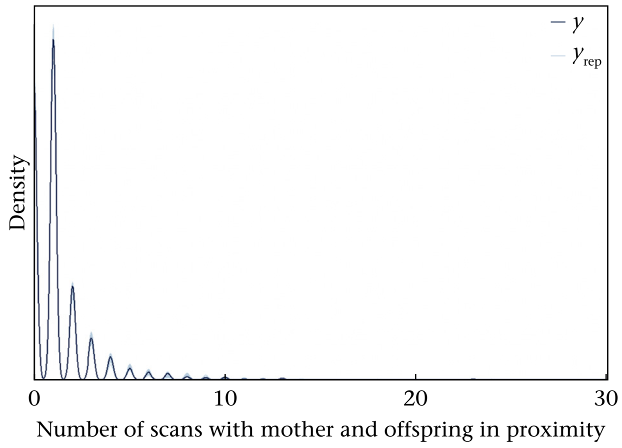

Figure A1. Posterior predictive check for the full model, model 1.

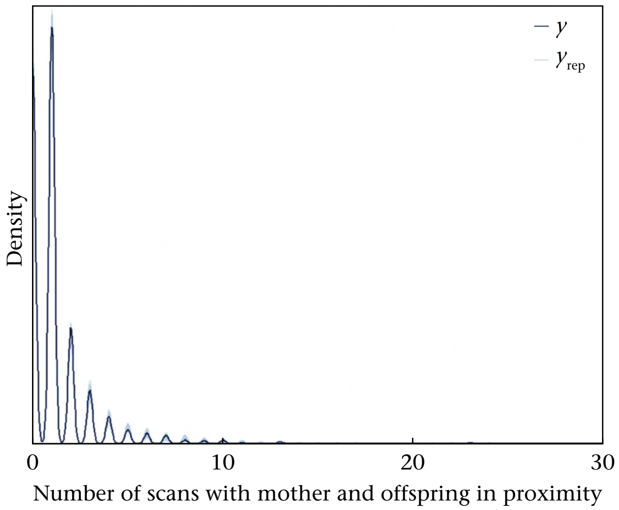

Figure A3. Posterior predictive check for the test kin model, model 2b.

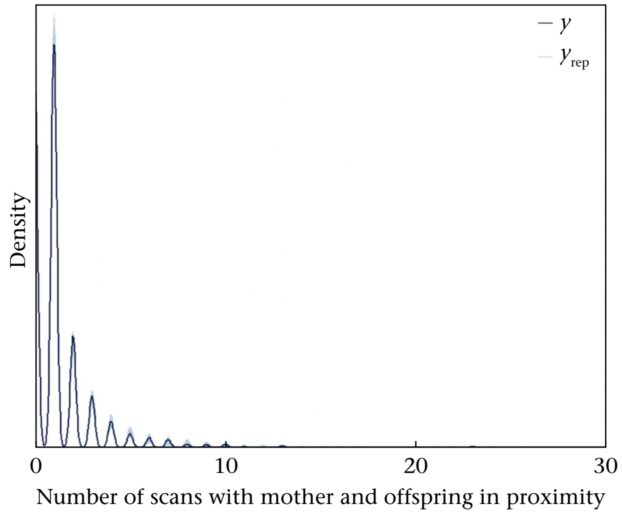

Figure A2. Posterior predictive check for the model controlling for kin presence, model 2a.

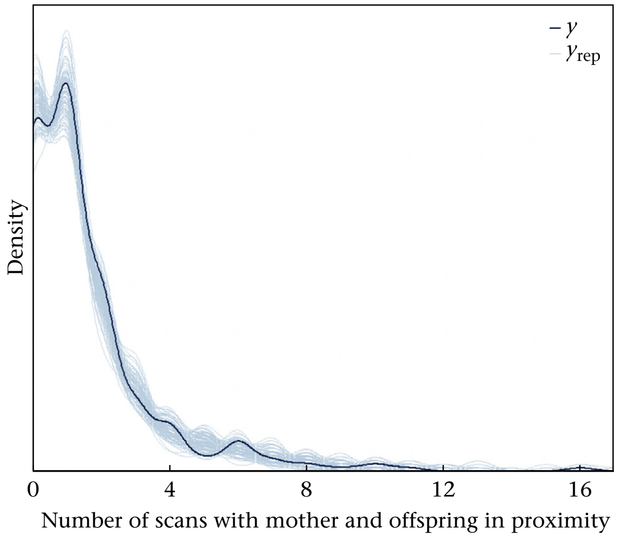

Figure A4. Posterior predictive check for the model controlling for the presence of infanticidal individuals, model 3a.

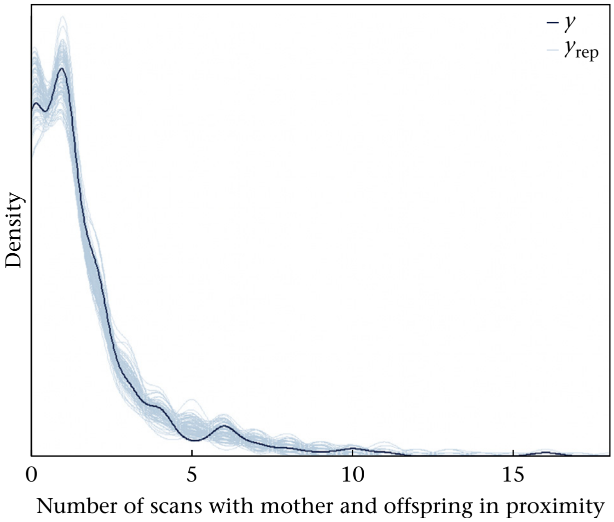

Figure A5. Posterior predictive check for the test infanticidal model, model 3b.