ASSESSING THE ROLE OF MATERNAL SOCIAL NETWORK INHERITANCE IN THE SOCIAL INTEGRATION OF IMMATURE VERVET MONKEYS (*CHLOROCEBUS PYGERYTHRUS*)

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Abstract

Specific mechanisms of social network integration in juvenile animals are still largely obscure. However, much research indicates that mothers have a wide range of effects on their offspring, including on their sociality. Using a Bayesian framework, I investigated factors of social integration, such as maternal proximity, network influences (i.e., inheritance), age, dominance rank, and offspring traits from May-July 2025 in wild vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. My results suggest that maternal influences exist mainly in proximity but less in grooming networks. Older offspring were more distant from their mothers and less central in proximity networks than younger offspring. Notably, offspring sex was a strong predictor of social ontogeny in vervet monkeys, with daughters being more integrated in grooming networks than sons. Overall, these results provide insight into the importance of mothers in social ontogeny, while also highlighting the pivotal role of offspring sex on their social integration.

Keywords: social ontogeny, social network analysis, network transmission, primates, proximity, grooming

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1.0 Introduction

1.1 Sociality

The social lives of animals are recognized as critically important to their fitness (Thompson, 2019). Most research has focused on adult social networks, but little is known about the sociality of immature individuals. Maternal effects have been found to have a profound effect on numerous aspects of offspring physiology, behaviour, and fitness, including in primates (Maestripieri, 2009), though few studies have explored the potential effects of mothers on juvenile social network in primates. For this project, I examined maternal effects and offspring characteristics on the social networks of immature offspring in wild vervet monkeys (*Chlorocebus pygerythrus*).

Thompson (2019) identified six pathways whereby sociality is related to fitness. First, cooperation such as alliances with and interventions by social partners within groups can protect individuals from physical harm and harassment (i.e., lowering risk exposure), support resource acquisition and retention, and establish and maintain social status (i.e., dominance rank) (Thompson, 2019). Possessing more social ties can shield individuals from predators, food paucity, and cold temperatures (Thompson, 2019). Living in a group reduces the risk of being targeted by a predator since many other prey items are available at once. Concurrently, familiarity with other group members facilitates more effective communication (Thompson, 2019). For instance, adult female Celebes crested macaques (*Macaca nigra*) that shared a tighter bond were able to respond to their partner's eye motions faster than with others (Micheletta & Waller, 2012). Additionally, individuals with many social ties are often better tolerated at feeding sites, which decreases competition when resources (e.g., food) are limited (Thompson, 2019). In vervet monkeys, tolerance of physical contact with other group members facilitates thermoregulation during cold winter months (McFarland et al., 2015) and frequent associations can shield individuals from isolation, especially during or after stressful events (Charuvastra & Cloitre, 2008). Although glucocorticoid levels - a group of hormones involved in the body's stress response - can vary for a wide range of reasons, Crockford *et al.* (2008) found that regular interactions with fewer grooming partners could decrease baseline glucocorticoid levels through the downregulation of the hypothalamic-pituitary-adrenal axis in female chacma baboons (*Papio hamadryas ursinus*), thereby reducing their stress levels (but see but see Creighton et al., 2024). However, wild chimpanzees (*Pan troglodytes*) displayed lower baseline glucocorticoid levels when associating or interacting with their close social partners than other individuals across several contexts (Wittig et al., 2016). Resource monopolization is also enhanced with coalitions. Whilst female primates can secure more food and nesting sites in this way, males tend to use alliances to access and retain mates, which allows them to increase their reproductive success (Thompson, 2019; Watts, 1998). In some species such as wild tufted capuchin females (*Cebus apella nigritus*), social ties, such as frequent grooming of dominant individuals, can be used by group members to climb up the hierarchy (Tiddi et al., 2012).

Communal offspring caretaking and competence acquisition (i.e., social learning) of young animals are other potential advantages of sociality. Allomothering allows biological mothers to spend less time carrying their offspring and more time foraging, whilst also benefitting carers who gain mothering experience for their own future offspring (Fairbanks, 1990). House mouse (*Mus domesticus*) mothers who raised their pups with the help of other group members had a greater number of litters, pups with improved survival rates, and a higher lifetime reproductive success than mothers who did not receive help (König, 1994).

Similarly, early life experiences (e.g., food availability, population density), including offspring's relationship with their mothers, can affect their own sociality, parenting style (Margulis et al., 2005), partner preferences (Jarrett et al., 2018), affiliative and aggressive patterns (Bastian et al., 2002; Jarrett et al., 2018), emotional regulation (Branchi et al., 2009), dominance tendencies (Bastian et al., 2002), and reproductive success (Altmann, 1991). Associating with social partners can support learning and skill acquisition. Play allows infants and juveniles to test and gauge their physical limits and abilities (Thompson, 2019) while learning about others. High levels of play during development have been linked to enhanced motor-skills (Nunes et al., 2004), earlier onset of the first mating attempt (Heintz et al., 2017), the appropriateness of submissive behavioural responses to dominant individuals (Pellis & Pellis, 2007), greater territoriality during female gestation, and improved offspring survival for future mothers (Nunes, 2014). Social relationships provide crucial opportunities for learning. Baboons learn the location of food patches by observing others while they forage and inspect the same food items thereafter (Alberts, 2019). It is among others that social learning can operate.

1.2 Social Network Analysis

Three main categories of sociality measurements correlated with fitness are commonly used in the literature: gregariousness, bondedness, and integration (Thompson, 2019). Gregariousness tends to be assessed by observing individuals' activity budget (i.e., proportion of time spent being social) and affiliation rates relative to the individual average rate (Thompson, 2019). Tie strength, stability, and symmetry are relevant measures of bondedness that have been linked to fitness outcomes (Thompson, 2019). As for integration, the diversity of social partners and individuals' position in a social network can be measured using social network analysis, a common technique used to assess sociality (Jarrett et al., 2018; Thompson, 2019).

Social networks are composed of nodes and edges/ties; the former being individuals and the latter being the type and frequency of connections between these individuals (Farine & Whitehead, 2015). Social network analysis can evaluate both the centrality of individuals and characterize all connections in a group by assessing direct (i.e., immediate connection) or indirect (i.e., connection is more than one node away) interactions between individuals (Pinter-Wollman, 2014; Wey et al., 2008). Interactions are differentiated from associations in that interactions constitute observations of an individual's behaviours with a conspecific where one influences the behaviour or directs a behaviour towards the other, whereas an association is achieved with mere spatial proximity or co-membership of two individuals in a subgroup (Whitehead & Dufault, 1999; Whitehead, 2008; Whitehead, 2009). Associations provide opportunities for interactions and both processes tend to be affected by rank, sex, age, kinship, and philopatry (e.g., Kulik et al., 2015). Social network measures can depict the interactions of one individual (ego-centric level), two individuals (dyad level), or an entire group (network level) (Bonnell & Vilette, 2020; Wey et al., 2008). At each of these scales, the associations and interactions that compose social networks can be characterized with a wide range of quantitative metrics (see Table 1) (Croft et al., 2008, Wey et al., 2008). Networks can be differentiated into separate proximity, grooming, aggression, and play networks with studies investigating all - but most often only some - types of networks (e.g., Canteloup et al., 2021; Roatti et al., 2023; Vilette et al., 2022). Network metrics might then be weighted, where edges are weighted by the strength (see Figure 1) of each association or interaction, or unweighted (binary) (Wey et al., 2008). Similarly, networks may be directed (i.e., presence of an actor and receiver so the relationship between nodes can be unequal) or undirected (i.e., two nodes are connected) (Wey et al., 2008). For instance, in-strength is the frequency of associations and interactions *received* by an individual whilst out-strength is the frequency of associations or interactions *initiated* by that individual (Kulahci et al., 2016). As such, there is a lack of consensus, and therefore of consistency, in the literature regarding the appropriate measures for describing sociality (Vilette, 2022). Although this makes comparison between studies challenging, the diversity of available metrics may also be beneficial for addressing a range of specific and targeted questions about sociality (Canteloup et al., 2021).

Table 1. Social Network Metrics. Network type: B = binary only, W = weighted only, BW = weighted and binary networks (Farine & Whitehead, 2015). Adapted from Farine & Whitehead (2015). All quoted excerpts are from Box 2 (page 1153) of Farine & Whitehead (2015), unless indicated otherwise.

Node-level Metrics		
Metric	*Definition*	*Type*
Degree (binary degree)	"Number of edges connected to a node." For a directed network, degree can be separated into in-degree (i.e., number of incoming edges) and out-degree (i.e., number of outgoing edges). This metric represents individuals' gregariousness by providing the number of associates or interactants.	B
Strength (weighted degree)	"Sum of all edge weights connected to the node" (strength = binary degree if all edges have a weight of 1). For a directed network, strength can be separated into in-strength (i.e., frequency of incoming edges) and out-strength (i.e., frequency of outgoing edges). This measure captures "the expected total interaction or association rate per sample." For instance, we expect for approximately two other individuals to be associated (or interacting) with a node if this node has a strength of 2 (for most association indices).	W
Cosine Similarity	Measures whether "the patterning of values in two vectors (a, b) is similar" (Jarrett et al., 2018; Newman, 2010). This measure evaluates the similarity of edge weights between two networks (Vilette et al., 2022). Its value ranges between 0 and 1, with 0 being complete dissimilarity (i.e., partners are completely different at time t and t+1 within the same individual or partners are completely different between two individuals) and 1 being identical partner choices (i.e., partners are the same at time t and t+1 within the same individual or partners are the same between two individuals) (Vilette et al., 2022)	BW (Han et al., 2015)
Skewness	Measures the symmetry of the edge weights distribution (Vilette et al., 2022). A positive skewness (i.e., right-	BW (Cain et al.,

	skewed) suggests that an individual is weakly associated (low strength) with many individuals (high degree) and strongly associated (high strength) with few individuals (low degree) whereas a negative skewness (i.e., left-skewed) reveals that an individual disproportionately associates with many individuals (high degree) very often (high strength) (Vilette et al., 2022). When zero, skewness reveals an equal distribution across all social partners (Vilette et al., 2022).	2017; Matsumoto et al., 2012)
Betweenness Centrality	"Number of shortest paths that flow through the node." This metric evaluates the level of importance of a node for connecting parts of a network which are not connected otherwise. For instance, a node with a high betweenness often connects mostly independent communities. This reveals individuals that tend to switch groups more often than others.	BW
Eigenvector Centrality	"Sum of centralities of an individual's neighbours." For example, individuals with high centrality have "a large degree or [are] connected to associates with a high degree (or both)." This metric allows to show the 'importance' of nodes in the network, as social hubs or for disease and information transmission in populations.	BW
Page Rank	For directed networks, it measures centrality by dividing a node's centrality acquired through associates by each associate's out-degree. As such, very central nodes only give a small amount of centrality to the nodes they are connected to, which controls "the measure of eigenvector centrality for long tails in the degree distribution." For example, individuals with a greater page rank are critically important for connecting different parts of the network, which is relevant to studying flows through networks.	BW
Reach / Power	"Proportion of all other nodes [that] can be reached in one step, two steps", etc. This allows to estimate the number of separations. This metric is not often used in animal social networks but can be useful when studying differences or changes (and their implications) in social structure (e.g., removal of central individuals). It can also likely be helpful in models of information or disease propagation as it can evaluate how fast most nodes of a population become infected or knowledgeable.	BW
Network-level Metrics		
Density	"Number of edges in a network divided by the total number of possible edges (B), or the sum of edge	BW

	weights divided by the total number of possible edges (W).” This metric can be important to normalize the degree distributions observed since densities tend to be lower as networks grow larger.	
Homophily / Assortativity	“Correlation in the phenotype of connected individuals.” If positive, this means that individuals are more connected than expected whereas, if negative, they might be avoiding similar individuals. It can be measured on weighted networks and allows to identify the phenotypic structure of a social network. For instance, assortment by degree (high gregariousness) was associated with a fast spread of information or disease in a social network.	BW
Transitivity / Clustering Coefficient	“Proportion of triads [with] three edges divided by number of triads [with] two edges. When compared to null models, this identifies whether trios have a tendency to be more or less connected than expected.” It “captures the level of clustering in the network”, which can be important when measuring interactions. “For example, grooming networks may have low transitivity if grooming is directed up or down a linear hierarchy.” This metric can also be assessed at the node level. If using the gambit of the group approach, one should be careful as the transitivity measure closes triads (but consequences of this are unknown).	BW

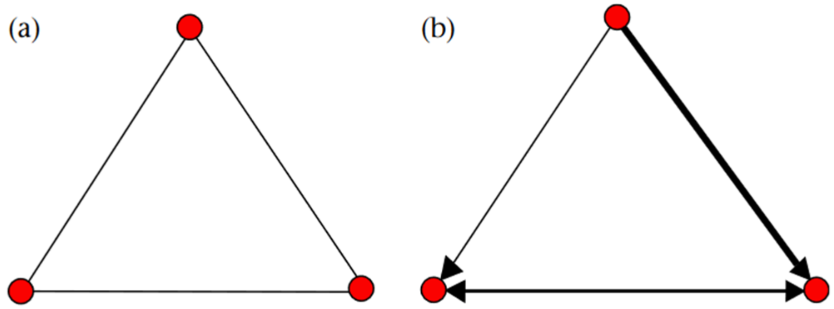


Figure 1. Triadic networks with ties that are **(a)** unweighted and undirected, and **(b)** weighted and directed. Red circles are nodes (or individuals) and black lines are edges (associations or interactions). Adapted from Wey *et al.* (2008).

Not all members of a group incur the same costs and gain the same benefits of sociality (King et al., 2008) and social network analysis is useful in describing and quantifying such disparities. Different positions (or centralities) in social networks have been associated with specific fitness outcomes in several taxa (e.g., influencing offspring survival and adult and offspring longevity) (Brent, 2015; McFarland et al., 2017). Centrality can be defined as the relative importance of a node in the general structure of a community (Wey et al., 2008), with socially central individuals tending to fare better than more peripheral group members (Brent, 2015). More central individuals tend to know and spread more information, and potentially spread more disease as well (Brent, 2015). Fitness outcomes can vary based on the social context and species. In juvenile male bottlenose dolphins (*Tursiops* sp.), being more central allowed them to avoid harassment from other community members (Stanton & Mann, 2012). Vervet monkeys with stronger bonds (strength centrality) in their grooming networks experienced lower risks of predation (Josephs et al., 2016) and were more protected from nocturnal hypothermia (McFarland et al., 2015). Nonetheless, centrality may not always be advantageous to individuals. For instance, more spatially central female white-faced capuchin monkeys (*Cebus imitator*) and their infants were more frequent targets of harassment (Kalbitzer et al., 2017).

Additionally, dominance rank can affect social networks with dominant individuals tending to be more central than subordinates (Blaszczyk, 2018; Borgeaud et al., 2017). For instance, higher-ranking vervet monkeys were groomed more often than others and displayed more aggression towards other group members, which made them more central in grooming and aggression networks (Blaszczyk, 2018; Borgeaud et al., 2017). Dominant vervets represent ideal associates as they can grant access to resources (Borgeaud et al., 2015) and represent more useful alliance partners during agonistic encounters (Seyfarth, 1977). However, associations among vervet kin are preferred by individuals since kin are similarly ranked in the group hierarchy and therefore are more accessible than dominant individuals (Seyfarth, 1977; Seyfarth, 1980), as well as providing inclusive fitness benefits (Hamilton, 1964). Identifying more central members is informative on (1) the mechanisms by which social structure remains stable, even amidst disruptions and diverging interests within groups, (2) the characteristics of a central individual, and (3) the spread of information and disease across group members (Canteloup et al., 2020a; Canteloup et al., 2021; Flack et al., 2006; Romano et al., 2016).

1.3 Social Network Analysis for Juveniles

Immature individuals undergo rapid changes throughout their development (Vilette et al., 2022). For instance, the affiliative networks of juvenile ravens (*Corvus corax*) were denser than subadult networks (Kulahci et al., 2016). Additionally, juvenile ravens with more frequent affiliative ties selectively observed and therefore learned from each other more often (Kulahci et al., 2016). Juveniles play a significant role in shaping their social environment and their affiliative patterns might change over time to match their future social roles as adults (Kulik et al., 2015). For example, young long-tailed manakins (*Chiroxiphia linearis*) who were more central in non-aggression contact networks were more likely to become the alpha male in their leks as adults (McDonald, 2007). In primates, the juvenile period is notably long (Jones, 2011; Pusey, 1990), which allows immatures to develop, modify, and maintain relationships with other group members. This long juvenile period might be linked to higher fitness as it allows primates to acquire the adequate cognitive proficiency needed for social competence (Joffe, 1997). During this period, juveniles build their social niche, whereby their social environments start to develop in accordance with the social niches that are available (Odling-Smee et al., 2013). There can be different paths leading to this, such as a ‘social revolution’ as can be seen in rhesus macaques (*Macaca mulatta*) who reach a milestone, at which point they express sex-specific social behaviours that match very closely to their adult roles (Kulik et al., 2015). Conversely, the attainment of a social niche might also be a more progressive and slow transition throughout primate development. Juveniles might shape their niche by social assortment (i.e., associating more frequently with individuals who share phenotypic characteristics with them; Deputte, 2000). In many species, association and interaction patterns change during juvenile development. Roatti et al. (2023) found that juvenile chacma baboon integration into grooming networks increased as they aged whereas their associations in proximity networks decreased. The authors suggested that older juveniles might need less agonistic support, play more, become less attractive to adults than younger juveniles (i.e., lower integration in proximity networks), and may become better groomers as they age (i.e., higher integration in grooming networks), since grooming is a learnt behaviour. Grooming may also represent a more important activity to adults than to juveniles, motivating adults to cooperate and establish coalitions.

Juveniles across species might be more socially active to provide themselves with more opportunities for social learning and be better prepared for adulthood (Laland, 2004). Juveniles of several taxa display a greater interest in pursuing social opportunities (e.g., muzzle contact, proximity, play) than adults, as seen in rhesus macaques (Liao et al., 2018), bottlenose dolphins (*Tursiops aduncus*) (Krzyszczyk et al., 2017), vervet monkeys (Nord et al., 2021), and mantled howler monkeys (*Alouatta palliata*) (Rodrigues, 2007). Effectively, integration in social networks is crucial to juveniles' social, motor, and cognitive development, and therefore, to their future adult selves (Pellis & Pellis, 2007).

1.4 Maternal Network Inheritance

Mothers influence their offspring through a variety of pathways, such as hormonal, cognitive, genetic, nutritional, social, environmental, emotional, and learning (Maestripieri, 2009). Observations of primate mother and infant or juvenile interactions revealed the occurrence of teaching (e.g., locomotion, foraging, gestural communication) (Maestripieri, 1995a), suggesting mothers can be a key source of information during offspring development. For example, maternal parenting style is transmitted to daughters in some species (Maestripieri, 2018). Moreover, mothers may also influence the types of partners their offspring associates with (Maestripieri, 2018). In rhesus macaques, maternal and infant relationships tend to mirror each other since infants spend most of their time with their mothers (Berman, 2004). In this way, mothers not only introduce their offspring to specific social opportunities, but their behaviour also constitutes a model that is observed and reproduced by their offspring (Kulik et al., 2015). Although there is limited evidence that mothers encourage their offspring to interact with specific partners, rhesus macaque mothers have been seen trying to prevent them from associating with certain social partners (Maestripieri, 1995b; Maestripieri, 2018). Thus, mothers can have long-term effects on the social lives of their offspring, including their behavioural tendencies and social preferences (Maestripieri, 2018).

In recent years, there have been reports of intergenerational inheritance of maternal social connections in several taxa (Ilany & Akçay, 2016). Mammals, including cercopithecine primates, have been observed to display this pattern (Roatti et al., 2023; Berman, 1982; Brent et al., 2013). For example, young chacma baboons inherited their mothers' networks and branched off from them later in life to become more selective and associate more with same-sex and same-age partners, though their mothers' connections continued to affect their bonds later in life (Roatti et al., 2023). Similarly, social networks of immature rhesus macaques matched their mothers' networks and were still influenced by these as they aged and reached locomotor independence (Berman, 1982; Brent et al., 2013). The process of maternal social inheritance is often recorded in taxa with multigenerational and stable social groups such as African elephants (*Loxodonta* *africana,* Goldenberg et al., 2016; Ilany & Akçay, 2016). Social network inheritance can be adaptive as it allows for the maintenance of network centralities from one generation to the next (Goldenberg et al., 2016), an idea supported by the observation that it was related to greater longevity in both spotted hyena (*Crocuta crocuta*) offspring and their mothers (Ilany et al., 2021).

Network inheritance may happen passively through spatial associations and not necessarily following active introductions of social partners (Ilany & Akçay, 2016). Maternal inheritance of social connections may reflect the young age of infants and juveniles, such that they may lack the assertiveness to choose partners based on their affiliative preferences, as suggested by Vilette et al. (2023) in relation to strong grooming ties. Furthermore, network inheritance may only apply to certain social network metrics and not others. Studies have shown that specific network metrics are heritable in some species whilst others are not (e.g., Brent et al., 2013). While the process of network trait inheritance might also have a genetic basis (i.e., social preferences from parents), at least some of the traits' heritability is social (i.e., emulating their parents; Ilany & Akçay, 2016). This social heritability might occur through repeated interactions with mothers' social circles due to mother-offspring proximity, which is common in mammals until the weaning of offspring (Ilany & Akçay, 2016). Overall, juveniles' selective preferences of certain social partners over others could be the result of passive observation of mothers (i.e., social learning), familiarity (i.e., spatial association), or maternal actions (i.e., mothers promoting certain associations for their offspring) (de Waal, 1990; de Waal, 1996).

Social ontogeny represents a complex process such that the inheritance of maternal connections should be nuanced. The social integration of immatures may occur through several pathways independent from maternal social network inheritance. A possible explanation to juvenile social tendencies throughout development is that individuals tend to prefer to associate with similar individuals as themselves (i.e., assortativity) (Ilany & Akçay, 2016), regardless of maternal preferences. Effectively, offspring networks tend to be similar but not be identical replicas of their mothers' (e.g., Roatti et al., 2023). Maternal networks can change frequently over time, which might prevent infants and juveniles from keeping up with these changes (i.e., moving target postulate: Jarrett et al., 2018). Alternatively, gradual distancing between mother-offspring dyads throughout development might predict their future divergence in social partner preferences. For example, proximity between mother-offspring dyads decreased between one and three years of age in captive green monkeys (*Chlorocebus sabaeus*) (Fairbanks & McGuire, 1985). Similarly, chacma baboons associated less often with their mothers and her social partners as they aged (Roatti et al., 2023). This pattern may reflect the growing independence of juveniles, notably ecological competence (e.g., foraging) and social competence, leading them to need less maternal care and protection (Alberts, 2019).

1.5 Sex and Age-specific Network Inheritance

Even when mother-offspring dyads are frequently in proximity, juvenile networks can start to diverge from their mother's networks due to contrasting sex-specific life history strategies. The sex-specific social behaviours of offspring during development can emerge early on and may reveal adaptive differences in male and female life history strategies. Individuals are predicted to express behaviours in accordance with their future paths: philopatry or dispersal (Maestripieri, 2018). In female-philopatric species, young females emphasize socializing and thus are more central in their social groups, whilst young males tend to spend more time playing and become more distant from the group as dispersal approaches (Maestripieri & Ross, 2004; Roatti et al., 2023; opposite trends are observed in male-philopatric species, Cords et al., 2010). As such, in female-philopatric species, immature females often have more social associates and devote greater efforts to grooming than immature males (Roatti et al., 2023). These patterns allow parenting skills to develop in females while males tend to develop skills that aid in dispersal (e.g., competitive behaviour) (Maestripieri & Ross, 2004). Philopatric females find high benefits in building long-lasting ties as they will be spending their entire lives in the natal group (Smith et al., 2003). By contrast, males in female-philopatric species tend to become peripheralized from the social group as time goes by (Roatti et al., 2023; Lonsdorf, 2017). While many philopatric females directly inherit maternal rank (e.g., Holekamp & Smale, 1993; Kutsukake, 2000), dispersing males often establish their dominance rank by competing in agonistic interactions with other group members and without matrilineal support (McGuire, 1982). Matrilineal bonds will allow females to be supported during agonistic conflicts, thereby helping them in maintaining the rank they inherited (Silk et al., 2004). However, even the dispersing sex might benefit from forming bonds with other group members prior to dispersal (Schoof et al., 2009). For example, engaging in parallel dispersal (i.e., dispersal with peers or close kin or immigration into a group containing familiar or related individuals; van Hooff, 2000) can be very advantageous to young males (e.g., reducing predation risk, higher takeover success; Pusey & Packer, 1987; Pope, 1990). This process can occur as both natal group dispersal and secondary dispersal (Schoof et al., 2009). In turn, parallel dispersal provides these males with the opportunity to form long-term social bonds with their dispersing peers and/or kin (van Hooff, 2000).

Furthermore, sex-specific differences in immature social patterns can be related to differential treatment of offspring by mothers and can result in offspring exhibiting different patterns of network inheritance. For instance, chimpanzee mothers appear to encourage patterns of socialization in their infants that are congruent with their future sex-specific adult roles (Lonsdorf, 2017). In cercopithecine primates, mothers tend to spend more time with their daughters than their sons and groom them more often, while also showing aggression more often to their sons than their daughters (Kulik et al., 2016). As such, mothers likely adjust their investment to favour the philopatric sex (Soben et al., 2023a). Macaque daughters groomed group members more often and started doing so at an earlier age than sons did, likely due to the greater frequency of grooming received by daughters from adult females (Maestripieri, 2018; Roney & Maestripieri, 2003). In contrast, male chacma baboons had shallower bonds with their mothers and her social partners than daughters did, possibly due to greater mother-offspring distance from sons than daughters, with males progressively peripheralizing from the group compared to females (Roatti et al., 2023). Taken together, these patterns reveal that mothers in female-philopatric species might be fostering closer ties with their daughters than with their sons (Kulik et al., 2016). As such, daughters' social ties may more closely mirror those of their mothers than those of sons (Suomi, 2005).

1.6 Maternal Rank and Age Effects on Offspring Network Inheritance

Dominance rank tends to be strongly related to fitness outcomes (Thompson, 2019), and maternal effects on offspring can extend to maternal dominance rank. Dominance can be defined as the consistent outcome in which the triumph of one member of a dyad over the other during agonistic interactions leads to the yielding of the unsuccessful individual (Drews, 1993); dominant and subordinate status in dyads can then be mapped onto a dominance hierarchy, yielding an individual rank within said hierarchy. Holding a high rank within the group may confer priority of access to food, mating partners, and reproductive success (Majolo et al., 2012; Alberts et al., 2006).

Dominance is highly relevant to social relationships, and coalitions can be important in the attainment and maintenance of dominance rank (Thompson, 2019). For example, tighter bonds between male Assamese macaques (*Macaca assamensis*) led to the formation of alliances which, in turn, raised their rank and reproductive success (Schülke et al., 2010). Reciprocally, individual rank can also affect social behaviour. Seyfarth (1980) showed that adult female vervet monkeys higher in the social hierarchy were groomed more often than others, likely because group members attempt to buy tolerance (e.g., feeding, mating) from higher-ranked members (Seyfarth, 1977). Dominance rank has been associated with network centrality in primates, whereby higher-ranking individuals tend to associate and interact with more social partners than lower-ranking individuals (Jarrett et al., 2018; Schino, 2001), though this can be context-dependent (Teichroeb et al., 2015).

In most cercopithecine primates, dominance ranks are inherited from mothers due to several pathways, such as maternal agonistic support and offspring's observation of their mothers and their interactions (Holekamp & Smale, 1991; Chapais, 1992). Rank inheritance is likely not genetically determined in cercopithecine primates, as adopted monkeys inherit their adoptive instead of their biological mother's rank (Chapais, 1992). Furthermore, maternal rank can affect mothers' behaviour towards their offspring. High-ranking captive green monkey mothers sought proximity with their offspring, especially daughters, more than low-ranking mothers (Fairbanks & McGuire, 1985). While high-ranking mothers expressed more frequent agonism towards their offspring, they also supported them more than low-ranking mothers did (Fairbanks & McGuire, 1985). Maternal rank can also affect offspring behaviour (e.g., grooming more high- than low-ranking mothers), with captive green monkey maternal rank affecting the behaviours of both mothers and offspring in most of the behaviours studied (Fairbanks & McGuire 1985). As suggested by de Waal (1996), matrilineal ranks have been found to have branching consequences on matrilines, such as spatial associations and affiliations among kin (e.g., Sade, 1972; Kurland, 1977), and bonds and tolerance among similarly ranked non-kin (de Waal, 1991; de Waal & Luttrell, 1986; Seyfarth, 1977; Seyfarth, 1980). Even in non-primate species, such as spotted hyenas, higher maternal ranks are linked with higher mother-offspring network similarity (Ilany et al., 2021).

Few studies have investigated the effects of maternal dominance on their juvenile's network structures, likely because this relationship is indirect. We know that in some species, dominance rank affects maternal social networks, and that juvenile offspring can inherit these maternal networks. For example, higher-ranking juvenile rhesus macaques of higher-ranking mothers had more extensive social networks than low-ranking juveniles of low-ranking mothers, indicating that maternal dominance ranks had indirect effects on juvenile networks from a very early age (Wooddell et al., 2020). Interestingly, Ilany et al. (2021) found that the network of spotted hyena mothers and offspring were very similar for up to six years and that these similarities were greater in mother-offspring dyads where mothers were high-ranking. Any influence of maternal rank on offspring networks would likely affect daughters more than sons in female-philopatric species, since sons are mostly freed from the influences of maternal rank upon their dispersal (Fairbanks & McGuire, 1985).

While little research has been done on the potential effects of maternal age on their juveniles' social networks, we know that the relationship between maternal rank and age as well as the consequences of maternal age on their offspring are complex (Machanda & Rosati, 2020). Regarding the influences of age on dominance rank, captive adult female green monkeys did not decrease their involvement in agonistic interactions as they aged (Fairbanks and McGuire, 1986). This trend is also observed in other cercopithecines such as female yellow baboons (*Papio cynocephalus*) who typically maintain their dominance rank as they age, experiencing rank declines only when their health deteriorates (Hausfater et al., 1982). Others have found that, as females age, their hierarchical position increases, as seen in wild eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Foerster et al., 2016). In parallel, in bonnet macaques (*Macaca radiata*) (Silk et al., 1981) and yellow baboons (Lea et al., 2014), rank reversals between mothers and their daughters were more prevalent when mothers were very old. As such, the effect of age on sociality may occur independently from that of dominance rank: yellow baboons experienced opposite effects of age and rank as older low-ranking females had larger networks (i.e., more partners) yet socialized less often with these partners and older high-ranking females had smaller networks yet socialized with them more often (Pavelka et al., 1991).

As such, it is important to investigate the effects of both dominance rank and age on offspring sociality. In long-lived species with multigenerational groups and kin-based interactions such as green monkeys, social strategies should adjust as individuals (e.g., mothers) age (Fairbanks & McGuire, 1986). Maternal investment in offspring should thus increase with age since older females have lower reproductive value due to limited prospective reproductive events (Clutton-Brock, 1984). Additionally, as females age, they tend to have more offspring (e.g., captive green monkeys: Fairbanks & McGuire, 1986), gain more life experience (including rearing experience), and this experience will likely increase commensurately with parity (Soben et al., 2023a). In captive green monkeys, neglect was the main cause of offspring death when mothers were qualified as marginal (i.e., very young or very old, lower-ranking, and with a low weight), with mothers spending less time in physical contact with their offspring than mothers in their prime (Fairbanks & McGuire, 1995). Multiparous mothers may have gained knowledge in their previous rearing experiences about specific critical windows of offspring development that they can then leverage to provide intensified care at these sensitive times to future offspring (e.g., Fairbanks, 1996). Similarly in mandrills (*Mandrillus sphinx*), mothers improved their ability to care for their offspring as they gained experience (Roura-Torres et al., 2025; but see captive green monkeys: Fairbanks, 1988a). As mandrill mothers aged and had more offspring, they were closer to their offspring and groomed them more often, both of which support successful social integration and overall development (Roura-Torres et al., 2025; Maestripieri et al., 2009). Having offspring at an advanced age grants mothers additional knowledge (e.g., social behaviours) from previous offspring (i.e., multiparity) and from pre-breeding experiences (e.g., raising siblings) which they can then apply to their future offspring.

1.7 Study Organism

Vervet monkeys (*Chlorocebus pygerythrus*) are one of the most widespread primates in Africa, with six identified taxa constituting the genus *Chlorocebus* (Turner et al., 2019). They are omnivorous, territorial (Struhsaker, 1967b), and found in a wide range of habitats (Turner et al., 2019). Adult vervets have a grey coat, a black face, hands, and feet, and white fur around their face and stomach (Turner et al., 2019), whereas infants have a pink face and a black coat (Lee, 1984). Adult males also have a red penis and blue scrotum (Turner et al., 2019), and male body size and weight are greater than that of females (Turner et al., 1997).

The juvenile period is estimated to start around 5-7 months of age (Lee, 1984). Females reach sexual maturity and tend to have their first infant at 3-5 years of age (Henzi et al., 2023). Males disperse from their natal group around 5 years of age, which is assumed the age of sexual maturity (Cheney, 1981; L'Allier et al., 2022), and this is followed by secondary dispersal every 2.5-3 years (Cheney et al., 1988). The Nabugabo vervet population expresses moderate breeding seasonality, with the birth peak spanning between October and January and year-around copulations (Schwegel et al., 2023). Each gestation period lasts about 163 days, with interbirth intervals of 1-2 year(s) (Kavanagh et al., 2011; Lee, 1984), though the Nabugabo vervet population has a mean interbirth interval of 11.5 months (Schwegel et al., 2023). Females birth a single offspring at a time (Jarrett et al., 2018). Infant survival to weaning has been linked with resource availability, maternal dominance rank, and the number of spatial partners in maternal networks (Blersch et al., 2023).

Vervets are group-living and social, with groups of 3 to 72 individuals composed of females and males and characterized by female-philopatry and male dispersal (Young & Isbell, 1994; Pasternak et al., 2013; Struhsaker, 1967c; Cheney, 1981). Vervets socially organize in linear dominance hierarchies where females and males may be co-dominant (Bramblett et al., 1982; Young et al., 2017), though sex-specific hierarchies are often used to characterize dominance relationships among males and females. Female dominance hierarchies are characterized by ranked matrilines, within which female rank is inherited maternally following a pattern of youngest ascendancy (i.e., youngest daughter ranks directly below her mother) (Bramblett et al., 1982; Horrocks & Hunte, 1983). Conversely, male dominance is generally established based on individual competitive ability, especially in adulthood (McGuire, 1982). While previous work has demonstrated that high-ranking vervet monkeys are more socially central (Canteloup et al., 2021), preliminary research suggests that female vervet centrality is not linked to dominance rank in the Lake Nabugabo population (Schwegel, 2023), making this population a particularly interesting one. Grooming is the main social interaction that occurs among vervet monkeys, taking up 90% of their social time and being expressed by both juveniles and adults (Jarrett et al., 2018).

Vervets are an excellent model species to address maternal network inheritance and effects of maternal dominance rank and age because of their long period of juvenescence (Pereira

& Altmann, 1985), multimale multifemale group structures, and multigenerational troops composed of multiple matrilines (Young et al., 2017; Struhsaker, 1967c; Kavanagh et al., 2011). Additionally, vervet monkeys maintain consistent proximity and grooming network centralities (Blaszczyk, 2018; Borgeaud et al., 2017; Canteloup et al., 2020b) and such stability allows a better detection of any trends in social network analysis. Very few studies have compared maternal and juvenile social networks in vervet monkeys, notably Jarrett et al. (2018) and Vilette et al. (2023), both of which were conducted on the same South African population. Jarrett et al. (2018) found that this South African population of vervets mostly did not show maternal network inheritance since grooming networks fluctuated a lot over time, and patterns of maternal partner identity alone were not sufficient to replicate daughters' grooming networks. Nonetheless, maternal strength was positively associated with daughters' out-similarity in grooming networks (Jarrett et al., 2018). Stability in mothers' networks increased similarity between mother-daughter networks and network stability was heritable to daughters, although the latter result had a small effect size (Jarrett et al., 2018). Additionally, Vilette et al. (2023) found that weak grooming ties were largely dissimilar for mothers and their offspring but were more similar in mother-daughter than mother-son dyads. While the only two studies done in vervets indicate an influence of maternal networks on juvenile networks, both found that juveniles failed to completely replicate maternal grooming networks (Jarrett et al., 2018; Vilette et al., 2023). However, neither study explored the effects of maternal rank or age on juvenile offspring social networks, which may play an important role in immature offspring social networks.

1.8 Research Questions, Hypotheses, and Predictions

To examine maternal effects and social network inheritance in vervet monkeys, I aimed to evaluate whether there is evidence for maternal social network inheritance in the Nabugabo study population, how mothers might affect immature offspring social networks, and whether this effect differs by offspring sex and/or age. I hypothesized that maternal social network inheritance occurs and differs by sex and age in vervet monkeys because of (1) mother-offspring proximity, (2) influences of maternal dominance rank and age, (3) social integration mechanisms in vervets, and (4) female philopatry.

I hypothesized that if social network inheritance occurs and this process is linked with mother-offspring proximity, then maternal social network metrics will explain variation in their offspring's network metrics, especially for close mother-offspring pairs. As such, I tested the prediction that mother-offspring proximity indices (1a) are positively correlated with mother-offspring cosine similarities, (1b) decline with offspring age with the rate of dissimilarity possibly being higher for males than females, and that (1c) immature daughters are spatially closer to their mothers than sons. In addition, I expected (1d) mothers with larger, denser, and more connected spatial and grooming networks will have immatures with similarly high values of network parameters.

I also hypothesized that maternal dominance rank and age will affect their offspring's social networks. Specifically, I predicted that (2a) more dominant and (2b) older mothers will have immatures with higher degree, strength, and centrality in their spatial and grooming networks reflective of their mother's network metrics.

Thirdly, I hypothesized that offspring age will be associated with different social network trends for daughters and sons due to social integration mechanisms in vervet monkeys, including youngest ascendancy in females and the approach of dispersal in males. Older immature offspring are expected to (3a) have fewer social associates (i.e., lower spatial degree) and (3b) have weaker relationships with those partners (i.e., lower spatial strength) than younger immatures (Vilette et al., 2022). I also predicted that (3c) social centrality will be lower for older than younger offspring. Additionally, I predicted (3d) less similarity between immature offspring social partners and their mother's networks (i.e., lower mother-offspring cosine similarities) for older compared to younger immatures, with the rate of dissimilarity possibly being faster for sons than for daughters (chacma baboons: Roatti et al., 2023; vervets: Jarrett et al., 2018; spotted hyenas: Ilany et al., 2021). Lastly, I predict that (3e) grooming degree and strength will be higher for older offspring and grooming strength is expected to have a stronger positive relationship with offspring age in daughters than in sons (i.e., differences in grooming strengths in older compared to younger daughters will be greater (or more positive) than differences in older compared to younger sons) (Vilette et al., 2022).

Finally, I hypothesized that female and male immatures will display different network patterns and dynamics because vervets are characterized by female philopatry and male-biased dispersal. As such, I predicted that (4a) immature females will have similar spatial but higher grooming network parameter values and be more central overall than immature males (Vilette et al., 2022), and (4b) daughters are expected to have more similar network metrics to their mothers' than sons.

2.0 Materials and Methods

2.1 Study Site, Population, and Data Collection

Data were collected on one group of habituated vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo in southern Uganda (0°22' S 31°54' E) between May 13th and July 26th, 2024. Lake Nabugabo, a satellite lake of Lake Victoria, is surrounded by a combination of dense wetland and human-modified landscape on the west side, which is composed of grasslands, areas of regenerating vegetation, forest patches, agricultural fields, and a couple of buildings (Chapman et al., 2016).

The study group has been the subject of research since 2011, and was composed of 39 adult, subadult, and juvenile individuals at the mid-point of the study (June 19th, 2024), including 11 adult females (after first birth), six adult males (with one disappearance July 5th, 2024), five subadult females (3 years - first birth), one subadult male (4 years - first dispersal), four juvenile females (6 months - 3 years), 11 juvenile males (6 months - 4 years), and a juvenile of unknown sex. Of the 11 adult females, behavioural data were collected on eight mothers. As for the 22 juveniles and subadults (i.e., immatures or offspring herein), 17 were used in subsequent analyses. Fewer immatures were used in the analyses than sampled due to changes in age-sex classifications as well as the fact that some immature individuals were orphans. In my analyses, I considered individuals' ages (in months) precisely at the mid-point of the field season (June 19th, 2024). Some mothers' exact age was unknown as they were already present in the group when it was first habituated. In these cases, maternal age was estimated by evaluating age when the individual was first found based on age categories (e.g., found as a juvenile female so individual must be at least 6 months of age), and adding the number of months that had passed since then. Sex was obtained from our observations during the field season.

I collected instantaneous focal follows and *ad libitum* data. For each instantaneous focal follow, instantaneous scans were taken every 20 seconds; follows lasted 15 minutes for mothers (N = 8) and 5 minutes for immatures (N = 17), given that the latter tend to be more active and difficult to follow. I conducted a total of 334 focal follows (mean ± SD: 41.75 ± 5.42, range: 34-49) on mothers and 946 focal follows on immatures (mean ± SD: 55.65 ± 7.53, range: 39-67), excluding follows where the focal individual was out of sight for ≥ 20% of total focal time and excluding some immatures (see above). One immature, the only subadult male, was not focaled but was considered in subsequent analyses using *ad libitum* data and data from other individuals' focal follows. Data were collected six days a week between 7 am and 6 pm. Variables collected included focal identity (i.e., mother or immature), behaviour (see Ethogram), and (if any) interactant(s), and nearest neighbour(s) (within 2 meters). I collected *ad libitum* data by recording individual identity, behaviour (except for associations and behaviours that included only one individual), and interactant(s). *Ad libitum* data collection and focal follows were conducted using hand-held PSION computers, with focal animals selected haphazardly based on availability while trying to keep data collection balanced.

I used all dyadic intragroup agonistic interactions (i.e., avoid, chase, bite, bob, hit, supplant, lunge, eyelid flash) from *ad libitum* and focal data to develop an intersexual dominance hierarchy, given previous studies that indicate female-male co-dominance in vervet monkeys (e.g., Bramblett et al., 1982; Young et al., 2017). I calculated individual ranks using Elo-scores (Neumann et al., 2011) on the last day of the field season with the *EloRating* package (Neumann & Kulik, 2019) in RStudio version 2023.09.1+494 (R Core Team, 2024). Extracting Elo-scores on the last day of the sampling period allowed for an extensive burn-in period of 2.5 months. Compared to traditional matrix-based methods, Elo-rating scores are dynamic in that they account for changes in group composition and incorporate all hierarchy changes that arise over time due to the sequential nature of agonistic interactions (Neumann et al., 2011). Any two agonistic behaviours occurring within 15 minutes of each other involving the same dyad members were considered as part of the same agonistic bout (Schwegel et al., 2023). For each bout, a winner was defined as the individual who performed an aggressive behaviour and/or received a submissive behaviour, whereas a loser was on the receiving end of aggressive behaviours and/or submitted to the other individual. Interactions during which both members of the dyad displayed aggressive behaviours towards one another were classified as draws (Schwegel et al., 2023). I first generated a dominance hierarchy using a default starting Elo-score value of 1000 and a k-value of 100, with k being the increment by which an individual's Elo-score changes when they win or lose an agonistic interaction (Neumann at al., 2011). This initial hierarchy allowed me to calculate the optimized k-value with the function "optimizek" which uses a maximum likelihood approach (Neumann & Kulik, 2019). I provided a range of 4 to 200 for k values and a resolution of 491, such that each tested value of k was separated by 0.4 units (Schwegel, et al., 2023). This process yielded an optimized k-value of 171.2. Hereafter, I isolated the Elo-scores of all 8 mothers (Figure 2) and converted them to ordinal ranks, where 1 represents the highest rank. These ordinal ranks were then standardized across mothers to obtain proportional dominance ranks by calculating (hierarchy size – ordinal rank) ÷ (hierarchy size – 1), which allowed to account for maternal group size (Levy et al., 2020; Schwegel et al., 2023). I also ran the same exact statistical models prior to the conversion of Elo-scores to ordinal ranks (i.e., proportional ranks taken directly from the final hierarchy scores with all group members and no standardizing across mothers) and observed the same trends with very similar estimates and credible interval (CrI) values, including for the maternal dominance rank predictor.

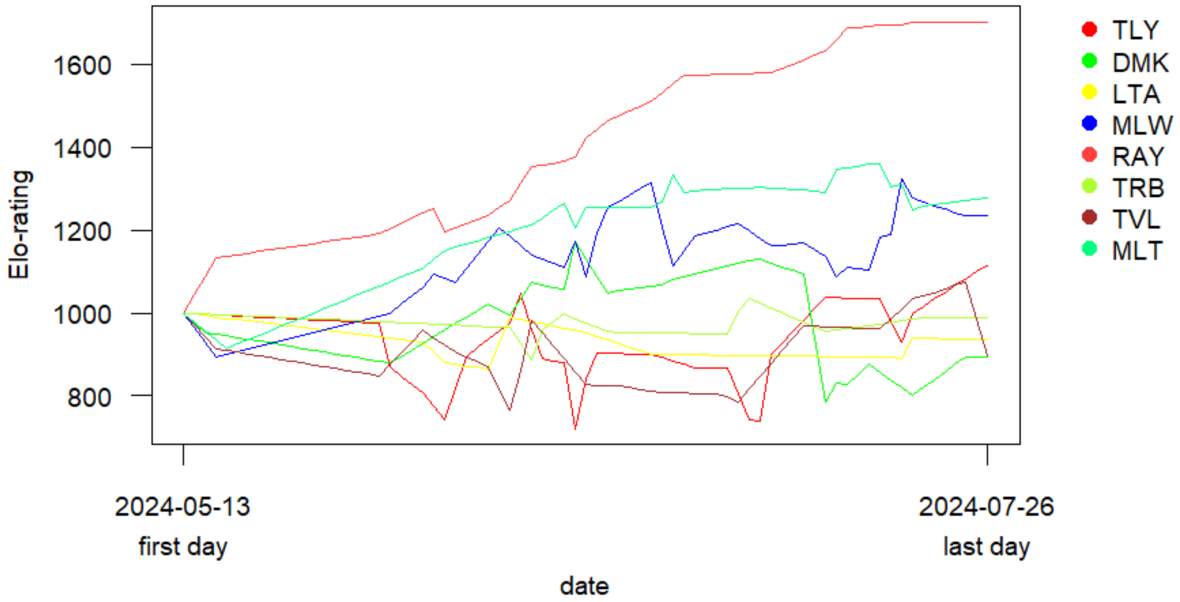


Figure 2. Elo-plot depicting dominance relationships between all mothers of immature offspring (N = 8) in one group of vervet monkeys between May 13th, 2024 and July 26th, 2024 at Lake Nabugabo, Uganda. Legend on the right side represents individual identity codes.

2.2 Social Network Analyses

I used social network analyses to detect patterns of social change across immature ages and sexes using a cross-sectional approach. I considered proximity networks (i.e., nearest neighbour) from focal data and grooming networks from both focal and *ad libitum* data. I built undirected networks since my predictions are independent of the direction of associations and interactions, as well as networks weighted by the frequency of associations/interactions (Figure 1). For each network, I quantified four metrics: degree, strength, eigenvector centrality, and cosine similarity. Degree is the number of partners an individual has, whereas strength is the frequency of associations and/or interactions with those partners (Farine & Whitehead, 2015) (Table 1). Eigenvector centrality can be defined as the sum of the centralities of a node's neighbours and is a metric frequently examined in relation to dominance rank and fitness metrics

(Farine & Whitehead, 2015). Cosine similarity is used here to quantify the similarity of social partners across two different individuals (i.e., mother-offspring dyads) (Jarrett et al., 2018). Using focal data, I also estimated mother-offspring proximity indices (i.e., Simple Ratio Index; SRI) by calculating the proportion of scans for which offspring and mothers were nearest neighbours, which was calculated as the number of scans for which the pair are nearest neighbours ÷ (total number of scans in which the mother appears + total number of scans in which the offspring appears + total number of scans in which the pair are nearest neighbours), which allowed me to control for sampling effort (Whitehead, 2008).

We built undirected grooming and proximity networks using the *bisonR* package in R, which operates under a Bayesian framework (Hart et al., 2024; Hart et al., 2023) and used AI-software ChatGPT (Version GPT-5) to help with code errors. From these networks, I ran three edge weight models using the “bison_model” function to extract 1,000 iterations of weight separately for grooming networks using focal and *ad libitum* data, and focal data only for proximity networks. The BISoN (Bayesian Inference of Social Networks) framework accounts for sampling effort and subsequently propagates uncertainty in downstream analyses (Hart et al., 2023). Network edge weights represented the number of times each dyad associated or interacted for proximity or grooming networks, respectively, relative to the sampling effort over the field season (i.e., for focal data: total number of scans where focal is present + total number of scans where interactant is present if interactant was also a focal subject during the field season; for *ad libitum* data: total number of observation hours during the field season). Given that focal data sampling had known sampling maximums that needed to be accounted for, binomial probability distributions were specified to focal edge weight models (grooming and proximity), whereas a Poisson distribution was provided for the *ad libitum* edge weight model (grooming networks) for the outcome variables (i.e., all count data). I selected weakly informative priors for edge weight models, using a normal distribution with mean = -1 and sd = 1 for grooming networks and mean = -0.5 and sd = 1 for proximity networks as individuals were expected to associate more than they interacted (Vilette et al., 2022). Traceplots revealed that the Markov chain Monte Carlo (MCMC) chains were well-mixed and had converged (Figure S1) (Hart et al., 2024). Edge weight networks displayed relationship trends that were congruent with my field experience (Figure 3), and posterior predictive plots demonstrated that predictions of all models were able to recreate the data they were fit on (Figure S2) (Hart et al., 2024). I then conducted a non-random edge weight analysis for each model; this analysis is the Bayesian analog of the Bejder *et al.* (1998) non-random association test (Hart et al., 2023). As such, I could compare the probabilities of the actual edge weight models with null versions of the models (i.e., in which all weights are the same) to see if observed network structures were due to sampling alone (Hart et al., 2023). All networks were non-random (model weight: non-random = 1, random = 0) and therefore were not due to sampling alone.

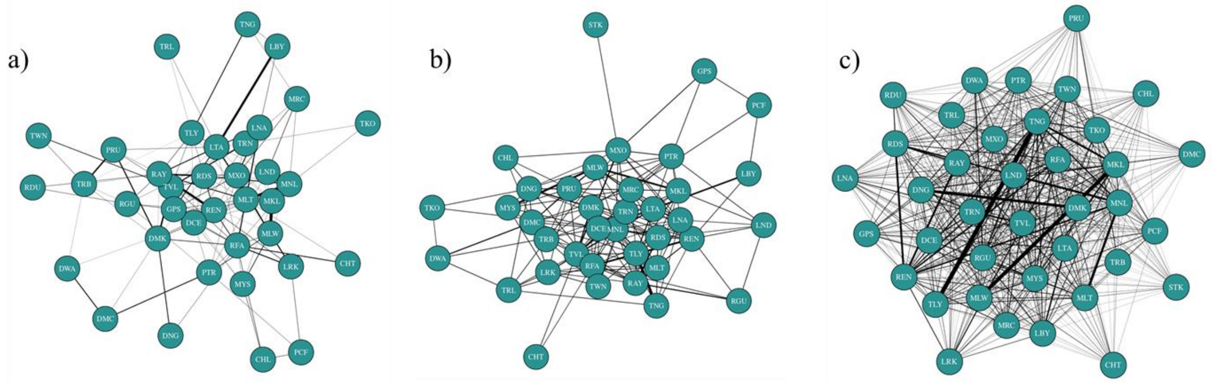


Figure 3. Grooming networks using **a)** focal data (N = 37 individuals), **b)** *ad libitum* data (N = 37 individuals), and **c)** proximity networks using focal data (N = 38 individuals) generated from fitted edge weight models with uncertainty. Grooming sociograms were attributed a line width scale "lwd" of 100 whereas the proximity sociogram was assigned a scale of 25 to allow a full visualization of edge weight variation since there were more associations than interactions. Edges were each plotted using their lower and upper credible intervals, with the expectation that the true weight is found between these two values.

After (1) fitting the three edge weight models (i.e., grooming focal data, grooming *ad libitum* data, proximity focal data), I conducted the following metric extractions. Using code inspired by Motes-Rodrigo et al. (2024), (2) I drew 1,000 posterior samples of edge weights from each model, transformed matrices into graphs, combined edges with two directions, (3) converted edge weights from the logit scale back to probabilities to create networks from these edge weight probabilities. These steps allowed me to (4) extract network measures from the model. This process was then (5) repeated 1,000 times such that I obtained 1,000 data points for each individual and for each metric. For the degree metric specifically, since each edge had a posterior sample (i.e., estimate of the likelihood that two edges will associate or interact), an additional step was necessary: I used the probabilities that were converted from the logit scale in step (3) to randomly create networks using a binomial distribution. As such, I simulated binary outcomes for all edge probabilities by drawing random probabilities from a binomial distribution. To obtain a wide range of interindividual variation of degree, selecting the number of trials (i.e., grooming or proximity events that could have occurred) was necessary. I used the mean total number of scans per focal individual to select this number for focal grooming data, specifying 1,111 trials, and the total sampling hours over the field season for grooming *ad libitum* data, thereby specifying 407 trials. For the proximity networks, I specified 278 trials for focal data (i.e., mean total number of scans per focal individual divided by four: 1,111/4) since proximity degree otherwise displayed a visible left skew given that most individuals within the study group had associated with each other. I then removed edges with a weight of zero before extracting degree. Using the R package *igraph* by Csárdi et al. (2025), I obtained degree, strength, and eigenvector centrality from each 1,000 instantiations. For cosine similarity, I converted graphs back into matrices, removed edges within the same dyads, and manually populated the values for each possible dyad using the package *lsa* (Wild, 2022). Thereafter, I combined focal and *ad libitum* metrics into the same dataset for all subsequent grooming network analyses. I also standardized all continuous predictor variables into z-scores to increase model sampling efficiency and to allow comparisons of effect sizes across predictors in later analyses (Pavez-Fox et al., 2024): offspring age, maternal age, SRI, maternal rank, maternal degree, maternal strength, and maternal eigenvector centrality.

We then used the R package *miceadds* to organize data from each 1,000 iterations into individual imputed datasets (Robitzsch & Grund, 2024) and put these datasets in a list which I then converted into a mids object. Hereupon, I plotted histograms of network metrics for a few offspring with 1,000, 50, and 30 datasets and decided to extract 30 imputed datasets as the histograms revealed a sufficient account of uncertainty.

2.3 Statistical Analyses

For each offspring grooming and proximity network measure, as well as for SRI, I ran a generalized linear mixed effects model (GLMM). As such, offspring grooming and proximity degree, strength, eigenvector centrality, and mother-offspring cosine similarity were the outcome variables, as well as SRI, an additional outcome variable (i.e., total = 9 models). The offspring grooming degree (Model I), strength (Model II) and eigenvector centrality model (Model III) had offspring age and sex, offspring age*sex, maternal age, maternal rank, SRI, as well as maternal grooming network metrics (i.e., degree, strength, and eigenvector centrality) as fixed effects (Table S1). For the mother-offspring cosine similarity models (Model IV for grooming networks), only offspring age, sex, age*sex, and SRI were included as fixed effects (Table S1). This process was repeated for proximity network metrics: offspring degree (Model V), strength (Model VI), eigenvector centrality (Model VII), and mother-offspring cosine similarity (Model VIII). For each of my response variables, I used the function "brm_multiple" from the package *brms*, which allowed me to run the same brm model on my 30 imputed datasets and combine these results into one fitted model (Bürkner, 2021). The package *future* was selected to run these models in parallel (Bengtsson, 2021). For the SRI model (Model IX), I ran a simple brm model (i.e., no imputed dataset) since SRI is an aggregate measure of the observed count data. Fixed effects included offspring sex, offspring age, and the interaction between offspring age and sex (Table S1). Maternal identity was included as a random effect in all models since some offspring shared the same mother.

While I collected and used both focal and *ad libitum* data, those data types may capture different trends (Altmann, 1974). As such, I explored the possibility of this by including a categorical data type variable (i.e., focal vs. *ad libitum* data) as a fixed effect in all grooming models (Model I - IV). I then ran each of my grooming models with both the data type variable and data type interaction terms with other variables as fixed effects. These other variables included offspring age, SRI, maternal age, maternal rank, maternal degree, strength and eigenvector centrality for models I-III, and only offspring age and SRI for model IV. Hereupon, I compared the models containing these interactions to those that did not using the Bayesian leave-one-out cross-validation (LOO-CV) and 10-fold cross-validation (K-fold) methods and compared these models with the function "loo_compare" from the R package *brms* (Bürkner, 2021). All models without the data type interaction terms (i.e., only the data type variable as a fixed effect) either performed similarly or outperformed the models with data type interaction terms (Table 2). The mother-offspring cosine similarity model comparison was the only exception that yielded opposite results (LOO-CV comparison: ΔELPD = -4.5, ΔSE = 7.5, favouring the simpler model; K-fold comparison: ΔELPD = -6.0, ΔSE = 2.7, favouring the more complex model), where ELPD is the expected log pointwise predictive density. Since I ran all the grooming models with the same data, I chose the simpler model structure (i.e., no data type interaction terms) to ensure consistency across models (Table S1). Additionally, as data were limited to 33 data points (i.e., 17 immature offspring in focal data and 16 in *ad libitum* data) in the mother-offspring grooming cosine similarity model, selecting fewer terms through a simpler model structure supported model convergence.

Table 2. Summary statistics of model comparisons using the expected log pointwise predictive density (ELPD) to evaluate how two models' (e.g., simple versus complex) predictive accuracies compare to each other (Bürkner, 2021). Each value corresponds to the difference between the preferred model and the model of interest, which is 0 if it is the preferred model (Bürkner, 2021). SE =ELPD standard error. * = Interaction with Data Type (focal vs. *ad libitum*) for grooming networks only.

			LOO-CV Comparison		**K-fold comparison**	
Response Variable	**Model Complexity**	**Additional Fixed Effects**	*ELPD Difference*	*SE Difference*	*ELPD Difference*	*SE Difference*
Mother-Offspring Cosine Similarity	Simple	Data Type	0	0	-6.0	2.7
	Complex	Data Type + Offspring Age* + SRI*	-4.5	7.5	0	0
Offspring Degree	Simple	Data Type	0	0	0	0
	Complex	Data Type + Offspring Age* + SRI* + Maternal Age* + Maternal Rank* + Maternal Degree* + Maternal Strength* + Maternal Eigenvector Centrality*	-232.8	54.5	-7.2	1.7
Offspring Strength	Simple	Data Type	0	0	0	0
	Complex	Data Type + Offspring Age* + SRI* + Maternal Age* + Maternal Rank* + Maternal Degree* + Maternal Strength* + Maternal Eigenvector Centrality*	-262.4	68.0	-8.5	4.1
Offspring Eigenvector Centrality	Simple	Data Type	0	0	0	0
	Complex	Data Type + Offspring Age* + SRI* + Maternal Age* + Maternal Rank* + Maternal Degree* + Maternal Strength* + Maternal Eigenvector Centrality*	-89.0	42.9	-2.2	2.9

I ran each model with 4 chains per imputed dataset and selected a normal distribution for my priors with a mean of 0 and standard deviation of 1 for the model slopes. For each chain, I specified 5,000 iterations with a 1,000-iteration warm-up, as well as adapt_delta values of 0.9999 for all models to better support model convergence here again. I selected a zero-inflated beta and a simple beta distribution for grooming and proximity mother-offspring cosine similarity, respectively, since grooming cosine similarity had some zero values. I chose a Poisson and negative binomial distribution for the offspring grooming and proximity degree models, respectively, a Gamma distribution with a logarithmic link function for the offspring grooming and proximity strength models, a zero-one-inflated beta distribution for offspring grooming and proximity eigenvector centrality, and a beta distribution for the SRI model. To interpret the results, several measurements were used, such as credible intervals (CrIs) and the probability of direction (pd). Pd ranges 50 - 100% and corresponds to the probability that the posterior distribution of a parameter is positive or negative (Makowski et al., 2019). There is no consensus on the pd threshold for hypothesis testing in the literature, but it remains an important metric to report (Kelter, 2023). As such, I considered any predictor's pd of 90-94% to have a slight directionality, while pd values of 95% and above were considered to have moderate directionality. This remained a conservative approach relative to suggestions from other studies (Kelter, 2020).

As noted above, one juvenile was unsexed. To account for this, I ran all analyses mentioned above with this juvenile as a female and then conducted a sensitivity analysis by rerunning the exact same models but with the unsexed juvenile as a male. General trends were similar across all model pairs. Nonetheless, the grooming degree, strength, and eigenvector centrality model analyses with the unsexed juvenile as a male did yield an upper CrI around zero for the posterior of the age*sex interaction term, which it did not in its female model analog (see Results section). However, all proximity network and SRI models exhibited the same general results.

We ensured models performed appropriately through several methods. I checked that all models converged (i.e., all $\hat{R} \approx 1.00$ and $ESS > 500$). Additionally, I used posterior predictive checks to verify model fit to the data, and the R package *DHARMa* by Hartig (2024) was used to investigate any potential issues with overdispersion. I ran null models to aid in interpretation of the models, with null models created using only fixed but no random effects. Models II, IV, VIII, & IX all converged (i.e., all $\hat{R} = 1.00$). For model IV, all $\hat{R}$ values were approximately 1.00, suggesting the model had converged, except for the precision parameter (phi) of the beta distribution, with a slightly higher $\hat{R}$ value of 1.06. A few of the models, notably model I, III, V, VI, and VII yielded a few $\hat{R}$ values above 1.00. Nonetheless, running these same models with one imputed dataset (instead of 30 datasets) three to five times revealed that the models were converging within each dataset (i.e., all $\hat{R} = 1.00$), just not across all 30 datasets. Results were very similar between the model pairs with one relative to 30 imputed datasets. I used posterior predictive checks which revealed appropriate model fit for most models (Figure S3a, b, & c, S4b, c, & d, & S5). For model IV, although peaks were slightly underestimated in the middle range of cosine similarity values, posterior predictive checks revealed that the model fitted the observed data distribution reasonably well (Figure S3d). However, posterior predictive curves of model V did not match observed data very closely (Figure S4a, with negative binomial family distribution). Since degree is count data (model V), I initially selected a Poisson family distribution, specifying normal priors with a zero-centred mean and a standard deviation of one for all predictor slopes. However, this model did not fit the data well as suggested by posterior predictive checks and an overdispersion test run using the package *DHARMa* (Hartig, 2024). The latter revealed that the data display less variation (i.e., underdispersion) than the model was simulating (i.e., overdispersion), most likely due to the small sample size of 17 immature offspring. As such, I selected a negative binomial family, which resulted in a slight but negligeable improvement in model fit (Figure S4a). Hereupon, I reran these analyses with the addition of an observation-level random effect as per Harrison (2014), which yielded the same model fit. Consequently, I stuck with a simple negative binomial distribution with no observation-level random effect, specifying a normal prior with a mean of zero and standard deviation of 1. Model V might therefore not capture evidence of the predictors' potential effect on offspring degree, so I recommend interpreting these results with caution.

Additionally, social network data involve social relationships and therefore are non-independent observations (Roatti et al., 2023). Although data permutations have been commonly used in social network analyses to mitigate this, recent work has demonstrated that permutations often yield high type I and type II errors as well as unreliable effect sizes, while failing to control for the non-independence of relational data (Croft et al., 2011; Hart et al., 2022; Weiss et al. 2021 but see Farine, 2017). Instead, parametric regression models are recommended (e.g., generalized linear mixed models) (Croft et al., 2011; Hart et al., 2022; Weiss et al. 2021).

3.0 Results

3.1 Grooming Networks

Mother-level random effect variance in offspring degree was small (SD = 0.29). Although the CrI excluded zero, its lower bound lay very close to zero and the interval was wide (95% CrI [0.01, 0.90]), indicating weak and uncertain support for any among-mother variation (Table 3). The CrI of offspring sex excluded zero (posterior mean = -0.79, 95% CrI [-1.09, -0.49], pd =

100%) (Figure 4), indicating that daughters had more grooming partners than sons (Figure 5a). The upper CrI for offspring age*sex distribution barely bounded zero, suggesting a slight negative direction (posterior mean = -0.22, 95% CrI [-0.54, 0.08], pd = 92%). Running the same model with the unsexed juvenile as a male yielded an upper 95% CrI at zero (posterior mean = -0.32, 95% CrI [-0.65, 0.00], pd = 98%), indicating that the slightly positive relationship between offspring age and degree may be stronger in daughters than sons. The CrIs of all other predictors included zero and had pd < 90%, notably maternal eigenvector centrality (posterior mean = 0.22, 95% CrI [-0.63, 0.99], pd = 73%), data type (posterior mean = -0.20, 95% CrI [-0.88, 0.53], pd = 73%), the Simple Ratio Index (SRI) (posterior mean = -0.08, 95% CrI [-0.42, 0.26], pd = 68%), offspring age (posterior mean = 0.05, 95% CrI [-0.23, 0.34], pd = 63%), maternal Elo-rating (posterior mean = 0.04, 95% CrI [-0.31, 0.43], pd = 60%), maternal age (posterior mean = -0.03, 95% CrI [-0.37, 0.30], pd = 59%), maternal strength (posterior mean = -0.03, 95% CrI [-0.60, 0.59], pd = 55%), and maternal degree (posterior mean = -0.00, 95% CrI [-0.55, 0.55], pd = 53%) (Figure S6).

Table 3. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the number of grooming partners (degree) of offspring. CrI = credible interval, sd()= the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.29	0.24	0.01	0.90	1.01	7127	157667
Population-Level Effects	Intercept	2.46	0.26	1.92	2.95	1.06	1194	3419
	Simple Ratio Index (SRI)	-0.08	0.17	-0.42	0.26	1.02	3216	14246
	Offspring Age	0.05	0.15	-0.23	0.34	1.02	3470	16410
	Offspring Sex (is male, not female)	-0.79	0.15	-1.09	-0.49	1.02	2859	15513
	Maternal Age	-0.03	0.17	-0.37	0.30	1.01	8518	211653
	Maternal Elo-Rating	0.04	0.18	-0.31	0.43	1.02	3346	14769
	Maternal Degree	-0.0	0.28	-0.55	0.55	1.09	765	1819
	Maternal Strength	-0.03	0.30	-0.60	0.59	1.02	2762	7929
	Maternal Eigenvector Centrality	0.22	0.40	-0.63	0.99	1.04	1679	4126
	Data Type (is focal not *ad libitum*)	-0.20	0.36	-0.88	0.53	1.06	1078	1669
	Offspring Age and Sex Interaction	-0.22	0.16	-0.54	0.08	1.02	3855	24018

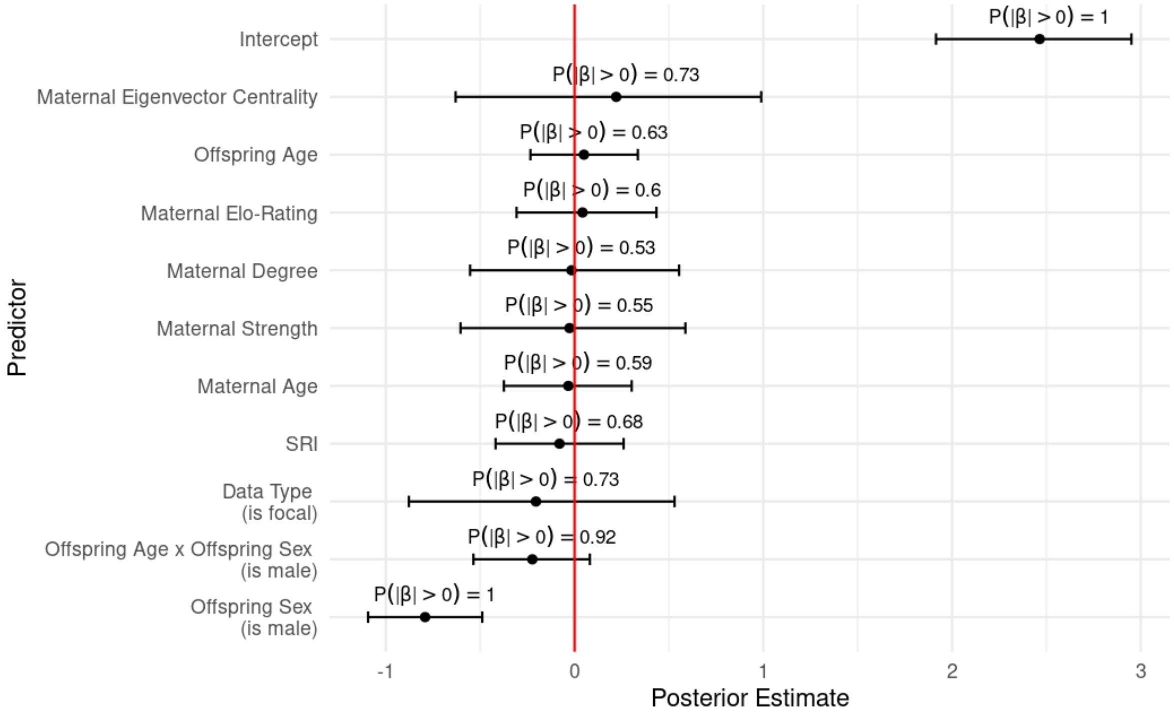


Figure 4. Forest plot of offspring grooming degree model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

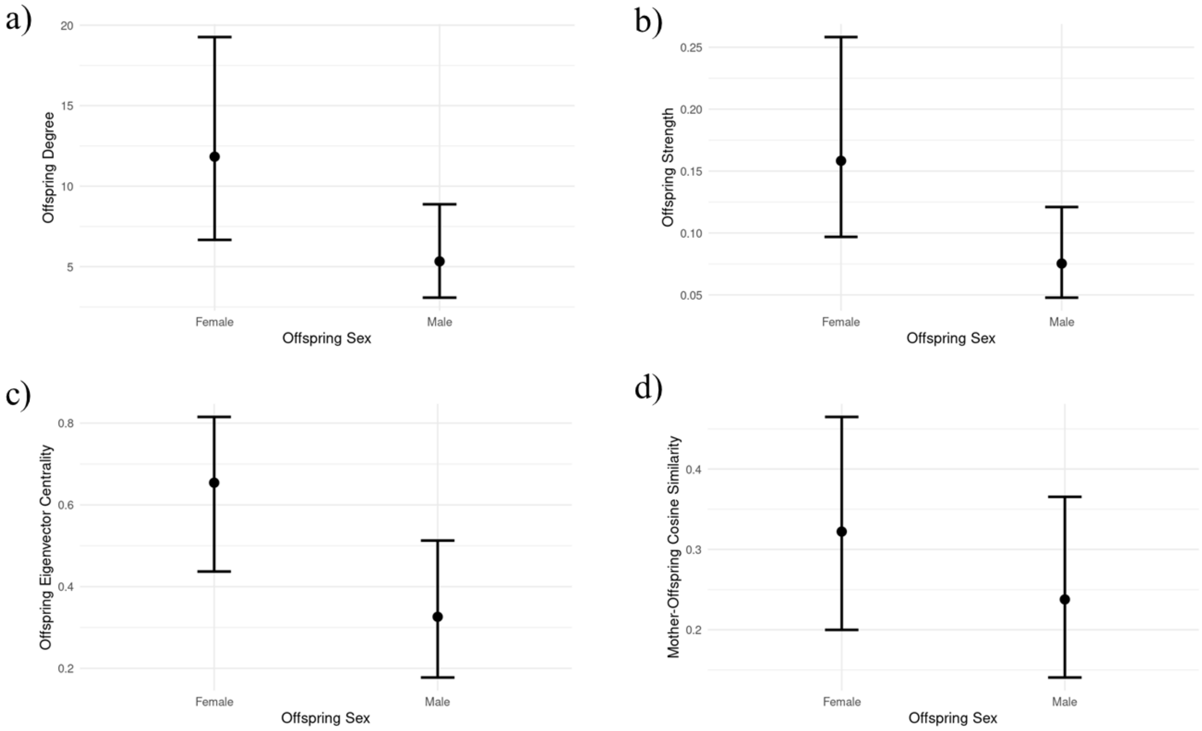


Figure 5. Relationship between offspring sex and posterior estimates of outcome variables a-d and their 95% credible intervals (CrIs), where **a)** number of grooming partners (degree) of offspring, **b)** frequency of grooming interactions (strength) of offspring, **c)** grooming centrality (eigenvector centrality) of offspring, **d)** similarity in grooming partners (cosine similarity) across mother-offspring dyads. There is a 100% probability that the effect of offspring sex on a-c grooming metrics is negative, and a 93% probability that the effect of offspring sex on mother-offspring grooming cosine similarity is negative.

Mother-level random effect variance in offspring strength was small (SD = 0.24). Although the CrI excluded zero, its lower bound lay very close to zero and the interval was wide (95% CrI [0.01, 0.80]), indicating weak and uncertain support for any among-mother variation (Table 4). Offspring sex (posterior mean = -0.74, 95% CrI [-1.09, -0.40], pd = 100%) and data type (posterior mean = -0.81, 95% CrI [-1.46, -0.14], pd = 99%) both had CrIs which excluded zero (Figure 6), indicating that daughters expressed higher grooming frequencies than sons and focal data yielded lower grooming frequencies than *ad libitum* data (Figure 5b & S7i). Offspring age*sex displayed weak evidence for negative directionality on offspring strength (posterior mean = -0.29, 95% CrI [-0.68, 0.11], pd = 93%). This contrasted with SRI (posterior mean =

0.28, 95% CrI [-0.13, 0.67], pd = 92%) and offspring age (posterior mean = 0.26, 95% CrI [-0.13, 0.64], pd = 91%) which showed weak evidence for a positive effect on offspring strength. Nonetheless, posterior distributions of maternal eigenvector centrality (posterior mean = 0.35, 95% CrI [-0.44, 1.14], pd = 82%), maternal degree (posterior mean = -0.15, 95% CrI [-0.58, 0.29], pd = 76%), maternal strength (posterior mean = 0.14, 95% CrI [-0.46, 0.73], pd = 69%), maternal Elo-rating (posterior mean = 0.02, 95% CrI [-0.37, 0.40], pd = 56%), and maternal age (posterior mean = 0.02, 95% CrI [-0.31, 0.35], pd = 54%) offered little evidence of any effect on grooming strength (Figure S7). After running the same model with the unsexed juvenile as a male, I found an upper 95% CrI below but close to zero for the offspring age*sex predictor (posterior mean = -0.44, 95% CrI [-0.86, -0.01], pd = 98%), indicating that the relationship between offspring age and strength may be steeper in daughters than sons.

Table 4. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the frequency of grooming interactions (strength) of offspring. CrI = credible interval, sd()= the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.24	0.22	0.01	0.80	1.00	4554	6326
Population-Level Effects	Intercept	-1.83	0.25	-2.31	-1.35	1.00	10460	10123
	Simple Ratio Index (SRI)	0.28	0.20	-0.13	0.67	1.00	9181	8520
	Offspring Age	0.26	0.20	-0.13	0.64	1.00	9257	9032
	Offspring Sex (is male, not female)	-0.74	0.18	-1.09	-0.40	1.00	16220	11306
	Maternal Age	0.02	0.17	-0.31	0.35	1.00	10264	8919
	Maternal Elo-Rating	0.02	0.19	-0.37	0.40	1.00	8767	9135
	Maternal Degree	-0.15	0.22	-0.58	0.29	1.00	9544	10732
	Maternal Strength	0.14	0.30	-0.46	0.73	1.00	10549	10412
	Maternal Eigenvector Centrality	0.35	0.40	-0.44	1.14	1.00	8542	9062
	Data Type (is focal not *ad libitum*)	-0.81	0.33	-1.46	-0.14	1.00	9192	11318
	Offspring Age and Sex Interaction	-0.29	0.20	-0.68	0.11	1.00	15662	11327
Family-Specific Parameters (Gamma, log link)	Shape	5.38	1.56	2.82	8.84	1.00	11699	11440

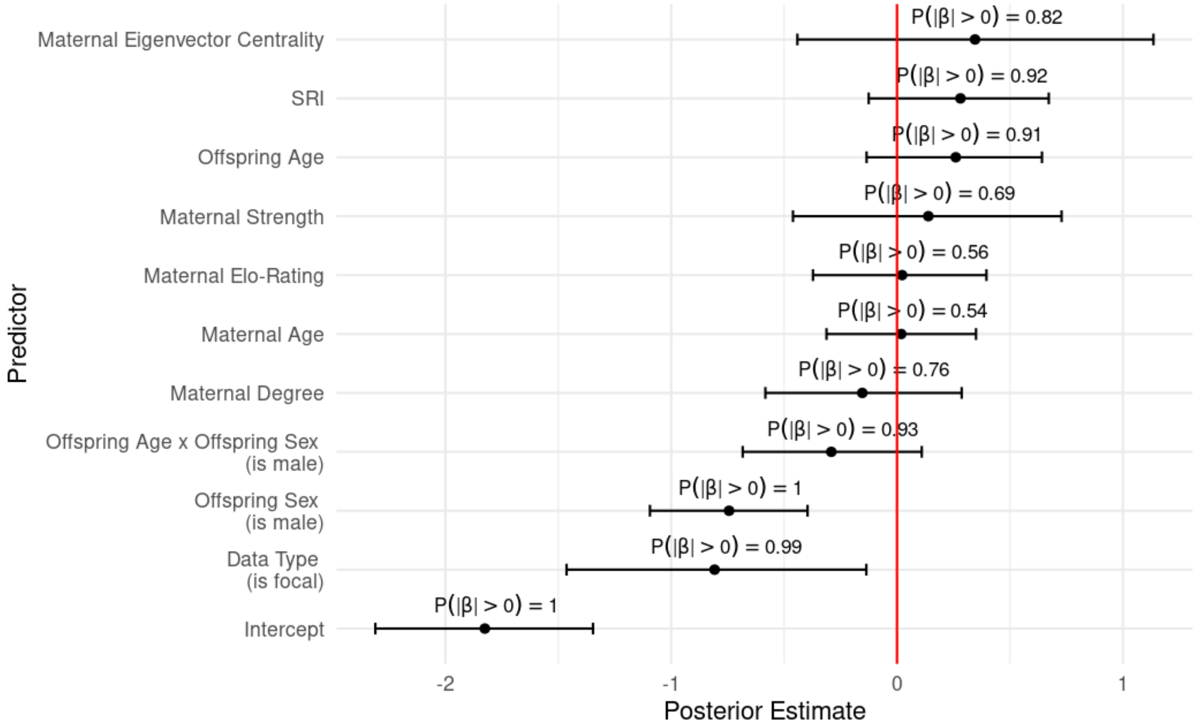


Figure 6. Forest plot of offspring grooming strength model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

Mother-level random effect variance in offspring eigenvector centrality was small (SD = 0.36). Although the CrI excluded zero, its lower bound lay very close to zero and the interval was wide (95% CrI [0.01, 1.18]), indicating weak and uncertain support for any among-mother variation (Table 5). Here again, results from this model suggested that offspring sex influenced offspring eigenvector centrality (posterior mean = -1.42, 95% CrI [-2.05, -0.79], pd = 100%) (Figure 7), with daughters being more central in grooming networks than sons (Figure 5c). Maternal eigenvector centrality exhibited a slight positive directionality (posterior mean = 0.83, 95% CrI [-0.38, 1.98], pd = 92%), whereas data type showed a minor negative directionality (posterior mean = -0.75, 95% CrI [-1.86, 0.40], pd = 90%), though both 95% CrIs bounded zero

(Figure S8b & i). All other fixed effects, that is, offspring age*sex (posterior mean = -0.29, 95% CrI [-0.89, 0.30], pd = 84%), maternal degree (posterior mean = -0.25, 95% CrI [-1.02, 0.56], pd = 74%), SRI (posterior mean = 0.13, 95% CrI [-0.47, 0.74], pd = 67%), maternal strength (posterior mean = 0.08, 95% CrI [-0.86, 1.09], pd = 55%), offspring age (posterior mean = 0.04, 95% CrI [-0.57, 0.66], pd = 55%), maternal Elo-rating (posterior mean = 0.03, 95% CrI [-0.51, 0.59], pd = 55%), and maternal age (posterior mean = 0.01, 95% CrI [-0.55, 0.55], pd = 52%) showed no evidence of an effect on offspring eigenvector centrality (Figure S8a, c-h). In contrast to models with the unsexed juvenile as male, when re-running the same model with the unsexed offspring as a male, the upper CrI of offspring age*sex predictor was below zero (posterior mean = -0.70, 95% CrI [-1.38, -0.03], pd = 98%), indicating a negative effect on grooming eigenvector centrality.

Table 5. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the grooming centrality (eigenvector centrality) of offspring. CrI = credible interval, sd()= the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.36	0.32	0.01	1.18	1.02	3917	11035
Population-Level Effects	Intercept	0.67	0.45	-0.22	1.53	1.12	589	1994
	Simple Ratio Index (SRI)	0.13	0.31	-0.47	0.74	1.05	1421	4213
	Offspring Age	0.04	0.31	-0.57	0.66	1.08	854	2635
	Offspring Sex (is male, not female)	-1.42	0.32	-2.05	-0.79	1.08	829	2243
	Maternal Age	0.01	0.28	-0.55	0.55	1.05	1325	5540
	Maternal Elo-Rating	0.03	0.28	-0.51	0.59	1.06	1086	3242
	Maternal Degree	-0.25	0.40	-1.02	0.56	1.05	1253	2856
	Maternal Strength	0.08	0.49	-0.86	1.09	1.10	713	2803
	Maternal Eigenvector Centrality	0.83	0.60	-0.38	1.98	1.07	998	4266
	Data Type (is focal not *ad libitum*)	-0.75	0.57	-1.86	0.40	1.08	830	3099
	Offspring Age and Sex Interaction	-0.29	0.30	-0.89	0.30	1.04	1660	5310
Family-Specific Parameters (zero-one-inflated beta)	Precision Parameter (phi)	9.45	3.00	4.64	16.32	1.12	596	1343
	Zero-One Inflation (zoi)	0.04	0.03	0.00	0.13	1.09	759	3602
	Conditional One Inflation (coi)	0.55	0.28	0.04	0.98	1.04	1792	7864

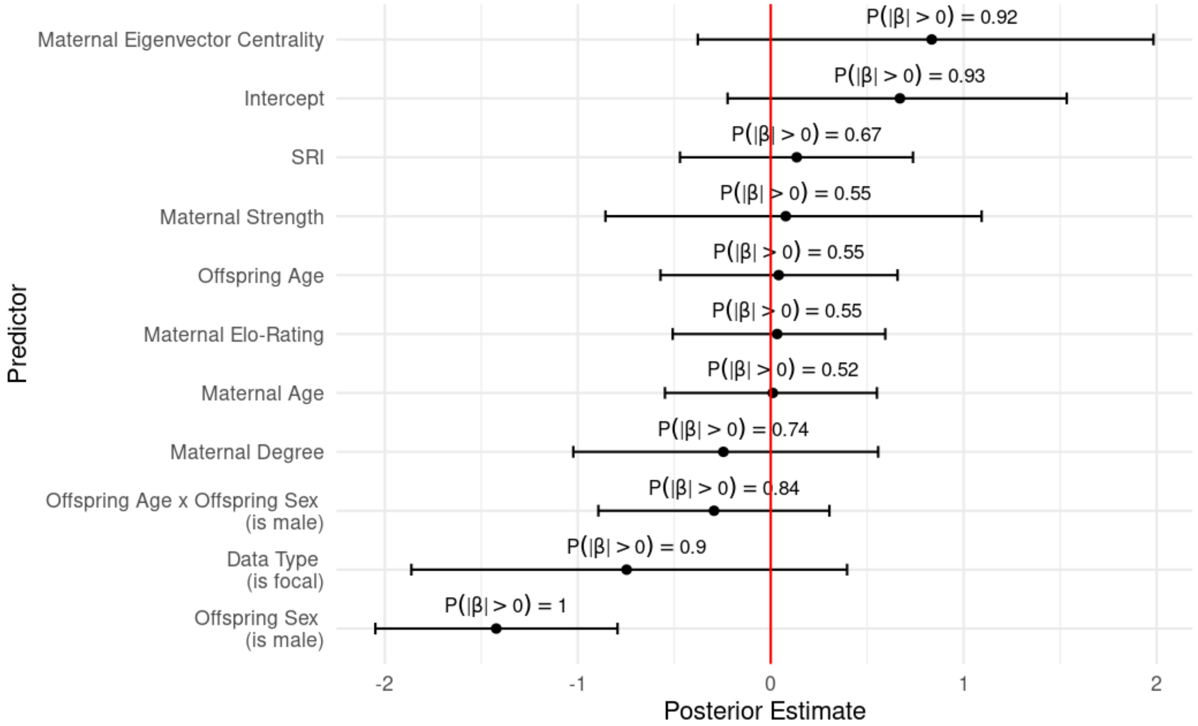


Figure 7. Forest plot of offspring grooming eigenvector centrality model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

Mother-level random effect variance in cosine similarity with offspring was small (SD = 0.39). Although the CrI excluded zero, its lower bound remained close to zero and the interval was wide (95% CrI [0.03, 1.02]), indicating weak and uncertain support for any among-mother variation (Table 6). There was little evidence of any notable effect of any fixed predictors on mother-offspring cosine similarity since all CrIs overlapped zero. That is, while the posterior distribution of offspring sex (posterior mean = -0.45, 95% CrI [-1.06, 0.17], pd = 93%) slightly favoured negative effects, offspring age (posterior mean = -0.33, 95% CrI [-0.96, 0.30], pd = 85%), SRI (posterior mean = -0.26, 95% CrI [-0.91, 0.39], pd = 79%), offspring age*sex (posterior mean = -0.16, 95% CrI [-0.78, 0.45], pd = 70%), and data type (posterior mean = -0.14, 95% CrI [-0.88, 0.60], pd = 64%) all had pd < 90% with 95% CrIs that bounded zero (Figure 8, 5d, & S9).

Table 6. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the similarity in grooming partners (cosine similarity) between mothers and their offspring. CrI = credible interval, sd()= the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.39	0.26	0.03	1.02	1.02	4817	96976
Population-Level Effects	Intercept	-0.51	0.32	-1.16	0.12	1.04	1800	8040
	Simple Ratio Index (SRI)	-0.26	0.33	-0.91	0.39	1.03	1988	8106
	Offspring Age	-0.33	0.32	-0.96	0.30	1.03	2039	10306
	Offspring Sex (is male, not female)	-0.45	0.31	-1.06	0.17	1.03	2504	13212
	Data Type (is focal not *ad libitum*)	-0.14	0.38	-0.88	0.60	1.04	1673	7687
	Offspring Age and Sex Interaction	-0.16	0.31	-0.78	0.45	1.02	3914	22024
Family-Specific Parameters (zero-inflated beta)	Precision Parameter (phi)	7.76	2.36	4.02	13.21	1.06	1080	3899
	Zero-Inflation Probability (zi)	0.14	0.06	0.05	0.27	1.00	553608	304047

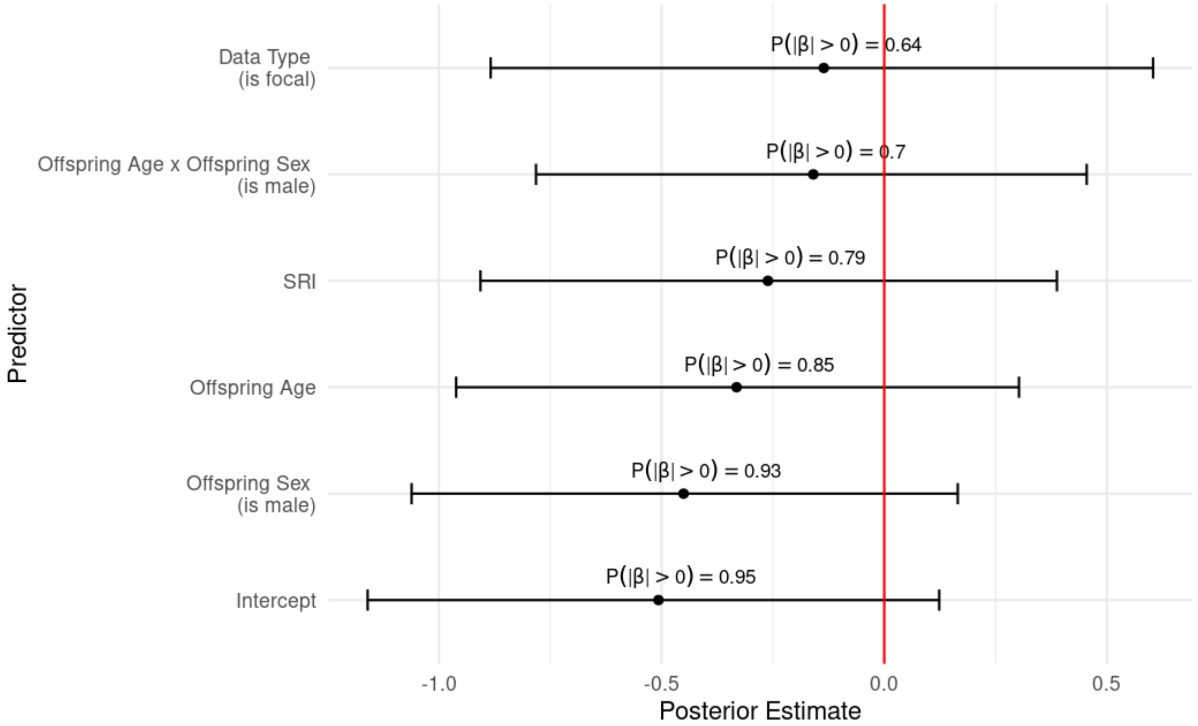


Figure 8. Forest plot of mother-offspring grooming cosine similarity model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

3.2 Proximity Networks

Mother-level random effect variance in offspring degree was very small (SD = 0.16). The CrI included values at or near zero and was wide (95% CrI [0.00, 0.63]), indicating weak and uncertain support for any among-mother variation (Table 7). There was little evidence that any of the fixed predictors affected offspring degree (Figure 9; S10): offspring age*sex (posterior mean = -0.05, 95% CrI [-0.33, 0.22], pd = 65%), SRI (posterior mean = -0.04, 95% CrI [-0.28, 0.20], pd = 63%), offspring age (posterior mean = -0.04, 95% CrI [-0.32, 0.24], pd = 61%), offspring sex (posterior mean = -0.02, 95% CrI [-0.28, 0.24], pd = 56%), maternal age (posterior mean = -0.05, 95% CrI [-0.74, 0.66], pd = 56%), maternal Elo-rating (posterior mean = 0.02, 95% CrI [-

0.43, 0.46], pd = 54%), maternal eigenvector centrality (posterior mean = -0.04, 95% CrI [-0.89, 0.81], pd = 53%), maternal strength (posterior mean = 0.03, 95% CrI [-1.16, 1.21], pd = 52%), and maternal degree (posterior mean = -0.00, 95% CrI [-0.57, 0.57], pd = 50%) all had pd < 90% with 95% CrIs that bounded zero.

Table 7. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the number of proximity partners (degree) of offspring. CrI = credible interval, sd() = the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.16	0.18	0.00	0.63	1.00	117572	160910
Population-Level Effects	Intercept	3.50	0.14	3.22	3.78	1.01	6811	29513
	Simple Ratio Index (SRI)	-0.04	0.12	-0.28	0.20	1.01	4595	34883
	Offspring Age	-0.04	0.14	-0.32	0.24	1.02	3339	21821
	Offspring Sex (is male, not female)	-0.02	0.13	-0.28	0.24	1.02	3287	18405
	Maternal Age	-0.05	0.35	-0.74	0.66	1.01	10151	16132
	Maternal Elo-Rating	0.02	0.22	-0.43	0.46	1.01	6682	24046
	Maternal Degree	-0.00	0.27	-0.57	0.57	1.08	6117	1952
	Maternal Strength	0.03	0.59	-1.16	1.21	1.01	7895	14868
	Maternal Eigenvector Centrality	-0.04	0.43	-0.89	0.81	1.01	8010	13464
	Offspring Age and Sex Interaction	-0.05	0.14	-0.33	0.22	1.02	4050	21732
Family-Specific Parameters (negative binomial)	Shape	100.44	81.39	14.58	317.59	1.00	337089	280632

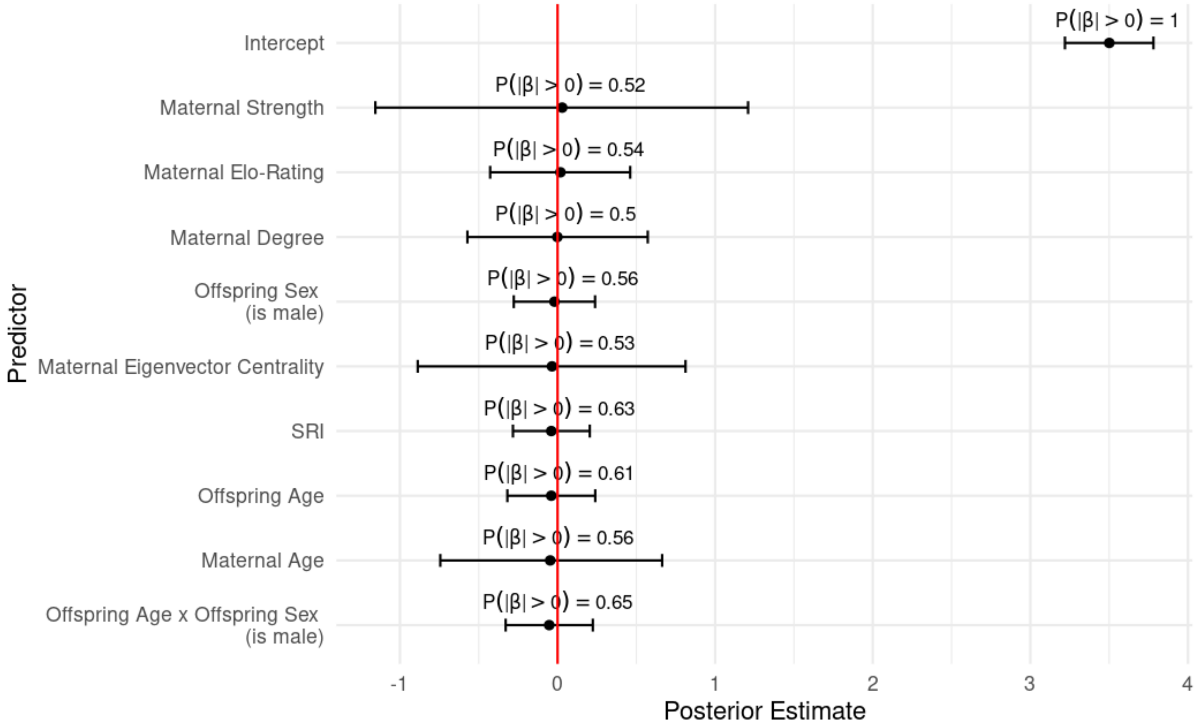


Figure 9. Forest plot of offspring proximity degree model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

Mother-level random effect variance in offspring strength was very small (SD = 0.16). The CrI included values at or near zero and was wide (95% CrI [0.00, 0.62]), indicating weak and uncertain support for any among-mother variation (Table 8). While there was moderate evidence that the posterior distribution of offspring age favoured a negative direction (posterior mean = -0.22, 95% CrI [-0.48, 0.05], pd = 95%), its associated CrI did include zero (Figure 10). Here again, there was no evidence for an effect of any of the fixed predictors on offspring strength (Figure 10). Effectively, maternal Elo-rating (posterior mean = 0.10, 95% CrI [-0.34, 0.53], pd = 71%), offspring sex (posterior mean = -0.06, 95% CrI [-0.31, 0.19], pd = 70%), offspring age*sex (posterior mean = -0.04, 95% CrI [-0.30, 0.23], pd = 62%), maternal age (posterior mean = -0.05, 95% CrI [-0.74, 0.65], pd = 56%), SRI (posterior mean = 0.01, 95% CrI [-0.22, 0.25], pd = 54%), maternal eigenvector centrality (posterior mean = 0.04, 95% CrI [-0.78, 0.89], pd = 53%), maternal strength (posterior mean = 0.03, 95% CrI [-1.16, 1.18], pd = 53%), and maternal degree (posterior mean = 0.00, 95% CrI [-0.57, 0.58], pd = 51%) all had pd < 90% and CrIs that included zero (Figure S11).

Table 8. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the frequency of associations (proximity strength) of offspring. CrI = credible interval, sd() = the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.16	0.18	0.00	0.62	1.00	117819	155859
Population-Level Effects	Intercept	-0.09	0.14	-0.36	0.19	1.01	8776	39202
	Simple Ratio Index (SRI)	0.01	0.12	-0.22	0.25	1.00	280333	272204
	Offspring Age	-0.22	0.13	-0.48	0.05	1.00	224143	255064
	Offspring Sex (is male, not female)	-0.06	0.12	-0.31	0.19	1.00	364620	291428
	Maternal Age	-0.05	0.34	-0.74	0.65	1.01	7514	21782
	Maternal Elo-Rating	0.10	0.22	-0.34	0.53	1.01	18317	186998
	Maternal Degree	0.00	0.27	-0.57	0.58	1.08	1346	1521
	Maternal Strength	0.03	0.58	-1.16	1.18	1.02	4758	5977
	Maternal Eigenvector Centrality	0.04	0.42	-0.78	0.89	1.01	5860	8222
	Offspring Age and Sex Interaction	-0.04	0.13	-0.30	0.23	1.00	40084	280351
Family-Specific Parameters (Gamma, log link)	Shape	30.22	15.83	7.93	68.50	1.00	149571	214822

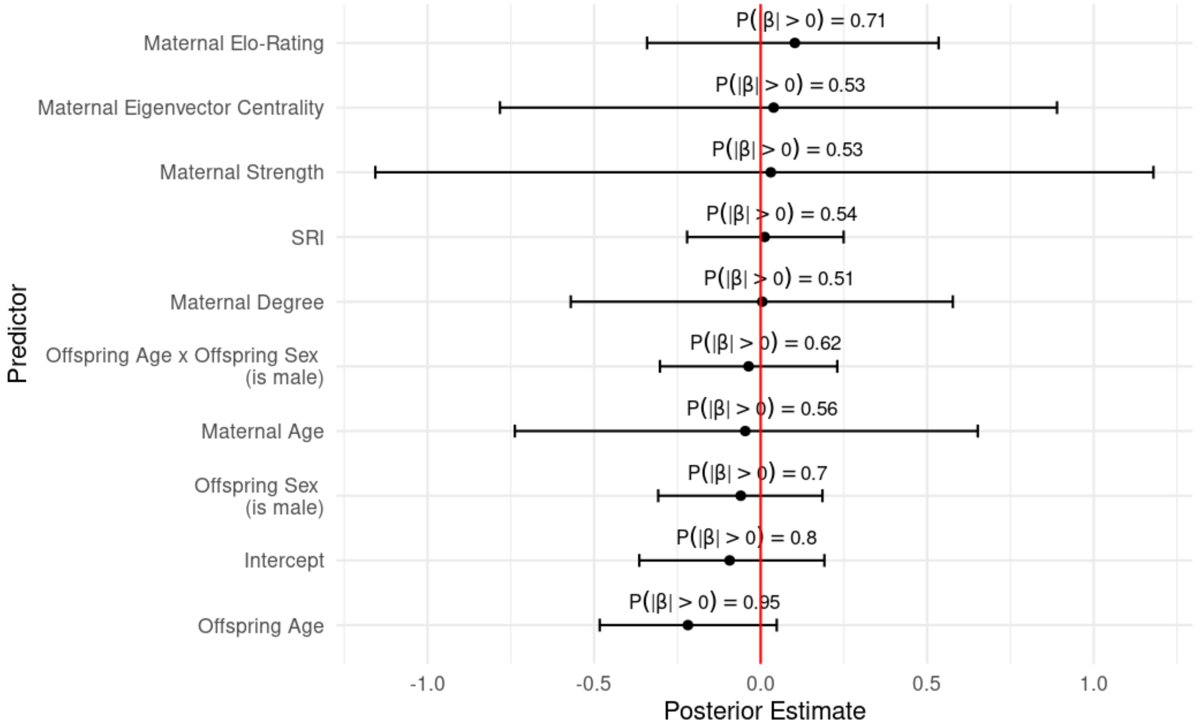


Figure 10. Forest plot of offspring proximity strength model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

Mother-level random effect variance in offspring eigenvector centrality was moderate (SD = 0.40). Although the CrI excluded zero, its lower bound was near zero and the interval was wide (95% CrI [0.01, 1.40]), indicating weak and uncertain support for any among-mother variation (Table 9). There was strong evidence that offspring age (posterior mean = -0.78, 95% CrI [-1.30, -0.21], pd = 99%) explained variation in offspring eigenvector centrality (Figure 11), with older offspring being less central than younger offspring (Figure 12). The posterior distribution of offspring sex (posterior mean = -0.38, 95% CrI [-0.89, 0.18], pd = 92%) slightly favoured a negative direction, with sons possibly being less central than daughters. The posterior distributions of the remaining predictors, namely offspring age*sex (posterior mean = 0.30, 95%

CrI [-0.26, 0.83], pd = 88%), maternal Elo-rating (posterior mean = 0.45, 95% CrI [-0.41, 1.22], pd = 87%), maternal age (posterior mean = -0.26, 95% CrI [-1.34, 0.90], pd = 69%), maternal strength (posterior mean = 0.06, 95% CrI [-1.40, 1.53], pd = 53%), SRI (posterior mean = 0.02, 95% CrI [-0.43, 0.50], pd = 52%), maternal degree (posterior mean = 0.01, 95% CrI [-1.01, 1.04], pd = 51%), and maternal eigenvector centrality (posterior mean = -0.02, 95% CrI [-1.30, 1.31], pd = 51%) did not provide strong evidence of an effect on offspring eigenvector centrality since all had pd < 90% and CrIs that included zero (Figure S12).

Table 9. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the proximity centrality (eigenvector centrality) of offspring. CrI = credible interval, sd() = the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.40	0.38	0.01	1.40	1.01	15186	215811
Population-Level Effects	Intercept	0.35	0.32	-0.27	1.00	1.02	3430	8568
	Simple Ratio Index (SRI)	0.02	0.23	-0.43	0.50	1.00	37132	275440
	Offspring Age	-0.78	0.27	-1.30	-0.21	1.00	33530	249576
	Offspring Sex (is male, not female)	-0.38	0.27	-0.89	0.18	1.00	302720	289775
	Maternal Age	-0.26	0.56	-1.34	0.90	1.02	4513	13018
	Maternal Elo-Rating	0.45	0.41	-0.41	1.22	1.01	12873	190721
	Maternal Degree	0.01	0.50	-1.01	1.04	1.10	689	2108
	Maternal Strength	0.06	0.75	-1.40	1.53	1.02	4261	16267
	Maternal Eigenvector Centrality	-0.02	0.66	-1.30	1.31	1.01	13011	299842
	Offspring Age and Sex Interaction	0.30	0.27	-0.26	0.83	1.00	27465	274558
Family-Specific Parameters (zero-one-inflated beta)	Precision Parameter (phi)	31.49	15.94	9.30	70.28	1.00	29373	255278
	Zero-One Inflation (zoi)	0.11	0.07	0.01	0.27	1.00	555005	265446
	Conditional One Inflation (coi)	0.67	0.24	0.16	0.99	1.00	596362	256955

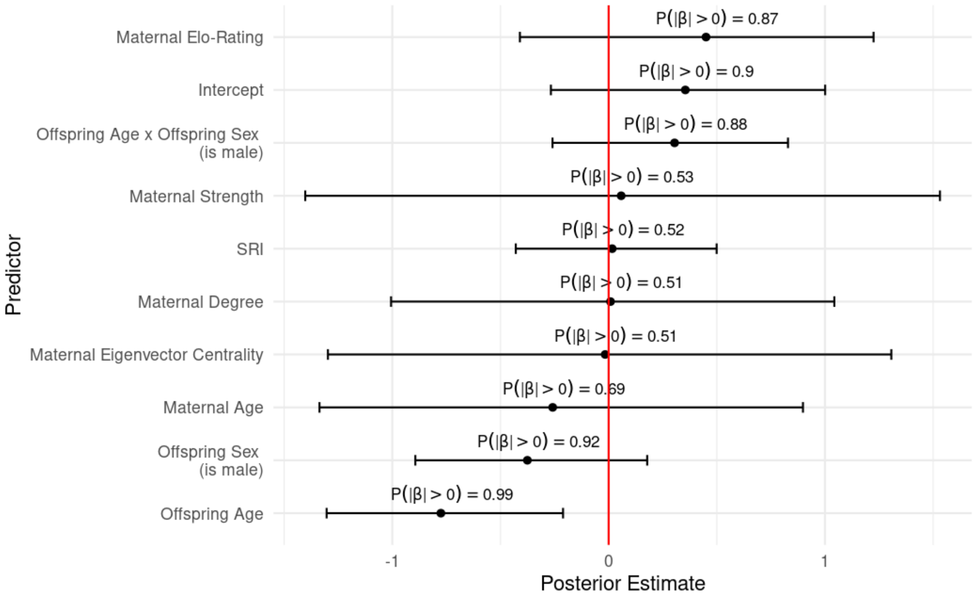


Figure 11. Forest plot of offspring proximity eigenvector centrality model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

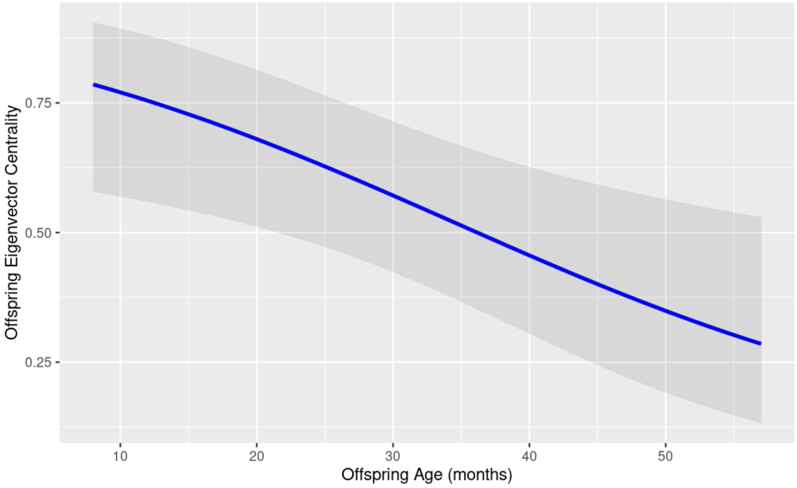


Figure 12. Relationship between offspring age (in months) and posterior estimates of offspring proximity eigenvector centrality, with its associated 95% credible intervals (shaded area). There is a 99% probability that the effect of offspring age on proximity eigenvector centrality is negative (i.e., older offspring are less central in proximity networks than younger offspring).

Mother-level random effect variance in cosine similarity with offspring was small (SD = 0.33). Although the CrI excluded zero, its lower bound was near zero and the interval was wide (95% CrI [0.03, 0.82]), indicating weak and uncertain support for any among-mother variation (Table 10). I found evidence that SRI had an effect on mother-offspring cosine similarity (posterior mean = 0.42, 95% CrI [0.03, 0.80], pd = 98%) (Figure 13), in which offspring with higher SRI values had higher mother-offspring cosine similarity values (Figure 14). However, there appeared to be no effect of any of the remaining predictor variables on mother-offspring cosine similarity, with offspring sex (posterior mean = 0.10, 95% CrI [-0.39, 0.59], pd = 67%), offspring age*sex (posterior mean = -0.04, 95% CrI [-0.51, 0.46], pd = 57%), and offspring age (posterior mean = -0.02, 95% CrI [-0.50, 0.44], pd = 52%) (Figure S13) all having pd < 90% and 95% CrIs that bounded zero.

Table 10. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the similarity of proximity partners (cosine similarity) between mothers and their offspring. CrI = credible interval, sd() = the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.33	0.21	0.03	0.82	1.00	125689	140679
Population-Level Effects	Intercept	0.60	0.23	0.14	1.08	1.00	242499	267272
	Simple Ratio Index (SRI)	0.42	0.19	0.03	0.80	1.00	216986	282516
	Offspring Age	-0.02	0.24	-0.50	0.44	1.00	210678	261040
	Offspring Sex (is male, not female)	0.10	0.25	-0.39	0.59	1.00	339913	306357
	Offspring Age and Sex Interaction	-0.04	0.25	-0.51	0.46	1.00	210730	289485
Family-Specific Parameters (zero-inflated beta)	Precision Parameter (phi)	27.92	12.96	9.62	59.37	1.00	171472	286481

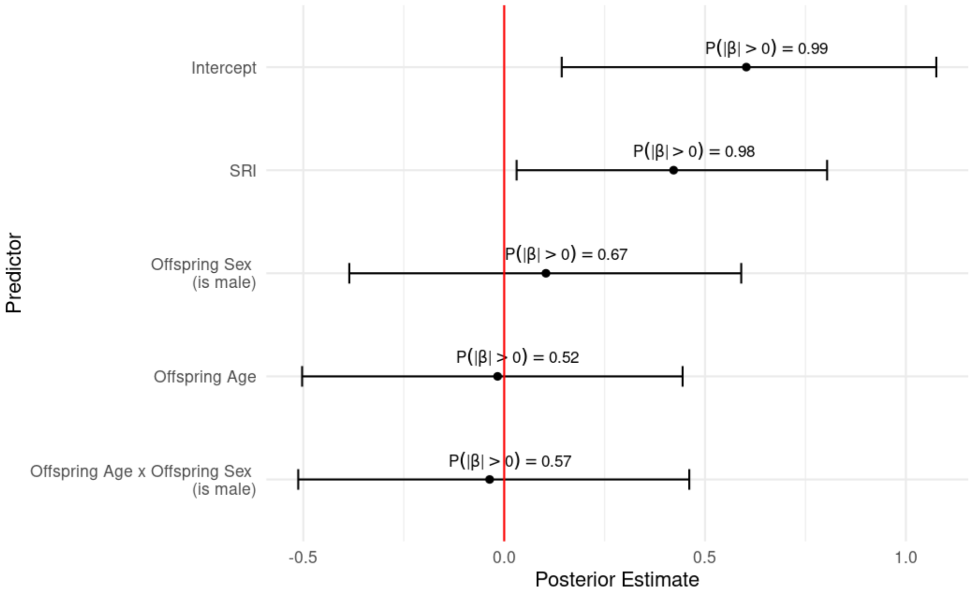


Figure 13. Forest plot of mother-offspring proximity cosine similarity model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

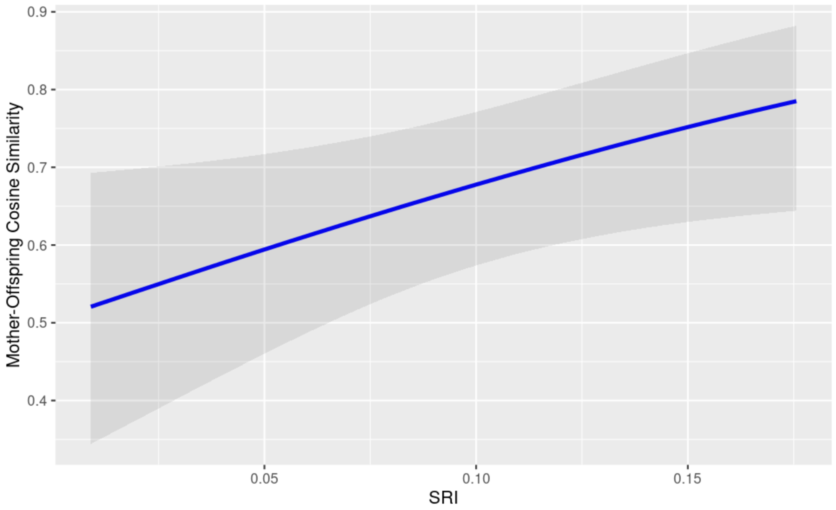


Figure 14. Relationship between Simple Ratio Index (SRI) and posterior estimates of mother-offspring proximity cosine similarity, with its associated 95% credible intervals (shaded area). There is a 98% probability that the effect of SRI on proximity mother-offspring cosine similarity is positive (i.e., offspring who stayed in proximity with their mothers more often had more similar associates to that of their mothers than those who did not).

3.3 Simple Ratio Index Model

Mother-level random effect variance in the Simple Ratio Index (SRI) was moderate (SD = 0.42). Although the CrI excluded zero, its lower bound was near zero and the interval was wide (95% CrI [0.02, 1.15]), indicating weak and uncertain support for any among-mother variation (Table 11). The posterior distribution of offspring age was the only fixed predictor that provided strong evidence of an effect on SRI, due to a narrow CrI and very high pd (posterior mean = -0.04, 95% CrI [-0.07, -0.01], pd = 100%), (Figure 15), suggesting that older offspring associated less often with their mothers than younger offspring (Figure 16). However, there was strong evidence, due to a narrow CrI, that offspring age*sex (posterior mean = -0.00, 95% CrI [-0.04, 0.04], pd = 51%) had no effect on SRI (Figure S14). As offspring age*sex, offspring sex also did not explain variation in SRI (posterior mean = -0.30, 95% CrI [-1.35, 0.79], pd = 72%) both having pd < 90% and 95% CrIs that bounded zero.

Table 11. Summary statistics of a Bayesian generalized mixed effects model (GLMM) for the proximity between mothers and their offspring (SRI). CrI = credible interval, sd() = the standard deviation.

Type	Parameter	Posterior Mean Estimate	Estimated Error	Lower 95% CrI	Upper 95% CrI	R-hat Value	Bulk Effective Sample Size	Tail Effective Sample Size
Group-Level Effects	sd(Intercept)	0.42	0.30	0.02	1.15	1.00	3198	5662
Population-Level Effects	Intercept	-1.29	0.43	-2.17	-0.47	1.00	7718	8339
	Offspring Age	-0.04	0.01	-0.07	-0.01	1.00	9919	10661
	Offspring Sex (is male, not female)	-0.30	0.55	-1.35	0.79	1.00	7132	8489
	Offspring Age and Sex Interaction	-0.00	0.02	-0.04	0.04	1.00	7355	9018
Family-Specific Parameters (zero-inflated beta)	Precision Parameter (phi)	42.32	20.15	14.80	92.04	1.00	5660	8911

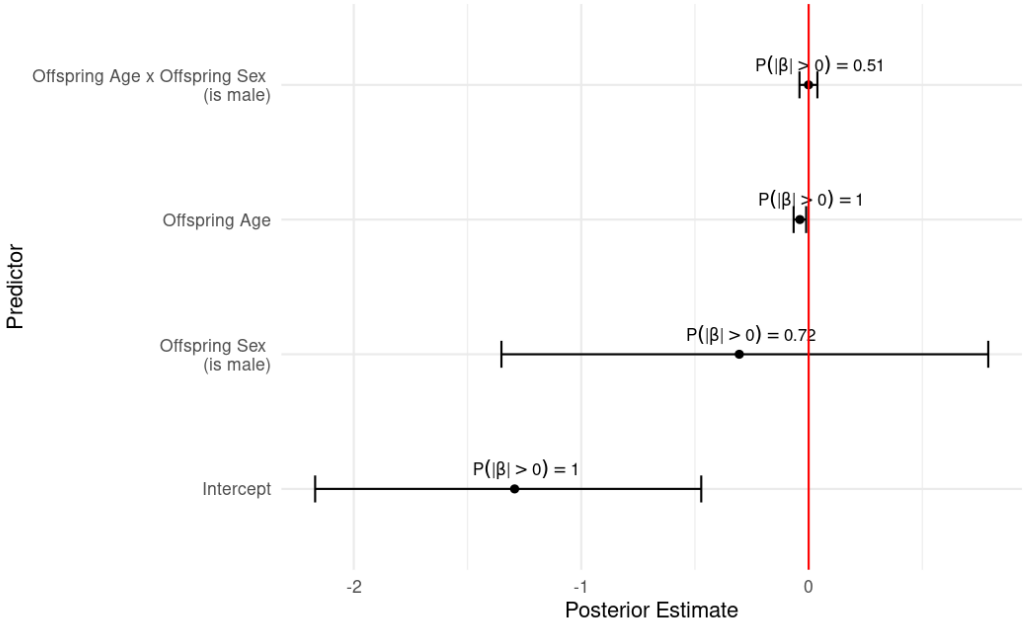


Figure 15. Forest plot of Simple Ratio Index (SRI) model results. Points represent posterior mean regression coefficients (β) of each predictor and lines display their associated 95% credible intervals (CrIs). Each value above CrIs corresponds to the probability of direction (pd), which is the probability that the effect of a predictor is positive or negative, depending on the direction of its posterior estimate. As such, higher values of pd suggest greater evidence of a specific direction.

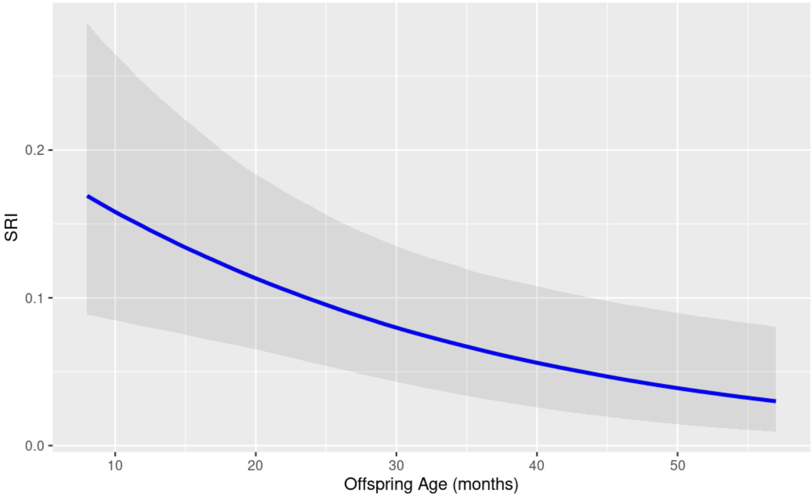


Figure 16. Relationship between offspring age (in months) and posterior estimates of SRI, with its associated 95% credible intervals (shaded area). There is a 100% probability that the effect of offspring age on SRI is negative (i.e., older offspring tend to spend less time around their mothers than younger offspring).

4.0 Discussion

Vervet monkey mothers at Lake Nabugabo, Uganda, did not fully transmit their grooming and proximity networks to their offspring, as more integrated mothers did not always rear more integrated immatures. Although my results suggest that maternal age and dominance rank did not influence offspring social networks, immature offspring were nonetheless clearly influenced by their mothers, especially in proximity networks: those who associated with their mothers more often had more similar associates to their mother’s than offspring who associated less often with their mothers. There was also evidence that older offspring associated less often with their mothers and that this relationship did not depend on offspring sex. Additionally, older offspring were less central in proximity networks, which was consistent with social integration processes observed in vervet monkeys such as patterns of youngest ascendancy in females & age-related changes in social behaviour related to the approach of dispersal for males. The slightly positive relationship between age and most grooming metrics may be stronger in daughters than sons. Lastly, consistent with female-philopatry and male-biased dispersal, daughters were more integrated in grooming networks but not in proximity networks: daughters had more partners, groomed them more often, and were more central in grooming networks than sons.

4.1 Maternal Network Inheritance and Effects of Mother-Offspring Proximity

Overall, results suggested immature offspring mostly do not inherit their mothers’ networks, despite the presence of some maternal influences. Offspring of mother-offspring pairs with higher proximity (i.e., higher simple ratio index, SRI) may groom or be groomed by others more frequently (i.e., grooming strength). Additionally, mother-offspring pairs had more similar proximity partners (i.e., proximity cosine similarity) when mothers and offspring expressed higher levels of proximity. Although more central mothers may rear more central offspring in grooming networks (i.e., eigenvector centrality), other metrics did not show such a relationship. Mother-offspring proximity was lower for older offspring, which did not vary by offspring sex. Overall, daughters did not express higher proximity with their mothers than sons.

While some studies (e.g., wild great tits, *Parus major*, Wild et al. 2024) similarly found limited evidence for maternal network inheritance, my results were mostly inconsistent with results from other species. For instance, in-degree was heritable in affiliative networks of yellow-bellied marmots (*Marmota flaviventris*) (Lea et al., 2010). Similarly, several studies report that rhesus macaque mothers transmitted their social network tendencies to their offspring (Berman et al., 1997; Brent et al., 2013; de Waal, 1996; Wooddell et al., 2020). More specifically, rhesus macaque grooming betweenness and eigenvector centrality were inherited by offspring from their mothers (Brent et al., 2013). This process started in infancy, whereby infant social connections echo those of their mothers and infants may even retain these tendencies after gaining independence from their mothers (Berman, 1982; Roney & Maestripieri, 2003). As such, maternal ties were a very strong predictor of daughters' affiliative ties in rhesus macaques, accounting for 64% of variance, which was stipulated to result from cultural learning (de Waal, 1996). Similarly, more spatially integrated white-faced capuchin mothers were more likely to rear daughters who themselves spent more time around other individuals, and such effects of maternal bonds lasted into offspring's juvenile and subadult stages (Godoy et al., 2024). White-faced capuchin mothers with male infants also spent more time associating with adult males than mothers with female infants (Jack et al., 2025), with the authors hypothesizing that males start creating bonds with other males very early on, which would then support a smooth transition to a different group at dispersal (i.e., engaging in parallel dispersal). Moreover, maternal bonds with adult males encouraged infant-adult male bonds in both Assamese macaques (Ostner et al., 2013) and chacma baboons (Moscovice et al., 2009). Chacma baboon immatures take on their mothers' grooming networks but differentiate from them over time, while conserving some influences from their mothers' connections throughout their development (Roatti et al., 2023). Additionally, wild bottlenose dolphins (particularly daughters) expressed similar networks as their mothers, and these maternal influences lasted well into adulthood (Frère et al., 2010; Stanton & Mann, 2012; Evans et al., 2021).

One unexpected maternal influence I found was that offspring closer to their mothers may groom or be groomed by others more frequently. This supports Vilette *et al.* (2023) hypothesis that tight associations with vervet mothers may encourage offspring to connect with a variety of grooming partners. Closeness with mothers is pivotal to the social integration of immature individuals (Deputte, 2000). Being near mothers may put offspring at ease such that they feel bolder and more confident when approaching grooming partners, and mothers may also represent reliable allies. Bottlenose dolphin calves who were closer to their mothers had a higher eigenvector centrality, and the latter protected them from being harassed by older juveniles (Stanton & Mann, 2012). This pattern could also be explained by the fact that some immatures simply have more social personalities (e.g., grooming/being groomed more often) and therefore are more social towards group members, which includes their mothers (i.e., maternal proximity) (e.g., Siberian hamsters: Adaniya et al., 2021). Proximity with mothers may also encourage immature offspring to groom others, either actively or passively (e.g., leading by example) (de Waal, 1990; de Waal, 1996). Maternal investment in male-philopatric black-handed spider monkeys increased the likelihood of social play behaviours in sons (Soben et al., 2023b), supporting the social integration of their sons. Social learning can only operate when individuals are in proximity to one another, and juveniles rely more on social than asocial learning (e.g., trial-and-error foraging, operant conditioning) compared to adults (Alberts, 2019; Carter et al., 2016; Laland, 2004). Mother-offspring proximity may even influence the identity of offspring's social partners. Infant rhesus macaques who were spatially closer to their mothers and those whose mothers sustained greater proximity exhibited networks that were more centered around kin (Berman et al., 1997) and these effects persisted past infant independence (Berman, 1982; de Waal, 1996).

Furthermore, offspring who associated more often with their mothers had more similar associates as their mothers than offspring who did so less often (Prediction 1a). This is consistent with the concept of triadic closure (i.e., friends of friends are also friends), which has been previously demonstrated in vervet monkeys (Borgeaud et al., 2016). Moreover, mothers who are more central in grooming networks may rear offspring who are themselves more central in grooming networks (Prediction 1d). Similarly, blue monkey (*Cercopithecus mitis stuhlmanni*) maternal sociality during infancy could affect the future grooming tendencies of their offspring (Thompson & Cords, 2020). Effectively, socially complex environments in early life provide greater learning opportunities and thus support future social competency (Wooddell et al., 2020). For instance, rhesus yearlings reared with the presence and support of multigenerational kin, which constitutes a complex social environment, displayed a more central position in the group (Wooddell et al., 2020).

Maternal network inheritance appears to constitute a spectrum that ranges from minor influences to full inheritance in stable social systems. In spotted hyenas, offspring's associations with other group members mirror those of their mothers for up to their sixth year of life (Ilany et al., 2021). Another species that appears to be at the extreme end of the network inheritance spectrum is the African elephant for which mothers' network betweenness was the main predictor of their daughters' social position ten years later (Goldenberg et al., 2016). Similarly, elephant mothers who associated frequently had offspring who themselves expressed high proximity strengths and this remained true even after the death of the mother (Goldenberg et al., 2016). Results from Ilany et al. (2021) in spotted hyenas supported the hypothesis that social network inheritance from parents to offspring is a pillar in species with a high level of stable social groups. In contrast, vervet monkeys find themselves at the lower end of the maternal network inheritance spectrum. There are several potential reasons for this. First, mothers may not transmit all their social connections directly, but instead, they may bias their offspring' associations and interactions towards certain types of partners, potentially even non-maternal partners. In parallel, while mothers may associate and interact more with other adults, immature vervets may prefer similar-aged peers. Prior research found weak to moderate evidence that the more stable vervet maternal grooming networks were over time, the higher the network similarity was between mothers and their daughters (Jarrett et al., 2018). This suggests that offspring are only able to keep up with maternal network changes when their mothers have stable networks, which they often did not (Jarrett et al., 2018). As such, maternal networks may represent a moving target to their offspring (Jarrett et al., 2018). Alternatively, inheritance of avoidances rather than the transmission of affiliative networks may be an important pathway of immatures' social development (Frère et al., 2023).

I also found that older offspring associate less often with their mothers than younger offspring (Prediction 1b). These results were generally consistent with other studies, such as in closely related captive green monkeys, for whom mother-offspring proximity decreased as juveniles aged from one to three years of age (Fairbanks & McGuire, 1985). Immatures of other primate species also exhibit similar patterns of age-related distancing from mothers (e.g., baboons: Roatti et al., 2023; Altmann, 1980, rhesus macaques: Berman, 1982; Assamese macaques: Arbaiza-Bayona et al., 2025; black-handed spider monkeys: Soben et al., 2023a). Distancing can start early in infancy (e.g., captive green monkeys: Fairbanks & McGuire, 1995) and tends to be driven more by mothers than their offspring (e.g., Fairbanks & McGuire, 1995; Fairbanks, 1996; Lindburg, 1971, but see Fairbanks & McGuire, 1985). Maternal distancing allows offspring to expand, diversify, and establish their social networks to same-age peers (including siblings) and non-maternal partners (e.g., rhesus macaques: Berman, 1982; baboons: Altmann, 1980; bottlenose dolphins: Tsai & Mann, 2013; Stanton et al., 2011; great tits: Wild et al., 2024, hihi (*Notiomystis cincta*): Franks et al., 2020). As such, offspring may need less support from their mothers once they acquire ecological competence (e.g., foraging knowledge) (Roatti et al., 2023). In parallel, they might associate or interact more often with peers of similar age, who seem to be pivotal sources of social knowledge across several taxa, especially information that is important to their own developmental stage (Templeton et al., 2012; Gallois et al., 2018). Juvenile vervets also exhibit a high social tolerance with each other, which further promotes horizontal information transmission (Grampp et al., 2019).

The relationship between mother-offspring proximity and offspring age did not vary depending on offspring sex. Overall, females were not spatially closer to their mothers than male offspring (Prediction 1c). Similar to my findings, immature bottlenose dolphins (Stanton et al., 2011) and black-handed spider monkeys (Soben et al., 2023a) did not express a sex difference in their spatial distancing from mothers as they aged or an overall sex-based difference in their maternal proximity. This contrasts with trends in cercopithecine primates, where mothers tend to have higher proximity with daughters and groom them more often (Kulik et al., 2016; but see results in Assamese macaques: Arbaiza-Bayona et al., 2025), including free-ranging vervet in which female infants become independent from their mothers earlier than male infants (Lee, 1984). In several species, daughters expressed greater proximity rates with their mothers and maternal relatives than sons during development in both female-philopatric (e.g., mandrills: Roura-Torrres et al., 2025; Japanese macaques (*Macaca fuscata*): Nakamichi, 1989; red deer (*Cervus elaphus*): Andres et al., 2013; chacma baboons: Roatti et al., 2023; savannah baboons (*Papio cynocephalus cynocephalus*): Pereira, 1988; stump-tailed macaques (*Macaca arctoides*): Mondragón-Ceballos et al., 2010; geladas (*Theropithecus gelada*): Barale et al., 2015) and male-philopatric species (e.g., chimpanzees: Lonsdorf et al., 2014; black-handed spider monkeys: Rodrigues, 2014). Given my results, there could be a need for high maternal investment in immature vervet daughters as well as sons. Sons need many learning opportunities from their mothers prior to their dispersal, and learning is generally facilitated by maternal proximity. Vervet juveniles learn mostly from their mothers and maternal kin (Grampp et al., 2019). Alternatively, an environmental factor specific to the Lake Nabugabo site (e.g., reliance on crops for feeding) could allow daughters to gain independence earlier than expected, thereby aligning their independence from mothers to that of sons.

4.2 Effects of Maternal Dominance Rank and Age

Contrary to my predictions, maternal dominance rank and age did not affect offspring network metrics (Prediction 4a & b). As such, older and more dominant mothers did not raise immature offspring who were more or less integrated in proximity and grooming networks than younger and less dominant mothers. This suggests that from a social network perspective, there is little advantage in having a high-ranking or older mother, which contrasts with findings from other species. Mandrill mothers higher up in the dominance hierarchy facilitated the social integration in their offspring (Roura-Torres et al., 2025), while spatial and affiliative networks of semi-free ranging immature robust capuchin monkeys (*Sapajus spp.*) were predicted by their mothers' dominance rank, with more dominant mothers rearing immatures who expressed higher grooming strength values and reach, as well as higher spatial degree values (de Lima & Ferreira, 2021). Hence, my results were surprising as dominance status is closely connected to and deeply intertwined with sociality in many species (e.g., rhesus macaques: Wooddell et al., 2020). For instance, vervet monkeys with higher centrality in aggression networks (i.e., higher rank) were also more central in grooming networks (Canteloup et al., 2021). That said, I found that mother-offspring proximity may encourage sociality in offspring, suggesting that an indirect relationship between maternal rank and offspring sociality in our Nabugabo population could exist. In addition to rank being inherited maternally in vervets, especially in daughters (captive vervets: Bramblett et al., 1982), infant vervets encounter markedly different early social experiences overall according to their mothers' dominance rank (Struhsaker, 1971). Fairbanks and McGuire (1985) found that maternal rank affected both mothers' behaviour as well as their offspring's behaviour in captive green monkeys, and that this pattern held true across most of the behaviours examined. Rhesus macaque mothers also limit access to their infants and the amount of time individuals are granted this access varies based on maternal actions and rank (Berman, 1982). There are several potential reasons for the lack of an effect of maternal rank and age on offspring network metrics in our population. First, female vervet centrality does not appear to be linked to dominance rank in the Lake Nabugabo population (Schwegel, 2023), which may explain my findings. It was also observed that the effect of dominance rank on grooming tendencies is significantly reduced in larger vervet monkey groups (Henzi et al., 2013) and as mentioned previously, our study group was somewhat large (N = 39), which might explain why I found no effect of maternal rank. Group composition might have also affected this relationship. In rhesus macaques, both group size and group composition influenced infants' bonds with group members (Berman et al., 1997). Additionally, while I explored the effects of maternal rank and age on offspring proximity and grooming networks, such effects may only apply to other network types not assessed in the current study. For instance, offspring with mothers of similar rank engaged in more play and maintained greater contact with each other than with other offspring (Caine & Mitchell, 1979; Tartabini & Dienske, 1979). Furthermore, offspring of low-ranking mothers may compensate for the low rank of their mothers by trying to bond with non-maternal partners to acquire and maintain successful social integration (Ilany et al., 2021; Kutsukake, 2000), whereas those of high-ranking mothers may leverage their mothers' social connections (Strauss & Holekamp, 2019). As such, analyzing both offspring of high- and low-ranking mothers together could nullify any effect of maternal rank on offspring networks.

4.3 Offspring Age Effects

Overall, I found that older vervet immature offspring likely do not have fewer associates (i.e., proximity degree), but there was moderate evidence that they may associate with others less often (i.e., proximity strength) than younger offspring and they were also less central (i.e., proximity eigenvector centrality) than younger individuals. Older immatures were not necessarily more central in grooming networks (i.e., grooming eigenvector centrality). There was no effect of offspring age on similarity to maternal grooming or proximity partner choices (i.e., mother-offspring cosine similarity), which did not vary based on offspring sex. While the number of grooming partners (i.e., grooming degree) also did not vary by offspring age, older offspring may groom or be groomed by others more often (i.e., grooming strength) than younger offspring. Finally, the slightly positive relationship between age and most grooming metrics (i.e., degree, strength, and eigenvector centrality) may be stronger in daughters than sons.

That older vervet offspring did not have fewer associates than younger offspring at Nabugabo (Prediction 3a) contrasts with findings where juvenile vervets of a South African population associated with fewer spatial partners as they aged (Vilette et al., 2022). Conversely, African elephants actually possessed more proximity partners as they aged (Goldenberg et al., 2016). However, consistent with my results, bottlenose dolphins demonstrated a high stability in the number of association partners over time (Evans et al., 2021). In addition, I found moderate evidence that older offspring associate less often with others than younger offspring (Prediction 3b), and this was consistent with overall declines in vervet association frequency observed in a South African vervet population, though both spatial degree and strength peaked during the birth seasons, most likely due to changes in group dynamics, notably attraction to newborns seen in vervet monkeys (Vilette et al. 2022). White-faced capuchins decreased their time in proximity with other individuals while also decreasing their number of associates as they aged, with both patterns being observed throughout their lifetime (Godoy et al., 2024; Godoy et al., 2022). In contrast to my results, older juvenile blue monkeys expressed higher spatial strengths than younger juveniles (Cords & al., 2010). Similarly, fledglings increased their frequency of dyadic associations within their first few weeks, which suggested that they were successfully integrating into local flocks (Wild et al., 2024). Overall, my results suggest that, without needing to increase the number of associates, older Nabugabo vervets may be more selective with their proximity partners than younger individuals. This could be due to less of a need for external support as they reach independence and therefore a reduced interest in associations and/or more partner selectivity (Roatti et al., 2023). Analogous to chacma baboons (Roatti et al., 2023), they may prefer similar-aged peers and partners with the same sex as their own, who may act as important sources of knowledge (Templeton et al., 2012; Gallois et al., 2018). Alternatively, immatures may also become less attractive to other group members as they age, thereby experiencing a reduction in spatial tolerance from fellow group members (Roatti et al., 2023; Silk, 1999).

Moreover, older offspring expressed lower centrality in proximity networks than younger individuals (Prediction 3c). These results are consistent with developmental processes of social integration. In females, this pattern aligns with youngest ascendancy, whereby younger daughters are more likely to be ranked higher in the hierarchy than their older sisters (Horrocks & Hunte, 1983), and higher rank is often associated with higher network centrality (Canteloup et al., 2021; but see Schwegel, 2023). Reciprocally, older age may be associated with lower centrality due to a declining rank for older immature females. In males, age-related changes in social behaviour associated with the onset of dispersal may similarly reduce spatial centrality in older immatures. As such, younger individuals are expected to be more central than older individuals. To confirm an indirect relationship between age and centrality, offspring dominance rank would have to be compared to centrality at Nabugabo. That said, preliminary analyses indicate that centrality is not linked to dominance rank in female vervets at Nabugabo (Schwegel, 2023), suggesting that dominance rank is not responsible for the observed connection between age and proximity centrality. In contrast with my results, robust capuchins exhibited no effect of age on proximity centrality (de Lima & Ferreira, 2021).

Contrary to my prediction (3c), there was no effect of offspring age on grooming centrality. Several studies in other species have recorded a positive effect of age on grooming centrality (Wooddell et al., 2020; Shimada & Sueur, 2018; de Lima & Ferreira, 2021). Effectively, immatures appear to shift their interest from play networks to grooming interactions, which allows them to build bonds with group members and integrate into affiliative networks (Kulik et al., 2015). Grooming centrality may be high in infancy and early juvenile years in vervet monkeys due to infant attraction and patterns of youngest ascendancy in females. Thereafter, grooming direction may progressively shift from co-residents grooming immatures to immatures initiating grooming bouts more often, and therefore compensating for the decline in grooming received by immatures, which could explain the lack of an effect of age on grooming centralities in the current study.

Contrary to my prediction (3d), partners of older offspring were not more or less similar to maternal spatial and grooming partners than partners of younger offspring. While immature females may choose more similar grooming partners to their mothers than males, proximity partner similarity did not vary by immature sex (Prediction 3d). Similarly, Jarrett *et al.* (2018) found that partner similarity between mother-offspring pairs did not increase with age in a South African population of vervet monkeys, such that juvenile and maternal networks did not converge over time. Conflicting results were reported in other species, with some exhibiting more similarity with maternal partners when older (e.g., rhesus macaques: de Waal, 1996), and others diversifying their partner choices from maternal patterns with age (e.g., chacma baboons: Roatti et al., 2023; infant rhesus macaques: Berman, 1982; white-faced capuchins: Godoy et al., 2024). Maternal influences tend to decline as offspring age (Lindholm et al., 2006), particularly after mother-offspring distancing (e.g., Berman, 1982) which was observed in our vervet group. Overall, my results suggest that immature vervets may retain maternal influences as they grow older, which may serve to benefit from the protection of mothers and her partners against external aggression, as well as possibly to buy feeding tolerance from maternal allies (Packer & Pusey, 1983; McFarland & Majolo, 2013).

Immature age had some effects on their grooming networks and these effects may vary by sex. Surprisingly, older immatures did not have more grooming partners than younger individuals (Prediction 3e), which contrasted with findings in robust capuchin monkeys (i.e., grooming degree) (de Lima & Ferreira, 2021). However, older individuals may groom or be groomed more frequently than younger individuals (Prediction 3e), which may be due to a shift in activity budgets. As mentioned, rhesus macaques may shift their focus from playing to grooming as they aged (Kulik et al., 2015) and simultaneously, become more skilled and desirable groomers (baboons: Altmann, 1980). Interestingly, most grooming metrics (i.e., degree, strength, and centrality) may show a stronger positive relationship with age among daughters than sons when the unsexed juvenile in this present study was classified as "male" (Prediction 3e). This was consistent with immature vervet females from another population, who increased the number of and relationship strength with grooming partners faster than male immatures, and this pattern became more pronounced over time (Vilette et al. 2022). Immature male grooming frequency was even reported to decline with age (Vilette et al., 2022). Nonetheless, it should be noted that social integration remains crucial to young males. For instance, adult male vervet monkeys who maintained many female spatial partners and groomed more with well-integrated females increased their dominance rank more rapidly than less integrated males, likely because females can represent important allies during conflict (Young et al., 2017), and a multilayer network approach revealed that this effect is transient, although it can influence other social layers, such as male-male aggression (Bonnell et al., 2021). In some species like chimpanzees, forming coalitions with other males may also be beneficial in accessing more estrous females and securing more copulations with them (Watts, 1998).

Overall, I found some effects of offspring age on their social network metrics, but these effects were not all as predicted. Many expected differences (e.g., grooming and proximity degree, grooming centrality) were not observed, which may be explained by the strong fluctuations exhibited by juvenile social networks, making it difficult to uncover trends and patterns of social ontogeny (Jarrett et al., 2018). Nonetheless, my results suggest that young individuals may spend less time in proximity with group members but more time grooming them, which directly echoed findings in chacma baboons (Roatti et al., 2023). Lastly, offspring sex appears to be a stronger predictor of offspring network changes than offspring age, as seen in chacma baboons (Roatti et al., 2023; but see robust capuchin monkeys: de Lima & Ferreira, 2021). In sum, vervet monkeys may express more social stability relative to other species, possibly similar to bottlenose dolphins whose social characteristics remain consistent from infancy all the way to older adulthood (Evans et al., 2021).

4.4 Offspring Sex Effects

Overall, immature females were more integrated in grooming networks than males, with females having more partners (i.e., grooming degree), stronger relationships with them (i.e., grooming strength), and being more central (i.e., grooming eigenvector centrality) than immature males. While immature females may be more central than males in proximity networks (i.e., proximity eigenvector centrality), there were no sex-based differences in the number of spatial partners (i.e., proximity degree) or the frequency with which they associated with them (i.e., proximity strength). My results present limited evidence suggesting that immature daughters may choose more similar grooming (but not proximity) partners as their mothers (i.e., cosine similarity) than sons.

Male and female immature vervet monkeys displayed notably different network patterns, with females being more integrated than males. Like in many female-philopatric species (e.g., vervet monkeys: Vilette et al., 2022; Jarrett et al., 2018; Blaszczyk et al., 2018; baboons: Young et al., 1982; Roatti et al., 2023; Hanuman langurs (*Presbytis entellus*): Nikolei & Borries, 1997;

rhesus macaques: Kulik et al., 2015; blue monkeys: Cord et al., 2010; but see geladas: Barale et al., 2015), immature females had more grooming partners and stronger relationships with them, and were also more central in grooming networks than males (Prediction 4a). This could be explained by findings from Funk *et al.* (2024) which suggest that young vervet males are more inclined to spend their time playing with others relative to females, which may support the development of fighting skills and aid the acquisition of a higher rank in the dominance hierarchy through competition as they grow into adulthood (McGuire, 1982; Roatti et al., 2023). In female-philopatric species, immature females tend to possess a greater variety of social partners whereas males tend to peripheralize from the social group and prefer male peers than other group members as they get closer to dispersal (Cords et al., 2010; Lonsdorf, 2017; Roatti et al., 2023). Immature female vervets could be more integrated in grooming networks for several reasons. Overall, high grooming frequencies have been linked with a strong tendency to form female coalitions among adult vervet females (Seyfarth, 1980). In many primate species, grooming is often used to form and strengthen alliances in agonistic contexts (Schino, 2006) and generally, females tend to form more alliances with other group members than males, allowing them to claim resources such as food and nest sites (Thompson, 2019). Grooming may also increase longevity (Silk et al., 2010), shield from predation (Josephs et al., 2016), and protect from hypothermia (McFarland et al., 2015). In vervet females, grooming integration in adulthood can predict infant survival (McFarland et al., 2015). As such, social centrality is often associated with higher reproductive success in individuals (Silk et al., 2006), which is supported by preliminary findings from the Nabugabo vervet population (Schwegel, 2023). Additionally, early rearing experience is a strong determinant of later offspring grooming centrality, as bonobo (*Pan paniscus*) immatures reared without a mother were less central in grooming networks and thus less important players in maintaining group cohesion (Torfs et al., 2023). Grooming is also used as a technique to calm other individuals which allows to build and maintain peaceful relationships, averting conflict by grooming threatening individuals (Sade, 1965), which reveals the mediating role that our central vervet females may adopt. Socially central philopatric females tend to hold a lot of leverage and influence in their group; for instance, driving group movements is most often done by socially central individuals (e.g., chacma baboons: King et al., 2011). In line with this, the most successful group members at leading group movements at the Lake Nabugabo site were older female vervets (Lee & Teichroeb, 2016).

Greater integration in social networks may provide learning opportunities for young females to gain rearing experience prior to breeding, making them more successful when raising their own offspring (captive green monkeys: Fairbanks, 1990). Centrality can also support the knowledge acquisition of foraging techniques and sites (e.g., blue tit (*Cyanistes caeruleus*), great tit, marsh tit (*Poecile palustris*): Aplin et al., 2012). In parallel, adult females themselves are pivotal sources of knowledge to immatures and to immigrant adults since philopatric females remain in the group for their entire lives (van de Waal et al., 2010, van de Waal et al., 2013).

Grooming centrality in young females may be an indicator of the formation of localized matrilineal cultures within vervet groups. Knowledge transfer is shaped by grooming & proximity networks in chacma baboons (e.g., socially central individuals enjoy an easier access to information) (Carter et al., 2016), which may also be the case in other cercopithecines such as vervet monkeys. Grooming tends to be mostly done among relatives (e.g., rhesus macaques: Sade, 1965; vervet monkeys: Seyfarth & Cheney, 1984). Vervet monkeys are much more likely to consistently dedicate their attention to core group members (i.e., the philopatric sex, more socially central females) as models to learn innovative foraging techniques (van de Waal et al., 2010). As such, vervet monkeys are more selectively attentive to females than males (Renevey et al., 2013). Studies have shown that predictors of social learning patterns alone can result in the formation of "subcultures" in matrilineal clusters within vervet groups (van de Waal et al., 2014; Roatti et al., 2023). In some cases, social learning tendencies specific to matrilines may even lead to the emergence of ecotypes (e.g., killer whales (*Orcinus orca*): Riesch et al., 2012). Matrilineal cultures may arise in vervet monkeys as I know that even arbitrary food preferences can be passed on (van de Waal et al., 2013). van de Waal *et al.* (2010) have proposed that dispersals likely do not allow the transfer of social knowledge between groups, which may constrain information flow and result in highly localized traditions specific to matrilines (van de Waal et al., 2012; van de Waal et al., 2014). Transmitting non-arbitrary food preferences is also very important as vervet monkeys are omnivorous generalists (Nord et al., 2021), which can increase the chance of encountering toxic food items (Galef & Giraldeau, 2001).

Moreover, female immatures may be more central than males in proximity networks (Prediction 4a), echoing results from Dunbar (1991) in rhesus macaques and from Borgeaud *et al.* (2017) and Blaszczyk *et al.* (2018) who demonstrated that vervet females are more central in both grooming and proximity networks, which is also reflected later in adulthood. However, I also found that females did not have more or fewer spatial partners and did not associate with group members more or less often than male immatures (Prediction 4a). Interestingly, this was fully aligned with results from Cord *et al.* (2010) in female-philopatric blue monkeys but contrary to findings from female-philopatric immature Hanuman langurs (Nikolei & Borries, 1997). Despite sex differences in grooming integration, young vervet males still need to acquire knowledge that will be key to their success upon reaching adulthood. While being active in affiliative networks is crucial to learning processes during juvenile years (e.g., Kulahci et al., 2016), visual contact is also essential for information transmission and can only occur if individuals are in proximity to one another. Young males may also benefit from creating and maintaining connections with associates, specifically male peers, as they may need coalitionary support when engaging in parallel dispersal upon reaching sexual maturity (Schoof et al., 2009).

My results suggest that immature daughters may choose more similar grooming (but not proximity) partners as their mothers compared to sons (Prediction 4b). This was congruent with findings in chacma baboons whereby young males had looser relationships with maternal partners than young females, and immature male proximity and grooming networks were more dissimilar from that of mothers than the networks of females (Roatti et al., 2023). Mothers themselves may support integration of daughters and encourage the independence of sons (Kulik et al., 2016), contrasting with mothers of male-philopatric species (Boesch, 1997). Matching matrilineal bonds will also allow females to be supported during agonistic conflicts, thereby helping them to maintain the rank they inherited (Silk et al., 2004). As such, daughters may also invest more in kin (Widdig et al., 2016), who tend to make up many maternal partners.

Overall, my results provide strong support for my fourth hypothesis as daughters and sons displayed different network patterns because vervets are characterized by female philopatry and male-biased dispersal. Several studies report that immature female vervet monkeys are more integrated than male immatures (Blaszczyk et al., 2018; Jarrett et al., 2018; Vilette et al., 2022), which echoes findings in other female-philopatric species (e.g., Cords et al., 2010). Possible explanations of sex-dependent differences in sociality include cues from other group members, in particular cues directed to the philopatric sex (as suggested by Cords et al., 2010).

4.5 Limitations

My study has a few limitations that should be acknowledged. First, my data only included eight mothers and 17 immatures. Nonetheless, our vervet monkey group was considered quite large at 39 individuals, highlighting the broader challenge of sample sizes faced by primate researchers. Predictably, focal data yielded lower values for weighted metrics (i.e., strength and possibly eigenvector centrality) than *ad libitum* data in grooming networks, but not in proximity networks. Essentially, instantaneous focal follows do not capture grooming behaviours that occur between scans (i.e., grooming bouts are less prevalent than proximity: Vilette et al., 2022), whereas *ad libitum* data collection targeted behaviours of interest such as grooming and may be over-represented because these data were sought out (Altmann, 1974). Moreover, one maternal network type (e.g., proximity) may be transmitted to a different network type (e.g., grooming) in offspring, which I did not investigate in my work. For instance, the social position of rhesus macaque mothers in the grooming network corresponded to their offspring' position in the play network, congruent with the different demands of the two separate life-history stages that mothers and their juveniles are in (Wooddell et al., 2020). Another potential limitation is that I did not compare maternal networks with offspring networks at different times (i.e., time t with time t+1). Effectively, Jarrett *et al.* (2018) suggested that maternal networks may represent a moving target for their offspring. As such, mapping delays between maternal and offspring networks might reveal stronger maternal influences than what I observed in the current study (e.g., delay in kin bias in infants and mother rhesus macaques: Berman & Kapsalis, 1999). Additionally, partner identity, which I did not investigate, may provide important information on immature social integration. For instance, offspring may associate more often with offspring of their parents' associates instead of their parents' associates directly (e.g., Wild et al., 2024).

Furthermore, much research is needed to uncover more of the mechanisms behind primate social integration. Including betweenness as a network metric tested in future studies of mother-offspring network comparisons will be very informative given that this measure was found to be inherited by offspring of several mammalian species (e.g., rhesus macaques: Brent et al., 2013; African elephants: Goldenberg et al., 2016). More specifically, betweenness is pivotal in the process of cultural transmission (Mann et al., 2012; Brent, 2015), as this metric represents bridges between individuals who were not otherwise connected (Table S1). Moreover, offspring of lower-ranking mothers may compensate for the disadvantage of having a lower-ranking mother by not inheriting their mothers' social networks (Ilany et al., 2021). Effectively, social inheritance may be only seen in offspring of higher-ranking mothers for whom leveraging relationships with maternal allies can be more advantageous (Strauss & Holekamp, 2019). As such, investigating whether mother-offspring social partner similarity is higher for higher-ranking mothers than for lower-ranking mothers will shed light on the finer-scale mechanisms of social ontogeny. My results reveal clear maternal influences on immature social integration so comparing the social networks of orphaned wild juvenile vervets with networks of juveniles whose mother is present during formative juvenile years would allow us to determine the full extent of such maternal influences. For instance, bonobo immatures reared without a mother were less central and displayed lower out-strength values in grooming networks than individuals raised by mothers (Torfs et al., 2023). Concurrently, assessing the potential effects of the presence of grandmothers would provide additional insight (e.g., Fairbanks, 1988b). Lastly, conducting dynamic social network analysis by adapting the *bisonR* package may be an interesting future avenue of research to map the temporal social changes that immatures express. A dynamic analysis is allowed to vary in structure over time and is therefore more representative of the social fluctuations experienced by animals (Vilette, 2022). Similarly, environmental conditions (e.g., food availability, rainfall) can affect the spatial disposition of individuals in a group, thereby altering likelihoods of interaction between group members (Whitehead, 2008). One cohort for which the use of dynamic social network analysis is particularly appropriate is that of immature individuals due to the rapid changes unfolding throughout development (e.g., Vilette et al., 2022).

4.6 Conclusions

To conclude, while some maternal characteristics (i.e., maternal proximity, some sociality metrics) influenced immature offspring social networks, maternal dominance rank and age did not. Through these maternal influences, mothers may prepare their offspring for their future adult roles (e.g., chimpanzees: Murray et al., 2014). Furthermore, I found that maternal influences exist mainly in proximity but not in grooming networks, which highlights the need to investigate mechanisms of integration in proximity networks. Of more importance seems to be characteristics of the offspring themselves, specifically sex, which appear to be influential to the social ontogeny of vervet monkeys, whereas offspring age had fewer effects on their social networks. Overall, immature individuals experience dramatic changes in selection pressures and, as such, should consistently modify their social behaviour in response to these changes to maintain the fitness advantages of living in social groups (Silk, 2007). Studies have found that understanding immature social networks can inform us on adult networks, while excluding immatures in investigations of social network structure of a group can lead to drastically different findings (Wooddell et al., 2020). Uncovering mechanisms underlying social integration is crucial, because securing affiliative and cooperative relationships across a variety of social partners is associated with improved fitness (Thompson, 2019). Effectively, gaining insight into social ontogeny can reveal how developmental changes yield different fitness consequences (Wooddell et al., 2020).

4.7 Significance

Assessing which attributes can affect social networks is important because it informs our understanding of social developmental processes and overall niche construction (Vilette et al., 2022). Studies about sociality often fail to include the potential effects of maternal rank, whilst studies focusing on dominance rank often forget to address social integration (Blersch et al., 2023). In the present study, both dominance and social integration were included. Considering both in concert, and later how they affect reproductive success, would also allow us to isolate the factors that affect immature fitness across temporal and spatial contexts (Blersch et al., 2023). In turn, this may have conservation implications, allowing us to speculate on the potential effects of the absence of mothers (e.g., due to poaching) on the fitness of their offspring. Given my results that mothers do have some influences on their offspring, orphaned immatures may experience notable disadvantages relative to other immatures. In addition, although Jarrett et al. (2018) have already investigated maternal network inheritance in vervet monkeys, they excluded spatial networks and the possible effects of maternal dominance rank and age in mother-offspring network comparisons from their analyses, both of which are important and were considered by the present work. For instance, including spatial networks is crucial since social learning can only operate when individuals are spatially associated, particularly juveniles (e.g., visual contact) (Carter et al., 2016). Some research has found that the effects of affiliative bonds (i.e., measured with grooming networks) on social learning were weaker than the effects of proximity networks, showing the importance of considering spatial networks, especially in the context of social learning (Carter et al. 2016). Thus, incorporating multiple potential attributes in social developmental analyses is crucial to gain a fuller picture of the patterns at play (Kulahci et al., 2016).

Developing a more complete understanding of ecological and evolutionary processes that influence network formation also requires the study of interpopulation differences (Pinter-Wollman et al., 2014). As such, while Jarrett *et al.* (2018) and Vilette *et al.* (2023) investigated and touched on network inheritance in a South African population of vervet monkeys, my study explored maternal network inheritance in a Ugandan population. Furthermore, although the majority of social network studies have focused on adults (Canteloup et al., 2021), evaluating network changes over time requires the consideration of a broader age bracket. Including immatures in social network analysis is crucial since they can significantly affect the networks of adults (e.g., inclusion increased adult female centrality and decreased male centrality) (Canteloup et al., 2021; Fedurek & Lehmann, 2017). Not only do immatures often express more social activity than adults, but they also rely more on social than asocial learning (Laland, 2004).

My work on social network development and integration also provides insight into social learning and its potential constraints as I found that immature females are more integrated in grooming networks than immature males. Vervet monkeys were found to be selective with their associates at older ages, echoing findings that they prefer to observe and learn from females (van de Waal et al., 2010). In sum, connections between individuals differ in how effective they are at allowing information to be transmitted (Kulahci et al., 2016). For instance, the best predictors of information diffusion in juvenile ravens were an association of hierarchical rank and social transmission within the kinship network (Kulahci et al., 2016). As such, maternal social influences, particularly in daughters, combined with the greater social integration of immature females, suggest that sex and age clusters form at the matrilineal level which might constrain social learning and potentially lead to matrilineal ‘culture’ instead of ‘group’ culture (Roatti et al., 2023). This hypothesis was supported in vervet monkeys who displayed similarities among matrilines in food processing methods which remained stable over time (van de Waal et al., 2012), illustrating a case where cultural practices formed at the matrilineal level instead of the group level. Overall, understanding intra- and interspecific network variations as well as how social networks develop can allow us to build comprehensive theories, which is much needed (Ilany & Akçay, 2016). As such, a lot remains to be uncovered about social ontogeny within the field of primate behavioural evolution (Maestripieri, 2018).

5.0 References

Adaniya, C. H., Wellman, C. L., Demas, G. E. & Cusick, J. A. (2021). The ontogeny of personality: Repeatability of social and escape behaviors across developmental stages in Siberian hamsters (*Phodopus sungorus*). *Journal of experimental zoology. Part A, Ecological and integrative physiology* **335**(6), 10.1002/jez.2499. https://doi.org/10.1002/jez.2499

Alberts, S. C. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology* **88**(1), 47-66. https://doi.org/10.1111/1365-2656.12887

Alberts, S. C., Buchan, J. C. & Altmann, J. (2006). Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour* **72**(5), 1177-1196. https://doi.org/10.1016/j.anbehav.2006.05.001

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **49**(3), 227-267. https://doi.org/10.1163/156853974x00534

Altmann, J. (1980). Baboon mothers and infants, 1st edition. Chicago, IL: The University of Chicago Press.

Altmann, S.A. (1991). Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proceedings of the National Academy of Sciences of the United States of America* **88**(2), 420-423. https://doi.org/10.1073%2Fpnas.88.2.420

Andres, D., Clutton-Brock, T.H., Kruuk, L.E.B., Pemberton, J. M., Stopher, K. V. & Ruckstuhl, K. E. (2013). Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*). *Behavioral Ecology and Sociobiology* **67**, 1249-1258. https://doi.org/10.1007/s00265-013-1552-3

Aplin, L. M., Farine, D. R., Morand-Ferron, J. & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings. Biological sciences* **279**(1745), 4199-4205. https://doi.org/10.1098/rspb.2012.1591

Arbaiza-Bayona, A. L., Mundry, R., Malaivijitnond, S., Meesawat, S., Schülke, O. & Ostner, J. (2025). *Age-trajectory of mother-infant relationships in wild Assamese macaques.* [Preprint]. bioRxiv. https://doi.org/10.1101/2025.05.10.653242

Barale, C. L., Rubenstein, D. I. & Beehner, J. C. (2015). Juvenile social relationships reflect adult patterns of behavior in wild geladas. *American Journal of Primatology* **77**(10), 1086-1096. https://doi.org/10.1002/ajp.22443

Bardi, M., French, J.A., Ramirez, S.M. & Brent, L. (2004). The role of the endocrine system in baboon maternal behavior. *Biological Psychiatry* **55**, 724-732.

Bardi, M., Shimizu, K., Fujita, S., Borgognini-Tarli, S. & Huffman, M.A. (2001). Hormonal correlates of maternal style in captive macaques (*Macaca fuscata* and *M. mulatta*). *International Journal of Primatology* **22**, 647-662.

Bastian, M.L., Sponberg, A.C., Sponberg, A.C., Suomi, S.J. & Higley, J.D. (2002). Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Developmental Psychobiology* **42**(1), 44-51. https://doi.org/10.1002/dev.10091

Bejder, L., Fletcher, D. & Bräger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour* **56**(3), 719-725. https://doi.org/10.1006/anbe.1998.0802

Bengtsson, H. (2021). A Unifying Framework for Parallel and Distributed Processing in R using Futures. *The R Journal* **13**(2), 208-227. https://doi.org/10.32614/RJ-2021-048

Berman, C. M. (1982). The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys I. Social networks and differentiation. *Animal Behaviour* **30**(1), 149-162. https://doi.org/10.1016/S0003-3472(82)80250-9

Berman, C. M. (2004) Developmental aspects of kin bias in behavior. In: Chapais, B., Berman, C. M. (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 317-346.

Berman, C. M. & Kapsalis, E. (1999). Development of kin bias among rhesus monkeys: maternal transmission or individual learning? *Animal behaviour* **58**(4), 883-894. https://doi.org/10.1006/anbe.1999.1221

Berman, C. M., Rasmussen, K. L. R. & Suomi, S. J. (1997). Group size, infant development and social networks in free-ranging rhesus monkeys. *Animal Behaviour* **53**(2), 405-421. https://doi.org/10.1006/anbe.1996.0321

Blaszczyk, M. B. (2018). Consistency in social network position over changing environments in a seasonally breeding primate. *Behavioral Ecology and Sociobiology* **72**(11), 1-13. https://doi.org/10.1007/s00265-017-2425-y

Blersch, R. A., Bonnell, T. R., Clarke, M., Dostie, M. J., Lucas, M., Jarrett, J., McFarland, R., Nord, C., Takahashi, A., Varsanyi, S., Vilette, C., Young, C., Barrett, L. & Henzi, S. P.

(2023). Maternal social position and survival to weaning in arid-country vervet monkeys. *American Journal of Biological Anthropology* **181**(1), 3-9. https://doi.org/10.1002/ajpa.24689

Boesch, C. (1997). Evidence for dominant wild female chimpanzees investing more in sons. *Animal behaviour* **54**(4), 811-815. https://doi.org/10.1006/anbe.1996.0510

Bonnell, T. R. & Vilette, C. (2020). Constructing and analysing time-aggregated networks: The role of bootstrapping, permutation and simulation. *Methods in Ecology and Evolution* **12**(1), 114e126. https://doi.org/10.1111/2041-210X.13351

Bonnell, T. R., Vilette, C., Young, C., Henzi, S. P. & Barrett, L. (2021). Formidable females redux: male social integration into female networks and the value of dynamic multilayer networks. *Current zoology* **67**(1), 49-57. https://doi.org/10.1093/cz/zoaa041

Borgeaud, C., Alvino, M., van Leeuwen, K., Townsend, S. & Bshary, R. (2015). Age/sex differences in third-party rank relationship knowledge in wild vervet monkeys, *Chlorocebus aethiops pygerythrus*. *Animal Behaviour* **102**, 277e284. https://doi.org/10.1016/j.anbehav.2015.02.006

Borgeaud, C., Sosa, S., Bshary, R., Sueur, C. & van de Waal, E. (2016). Intergroup Variation of Social Relationships in Wild Vervet Monkeys: A Dynamic Network Approach. *Frontiers in psychology* **7**, 915. https://doi.org/10.3389/fpsyg.2016.00915

Borgeaud, C., Sosa, S., Sueur, C. & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Animal Behaviour* **134**, 155-165. https://doi.org/10.1016/j.anbehav.2017.09.028

Bramblett, C. A., Bramblett, S. S., Bishop, D. A. & Coelho, A. M. (1982). Longitudinal stability in adult status hierarchies among vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology* **2**(1), 43-51. https://doi.org/10.1002/ajp.1350020107

Branchi, I., D'Andrea, I., Gracci, F., Santucci, D. & Alleva, E. (2009). Birth spacing in the mouse communal nest shapes adult emotional and social behavior. *Physiology & Behaviour* **96**(4-5), 532-539. https://doi.org/10.1016/j.physbeh.2008.12.003

Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Animal Behaviour* **103**, 211-222. https://doi.org/10.1016/j.anbehav.2015.01.020

Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., Skene, J. H. P. & Platt, M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports* **3**, 1042. https://doi.org/10.1038/srep01042

Bürkner, P.-C. (2021). Bayesian Item Response Modeling in R with brms and Stan. *Journal of Statistical Software* **100**(5), 1-54. https://doi.org/10.18637/jss.v100.i05

Cain, M. K., Zhang, Z. & Yuan, K. H. (2017). Univariate and multivariate skewness and kurtosis for measuring nonnormality: Prevalence, influence and estimation. *Behavior Research Methods* **49**, 1716-1735. https://doi.org/10.3758/s13428-016-0814-1

Caine, N. & Mitchell, G. (1979). The relationship between maternal rank and companion choice in immature macaques (*Macaca mulatta* and *M. radiata*). *Primates* **20**, 583-590. https://doi.org/10.1007/BF02373440

Canteloup, C., Puga-Gonzalez, I., Sueur, C. & van de Waal, E. (2021). The consistency of individual centrality across time and networks in wild vervet monkeys. *American journal of primatology* **83**(2), e23232. https://doi.org/10.1002/ajp.23232

Canteloup, C., Hoppitt, W. & van de Waal, E. (2020a). Wild primates copy higher-ranked individuals in a social diffusion experiment. *Nature Communications* **11**, 459. https://doi.org/10.1038/s41467-019-14209-8

Canteloup, C., Puga-Gonzalez, I., Sueur, C. & van de Waal, E. (2020b). The effects of data collection and observation methods on uncertainty of social networks in wild primates. *American journal of primatology* **82**(7), e23137. https://doi.org/10.1002/ajp.23137

Carter, A. J., Torrents Ticó, M. & Cowlishaw, G. (2016). Sequential phenotypic constraints on social information use in wild baboons. *Elife* **5**, e13125. https://doi.org/10.7554/eLife.13125

Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In: Harcourt A, de Waal, F. B. M. (eds) Coalitions and alliances in humans and other animals. Oxford University Press, New York, pp 29-59.

Chapman, C. A., Twinomugisha, D., Teichroeb, J. A., Valenta, K., Sengupta, R., Sarkar, D. & Rothman, J. M. (2016). How do primates survive among humans? Mechanisms employed by the vervet monkey at Lake Nabugabo, Uganda. In: Waller, M., editor. Ethnoprimatology. Primate conservation in the 21st century. New York: Springer Press. p. 77-94.

Charuvastra, A. & Cloitre, M. (2008). Social Bonds and Posttraumatic Stress Disorder. *Annual Review of Psychology* **59**, 301-328. https://doi.org/10.1146%2Fannurev.psych.58.110405.085650

Cheney, D. L. (1981). Intergroup encounters among free-ranging vervet monkeys. *Folia primatologica; international journal of primatology* **35**(2-3), 124-146. https://doi.org/10.1159/000155970

Cheney, D. L., Seyfarth, R. M., Andelman, S. J. & Lee, P. C. (1988). Reproductive success in vervet monkeys. In T. H. Clutton-Brock (Ed.), Reproductive success: Studies of individual variation in contrasting breeding systems (pp. 384e402). University of Chicago Press.

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *The American Naturalist* **123**(2), 212-229. https://doi.org/10.1086/284198

Cords, M., Sheehan, M. J. & Ekernas, L. S. (2010). Sex and age differences in juvenile social priorities in female philopatric, non-despotic blue monkeys. *American journal of primatology* **72**(3), 193-205. https://doi.org/10.1002/ajp.20768

Creighton, M. J. A., Lerch, B. A., Lange, E. C., Silk, J. B., Tung, J., Archie, E. A. & Alberts, S. C. (2024). Reevaluating the relationship between female sociality and infant survival in wild baboons. *Proceedings of the National Academy of Sciences of the United States of America* **122**(20), e2417378122. https://doi.org/10.1073/pnas.2417378122

Crockford, C., Wittig, R., Whitten, P., Seyfarth, R. & Cheney, D. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior* **53**, 254-265. https://doi.org/10.1016/j.yhbeh.2007.10.007

Croft, D. P., Madden, J. R., Franks, D. W. & James, R. (2011). Hypothesis testing in animal social networks. *Trends in ecology & evolution* **26**(10), 502-507. https://doi.org/10.1016/j.tree.2011.05.012

Croft, D. P., James, R. & Krause, J. (2008). Exploring animal social networks. Princeton University Press.

Csárdi, G., Nepusz, T., Müller, K., Horvát, S., Traag, V., Zanini, F. & Noom, D. (2025). igraph for R: R interface of the igraph library for graph theory and network analysis (v2.1.4). *Zenodo* https://doi.org/10.5281/zenodo.14736815

Deputte, B. L. (2000). Primate socialization revisited: Theoretical and practical issues in social ontogeny. In Advances in the Study of Behavior 29 (pp. 99-157). Elsevier.

de Lima, V. C. C. & Ferreira, R. G. (2021). Social network changes during the development of immature capuchin monkeys (*Sapajus spp.*). *Primates* **62**(5), 801-815. https://doi.org/10.1007/s10329-021-00918-6

de Waal, F. B. M. (1990). Do rhesus mothers suggest friends to their offspring? *Primates* **31**, 597-600. https://doi.org/10.1007/BF02382543

de Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: A sociometric analysis. *Animal Behaviour* **41**, 383-398. https://doi.org/10.1016/S0003-3472(05)80669-1

de Waal, F. B. M. (1996). Macaque social culture: development and perpetuation of affiliative networks. *Journal of comparative psychology (Washington, D.C: 1983)* **110**(2), 147-154. https://doi.org/10.1037/0735-7036.110.2.147

de Waal, F. B. M. & Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia primatologica; international journal of primatology*, **46**(4), 215-234. https://doi.org/10.1159/000156255

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour* **125**(3-4), 283-313. https://doi.org/10.1163/156853993X00290

Dunbar, R. I. (1991). Functional significance of social grooming in primates. *Folia Primatologica* **57**, 121-131.

Evans, T., Krzyszczyk, E., Frère, C. & Mann, J. (2021). Lifetime stability of social traits in bottlenose dolphins. *Communications Biology* **4**, 759. https://doi.org/10.1038/s42003-021-02292-x

Fairbanks, L. A. (1988a). Mother-infant behavior in vervet monkeys: Response to failure of last pregnancy. *Behavioral Ecology and Sociobiology* **23**(3), 157-165. https://doi.org/10.1007/BF00300350

Fairbanks, L. A. (1988b). Vervet monkey grandmothers: Effects on mother-infant relationships. *Behaviour* **104**(1-2), 176-188. https://doi.org/10.1163/156853988X00665

Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour* **40**(3), 553-562. https://doi.org/10.1016/S0003-3472(05)80536-6

Fairbanks, L. A. (1996). Individual differences in maternal styles: causes and consequences for mothers and offspring. *Advances in the Study of Behavior* **25**, 579611.

Fairbanks, L. A. & McGuire, M. T. (1985). Relationships of vervet mothers with sons and daughters from one through three years of age. *Animal Behaviour* **33**(1), 40-50. https://doi.org/10.1016/S0003-3472(85)80118-4

Fairbanks, L. A. & McGuire, M. T. (1986). Age, reproductive value, and dominance-related behaviour in vervet monkey females: Cross-generational influences on social relationships and reproduction. *Animal Behaviour* **34**(6), 1710-1721. https://doi.org/10.1016/S0003-3472(86)80258-5

Fairbanks, L. A. & McGuire, M. T. (1995). Maternal Condition and the Quality of Maternal Care in Vervet Monkeys. *Behaviour* **132**(9/10), 733-754. https://doi.org/10.1163/156853995X00126

Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in ecology and evolution* **8**(10), 1309-1320. https://doi.org/10.1111/2041-210X.12772

Farine, D. R. & Whitehead, H. (2015). Constructing, conducting and interpreting animal network analysis. *Journal of Animal Ecology* **84**(5), 1144-1163. https://doi.org/10.1111/1365-2656.12418

Fedurek, P. & Lehmann, J. (2017). The effect of excluding juveniles on apparent adult olive baboons (*Papio anubis*) social networks. *PLOS One* **12**(3), e0173146. https://doi.org/10.1371/journal.pone.0173146

Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature* **439**(7075), 426-429. https://doi.org/10.1038/nature04326

Foerster, S., Franz, M., Murray, C. M., Gilby, I. C., Feldblum, J. T., Walker, K. K. & Pusey, A. E. (2016). Chimpanzee females queue but males compete for social status. *Scientific reports* **6**, 35404. https://doi.org/10.1038/srep35404

Franks, V. R., Ewen, J. G., McCready, M., Rowcliffe, J. M., Smith, D. & Thorogood, R. (2020). Analysing age structure, residency and relatedness uncovers social network structure in aggregations of young birds. *Animal Behaviour* **166**,7384. https://doi.org/10.1016/j.anbehav.2020.06.005

Frère, C. H., Class, B., Potvin, D. A. & Ilany, A. (2023). Social inheritance of avoidances shapes the structure of animal social networks. *Behavioral Ecology* **35**(1), arad088. https://doi.org/10.1093/beheco/arad088

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L. & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences of the United States of America* **107**(46), 19949-19954. https://doi.org/10.1073/pnas.1007997107

Funk, K. R., Barrett, L., Nord, C. M. & Henzi, S. P. (2024). Socioecological factors and partner preferences in the play behaviour of wild vervet monkeys, *Chlorocebus pygerythrus*. *Animal Behaviour* **214***,* 65-72. https://doi.org/10.1016/j.anbehav.2024.05.016

Galef, B. G., Jr & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal behaviour* **61**(1), 3-15. https://doi.org/10.1006/anbe.2000.1557

Gallois, S., Lubbers, M. J., Hewlett, B. & Reyes-García, V. (2018). Social Networks and Knowledge Transmission Strategies among Baka Children, Southeastern Cameroon. *Human nature (Hawthorne, N.Y.)* **29**(4), 442-463. https://doi.org/10.1007/s12110-018-9328-0

Godoy, I., Korsten, P. & Perry, S. E. (2022). Genetic, maternal, and environmental influences on sociality in a pedigreed primate population. *Heredity* **129**(4), 203-214. https://doi.org/10.1038/s41437-022-00558-6

Godoy, I., Korsten, P. & Perry, S. E. (2024). Mother of all bonds: Influences on spatial association across the lifespan in capuchins. *Developmental science* **27**(6), e13486. https://doi.org/10.1111/desc.13486

Goldenberg, S. Z., Douglas-Hamilton, I. & Wittemyer, G. (2016). Vertical transmission of social roles drives resilience to poaching in elephant networks. *Current Biology* **26**(1),75-79. https://doi.org/10.1016/j.cub.2015.11.005

Grampp, M., Sueur, C., van de Waal, E. & Botting, J. (2019). Social attention biases in juvenile wild vervet monkeys: implications for socialisation and social learning processes. *Primates; journal of primatology* **60**(3), 261-275. https://doi.org/10.1007/s10329-019-00721-4

Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology* **7**(1), 1-52. https://doi.org/10.1016/0022-5193(64)90038-4

Han, X., Wang, L., Crespi, N., Park, S. & Cuevas, Á. (2015). Alike people, alike interests? Inferring interest similarity in online social networks. *Decision Support Systems* **69**, 92-106. http://dx.doi.org/10.1016/j.dss.2014.11.008

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* **2**, e616. https://doi.org/10.7717/peerj.616

Hart, J. D. A., Franks, D. W., Brent, L. J. N. & Weiss, M. N. (2024). bisonR: Bayesian Inference of Social Networks in R. R package version 0.4.6, https://github.com/JHart96/bisonR

Hart, J. D. A., Weiss, M. N., Brent, L. J. N. & Franks, D. W. (2022). Common permutation methods in animal social network analysis do not control for non-independence. *Behavioral Ecology and Sociobiology* **76**(11), 151. https://doi.org/10.1007/s00265-022-03254-x

Hart, J. D. A., Weiss, M. N., Franks, D. W. & Brent, L. J. N. (2023). BISoN: A Bayesian framework for inference of social networks. *Methods in Ecology and Evolution* **14**, 2411-2420. https://doi.org/10.1111/2041-210X.14171

Hart, J. D. A., Franks, D. W., Brent, L. J. N. & Weiss, M. N. (2024). bisonR: Bayesian Inference of Social Networks in R. R package version 0.4.6, https://github.com/JHart96/bisonR

Hartig, F. (2024). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.7.

Hausfater, G., Altmann, J. & Altmann, S. (1982). Long-Term Consistency of Dominance Relations Among Female Baboons (*Papio cynocephalus*). *Science (New York, N.Y.)* **217**(4561), 752-755. https://doi.org/10.1126/science.217.4561.752

Heintz, M. R., Murray, C. M., Markham, A. C., Pusey, A. E. & Lonsdorf, E. V. (2017). The relationship between social play and developmental milestones in wild chimpanzees (*Pan troglodytes schweinfurthii*). *American journal of primatology* **79**(12), 10.1002/ajp.22716. https://doi.org/10.1002/ajp.22716

Henzi, S. P. (1982). *Some aspects of visual signalling and social organization in the vervet monkey (Cercopithecus aethiops pygerythrus).* [Doctoral dissertation, University of Natal].

Henzi, S. P., Blersch, R. A., Bonnell, T. R., Clarke, M., Dostie, M. J., Lucas, M., Jarrett, J., McFarland, R., Nord, C., Takahashi, A., Vilette, C., Young, C., Young, M. M. & Barrett, L. (2025). Estimates of life history parameters in a high latitude, arid-country vervet monkey population. *American journal of primatology* **87**(1), e23527. https://doi.org/10.1002/ajp.23527

Henzi, S. P., Forshaw, N., Boner, R., Barrett, L. & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **368**(1618), 20120351. https://doi.org/10.1098/rstb.2012.0351

Hiraiwa-Hasegawa, M. (1993). Skewed birth sex ratios in primates: Should high-ranking mothers have daughters or sons? *Trends in ecology & evolution* **8**(11), 395-400. https://doi.org/10.1016/0169-5347(93)90040-V

Holekamp, K. E. & Smale, L. (1991). Dominance Acquisition During Mammalian Social Development: The “Inheritance” of Maternal Rank. *American Zoologist* **31**(2), 306-317. https://doi.org/10.1093/icb/31.2.306

Holekamp, K. E. & Smale, L. (1993). Ontogeny of dominance in free-living spotted hyaenas: Juvenile rank relations with other immature individuals. *Animal Behaviour* **46**(3), 451-466. https://doi.org/10.1006/anbe.1993.1214

Horrocks, J. A. & Hunte, W. (1983). Rank Relations in Vervet Sisters: A Critique of the Role of Reproductive Value. *The American Naturalist* **122**(3), 417-421. http://www.jstor.org/stable/2461025

Horrocks, J. A. (1986). Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaeus*) in Barbados, West Indies. *International Journal of Primatology* **7**(1), 3147. https://doi.org/10.1007/BF02692308

Ilany, A. & Akçay, E. (2016). Social inheritance can explain the structure of animal social networks. *Nature Communications* **7**, 12084. https://doi.org/10.1038/ncomms12084

Ilany, A., Holekamp, K. E. & Akçay, E. (2021). Rank-dependent social inheritance determines social network structure in spotted hyenas. *Science* **373**(6552), 348e352. https://doi.org/10.1126/science.abc1966

Jack, K. M., Kulick, N. K., Schoof, V. A. M., Wikberg, E. C., Kawamura, S. & Fedigan, L. M. (2025). And Baby Makes Three: Postpartum Changes in Male-Female Affiliative Interactions in White-Faced Capuchins. *American journal of primatology* **87**(1), e23691. https://doi.org/10.1002/ajp.23691

Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L. & Henzi, S. P. (2018). Network integration and limits to social inheritance in vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences* **285**(1876), 20172668. https://doi.org/10.1098/rspb.2017.2668

Joffe, T. H. (1997). Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution* **32**(6), 593-605. https://doi.org/10.1006/jhev.1997.0140

Jones, J. H. (2011). Primates and the evolution of long, slow life histories. *Current biology* **21**(18), R708-R717. https://doi.org/10.1016/j.cub.2011.08.025

Josephs, N., Bonnell, T., Dostie, M., Barrett, L. & Henzi, S. P. (2016). Working the crowd: Sociable vervets benefit by reducing exposure to risk. *Behavioral Ecology* **27**(4), 988e994. https://doi.org/10.1093/beheco/arw003

Kalbitzer, U., Bergstrom, M. L., Carnegie, S. D., Wikberg, E. C., Kawamura, S., Campos, F. A., Jack, K. M. & Fedigan, L. M. (2017). Female sociality and sexual conflict shape offspring survival in a Neotropical primate. *Proceedings of the National Academy of Sciences of the United States of America* **114**(8), 1892-1897. https://doi.org/10.1073/pnas.1608625114

Kavanagh, K., Dozier, B. L., Chavanne, T. J., Fairbanks, L. A., Jorgensen, M. J. & Kaplan, J. R. (2011). Fetal and maternal factors associated with infant mortality in vervet monkeys. *Journal of medical primatology* **40**(1), 27-36. https://doi.org/10.1111/j.1600-0684.2010.00441.x

Kelter, R. (2020). Analysis of Bayesian posterior significance and effect size indices for the two-sample t-test to support reproducible medical research. *BMC Medical Research Methodology* **20**, 88. https://doi.org/10.1186/s12874-020-00968-2

Kelter, R. (2023). How to Choose between Different Bayesian Posterior Indices for Hypothesis Testing in Practice. *Multivariate behavioral research* **58**(1), 160-188. https://doi.org/10.1080/00273171.2021.1967716

King, A. J., Sueur, C., Huchard, E. & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour* **82**(6), 1337e1345. http://dx.doi.org/10.1016/j.anbehav.2011.09.017

King, J. E., Weiss, A. & Sisco, M. S. (2008). Aping humans: age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology* **122**(4), 418-427. https://doi.org/10.1037/a0013125

König, B. (1994). Components of lifetime reproductive success in communally and solitarily nursing house mice - a laboratory study. *Behavioral Ecology and Sociobiology* **34**, 275-283. https://doi.org/10.1007/BF00183478

Krzyszczyk, E, Patterson, E. M., Stanton, A. M. & Mann, J. (2017). The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins. *Animal Behaviour* **129**(2), 43-59. http://dx.doi.org/10.1016/j.anbehav.2017.04.011

Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N. & Schwab, C. (2016). Social networks predict selective observation and information spread in ravens. *Royal Society Open Science* **3**, 160256. https://doi.org/10.1098/rsos.160256

Kulik, L., Amici, F., Langos, D. & Widdig, A. (2015). Sex differences in the development of social relationships in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology* **36**, 353e376. https://doi.org/10.1007/s10764-015-9826-4

Kulik, L., Langos, D. & Widdig, A. (2016). Mothers make a difference: mothers develop weaker bonds with immature sons than daughters. *PLoS One* **11**(5), e0154845. https://doi.org/10.1371/journal.pone.0154845

Kurland, J. A. (1977). Kin selection in the Japanese monkey. *Contributions to primatology* **12**, 1-145.

Kutsukake, N. (2000). Matrilineal rank Inheritance varies with absolute rank in Japanese macaques. *Primates; journal of primatology* **41**(3), 321-335. https://doi.org/10.1007/BF02557601

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior* **32**(1), 4-14. https://doi.org/10.3758/BF03196002

L'Allier, S., Schwegel, M. A., Filazzola, A., Mastromonaco, G., Chapman, C. A. & Schoof, V. A. M. (2022). How individual, social, and ecological conditions influence dispersal decisions in male vervet monkeys. *American journal of primatology* **84**(9), e23426. https://doi.org/10.1002/ajp.23426

Lea, A. J., Blumstein, D. T., Wey, T. W. & Martin, J. G. (2010). Heritable victimization and the benefits of agonistic relationships. *Proceedings of the National Academy of Sciences of the United States of America* **107**(50), 21587-21592. https://doi.org/10.1073/pnas.1009882107

Lea, A. J., Learn, N. H., Theus, M. J., Altmann, J. & Alberts, S. C. (2014). Complex sources of variance in female dominance rank in a nepotistic society. *Animal Behaviour* **94**, 87-99. https://doi.org/10.1016/j.anbehav.2014.05.019

Lee, P. C. (1984). Early infant development and maternal care in free-ranging vervet monkeys. *Primates* **25**(1), 36-47. https://doi.org/10.1007/BF02382294

Lee, H. C. & Teichroeb, J. A. (2016). Partially shared consensus decision making and distributed leadership in vervet monkeys: older females lead the group to forage. *American journal of physical anthropology* **161**(4), 580-590. https://doi.org/10.1002/ajpa.23058

Levy, E. J., Zipple, M. N., McLean, E., Campos, F. A., Dasari, M., Fogel, A. S., Franz, M., Gesquiere, L. R., Gordon, J. B., Grieneisen, L., Habig, B., Jansen, D. J., Learn, N. H., Weibel, C. J., Altmann, J., Alberts, S. C. & Archie, E. A. (2020). A comparison of dominance rank metrics reveals multiple competitive landscapes in an animal society. *Proceedings of the Royal Society B* **287**, 20201013. http://dx.doi.org/10.1098/rspb.2020.1013

Liao, Z., Sosa, S., Wu, C. & Zhang, P. (2018). The influence of age on wild rhesus macaques' affiliative social interactions. *American Journal of Primatology* **80**(2), e22733. https://doi.org/10.1002/ajp.22733

Lindburg, D. G. (1971). The rhesus monkey in north India: An ecological and behavioral study. In L. A. Rosenblum (Ed.), Primate behavior: Developments in field and laboratory research (pp. 1-106, Vol. 1). Academic Press.

Lindholm, A. K., Hunt, J. & Brooks, R. (2006). Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. *Biology letters* **2**(4), 586-589. https://doi.org/10.1098/rsbl.2006.0546

Lonsdorf, E. V. (2017). Sex differences in nonhuman primate behavioral development. *Journal of Neuroscience Research* **95**(1-2), 213-221. https://doi.org/10.1002/jnr.23862

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), e99099. https://doi.org/10.1371/journal.pone.0099099

Machanda, Z. P. & Rosati, A. G. (2020). Shifting sociality during primate ageing. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **375**(1811), 20190620. https://doi.org/10.1098/rstb.2019.0620

Maestripieri, D. (1995a). Maternal encouragement in nonhuman primates and the question of animal teaching. *Human Nature* **6**, 361-378. https://doi.org/10.1007/bf02734206

Maestripieri, D. (1995b). Assessment of danger to themselves and their infants by rhesus macaque (*Macaca mulatta*) mothers. *Journal of comparative psychology (Washington, D.C.: 1983)* **109**(4), 416-420. https://doi.org/10.1037/0735-7036.109.4.416

Maestripieri, D. (2009). *Maternal influences on offspring growth, reproduction, and behavior in primates*. In D. Maestripieri & J. M. Mateo (Eds.), *Maternal effects in mammals* (pp. 256-291). University of Chicago Press. https://doi.org/10.7208/9780226501222-013

Maestripieri, D. (2018). Maternal influences on primate social development. *Behavioral Ecology and Sociobiology* **72**, 130. https://doi.org/10.1007/s00265-018-2547-x

Maestripieri, D., Hoffman, C. L., Anderson, G. M., Carter, C. S. & Higley, J. D. (2009). Mother-infant interactions in free-ranging rhesus macaques: relationships between physiological and behavioral variables. *Physiology & behavior* **96**(4-5), 613-619. https://doi.org/10.1016/j.physbeh.2008.12.016

Maestripieri, D. & Ross, S. R. (2004). Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: implications for adult behavior and social structure. *American Journal of Biological Anthropology* **123**(1), 52-61. https://doi.org/10.1002/ajpa.10295

Majolo, B., Lehmann, J., de Bortoli Vizioli, A. & Schino, G. (2012). Fitness-related benefits of dominance in primates. *American journal of physical anthropology* **147**(4), 652-660. https://doi.org/10.1002/ajpa.22031

Makowski, D., Ben-Shachar, M. S. & Lüdecke, D. (2019). bayestestR: Describing Effects and their Uncertainty, Existence and Significance within the Bayesian Framework. *Journal of Open Source Software* **4**(40), 1541. https://doi.org/10.21105/joss.01541

Mann, J., Stanton, M., Patterson, E., Bienenstock, E. J. & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications* **3**, 980. https://doi.org/10.1038/ncomms1983

Margulis, S.W., Nabong, M., Alaks, G., Walsh, A. & Lacy, R.C. (2005). Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. *Animal Behaviour* **69**(3), 627-634. http://dx.doi.org/10.1016/j.anbehav.2004.04.021

Matsumoto, Y., Tsugawa, S., Ohsaki, H. & Imase, M. (2012). Robustness of centrality measures against link weight quantization in social network analysis. *SIMPLEX '12: Proceedings of the Fourth Annual Workshop on Simplifying Complex Networks for Practitioners* 49-54. https://doi.org/10.1145/2184356.2184369

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences* **104**(26), 10910-10914. https://doi.org/10.1073/pnas.0701159104

McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P. & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology* **84**, 871-878. https://doi.org/10.1111/1365-2656.12329

McFarland, R. & Majolo, B. (2013). Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology letters* **9**(4), 20130428. https://doi.org/10.1098/rsbl.2013.0428

McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J. L., Pollet, T. V. & Barrett, L. (2017). The 'strength of weak ties' among female baboons: Fitness-related benefits of social bonds. *Animal Behaviour* **126**, 101e106. https://doi.org/10.1016/j.anbehav.2017.02.002

McGuire, M. T. (1982). Social dominance relationships in male vervet monkeys: A possible model for the study of dominance relationships in human political systems. *International Political Science Review* **3**(1), 11-32. https://doi.org/10.1177/019251218200300I

Micheletta, J. & Waller, B. M. (2012). Friendship affects gaze following in a tolerant species of macaque, *Macaca nigra*. *Animal Behaviour* **83**(2), 459-467. https://doi.org/10.1016/j.anbehav.2011.11.018

Mondragón-Ceballos, R., Chiappa, P., Mayagoitia, L. & Lee, P. (2010). Sex differences in learning the allocation of social grooming in infant stump-tailed macaques. *Behaviour* **147**(9), 1073-1099. https://doi.org/10.1163/000579510X505436

Moscovice, L. R., Heesen, M., Di Fiore, A., Seyfarth, R. M. & Cheney, D. L. (2009). Paternity alone does not predict long-term investment in juveniles by male baboons. *Behavioral ecology and sociobiology* **63**(10), 1471-1482. https://doi.org/10.1007/s00265-009-0781-y

Motes-Rodrigo, A., Albery, G. F., Negron-Del Valle, J. E., Philips, D., Cayo Biobank Research Unit, Platt, M. L., Brent, L. J. N. & Testard, C. (2025). A Natural Disaster Exacerbates and Redistributes Disease Risk Among Free-Ranging Macaques by Altering Social Structure. *Ecology letters* **28**(1), e70000. https://doi.org/10.1111/ele.70000

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 of the United States of America* **111**(51), 18189-18194. https://doi.org/10.1073/pnas.1409507111

Nakamichi, M. (1989). Sex differences in social development during the first 4 years in a free-ranging group of Japanese monkeys, *Macaca fuscata. Animal Behaviour* **38**(5), 737-748. https://doi.org/10.1016/S0003-3472(89)80106-X

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A. & Engelhardt, A. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour* **82**(4), 911-921. https://doi.org/10.1016/j.anbehav.2011.07.016

Neumann, C. & Kulik, L. (2019). EloRating: Animal Dominance Hierarchies by Elo Rating. R Package Version 0.46.8.

Newman, M. (2010). Networks: An introduction. Oxford University Press. https://books.google.ca/books?id=LrFaU4XCsUoC

Nikolei, J. & Borries, C. (1997). Sex Differential Behavior of Immature Hanuman Langurs (*Presbytis entellus*) in Ramnagar, South Nepal. *International Journal of Primatology* **18**, 415-437. https://doi.org/10.1023/A:1026390517948

Nord, C. M., Bonnell, T. R., Dostie, M. J., Henzi, S. P. & Barrett, L. (2021). Tolerance of muzzle contact underpins the acquisition of foraging information in vervet monkeys (*Chlorocebus pygerythrus*). *Journal of comparative psychology* **135**(3), 349-359. https://doi.org/10.1037/com0000258

Nunes, S. (2014). Juvenile social play and yearling behavior and reproductive success in female Belding's ground squirrels. *Journal of Ethology* **32**(3), 145-153. http://dx.doi.org/10.1007/s10164-014-0403-7

Nunes, S., Muecke, E.-M., Sanchez, Z., Hoffmeier, R. & Lancaster, L. (2004). Play behavior and motor development in juvenile Belding's ground squirrels (*Spermophilus beldingi*). *Behavioural Ecology and Sociobiology* **56**, 97-105. https://doi.org/10.1007/s00265-004-0765-x

Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W. & Laland, K. N. (2013). Niche construction theory: a practical guide for ecologists. *The Quarterly review of biology* **88**(1), 4-28. https://doi.org/10.1086/669266

Ostner, J., Vigilant, L., Bhagavatula, J., Franz, M. & Schülke, O. (2013). Stable heterosexual associations in a promiscuous primate. *Animal Behaviour* **86**(3), 623-631. https://doi.org/10.1016/j.anbehav.2013.07.004

Packer, C. & Pusey, A. E. (1983). Adaptations of Female Lions to Infanticide by Incoming Males. *The American Naturalist* **121**(5), 716-728. http://www.jstor.org/stable/2460874

Pasternak, G., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L. & Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe* **55**(1), a1078. https://doi.org/10.4102/koedoe.v55i1.1078

Pavez-Fox, M. A., Escabi-Ruiz, C. M., Hart, J. D. A., Negron-Del Valle, J. E., Phillips, D., Ruiz-Lambides, A., Bauman, S. E., Martinez, M. I., Montague, M. J., Platt, M. L., Higham, J. P., Snyder-Mackler, N. & Brent, L. J. N. (2024). Trade-offs between sociality and gastrointestinal parasite infection in the context of a natural disaster. *Animal Behaviour* **211**, 147-161 https://doi.org/10.1016/j.anbehav.2024.03.002

Pellis, S. M. & Pellis, V. C. (2007). Rough-and-tumble play and the development of the social brain. *Current Directions in Psychological Science* **16**(2), 95-98. http://dx.doi.org/10.1111/j.1467-8721.2007.00483.x

Pereira, M. E. (1988). Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio cynocephalus cynocephalus*. *Animal Behaviour* **36**(1), 184-204. https://doi.org/10.1016/S0003-3472(88)80262-8

Pereira, M. E. & Altmann, J. (1985). Development of social behavior in free-living nonhuman Primates.

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., De Silva, S., Waters, J. S., Prager, S. D., Sasaki, T., Wittemyer, G., Fewell, J. & McDonald, D. B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology* **25**(2), 242-255. https://doi.org/10.1093/beheco/art047

Pope, T. R. (1990). The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behavioral Ecology and Sociobiology* **27**, 439-446. https://doi.org/10.1007/BF00164071

Pusey, A. E. (1990). Behavioural changes at adolescence in chimpanzees. *Behaviour* **115**(3-4), 203-246. https://doi.org/10.1163/156853990X00581

Pusey, A. & Packer, C. (1987). Philopatry and dispersal. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, T. T. Struhsaker & R. W. Wrangham (Eds.), *Primate Societies* (pp. 250-266). Chicago: University of Chicago Press.

R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Renevey, N., Bshary, R. & van de Waal, E. (2013). Philopatric vervet monkey females are the focus of social attention rather independently of rank. *Behaviour* **150**(6), 599-615. http://www.jstor.org/stable/23435030

Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B. & Deecke, V. B. (2012). Cultural traditions and the evolution of reproductive isolation: Ecological speciation in killer whales? *Biological Journal of the Linnean Society* **106**(1), 1-17. https://doi.org/10.1111/j.1095-8312.2012.01872.x

Roatti, V., Cowlishaw, G., Huchard, E. & Carter, A. (2023). Social Network Inheritance and Differentiation in Wild Baboons. *Royal Society Open Science* **10**, 230219. https://doi.org/10.1098/rsos.230219

Robitzsch, A. & Grund, S. (2024). miceadds: Some Additional Multiple Imputation Functions, Especially for 'mice'. R package version 3.17-44. https://CRAN.R-project.org/package=miceadds

Rodrigues, M. A. (2007). Age and sex-based differences in social interactions and spacing in mantled howling monkeys: Implications for juvenile social development. *The Journal of Developmental Processes* 103.

Rodrigues, M. A. (2014). Emergence of sex-segregated behavior and association patterns in juvenile spider monkeys. *Neotropical Primates* **21**(2), 183-188. https://doi.org/10.1896/044.021.0204

Romano, V., Duboscq, J., Sarabian, C., Thomas, E., Sueur, C. & MacIntosh, A. J. (2016). Modeling infection transmission in primate networks to predict centrality-based risk. *American Journal of Primatology* **78**(7), 767-779. https://doi.org/10.1002/ajp.22542

Romero, L. M., Dickens, M. J. & Cyr, N. E. (2009). The Reactive Scope Model - a new model integrating homeostasis, allostasis, and stress. *Hormones and behavior* **55**(3), 375-389. https://doi.org/10.1016/j.yhbeh.2008.12.009

Roney, J. R. & Maestripieri, D. (2003). Social development and affiliation. In: Maestripieri, D. (ed) Primate psychology. Harvard University Press, Cambridge, pp 171-204.

Roura-Torres, B., Baniel, A., Cryer, A., Sauvadet, L., De Pastors, M., Havill, G., Kreyer, M., Meric de Bellefon, J., Abaga, S., Harté, M., Kappeler, P. M. & Charpentier, M. J. E. (2025). Toward independence: maternal social status and experience shape mother-infant relationships in mandrills. *Behavioral Ecology and Sociobiology* **79**, 42. https://doi.org/10.1007/s00265-025-03582-8

Sade, D. S. (1965). Some Aspects of Parent-offspring and Sibling Relations in a Group of Rhesus Monkeys, with a Discussion of Grooming. *American journal of physical anthropology* **23**(1), 1-17. https://doi.org/10.1002/ajpa.1330230115

Sade, D. S. (1972). Sociometrics of Macaca mulatta. I. Linkages and cliques in grooming matrices. *Folia primatologica; international journal of primatology* **18**(3), 196-223. https://doi.org/10.1159/000155480

Schino, G. (2001). Grooming, competition and social rank among female primates: A metaanalysis. *Animal Behaviour* **62**(2), 265-271. https://doi.org/10.1006/anbe.2001.1750

Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology* **18**(1), 115-120. https://doi.org/10.1093/beheco/arl045

Schoof, V. A. M., Jack, K. M. & Isbell, L. A. (2009). What traits promote male parallel dispersal in primates? *Behaviour* **146**(4-5), 701-726. https://doi.org/10.1163/156853908X399086

Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology* **20**(24), 2207-2210. https://doi.org/10.1016/j.cub.2010.10.058

Schwegel, M. (2023). Individual factors predicting the disappearance and reproductive success of vervet monkeys (*Chlorocebus pygerythrus*). [Master's thesis, York University].

Schwegel, M. A., Filazzola, A., Chapman, C.A. & Schoof, V. A. M. (2023). Breeding Seasonality in Female Vervet Monkeys (*Chlorocebus pygerythrus*) Living in an Anthropogenic Landscape. *International Journal of Primatology* **44**, 45-70. https://doi.org/10.1007/s10764-022-00313-y

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology* **65**(4), 671-698. https://doi.org/10.1016/0022-5193(77)90015-7

Seyfarth, R. M. (1980). The distribution of grooming and related behaviors among adult female vervet monkeys. *Animal Behaviour* **28**(3), 798-813. https://doi.org/10.1016/S0003-3472(80)80140-0

Seyfarth, R. & Cheney, D. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* **308**, 541-543. https://doi.org/10.1038/308541a0

Shimada, M. & Sueur, C. (2018). Social play among juvenile wild Japanese macaques (*Macaca fuscata*) strengthens their social bonds. *American Journal of Primatology* **80**(1), 10.1002/ajp.22728. https://doi.org/10.1002/ajp.22728

Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour* **57**(5), 1021-1032. https://doi.org/10.1006/anbe.1998.1065

Silk, J. B., Alberts, S. C. & Altmann, J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour* **67**(3), 573-582. https://doi.org/10.1016/j.anbehav.2003.07.001

Silk, J. B., Altmann, J. & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology* **61**(2), 183-195. https://doi.org/10.1007/s00265-006-0249-2

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology* **20**(5), 1359-1361. https://doi.org/10.1016/j.cub.2010.05.067

Silk, J. B., Samuels, A. & Rodman, P. S. (1981). Hierarchical organization of female *Macaca radiata* in captivity. *Primates* **22**(1), 84-95. https://doi.org/10.1007/BF02382559

Smith, K. L., Alberts, S. C. & Altmann, J. (2003). Wild female baboons bias their social behaviour towards paternal half-sisters. *Proceedings of the Royal Society B* **270**(1514), 503-510. https://doi.org/10.1098%2Frspb.2002.2277

Soben, C., Llorente, M., Villariezo, P., Liebal, K. & Amici, F. (2023a). Mother's Age and Social Integration Modulate Sex-biased Maternal Investment in Wild Spider Monkeys (*Ateles geoffroyi*). *International Journal of Primatology* **44**,1007-1025. https://doi.org/10.1007/s10764-023-00375-6

Soben, C., Llorente, M., Villariezo, P., Liebal, K. & Amici, F. (2023b). Maternal Investment Fosters Male but Not Female Social Interactions with Other Group Members in Immature Wild Spider Monkeys (*Ateles geoffroyi*). *Animals: an open access journal from MDPI* **13**(11), 1802. https://doi.org/10.3390/ani13111802

Stanton, M. A., Gibson, Q. A. & Mann, J. (2011). When mum's away: a study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops sp.*). *Animal Behaviour* **82**(2), 405-412. http://dx.doi.org/10.1016/j.anbehav.2011.05.026

Stanton, M. A. & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLoS One* **7**(10), e47508. https://doi.org/10.1371/journal.pone.0047508

Strauss, E. D. & Holekamp, K. E. (2019). Social alliances improve rank and fitness in convention-based societies. *Proceedings of the National Academy of Sciences of the United States of America* **116**(18), 8919-8924. https://doi.org/10.1073/pnas.1810384116

Struhsaker, T. T. (1967a). Behavior of vervet monkeys (*Cercopithecus aethiops*). Berkeley: University of California Press. pp. 74.

Struhsaker, T. T. (1967b). Ecology of Vervet Monkeys (*Cercopithecus aethiops*) in The Masai-Amboseli Game Reserve, Kenya. *Ecology* **48**(6), 891-904. https://doi.org/10.2307/1934531

Struhsaker, T. T. (1967c). Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour* **29**(2), 6-121.

Struhsaker, T. T. (1971). Social behaviour of mother and infant vervet monkeys (*Cercopithecus aethiops*). *Animal Behaviour* **19**(2), 233-250. https://doi.org/10.1016/S0003-3472(71)80004-0

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

Tartabini, A. & Dienske, H. (1979). Social play and rank order in rhesus monkeys (*Macaca mulatta*). *Behavioural processes* **4**(4), 375-383. https://doi.org/10.1016/0376-6357(79)90020-2

Teichroeb, J. A., White, M. M. J. & Chapman, C. A. (2015). Vervet (*Chlorocebus pygerythrus*) intragroup spatial positioning: Dominants trade-off predation risk for increased food acquisition. *International Journal of Primatology* **36**(1), 154-176. https://doi.org/10.1007/s10764-015-9818-4

Templeton, C. N., Reed, V. A., Campbell, S. E. & Beecher, M. D. (2012). Spatial movements and social networks in juvenile male song sparrows. *Behavioral ecology: official journal of the International Society for Behavioral Ecology* **23**(1), 141-152. https://doi.org/10.1093/beheco/arr167

Thompson, N. A. (2019). Understanding the links between social ties and fitness over the life cycle in primates. *Behaviour* **156**(9), 859-908. https://doi.org/10.1163/1568539X-00003552

Thompson, N. A. & Cords, M. (2020). Early life maternal sociality predicts juvenile sociality in blue monkeys. *American journal of primatology* **82**(11), e23039. https://doi.org/10.1002/ajp.23039

Tiddi, B., Aureli, F. & Schino, G. (2012). Grooming up the hierarchy: the exchange of grooming and rank-related benefits in a new world primate. *PloS one* **7**(5), e36641. https://doi.org/10.1371/journal.pone.0036641

Torfs, J. R. R., Stevens, J. M. G., Verspeek, J., Laméris, D. W., Guéry, J. P., Eens, M. & Staes, N. (2023). Multi-group analysis of grooming network position in a highly social primate. *PloS one* **18**(4), e0284361. https://doi.org/10.1371/journal.pone.0284361

Tsai, Y. J. J. & Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science* **29**, 261-279. https://doi.org/10.1111/j.1748-7692.2011.00559.x

Turner, T. R., Anapol, F. & Jolly, C. J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American journal of physical anthropology* **103**(1), 19-35. https://doi.org/10.1002/(SICI)1096-8644(199705)103:1<19::AID-AJPA3>3.0.CO;2-8

Turner, T. R., Schmitt, C. A. & Cramer, J. D. (2019). *Savanna monkey taxonomy*. In T. R. Turner, C. A. Schmitt, & J. D. Cramer (Eds.), *Savanna monkeys: The genus Chlorocebus* (pp. 31-54). Cambridge University Press.

van de Waal, E., Borgeaud, C. & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science (New York, N.Y.)* **340**(6131), 483-485. https://doi.org/10.1126/science.1232769 van de Waal, E., Bshary, R. & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour* **90***,* 41-45. https://doi.org/10.1016/j.anbehav.2014.01.015

van de Waal, E., Krützen, M., Hula, J., Goudet, J. & Bshary, R. (2012). Similarity in food cleaning techniques within matrilines in wild vervet monkeys. *PLoS ONE* **7**(4), e35694. https://doi.org/10.1371/journal.pone.0035694

van de Waal, E., Renevey, N., Favre, C. M. & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Science* **277**(1691), 2105-2111. https://doi.org/10.1098/rspb.2009.2260

van Hooff, J. A. R. A. M. (1962). Facial expressions in higher primates. *Symposium for the Zoological Society of London* **8**, 97-125.

van Hooff, J. A. R. A. M. (2000). Relationships among non-human primate males: A deductive framework. In P. Kappeler (Ed.), Primate males: Causes and consequences of variation in group composition (pp. 183–191). Cambridge University Press.

Vilette, C. (2022). The study of social dynamics in juvenile vervet monkeys. [Doctoral thesis, University of Lethbridge].

Vilette, C., Bonnell, T., Dostie, M. J., Henzi, S. P. & Barrett, L. (2022). Network formation during social integration in juvenile vervet monkeys. *Animal Behaviour* **194**, 205-223. https://doi.org/10.1016/j.anbehav.2022.10.006

Vilette, C., Bonnell, T. R., Dostie, M. J., Henzi, S. P. & Barrett, L. (2023). Strong ties formation, composition and processes at play during the developmental period of juvenile vervet monkeys. *Animal Behaviour* **201**, 137-156. https://doi.org/10.1016/j.anbehav.2023.05.003

Watts, D. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* **44**, 43-55. https://doi.org/10.1007/s002650050513

Weiss, M. N., Franks, D. W., Brent, L. J. N., Ellis, S., Silk, M. J. & Croft, D. P. (2021). Common datastream permutations of animal social network data are not appropriate for hypothesis testing using regression models. *Methods in ecology and evolution* **12**(2), 255-265. https://doi.org/10.1111/2041-210X.13508

Wey, T., Blumstein, D. T., Shen, W. & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* **75**(2), 333-344. https://doi.org/10.1016/j.anbehav.2007.06.020

Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. Chicago, IL: University of Chicago Press.

Whitehead, H. & Dufault, S. M. (1999). Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. *Advances in The Study of Behavior* **28**, 33-74. https://doi.org/10.1016/S0065-3454%2808%2960215-6

Widdig, A., Langos, D. & Kulik, L. (2016). Sex differences in kin bias at maturation: Male rhesus macaques prefer paternal kin prior to natal dispersal. *American journal of primatology* **78**(1), 78-91. https://doi.org/10.1002/ajp.22401

Wild, F. (2022). lsa: Latent Semantic Analysis. R package version 0.73.3, https://CRAN.R-project.org/package=lsa

Wild, S., Alarcón-Nieto, G. & Aplin, L. M. (2024). The ontogeny of social networks in wild great tits (*Parus major*). *Behavioral ecology: official journal of the International Society for Behavioral Ecology* **35**(2), arae011. https://doi.org/10.1093/beheco/arae011

Wittig, R. M. & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. *International Journal of Primatology* **24**(4), 847-867. https://doi.org/10.1023/A:1024632923180

Wittig, R.M., Crockford, C., Deschner, T., Langergraber, K.E., Ziegler, T.E. & Zuberbuhler, K. (2013). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* **281**.

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T. & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature communications* **7**, 13361. https://doi.org/10.1038/ncomms13361

Wooddell, L. J., Kaburu, S. S. & Dettmer, A. M. (2020). Dominance rank predicts social network position across developmental stages in rhesus monkeys. *American Journal of Primatology* **82**(11), e23024. https://doi.org/10.1002/ajp.23024

Young, C., Bonnell, T. R., Brown, L. R., Dostie, M. J., Ganswindt, A., Kienzle, S., McFarland, R., Henzi, S. P. & Barrett, L. (2019). Climate induced stress and mortality in vervet monkeys. *Royal Society Open Science* **6**(11), 191078. http://dx.doi.org/10.1098/rsos.191078

Young, G.H., Coelho, A.M. & Bramblett, C.A. (1982). The development of grooming, sociosexual behavior, play and aggression in captive baboons in their first two years. *Primates* **23**, 511-519. https://doi.org/10.1007/BF02373962

Young, T. P. & Isbell, L. A. (1994). Minimum group size and other conservation lessons exemplified by a declining primate population. *Biological Conservation* **68**(2), 129-134. https://doi.org/10.1016/0006-3207(94)90343-3

Young, C., McFarland, R., Barrett, L. & Henzi, S. P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. *Animal Behaviour* **125**, 61-67. https://doi.org/10.1016/j.anbehav.2017.01.006

6.0 Appendices

6.1 Supplementary Figures

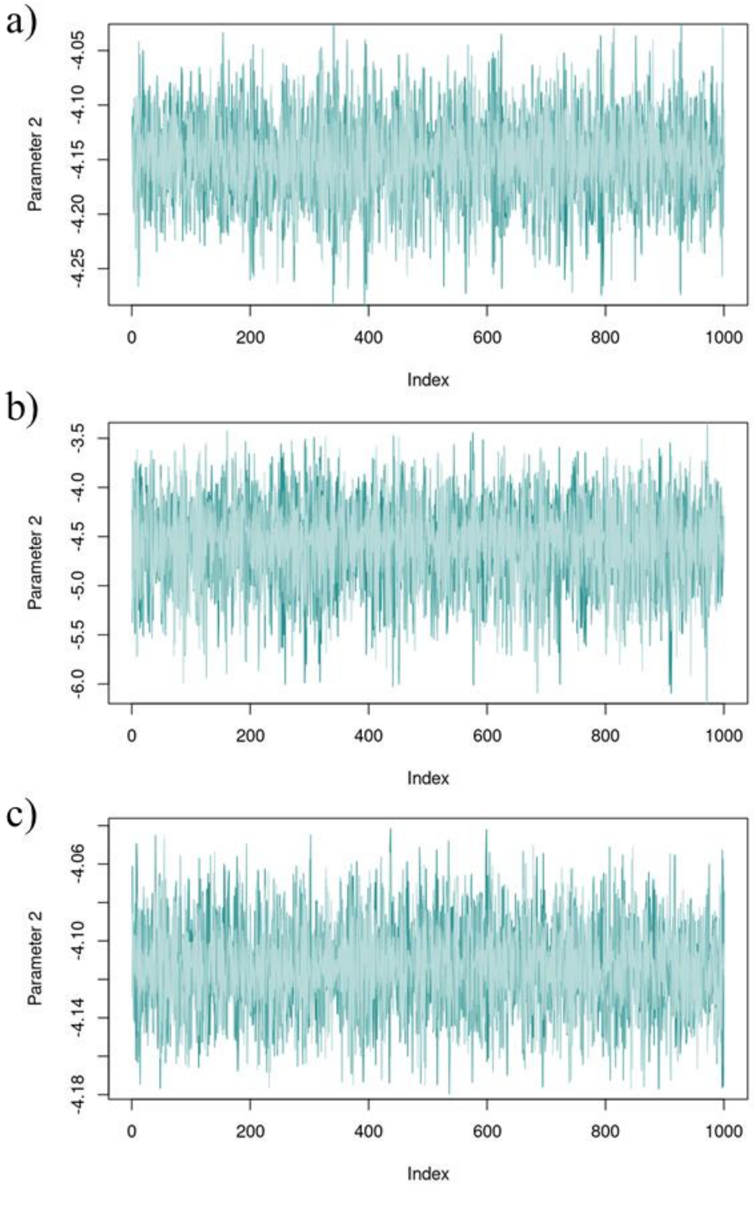


Figure S1. Traceplots of Markov chain Monte Carlo (MCMC) chains for the fitted edge weight models from **a)** grooming networks built using focal data, **b)** grooming networks built using *ad libitum* data, and **c)** proximity networks built using focal data. Chains were well-mixed and had converged, which suggests that the MCMC algorithm performed correctly.

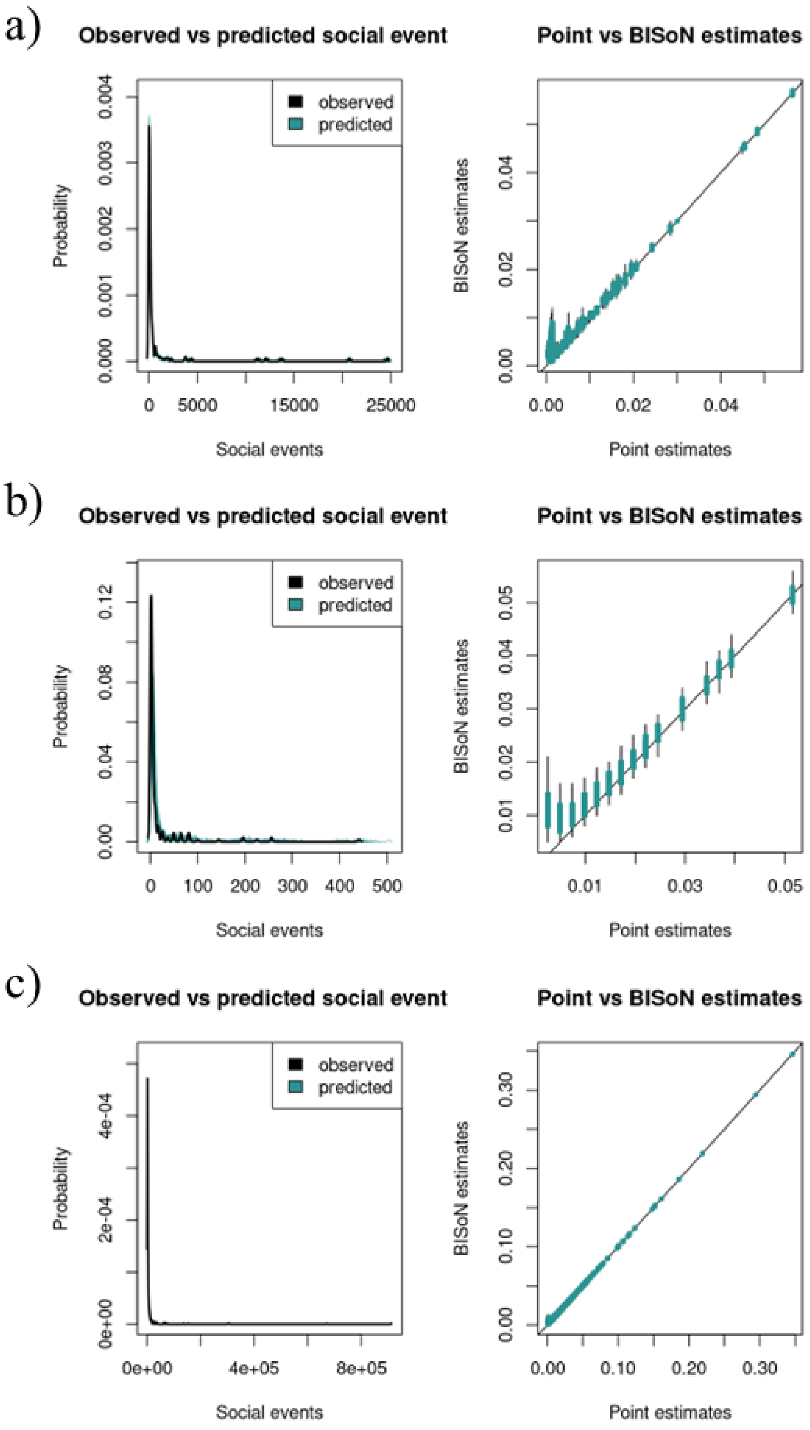


Figure S2. Posterior predictive plots showing summary statistics of observed data against predictions by the fitted edge weight models from **a)** grooming networks built using focal data, **b)** grooming networks built using *ad libitum* data, and **c)** proximity networks built using focal data. Predictions of all models matched the observed data, revealing that the models predicted the actual data appropriately and therefore performed properly.

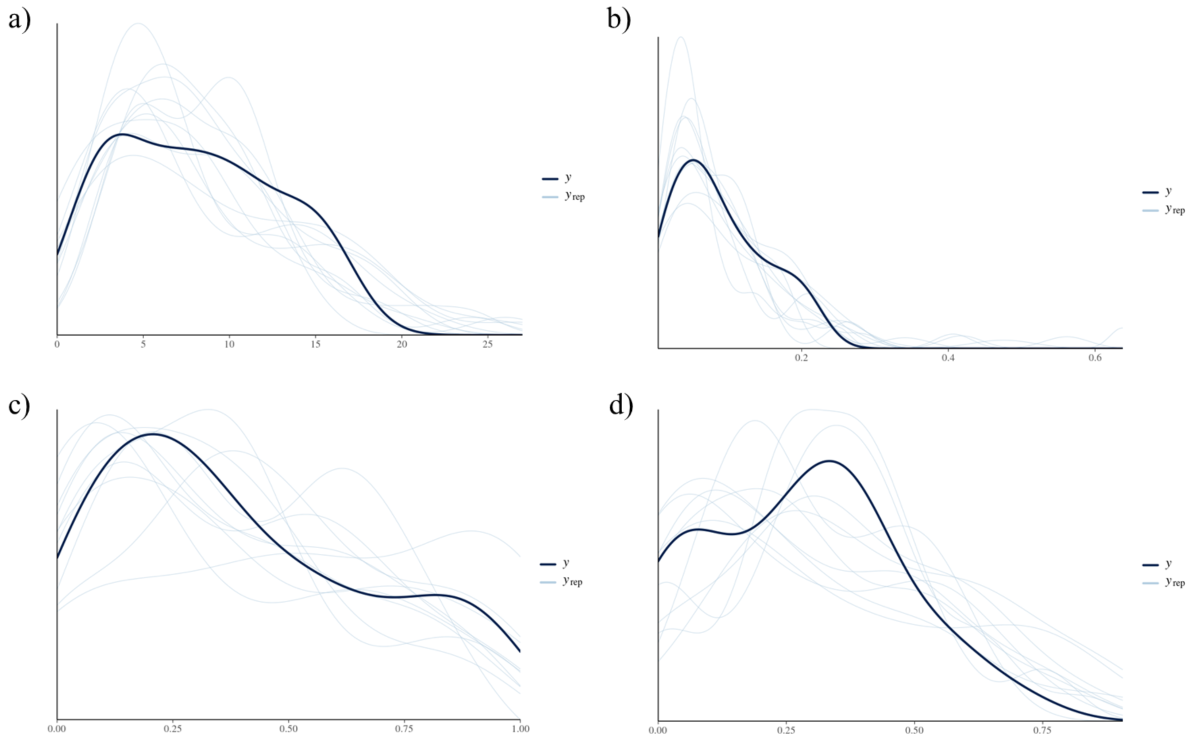


Figure S3. Posterior predictive check plots for the grooming **a)** degree, **b)** strength, **c)** eigenvector centrality, and **d)** mother-offspring cosine similarity models. Each plot was generated with the first imputed dataset whereas the models themselves were run using 30 imputed datasets. While *y* represents the observed network metric values, *yrep* curves display simulated datasets from the posterior predictive distribution (Bürkner, 2021).

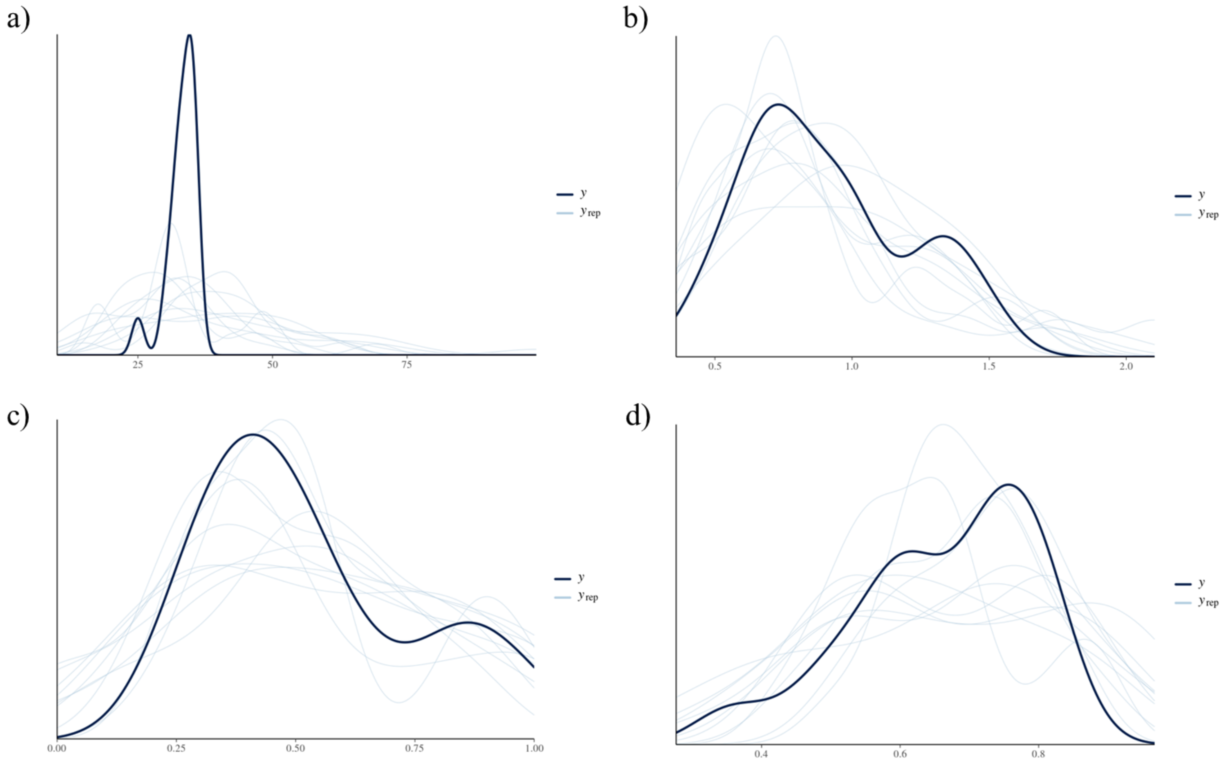


Figure S4. Posterior predictive check plots for the proximity **a)** degree, **b)** strength, **c)** eigenvector centrality, and **d)** mother-offspring cosine similarity models. Each plot was generated with the first imputed dataset whereas the models themselves were run using 30 imputed datasets. While *y* represents the observed network metric values, *yrep* curves display simulated datasets from the posterior predictive distribution (Bürkner, 2021).

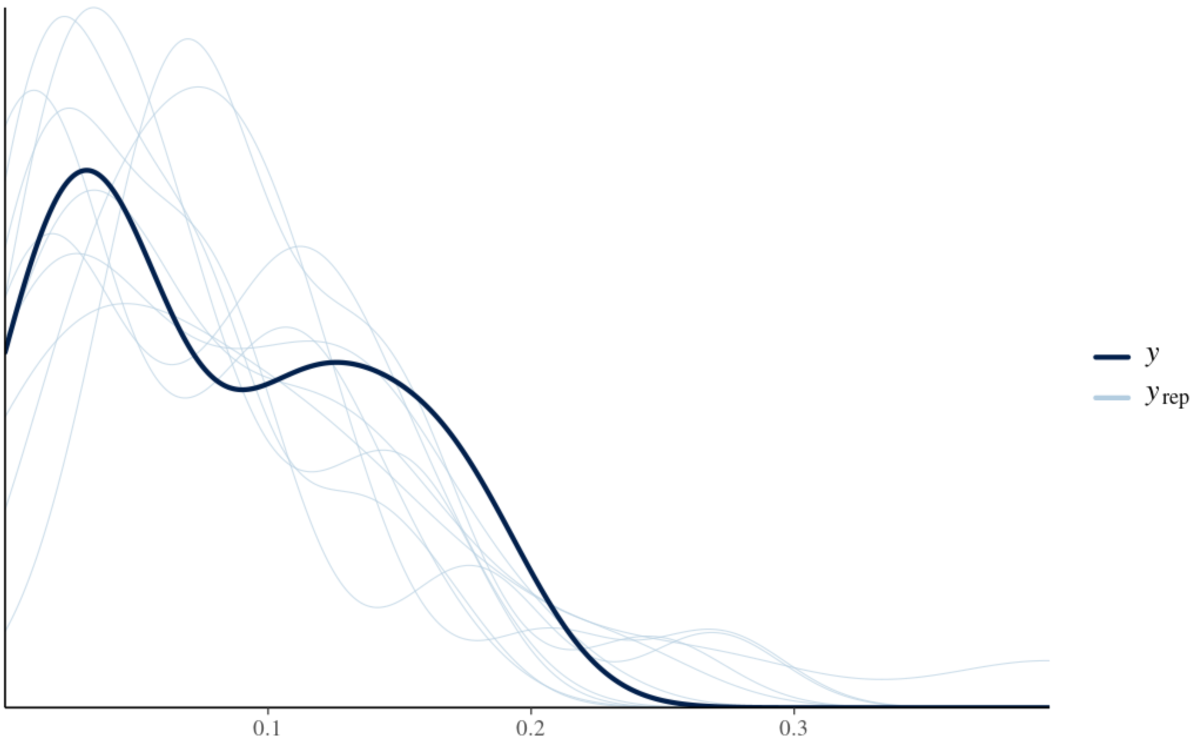


Figure S5. Posterior predictive check plot for the Simple Ratio Index (SRI) model. While *y* represents the observed SRI values, *yrep* curves display simulated datasets from the posterior predictive distribution (Bürkner, 2021).

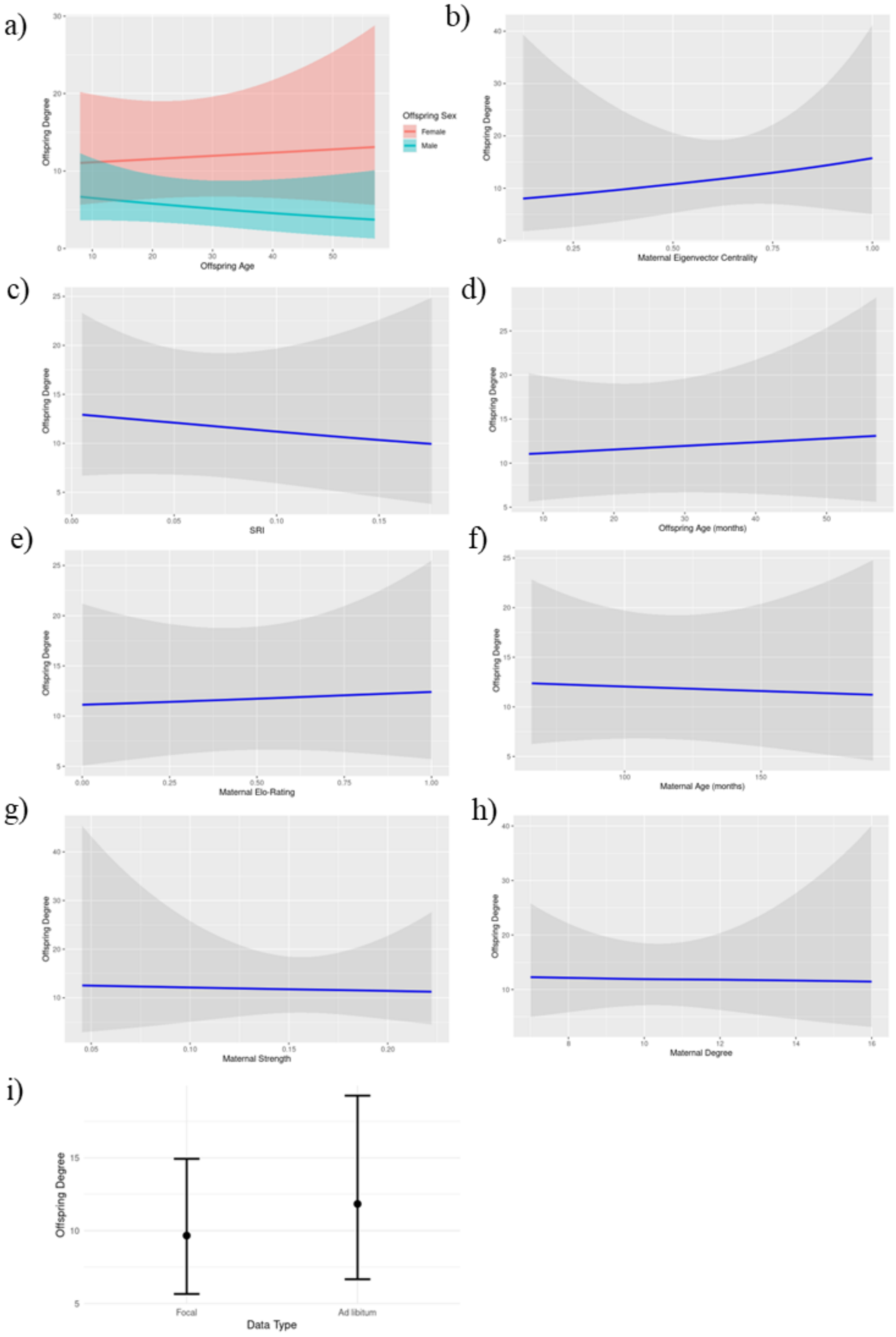


Figure S6. Posterior estimates of the number of grooming partners (degree) of offspring depending on **a)** offspring age*sex, **b)** maternal eigenvector centrality, **c)** SRI, **d)** offspring age (in months), **e)** maternal Elo-rating, **f)** maternal age (in months), **g)** maternal strength, **h)** maternal degree, and **i)** data type (focal versus *ad libitum*), with their associated 95% credible intervals.

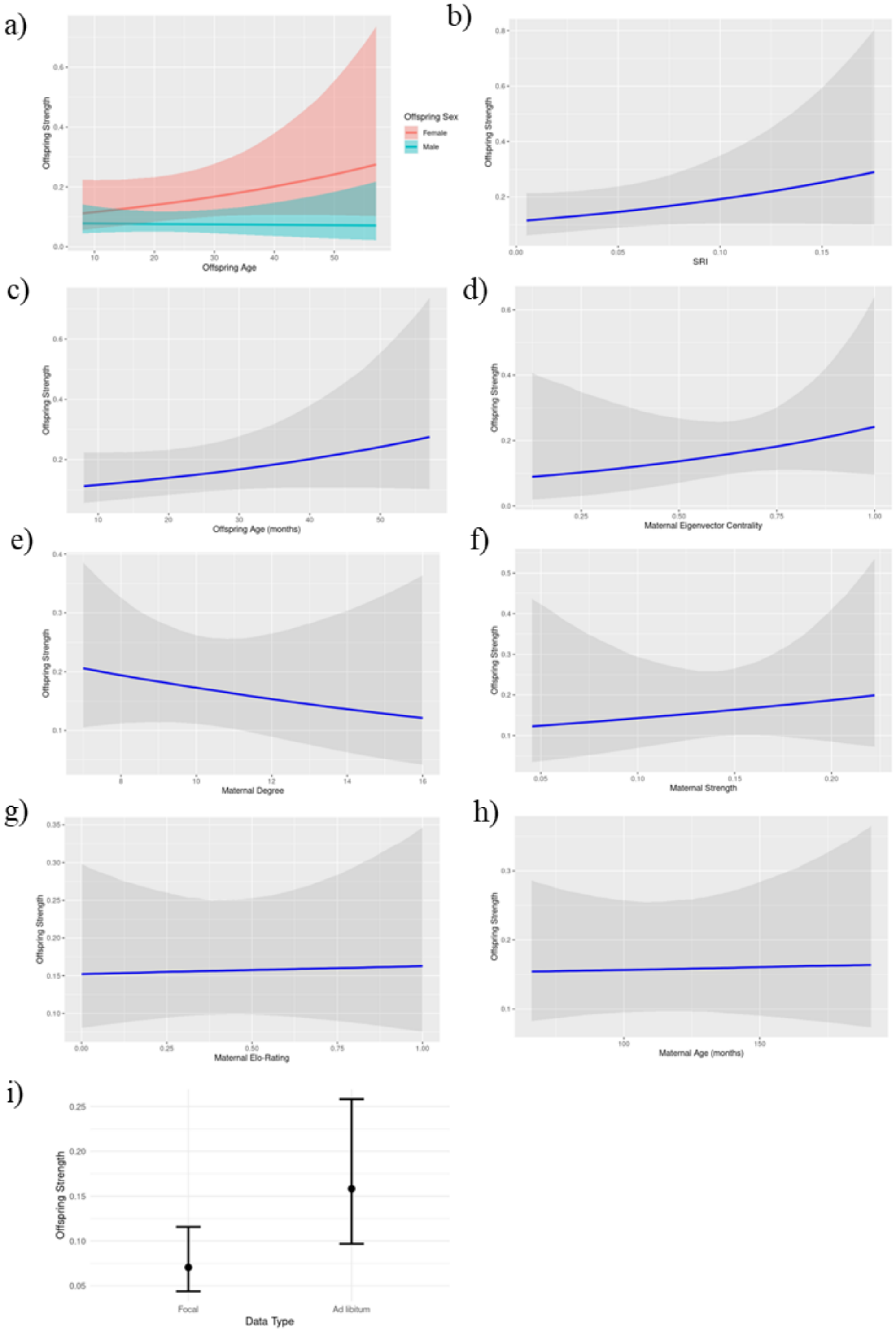


Figure S7. Posterior estimates of grooming frequency (strength) of offspring depending on **a)** offspring age*sex, **b)** SRI, **c)** offspring age (in months), **d)** maternal eigenvector centrality, **e)** maternal degree, **f)** maternal strength, **g)** maternal Elo-rating, **h)** maternal age (in months), and **i)** data type (focal versus *ad libitum*), with their associated 95% credible intervals.

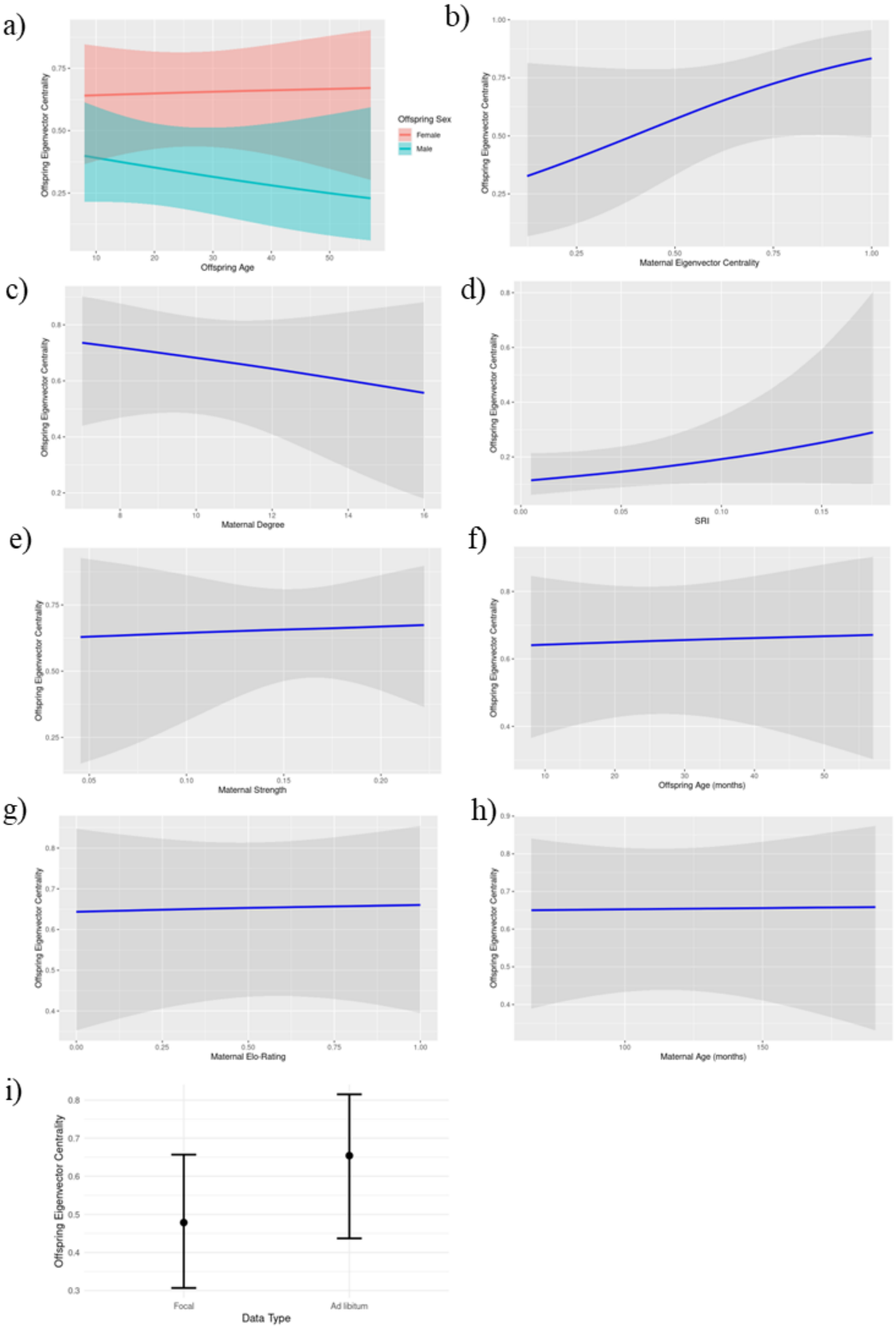


Figure S8. Posterior estimates of grooming centrality (eigenvector centrality) of offspring depending on **a)** offspring age*sex, **b)** maternal eigenvector centrality, **c)** maternal degree, **d)** SRI, **e)** maternal strength, **f)** offspring age (in months), **g)** maternal Elo-rating, **h)** maternal age (in months), and **i)** data type (focal versus *ad libitum*), with their associated 95% credible intervals.

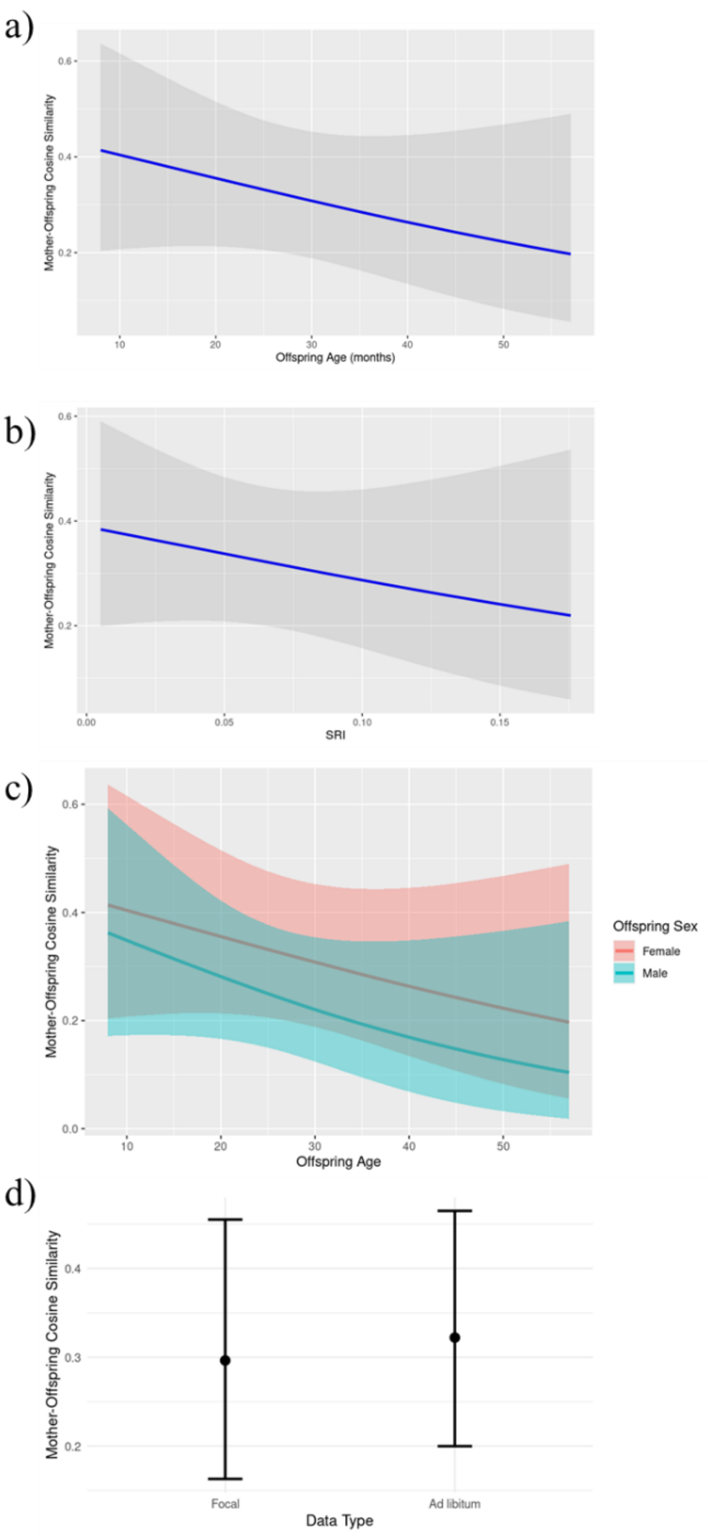


Figure S9. Posterior estimates of the similarity in grooming partners (cosine similarity) between mother-offspring dyads depending on **a)** offspring age (in months), **b)** SRI, **c)** offspring age*sex, and **d)** data type (focal versus *ad libitum*), with their associated 95% credible intervals.

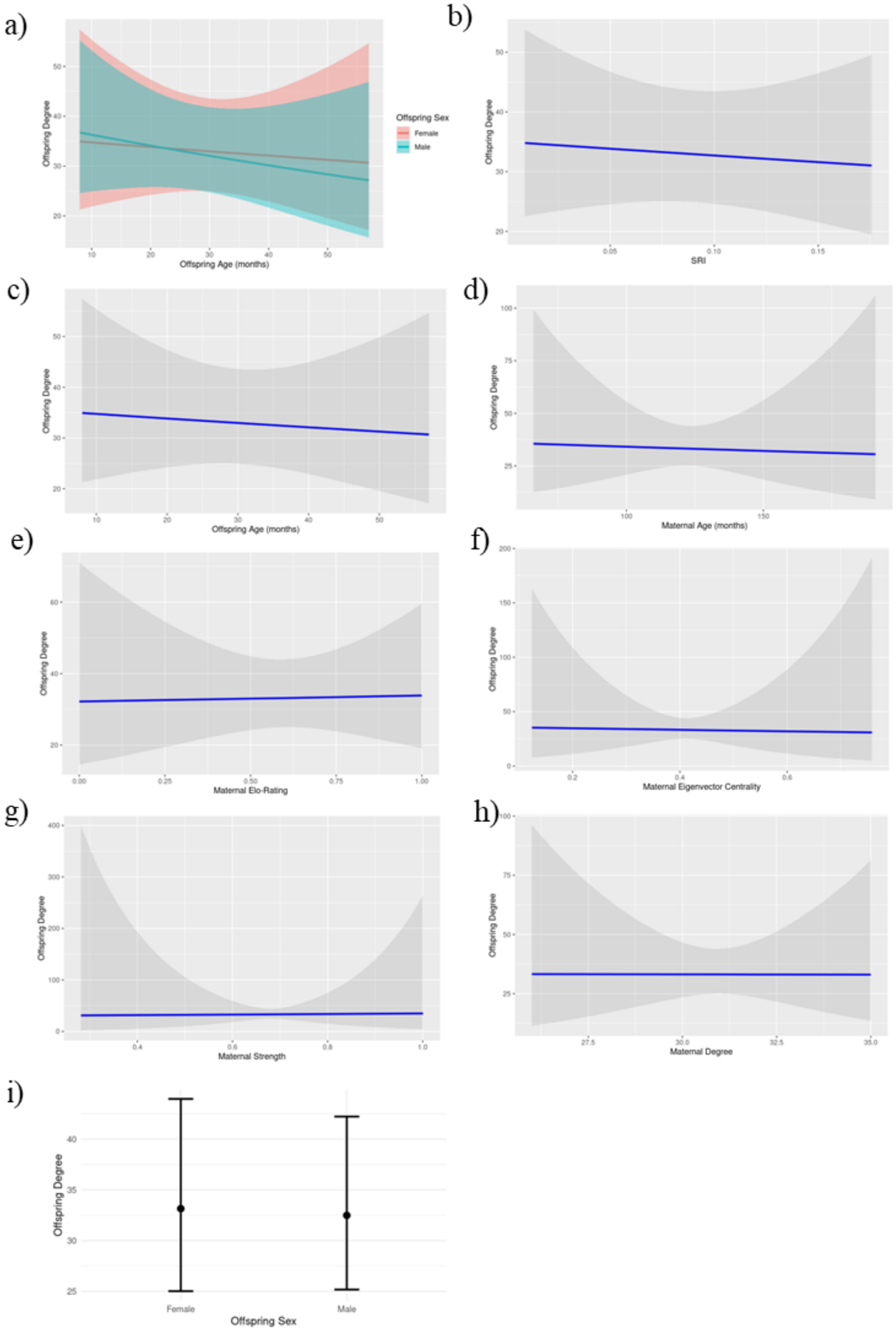


Figure S10. Posterior estimates of the number of associates (proximity degree) of offspring depending on **a)** offspring age*sex, **b)** SRI, **c)** offspring age (in months), **d)** maternal age (in months), **e)** maternal Elo-rating, **f)** maternal eigenvector centrality, **g)** maternal strength, **h)** maternal degree, and **i)** offspring sex, with their associated 95% credible intervals.

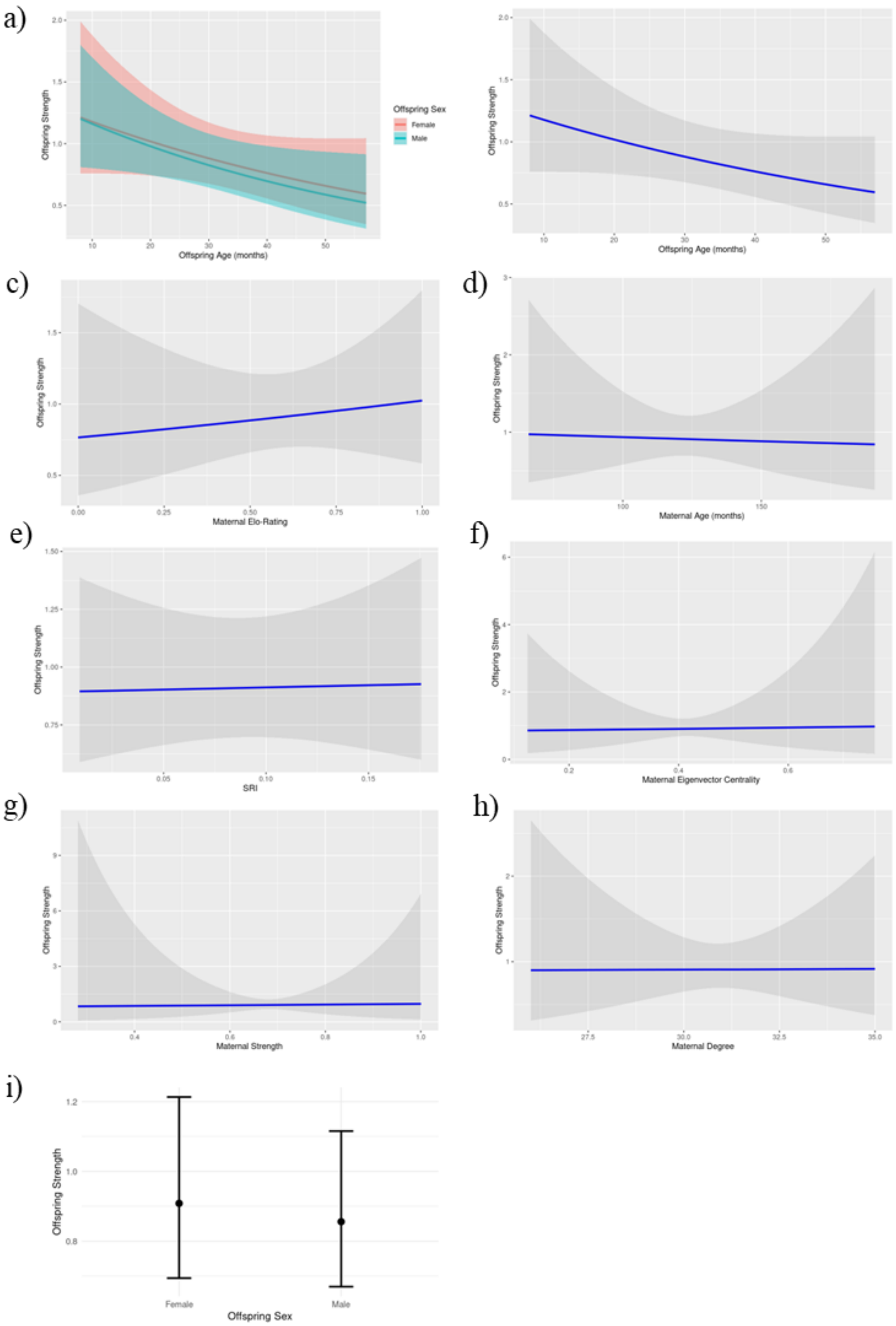


Figure S11. Posterior estimates of the frequency of association (proximity strength) of offspring depending on **a)** offspring age*sex, **b)** offspring age (in months), **c)** maternal Elo-rating, **d)** maternal age (in months), **e)** SRI, **f)** maternal eigenvector centrality, **g)** maternal strength, **h)** maternal degree, and **i)** offspring sex, with their associated 95% credible intervals.

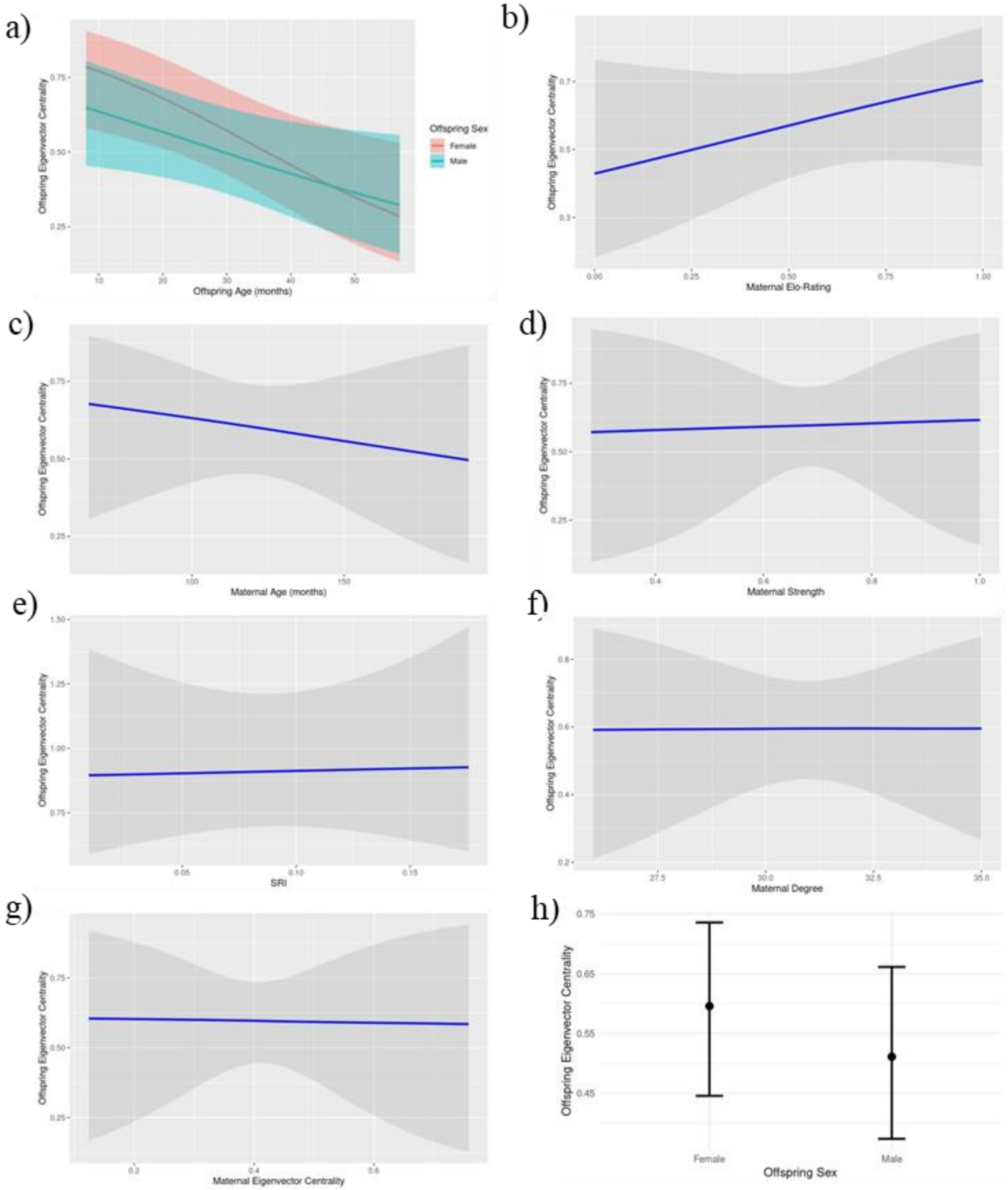


Figure S12. Posterior estimates of centrality (proximity eigenvector centrality) of offspring depending on **a)** offspring age*sex, **b)** maternal Elo-rating, **c)** maternal age (in months), **d)** maternal strength, **e)** SRI, **f)** maternal degree, and **g)** maternal eigenvector centrality, **h)** offspring sex, with their 95% credible intervals.

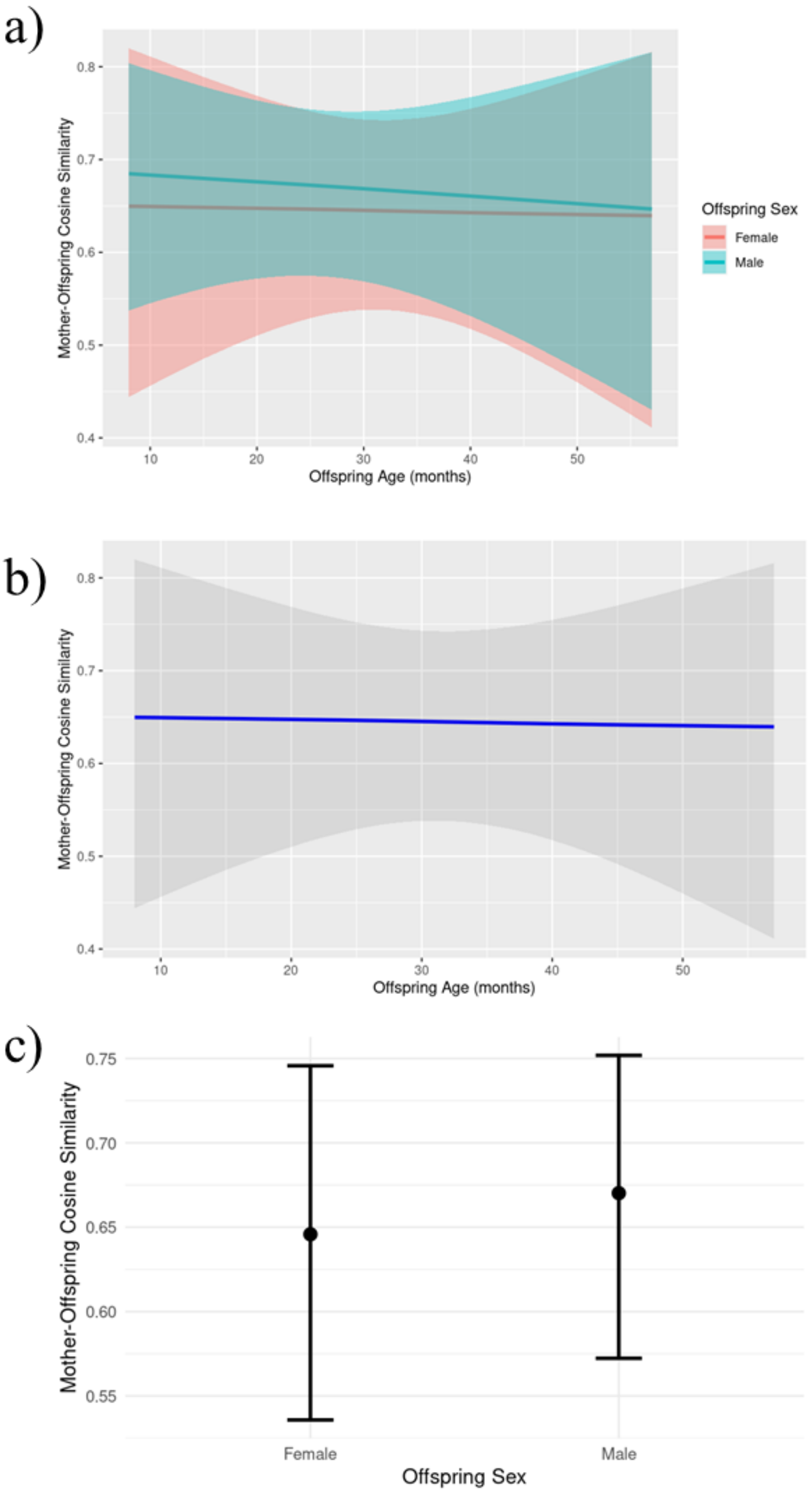


Figure S13. Posterior estimates of the similarity in associates (proximity cosine similarity) across mothers and their offspring depending on **a)** offspring age*sex, **b)** offspring age (in months), and **c)** offspring sex, with their 95% credible intervals.

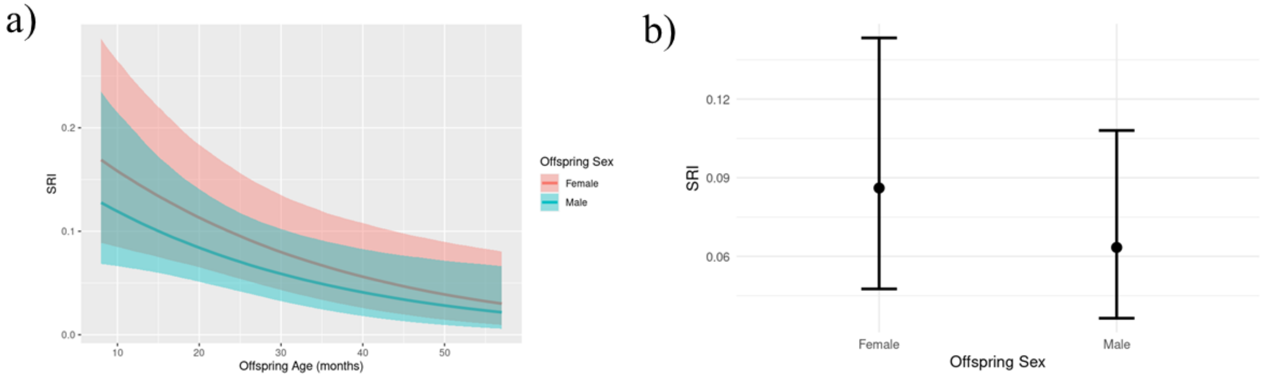
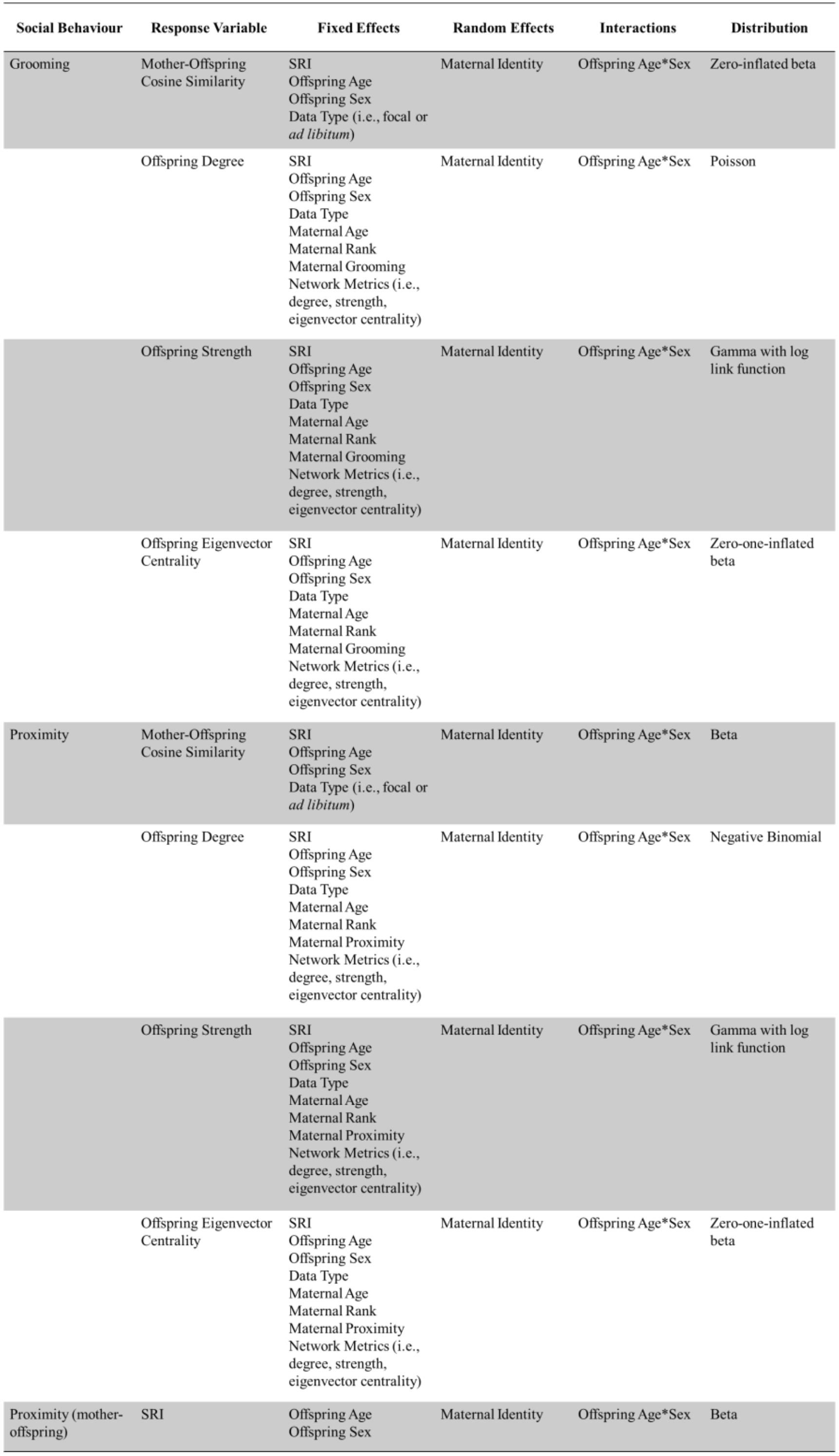


Figure S14. Posterior estimates of the Simple Ratio Index (SRI) across mothers and their offspring depending on **a)** offspring age*sex, and **b)** offspring sex, with their 95% credible intervals.

6.2 Supplementary Tables

Table S12. Bayesian Generalized Mixed Models (GLMMs) Summary. These models allowed to better understand vervet social integration through maternal effects, including maternal rank and age. Unlike other models which were computed using 30 imputed datasets, the SRI model was the only one that only included one imputed dataset.



Social Behaviour	Response Variable	Fixed Effects	Random Effects	Interactions	Distribution
Grooming	Mother-Offspring Cosine Similarity	SRI Offspring Age Offspring Sex Data Type (i.e., focal or *ad libitum*)	Maternal Identity	Offspring Age*Sex	Zero-inflated beta
	Offspring Degree	SRI Offspring Age Offspring Sex Data Type Maternal Age Maternal Rank Maternal Grooming Network Metrics (i.e., degree, strength, eigenvector centrality)	Maternal Identity	Offspring Age*Sex	Poisson
	Offspring Strength	SRI Offspring Age Offspring Sex Data Type Maternal Age Maternal Rank Maternal Grooming Network Metrics (i.e., degree, strength, eigenvector centrality)	Maternal Identity	Offspring Age*Sex	Gamma with log link function
	Offspring Eigenvector Centrality	SRI Offspring Age Offspring Sex Data Type Maternal Age Maternal Rank Maternal Grooming Network Metrics (i.e., degree, strength, eigenvector centrality)	Maternal Identity	Offspring Age*Sex	Zero-one-inflated beta
Proximity	Mother-Offspring Cosine Similarity	SRI Offspring Age Offspring Sex Data Type (i.e., focal or *ad libitum*)	Maternal Identity	Offspring Age*Sex	Beta
	Offspring Degree	SRI Offspring Age Offspring Sex Data Type Maternal Age Maternal Rank Maternal Proximity Network Metrics (i.e., degree, strength, eigenvector centrality)	Maternal Identity	Offspring Age*Sex	Negative Binomial
	Offspring Strength	SRI Offspring Age Offspring Sex Data Type Maternal Age Maternal Rank Maternal Proximity Network Metrics (i.e., degree, strength, eigenvector centrality)	Maternal Identity	Offspring Age*Sex	Gamma with log link function
	Offspring Eigenvector Centrality	SRI Offspring Age Offspring Sex Data Type Maternal Age Maternal Rank Maternal Proximity Network Metrics (i.e., degree, strength, eigenvector centrality)	Maternal Identity	Offspring Age*Sex	Zero-one-inflated beta
Proximity (mother-offspring)	SRI	Offspring Age Offspring Sex	Maternal Identity	Offspring Age*Sex	Beta

6.3 Ethogram

LETTER 1: Type of data to be entered

Self (S) – focal, self- or generally-directed behaviour
Contact (C) – focal in physical contact = 0m
Proximity (P) – focal within <1 body length from interactant
Direct (D) – focal gives, or directs, the behaviour
Receive (R) – focal receives the behaviour
Mutual (M) – mutual behaviour
OOO – out of sight

LETTERS 2&3: Behaviour Codes

SELF or GENERALLY DIRECTED (S/P/C)

Rest (RE), state – individual is sitting in a relaxed (i.e., non-vigilant) manner; may also be lying on side or straddling a tree branch (Struhsaker, 1967a)

Scan (SC), state – individual is looking around, turning its head, in the farther visual distance >2meters; often occurs as a standing pause during a "move"; differs from "rest" because the animal is usually not sitting or lying down.

Visual Forage (VF), state – individual is slowly moving or standing still while looking around in foreground <2m (on the ground, in tree or shrub branches, grasses); differs from "Move" because "Visual Forage" often includes locational displacement of less < 1 meter.

Move (MO), state – walking or galloping, occasionally including a hop, and may be preceded or interrupted by vigilance (Struhsaker, 1967a); locational displacement greater than 1 meter and excludes positional changes/adjustments with locational displacement of less than 1 meter (Schoof, 2016).

- Move between (**MB**) – moving between trees
- Move within (**MW**) – moving within a tree
- Move on ground (**MG**) – moving on the ground

Vigilant (VG), event – standing erect on hindlimbs staring in one direction or glancing in several directions (Struhsaker, 1967a); if in tree, the actor stands quadrupedally or sits with chest forward and stares or glances (Schoof, 2016).

Self-Groom (SG), state - an individual combs through its own pelage using fingers and/or mouth, and may place foreign particles in mouth (Schoof, 2016: included scratching)

Scratch (SK), event – includes scratching (*sensu* "self-cleaning" in Struhsaker, 1967a).

Feed (FE), state – individual is manipulating and/or ingesting food.

- When possible, the observer should note the food species and part in the "comments"

- Food parts include: Ripe Fruit (RF), Unripe Fruit (UF), Unknown Fruit (FR), Flower (FL), Young Leaf (YL), Mature Leaf (ML), Leaf Bud (LB), Young Leaf Petiole (YLP), Mature Leaf Petiole (MLP), Bark, Dead Wood, Pine Needles, Seeds, Seed pods, Pith, Soil, Tuber/Root/Potato

Drink (DR), state – individual is ingesting water from a ground or tree source (natural or man-made), normally involves lowering head towards standing water from water holes or rain pools; individuals may also lick water from hands, fingers, tree branches, or pelage of others (Struhsaker, 1967a).

Yawn (YW), event – Mouth open all the way, briefly, in the vertical rather than horizontal plane; head may go back a bit. Lips may cover teeth or roll back, exposing top and bottom canines.

Other (OT), state/event – any behaviour not described in the ethogram; use "comments" section to describe behaviour

Out of sight (OO), state – focal animal is out of sight of the observer, usually resulting from substantial visual obstruction such as a building or dense vegetation, or because the focal animal has been "lost".

<u>SOCIOSEXUAL</u> (S, P, C, D, occasionally M)

Hip grab (HG), event – actor will stand behind female and grab at her hips pulling her in as if to mount but does not mount.

Inspect (IN), state – actor visually inspects, touches, licks or smells the genital region of the recipient; this may include looking from a short distance (<1ft), manipulating with hands or mouth, touching with face and includes various forms of "muzzling" as described by Struhsaker (1967a). Self licking or manipulating (males' genitals) is S,P or C

Present (PR), event – female actor stands quadrupedally and orients her hindquarters towards the male recipient, sometimes glancing over shoulder; female may stop to present if followed by a male or male grabs hindquarters of a sitting female (i.e., behaviour of "estrous female" as described in Struhsaker, 1967a).

- Note: a male focal animal can therefore <u>Receive a Present</u> (RPR) from a female Interactant.

Mount (MT), state – actor holds mountee hips with its hands, and legs with its feet (i.e., foot clasping); mount with <u>no thrusting</u>; may be associated with grooming and individuals may alternate between role of actor and recipient; note: mount may be incomplete, with grasping of only one body part (Struhsaker, 1967a)

Thrusting mount (TM), state – actor mounts (see above) recipient <u>with pelvic thrusts</u>; thrusts may be relatively <u>rapid</u> and <u>short</u> and/or relatively <u>slow</u> and <u>long</u> (Struhsaker, 1967a); may be followed by a pause before dismount. (Field assistants call this copulation or mating (CO).

- In the comments" section, observer should attempt to (1) note whether the thrusts are rapid/short or slow/long, (2) count the **number of thrusts**, (3) note if the presence/absence of a "**pause**" before dismount, and (4) note the presence/absence of **ejaculate** on the male and female's genitals.

Mating refusal (MR), event –female actor who is being grabbed by male remains sitting, lies down, crouches low, or walks away; note that female may also hit, lunge, or make "anti-copulatory squeal-scream" vocalizations (i.e., behaviour of "anestrous female" as described in Struhsaker, 1967a).

Penile erection (PE), event – actor has a conspicuously erect red penis; may occur during 1) grooming when recipient is male, 2) intragroup agonism, usually by the aggressor (Struhsaker, 1976a).

AFFILIATIVE (D, occasionally M)

Approach (AP), event – One monkey moves into contact or within 2 meters of a second monkey (Jack, 1998).

Leave (LE), event – One monkey moves out proximity (2 meters) of another monkey (Jack, 1998).

***Breast feed (BF)** – actor suckles from one or both nipples simultaneously (Struhsaker, 1967a); this is a behaviour directed by an infant (sometimes a young juvenile) to a female recipient; a.k.a., nursing or suckling.

Carry (CA) – actor has another individual, usually an infant, clinging to its ventral surface or sitting/straddling on its back while engaged in locational movement.

Entwine tails (ET; Mutual behaviour) – two individuals sitting in close proximity on a branch criss-cross their tails (Struhsaker, 1967a)

Groom (GR), state – actor combs through the fur of recipient using fingers and/or mouth, and may place foreign particles in mouth; may be accompanied by lipsmacking or teeth chattering (Struhsaker, 1967a).

Groom solicit (GS), event – actor presents a specific body part to recipient for grooming (Struhsaker, 1967a)

Ignore (IG), event – actor presents a groom solicit that is not acted on by the recipient. (Event)

Hug (HU), event – actor wraps their arms around the recipient while sitting dorso-ventrally or ventro-ventrally (recipient-actor) and may be associated with grooming; a.k.a. embrace (Struhsaker, 1967a).

Play (PL; D, R, or M behaviour; or S for rare self-play), state – Play behaviours are quite variable and encompass a large number of behaviours described elsewhere (e.g., grab, chase, wrestle, mount, groom, embrace, hop, etc…)

- in play, these behaviours – such as chase or groom – are “alternated with one another in rapid sequence” and “may be the major distinctions between play and non-play encounters, rather than uniquely different behavior patterns” (Struhsaker 1967a: 33)
- intergroup play between juveniles and juvenile males of different groups may occur (Struhsaker, 1967a).

***Wean (WE)** – female actor refuses breast-feeding attempt, or nips and/or pushes away a suckling infant (Struhsaker, 1967a); this is a behaviour directed by a female to an infant or young juvenile.

Mouth to mouth (MM), event– actor approaches recipient and the two put their mouth close together touching (or nearly).

AGONISTIC

In “comments”, note the stimulus or context prior to the agonistic event(s), such as copulation/mount, male, infant, grooming, food, space, or unclear; do not leave blank (i.e., if you didn’t notice anything, write “unclear”).

Aggressive/Dominance Behaviours (D, occasionally M)

Bite (BI), event – as described, usually accompanied by grabbing (Struhsaker, 1967a)

Bob (BB), event – Jerking or bobbing of head or entire body in up and down motion (on sagittal plane); for body includes torso bobbing from quadrupedal to bipedal position – often associated with eyelid flash (*sensu* “jerking” in Struhsaker, 1967a)

Branch-shaking (BS), event – Actor deliberately bounces once or twice on a branch, sometimes associated with racing through trees creating noticeable noise, normally associated with intergroup encounters (Struhsaker, 1967c, Henzi, 1982)

Broadside (BD), event – Actor stands perpendicular to receiver, pauses, and then moves on; actor’s tail may be raised. Note: Receiver is usually sitting (Henzi, 1982; *sensu* “sideward-display” in Struhsaker, 1967a)

Chase (CH), **state**– Actor moves rapidly toward the recipient, who runs away (*sensu* “chase-and-attack” in Struhsaker, 1967a); recipient frequently looks back at actor while running away, and often emits submissive vocalizations

- note: some chases may be “false” (sensu “false-chase” in Struhsaker, 1967a), wherein the actor gallops slowly and hesitatingly towards the recipient that is never caught □ actor generally subordinate to the recipient

Coalitionary Display (CD) – any agonistic interaction involving three or more monkeys; the initial aggressor(s) is the “actor(s)”, while the initial victim(s) is the “recipient(s)”; additional details on the behaviours involved should be noted in the “comment” section.

Eyelid flash (EF), event – actor exposes lighter coloured eyelids by retracting brow while maintaining eye contact or staring at the recipient (Struhsaker, 1967a); may also be submissive ("defensive") in nature if actor is crouching (Struhsaker, 1967a)

Hit (HI), event – actor hits, or slaps, the recipient with its hand (Struhsaker, 1967a)

Lunge (LU), event – Actor leaps or jumps towards the recipient. Forward lurching of the chest.

Penile Display (PD), event– Male actor displays red and erect penis while standing bipedally or sitting upright with his hands on the recipient, whose face is directed towards the actor's genitals (Struhsaker, 1967a).

Red-white-and-blue display (RB), state – Male actor displays the red perianus, white pelage between anus and scrotum, and blue scrotum to the recipient; male encircles or paces next to recipient with tail lifted, or briefly stands on his hindlimbs while oriented towards the recipient, thereby exposing genitals; actors include only adult, subadult, and older juvenile males (Struhsaker, 1967a; Henzi, 1982). Note: Receiver is usually sitting and vocalizing. Like a male presenting/ may involved movement around receiving individual.

Solicit Assistance (SA) – aggressor or victim of aggressive behaviour solicits assistance from others by "head flagging", glancing back and forth between opponent and individual assistance is being solicited from, or vocalizing (e.g., chuttering)

Supplant (SU), event –the actor moves towards the recipient and occupies the space, eats the food, takes copulatory position, or assumes the grooming position of the recipient; the recipient or "supplantee" generally moves away, sometimes engaging in submissive behaviours such as lip-smacking or submissive vocalizations (Struhsaker, 1967a); a.k.a. displacement.

- Note: indicate in "comments" what the actor removed: food, grooming, or space (note that because "space" is generally taken when removing food or grooming from the recipient, "space" should only be used if neither food nor grooming were removed from the supplantee)

Submissive (D, occasionally M)

Avoid (AV), event– at the approach of another individual (i.e., the recipient of the avoidance behaviour), the actor spontaneously vacates and moves away without any threat or aggression from the other individual; the recipient may just be passing by and does not occupy the space vacated by the actor (i.e., the individual doing the "avoiding")

- note: if the space (or food/grooming partner) is then occupied by the approaching individual, this behaviour should be coded as a supplant directed by the approaching individual.

Cowering (CW), event – Actor lowers head/body by crouching towards the ground and avoids eye contact with recipient; actor may be moving away from recipient; usually associated with submissive vocalizations/lipsmacking (Henzi, 1982; sensu "crouching" in Struhsaker, 1967a)

Fear grimace (FG), event – actor opens mouth about halfway and exposes teeth by retracting lips on horizontal plane (resembles a "smile); often accompanied by submissive vocalizations and staring at the recipient (*sensu* "grimacing" in Struhsaker, 1967a).

VOCALIZATIONS (D, occasionally M)

Alarm call (AC), event – Alarm calls are often multi-syllabic barks can be emitted in response to a real or perceived threat, most notably for "other vervet group", snakes, eagles (i.e., *rraup*), leopards (i.e., *chirp*), & dogs and humans at Nabugabo (http://www.psych.upenn.edu/~seyfarth/Baboon%20research/vervet%20vox.htm)

Bark (BK), event – low-pitched and gruff uni-syllabic exhaled vocalization emitted by males during intergroup encounters and occasionally during intragroup agonism; given towards other vervet monkeys who are fighting, it is emitted to stop the fighting (Struhsaker, 1967c).

***Chutter (CT), event** – low-pitched, monotonal and staccato vocalization emitted by females and juveniles to express aggression and solicit assistance; mouth is closed and the teeth are covered (Struhsaker, 1967c).

Submissive vocalizations (SV), event – lipsmacking, teeth-chattering, purring (Struhsaker, 1967c; Henzi, 1982), and also includes:

- ***Woof woof (WW)***: This call is non-tonal, deep, and has a guttural sound (Struhsaker, 1967c) emitted with closed or slightly-open mouth to indicate submission (Struhsaker, 1967c).
- ***Wa (WA)***: This call is a continuous tonal exhalation that occurs with a grimace and indicates submission (Struhsaker, 1967c); may be combined with as "Woof-wa" vocalization.
- ***Rraugh (RR)***: For this call the mouth is closed or partially opened and the teeth are covered (Struhsaker, 1967c). This call is emitted by yearlings when they approach older members of the group, and is a signal of nonaggression (Struhsaker, 1967c); includes both the long and short rraugh, and the aarr-rraugh.
- ***Lipsmack (LS):*** Moving the lips together quickly, opening and closing the mouth repeatedly.

***Squeal-Scream (SS):** high-pitched, piercing calls usually are emitted by females and juveniles that are seeking help from threats by an aggressor, and may be anti-copulatory (Struhsaker, 1967c).

INFANT INTERACTIONS (C:Contact; R:Receive or D:Direct)

*When applicable, instantaneous samples of focal animal's infant should be recorded at 0, 5 10, and 15 mintues of focal follow.

Ventral contact (VC), event –actor initiates contact between torso of infant with the ventrum of mother (Bardi et al., 2004).

End ventral contact (EC), event –Actor separates torso of infant from the ventum of mother (Bardi et al., 2004)

Breast Feed (BF), event – infant's mouth is in contact with one or both nipples simultaneously (Struhsaker, 1967a)

End Breastfeed (EB), event – infant that was in nipple contact stops voluntarily (i.e., not "weaning")

Weaning (WN), event – infant that was in nipple contact is forced to stop breastfeeding by the action of the focal

Nursing refusal (NR), event – infant who reaches or comes into contact with nipple is pushed back by focal or focal moves away

Restrain (RS), event – Focal keeps infant from breaking contact (Bardi et al., 2004)

Reject (RJ), event – Focal prevents attempted contact by infant (Bardi et al., 2001)

INTERACTANT(S)

For identified monkeys, write their name or code in the Interactants (or NN) column;
For unidentified monkeys, use the following two or three letter codes; if there are multiple individuals of the same age/sex category, add number identifiers. For example, AM1, AM2
AM# – Adult male
AF# – Adult female without infant
AI# – Adult female with infant
AD# – Adult, unsexed
SM# – Subadult male
SF# – Subadult female
SB# – Subadult, unsexed
JM# – Juvenile Male
JF# – Juvenile Female
JV# – Juvenile, unsexed
IN# – infant (always unsexed)
XX# – Unidentified vervet
ZZ – other species (if known, indicate the species in the "comments"; e.g., snake, bird, dog, cow)
OO – observer
OH – other human

- If there are multiple interactants, use a comma to separate their IDs

ZRT- Red tailed monkey
BWC – Black and white colobus monkey
BBN - Baboon
DOG – Dog (indicate how many in the comments, and their behaviour)
COW – Cow
PIG – Pig
GOT – Goat
CKN – Chicken

ADDITIONAL NOTES:

***behaviours** identified with an asterisk (*) are not usually performed by adult or subadult males; e.g., Breast feed, Wean, Chutter and Squeal-Scream.

Copulatory harassment of a male or a mating pair has been observed, but the behaviours comprised in copulatory harassment include other behaviours described herein (e.g., biting, lunging, grabbing, etc…). As such, if copulatory harassment is observed, this should be noted in the "comments" of the associated behaviour.