THE STUDY OF SOCIAL DYNAMICS IN JUVENILE VERVET MONKEYS

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ABSTRACT

Using a longitudinal approach, I sought to deepen my understanding on social integration in wild juvenile vervet monkeys (*Chlorocebus pygerythrus*). First, I focused on the analytical tools used to capture the social and temporal dynamics within my data, which led me to provide my own flexible and reliable methods. Second, I used these methods to address theoretical questions regarding the development of social networks as well as the emergence of sex-specific social behaviours in male and female juveniles, throughout social development. Overall, my findings showed that juveniles develop social networks composed of few strong and many weak ties, through social niche construction. Taking a closer look at these strong ties, in turn, demonstrated that the value of sociality not only lies in the formation of a subset of strong ties, but also in the formation of a more extended social network, where the offspring's mother grooming partners were found.

CONTRIBUTIONS OF AUTHORS

This thesis is a collection of collaborative work.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Aims

Primates' individuals are embedded in changing networks of relationships with social group members. As such, there is a need to understand social life from a dynamic, multidimensional perspective because approaches that either ignore or do not adequately account for these temporal dynamics can result in inappropriate inferences. Addressing such temporal issues is, however, reliant on the availability of appropriate analytical techniques. My aims in this thesis, therefore, are to describe the development of such techniques and to use them to investigate aspects of the social dynamics of a non-human primate system: the juvenile vervet monkeys (*Chlorocebus pygerythrus*). That is, I propose to study in detail the development of social networks as an index of social integration into the group during the juvenile period, while addressing the need for flexible and reliable methods that can take into account the social and temporal dynamics. What follows here is a general overview of the relevant issues.

1.2 Background

1.2.1 Group living

Primates are long-lived mammals that exhibit a strong tendency to live in cohesive social groups (Isbell & Young, 2002), where one sex usually remains in its natal group (philopatry) while the other disperses. In the main, they form persistent, multi-generational societies. i.e., they comprise overlapping generations of matrilineal or patrilineal kin (Dunbar, 1988; Humphrey, 1976). Observed consistent cross-species differences in group structure suggested that social organisation reflected the evolutionary consequences of a species 'ecological niche and gave rise to a long-standing question in socioecology (Crook & Gartlan, 1966): what drives the structure of these groups? To explain the evolution of sociality in primates and the resulting variation in social systems, verbal models appealing to ecological factors were developed (Clutton-Brock, 1974; Crook & Gartlan, 1966; Sterck et al., 1997; Van Schaik, 1989; Wrangham, 1980). The principle debate hinged on whether the variation in group size, group composition, and social relationships among group members was the consequence of a need to defend patchily distributed resources, such as food for females (Wrangham, 1980) or reproductive access for males (Watts, 1998), or to reduce the risks of predation or infanticide (Dunbar, 1988; Harcourt & Greenberg, 2001; Sterck et al., 1997; Van Schaik & Van Hooff, 1983). Today, the general empirical consensus is that predation risk is the primary driver of primate sociality (Dunbar & Dunbar, 1988; Majolo et al., 2008; Schülke & Ostner, 2012; Van Schaik & Van Hooff, 1983; Van Schaik, 1989). This is based on the evidence that predation risk appeared to be lower in larger groups that were more efficient at detecting the presence of predators from a longer distance (Van Schaik & Van Hooff, 1983). The main expected cost with increasing group size, however, is an increase in the level of within-group food competition (Isbell, 1991; Janson & Van Schaik, 1988), which affects reproductive performance or survival through lower net food intake (Majolo et al., 2008). Group size and structure, therefore, represent a balance between predation risk and group competition, where the lower threshold to group size is set by predation and the upper limit is posed by feeding competition among group members (Van Schaik & Van Hooff, 1983).

While these socio-ecological studies highlighted the ultimate importance of ecological factors, determining the adaptive strategies of individuals, to alleviate the costs of living in groups and the consequent group social organisation, they also contributed to defining primate competitive regimes. In fact, with ecological competitors constrained to coexist within a social group, such gatherings had an effect, not only on the grouping and dispersal patterns of females, but also on the strength in the competition for resources. Extending on the theme of competition, Van Schaik (1989) argued that the role of dominance, in structuring social relationships between the philopatric sex, should depend on species ’local ecology (i.e., the distribution of food resources relative to group size), and the intensity level of intra-group competition. That is, despotic species have clearly established dominance relationships (de Waal, 1989) and usually have linear dominance hierarchies (Sterck et al., 1997). For instance, rhesus and Japanese macaques (*Macaca mulatta* and *M. fuscata*) engage in conflicts of high intensity, which are mainly asymmetric (Chaffin et al., 1995; De Waal & Luttrell, 1989). In egalitarian species, the dyadic dominance relationships are not detectable or poorly defined, resulting in uncertain and non-linear dominance hierarchies (Sterck et al., 1997). In these systems, therefore, social interactions are more symmetrical, and less kin biased (Tonkean macaques (*M. tonkeana*), (Matsumura, 1999)). van Schaik’s original slate of dominance styles reached its conceptual endpoint in the publication by Sterck et al. (1997), with a very detailed elaboration of four categories (resident-nepotistic, resident-nepotistic-tolerant, resident-egalitarian and dispersal-egalitarian), which describe the social responses that arise among female primates from the strength of within- and between-group contest competition. Overall, social competition in groups sets out the framework in which the social relationships of group members should be considered, and the establishment of competitive gradients allowed for predictions about the nature of affiliative relationships among females to be made.

The important point to note here is that these social relationships are taken to be categorical markers that apply to entire species. So, for example, baboon females (*Papio cynocephalus ursinus*) are ‘resident-nepotistic’, while blue monkeys (*Cercopithecus mitis*) are ‘resident-egalitarian’. In other words, while ecology structures social relationships, the relationship styles themselves, depicted at the level of the species, are considered to be fixed. Therefore, these relationships are relatively impervious to spatial or temporal variations in local ecology. Lastly, different dominance styles may reflect different behavioural strategies for contesting and defending resources, and individuals may be expected to adapt their strategies in response to their local and social environments. As such, these fixed relationships also fail to explain interspecific variation in individuals/populations/species (e.g., Kuester et al., 1998; Matsumura 1999).

1.2.2 The demands of social life

While socioecological studies investigated how environmental conditions influenced the social structures of animals, the intense nature of primate's sociality was investigated in relation to their unusual large brains (Jerison, 1975). Humphrey (1976) originally proposed that the social environment might select for primate intelligence. This idea was later elaborated by Whiten and Byrne (1988) with the Machiavellian Intelligence hypothesis (MIH). In essence, it argued that coexistence with ecological competitors selected for animals that could simultaneously deceive others while being able to detect and avoid deception in turn. Tactical deception (Byrne and Whiten 1992), hence, became one of the defining criteria for this hypothesis, where selection for a tactical intelligence relied incrementally on the ability to cope with increasingly elaborated strategies and counterstrategies, in order to 'outwit 'the competition. This explanation, however, suggests that social strategies are needed to alleviate these costs linked to living in social groups.

In 1992, Dunbar extended van Schaik's (1989) earlier analysis by quantitatively examining how different social and ecological indices correlate with different measures of relative neocortex size. This resulted in a series of influential papers, where Dunbar (1992, 1995,

1998) drew a clearer picture of the relationships between ecology, female sociality, and population structure. He argues that, as a means of solving an ecological problem (Dunbar, 1992, 1998; Dunbar & Shultz, 2007), individuals would be exposed to rising competition with increasing group size through (a) ecological competition and (b) the consequences of crowding in limited space (Dunbar & Shultz, 2017). To alleviate these costs, the capacity to form and sustain agonistic coalitions (Harcourt, 1988), mediated by grooming as an affiliative tactic (Dunbar, 1992, 2012; Seyfarth, 1980) and reconciliation (de Waal, 1989), would be increasingly difficult but also valuable. It would, therefore, necessitate an ability to track and monitor the social environment in order to exploit the knowledge of other individuals' behaviour (Whiten & Byrne, 1988; Cheney & Seyfarth, 1990), and hence to sustain beneficial alliances. This was thought to be cognitively demanding, thus driving selection for the increased brain size underpinning the necessary cognitive requirements. In other words, the need to cope with this unusually complex social life consequently necessitated a proportionally bigger brain to handle social relationships (Dunbar, 1992, 1995, 1998), generating the prediction that social group size (as index of social complexity) should predict the size of the primate neocortex (the most recently evolved part of the brain). That is, the cognitive demands from group life were linked to the need to manage an exponentially increasing number of potential relationships associated with linearly increasing group size. In support of this, Dunbar (1992, 1995, 1998; see Dunbar & Shultz 2007 for a more recent restatement of this position) pointed to empirical data indicating that the neocortex was relatively larger in primate species living in larger social groups.

In sum, anthropoid primate social societies result from a complex combination of cooperative and competitive interactions (Hinde, 1976; Walters, 1987), and are characterized by a high proportion of female-bonded social groups (Shultz & Dunbar, 2007). In other words, females have close, bonded relationships in which dyads maintain long-term close spatial proximity, interact frequently with each other, and come to each other's aid. This sets out the context under which highly differentiated social relationships evolve (Seyfarth, 1980; Silk et al., 2006b). Factors have been proposed to underpin the highly differentiated relationships, such as resource-holding potential, which describes the inherent ability of an animal to acquire and hold a resource (Parker, 1974), in conjunction with the inclusive fitness benefits of assisting close kin (Hamilton, 1964). Further determinants of primate social relationships were also proposed like dominance rank and the advantages of forming close bonds preferentially with high-ranking group members (Seyfarth, 1980). Put simply, these relationships are shaped by social status, friendships, alliances, and kinship. These differentiated relationships bring in the final piece of the puzzle, which is the link between environmentally induced sociality and fitness. Silk and her colleagues (2003, 2009) first demonstrated a link between strong social bonds and offspring survival in free-ranging baboons. Bringing things full circle, predation risk was linked to obligate sociality for primates, which gave rise to costs associated with group living, which then led to a need for advantageous cooperation with others, which in turn required cognitive skills that relied on a "social brain", that ultimately paid reproductive dividends.

In sum, socio-ecological studies assumed that a limited number of environmental factors affect population characteristics, leading to predictable differences in social systems. This categorical approach makes the assumption that species could be adequately characterized and placed in categories based on the 'average' behavioural characters for each taxonomic unit, ignoring the within-specific variation in social structure. The flexibility in primate social systems was, therefore, considered a consequence of the variation in ecology (Koenig et al., 2013). In addition, these studies emphasize entities above the individual level, such as dominance style (Van Schaik, 1989), and make the implicit assumption that patterns arise because all individuals respond uniformly to their ecological and social contexts (e.g., Sterck et al., 1997). Yet, group composition varies and modifies the social context under which social interactions. This suggests that optimal responses to the local and social environment may also be expected to vary, as individuals track changes in local resource availability and shift patterns of social affiliation in response to these ecological and demographic conditions (Barrett & Henzi, 2005; Henzi et al., 2013; McFarland et al., 2014). It, therefore, encourages a shift in focus from between to within species variation. Lastly, recent analyses (DeCasien et al., 2017; Lindenfors et al., 2021; Powell et al., 2017) provide no evidence that brain structure is tailored to social demand *per se*. There is also very little evidence that tracking changes requires the cognitive capacities suggested by the MIH. In line with this, Henzi and Barrett (2007), following the arguments of Biological Markets Theory (BMT: Noë & Hammerstein 1994a, 1995a) proposed that alliances and coalitions, and their generation and maintenance via grooming, occurred too infrequently to serve as an organizational principle on which natural selection could act to structure social relationships and therefore groups. Instead, they suggested that grooming was better seen as a service that can be exchanged either for itself or for immediately trade-able commodities. The BMT, therefore, proposes that cheating can be avoided through appropriate partner choice. As such, taking a more individual-based approach, ‘traders ’are predicted to behave differently depending on what they are trading and with whom (Barrett & Henzi, 2006). Consequently, individuals can vary in value depending on their health, reproductive state, seasonal changes in the competitive regime, and on the presence or absence of other individuals. Interactions, in other words, are contingent on context.

What we can take from all this, then, is that primates live in the company of others, in unpredictable local and social environments and have distinctively large brains that are presumably directed at tracking ecological and social contingency. If so, then an evaluation of the value of social relationships needs to begin with a better understanding of the dynamics of social interaction. Long-term studies have proven to be one of the best approaches to address such issues, as they have provided insights into primate social behaviour patterns, giving us the opportunity to shift towards more rigorous, quantitative approaches.

1.2.3 Social relationships

In line with this quantitative approach is the recognition that, to explain and predict the behaviour of individuals, simple description of who does what to whom and how often is not enough. Instead, a step back is required to identify, at a more abstract level, social relationships and the general principles that underlie them. Hinde's (1976) conceptual framework does so where social relationships, emerging from the patterning of interactions between pairs of individuals, lead to the emergence of a group's social structure. Hinde (1976) argues that social relationships can be described in terms of their content (what do two individuals do together?), quality (how do they do it?), and the frequency and patterning of social interactions through time (Hinde, 1976). He also emphasizes the dynamic aspect of social relationships, which he perceived as relationships that change, or are adjusted, over time. Although Hinde's framework doesn't consider the environment in which the social structure evolves, it allows for the quantification of social relationships. As such, it also contrasts with commonly used measures, like group size (Dunbar, 1998; Strier, 1989), which only indirectly reflect the social relationships between individuals and assume homogeneity of effect on all of them. Finally, with its three levels of structure (interactions, relationships, social structure), this framework depicts the complex multi-dimensional nature of sociality (Whitehead, 2008), where causal relationships between these three levels exist (Hinde, 1976). To understand the nature of feedback between social structure and social behaviour, detailed descriptions of social structure over the long-term are needed (Clutton-Brock & Sheldon, 2010). This includes the quantitative insights provided by network analysis (Cantor & Whitehead, 2013), which are not possible when using the verbal arguments of the socioecological model.

Given its multiple levels of organisation, and therefore, multiple levels of description, the multi-dimensional nature of sociality is difficult to represent accurately and to quantify (Hobson et al., 2019). Whereas interactions between two individuals sit at the core of Hinde's framework and most studies focus on dyadic relationships, the context of these relationships extends beyond the dyad itself (Arnold & Barton, 2001; Kutsukake & Castles, 2004). That is, the number and quality of social relationships formed depends not only on the individual's own position within the group's structure (McDonald, 2007) but also on the broader social context in which social interactions take place (Kutsukake, 2009), which includes the way the group is organized (Hock et al., 2010). These social interactions should therefore be studied in the context in which they emerge, which is the social group. With its ability to combine individual and group properties in analysis, Social Network Analysis (SNA) provides the appropriate analytical framework.

1.3 Studying Social Relationships: the case of SNA

1.3.1 General introduction

SNA offers the possibility to deconstruct a social group into nodes and edges, representing respectively, individuals and the interactions between individuals (Pinter-Wollman et al., 2014) at a point in time. By aggregating interactions over any relevant period of time, SNA can quantify the patterns of relationships that arise among interacting individuals. This can be done thanks to a well-established suite of quantitative social network metrics (Croft et al., 2008; Newman, 2010) that enables researchers to define and quantify sociality in a variety of ways. Thus, social network measures can be calculated to quantify the properties between two individuals (dyad scale), around the individual (ego scale) and at the entire group level (network scale) (Wey et al., 2008). In behavioural ecology, SNA is procuring researchers with tools to probe social groups and their dynamics, providing greater insights into how the group's social network structure and the individual's social network position impact fitness components. For instance, in mammalian species, studies have shown that survival may be negatively correlated with eigenvector centrality (Male Bottlenose dolphins (*Tursiops* sp.): Stanton & Mann 2012) and with variance in edge weights for spatial proximity (Rock hyrax (*Procavia capensis*): Barocas et al., 2011), but also positively associated with stability or quality of affiliative relationships (Chacma baboons (*Papio hamadryas ursinus*): Silk et al., 2010a; Barbary macaques (*Macaca sylvanus*): McFarland & Majolo 2013 both using the composite sociality index (CSI), and Blue monkeys (Thompson & Cords, 2018), using the annual dyadic sociality index).

If these examples reveal the wide applicability of SNA across diverse taxa, they also give us a quick glimpse into the overwhelming number of available measures with which to investigate social relationships. A recent study by Schülke et al. (2022) assessed the similarity of quantitative measures of sociality. Regarding social bonding, which concerns the strongest affiliative relationships individuals form, they extracted seven measures (e.g., CSI, the annual dyadic sociality index, strength, degree), revealing the plethora of measures that can be used and, therefore, the lack of consensus in how to quantify sociality. Furthermore, these measures can be inferred differently, depending on whether they focus on all ties or on different threshold values.

So, for example, we might include in an analysis an individual's top three partners using the CSI, or the number of strong ties with strength above either the 0.9 percentile, the 3rd quartile, or the mean value. We might, finally, also consider the strength of the strongest ties using the top three connections per individual (Schülke et al., 2022). The takeaway message here is that numerous indices exist to describe specific aspects of a social relationship between two individuals (Fraser et al., 2008). This calls, therefore, for transparency in terms of the measures used to quantify social relationships, which should clearly be defined and justified in analyses. This then raises the additional question of whether sociality is best captured from (i) grooming behaviour alone (Mcfarland et al., 2015), (ii) spatial association (Jones et al., 2020), (iii) both types of data (Brent et al., 2013a), or (iv) a combination that also includes agonistic behaviour (Crockford et al., 2013).

1.3.2 From static to dynamic

Until recently, most network analyses considered a network to be a static structure, providing "snapshots" of social structure at a predefined time, regardless of how long that time period was (Seyfarth et al., 2012; Silk et al., 2006a, 2006b, 2010a). This, however, did not depict the most accurate structure as not all relationships present in that timeframe may have existed at the same time, nor may the individuals have all been together simultaneously. In reality, patterns of social interactions shift in response to factors such as resource distribution, seasonal change, predation pressure or demography (Blonder et al., 2012). Consequently, to address particular theoretical and empirical concerns, measures of how social networks change over time are required (Aplin et al., 2015; Bonnell et al., 2019), and efforts have been made to incorporate the dynamic nature of social networks, which allows for the description of social structure based on a series of continuous measures. As such, if certain network positions or characteristics provide fitness benefits (Alberts, 2019), a dynamic approach can now be used to quantify the consistency with which individuals maintain these positions to achieve such benefits and might well reveal the mechanisms that underpin these functional outcomes (Ostner & Schülke, 2018). In the same way, the study of longitudinal networks allows us to investigate how social networks emerge and evolve over time and could further our understanding as to how variation in sociality arises. Although the introduction of SNA and its shift to a more dynamic approach has helped our understanding of sociality, the multi-dimensionality of social structure has, until recently, been ignored.

1.3.3 From a single to a multidimensional representation

Social networks have the capacity to capture the multi-dimensional nature of sociality. Yet, the early and traditional use of SNA has tended to aggregate animals 'social relationships into a single edge between nodes, often aggregating over long periods of time. This resulted in network structure being "flattened" into a single dimension, and social dynamics thereby necessarily being ignored (Finn et al., 2019). Consequently, variations that may exist across behaviours are lost (Chan et al., 2013; Hasenjager et al., 2021; Jones et al., 2020). Additionally, a single layer approach ignores the interdependencies that may exist between different types of interaction (Beisner, 2015). Multilayer network analysis (MLNA) has recently been proposed as an approach that can help to construct a more nuanced representation of social structure (Finn et al., 2019). In brief, a multilayer network incorporates multiple sets of relationships into the same structure, often with each layer representing a distinct type of interaction (Hasenjager et al., 2021). These layers are not limited to social interactions, as they can also represent non-social forms of relationship (e.g., genetic relatedness) and can include different types of entities (e.g., nodes may be physical locations in one layer and individual animals in another). Finally, because a multilayer network approach includes a series of layers within a single structure, the interdependencies between the different layers also can be modelled and investigated. To understand how behaviour and social context interact to influence individual variation in sociality, it is necessary to address the multidimensional nature of animal social associations (Finn et al., 2019) and MLNA holds a great potential to do so (Bonnell et al., 2021; Montiglio et al., 2020). For instance, it becomes possible to investigate whether grooming associations indicate an active social choice or merely the emergence of patterns due to shared space use. We can also start to identify how changes in an individual's social position cascade through the other network layers.

In this thesis, I capitalise on the methodological and analytical developments, which allow us to build on what has been found, in a more accurate and reliable way. But first, let's see what has been found more recently.

1.4 The importance of social relationships: where are we at?

The link between sociality and fitness components in primates, first mentioned above, has also been found across a diverse array of species (bottlenose dolphin: Frere et al., 2010; wild horses (*Equus caballus*): Cameron et al., 2009; killer whales (*Orcinus orca*): Brent et al., 2015), highlighting the taxonomic generalizability of this sociality–fitness link. Concretely, social relationships have been shown to predict higher health, greater longevity, fecundity, and offspring survival (McDonald, 2007; Schülke et al., 2010; Silk et al., 2003, 2009, 2010a), emphasizing the importance of social integration to ensure fitness benefits. Among primates, the benefits of increased social integration have been argued to derive from an improved ability to deal with 'social stress', as females with strong social bonds displayed lower glucocorticoid (GC) levels than did females with weaker bonds (Brent et al., 2011a; Crockford et al., 2008; Widdig et al., 2016). In line with this, lack of social support has been shown to correlate with elevated stress hormones (GC) in a wide variety of primate species (Abbott et al., 2003), while competition for resources has been shown to increase allostatic load, reflected in elevated GC concentrations (Goymann & Wingfield, 2004). Yet, this seemingly direct effect between GC levels and stress may not be that straightforward since the observed stress response (i.e., the physiological changes that occur when cortisol levels are elevated) comes from the individual's attempt to restore or maintain homeostasis when exposed to changes in their environment or their physiological status (Romero et al., 2009; Young et al., 2019a). Lastly, social instability, like changes in group composition (Kohn et al., 2011), also increases levels of aggression in the group (Marler, 1976) and can induce chronic social stress (Baranyi et al., 2005; Capitanio & Cole, 2015; Deputte, 2000; McCormick et al., 2012). For instance, female baboons who lost a close relative to predation experienced a dramatic increase in GC levels (Engh et al., 2006), which in turn may affect their reproductive success (Silk et al., 2003, 2006a, 2006b). Alternatively, female baboons showed lower GC levels when they concentrated their grooming on a few preferred partners compared to when their grooming was more equally distributed (Crockford et al., 2008). In sum, strong relationships (Crockford et al., 2008; Fuentes-González & Martins, 2019; Seyfarth et al., 2012) play a crucial role in enhancing primates' fitness between genetically related individuals (Chapais, 2001), but also when they involve non-kin (Seyfarth et al., 2012; Silk, 2002). These relationships are commonly seen as high frequency of affiliative interactions, and can include body contact, close spatial association, grooming, and huddling (Cords & Thompson, 2017).

Considering that prolonged activation of the stress system can have long-term negative effects on primate health and reproduction (Wingfield & Sapolsky, 2003), and that primates form permanent social groups, a certain notion of stability in social relationships is implied to maintain cohesive groups. Yet, this may be misleading as, to generate adaptive benefits, social relationships do not necessarily imply a stable pattern of highly frequent interactions (Henzi et al., 2009; Hinde, 1976). This notion is also amplified by the focus on the quality of social relationships and its link to fitness components. Yet again, weak social relationships, characterized by interactions that are deemed to be infrequent, have been also linked to fitness components (see Ellis et al., 2019; McFarland et al., 2017). For example, with minimal effort, individuals can increase the number of social partners in ways that may aid predator avoidance or thermoregulation (Josephs et al., 2016; Mcfarland et al., 2015; Ostner & Schülke, 2018). Such benefit comes at a low-cost as, all else being equal, a weakly-bonded partner would be as efficient as a strong one in such contexts (Ostner & Schülke, 2018). As such, while weak social relationships may serve different functions than strong ones (Mcfarland et al., 2015), and show different patterns, they too provide fitness-related benefits. Despite their differences, strong and weak social relationships may hence serve to complement each other with respect to the fitness benefits associated with relationship formation. Lastly, quantitatively speaking, these strong and weak social relationships distinguish each other by a required threshold value, above which a relationship is considered ‘strong ’and below which it is considered ‘weak ’(e.g., CSI values smaller than one, Silk et al., 2006b).

As social relationships have mainly been considered with respect to the ways that they contribute to fitness, there is an obvious reason to consider how these social relationships emerge and evolve across individuals’ lifetimes and how this leads to variation in fitness benefits across individuals.

1.5 The development of social relationships

When asking the question “how do social relationships develop”, it makes intuitive sense to look at their origin, which takes root either during infancy or the juvenile period. This juvenile period in primates is also of general interest because of its extended duration. Primates’ social developmental process spans years (Harvey & Clutton-Brock, 1985; Pereira & Fairbanks, 2002), during which young animals can shape their own social development through forming, maintaining, and reconstructing social relationships (Deputte, 2000; Fairbanks, 2002; Joffe, 1997; Kohn, 2019; Shimada & Sueur, 2014). The delayed maturation, characteristic of anthropoid primates, is part of an ongoing debate as to whether it represents a constraint imposed by the demands of growing a large brain (Aiello & Wheeler, 1995), or whether a long lifespan requires a large brain to cope with environmental unpredictability (Allman et al., 1993; Gibson, 1986; Sol, 2009). Several authors have also suggested that this prolonged juvenile period contributes positively to survival and fitness by enabling the acquisition of the cognitive skills needed to succeed in social groups (Joffe, 1997; Johnson & Bock, 2004; Leigh, 2004). Not surprisingly, there is a need for a better understanding of early life social experiences in the development of potentially long-lasting relationships, and how it affects later fitness benefits. In fact, considering the potential costs entailed by a delayed maturation from a life history perspective, and the risk of mortality as a juvenile (Fairbanks & Pereira, 1993), it becomes relevant to understand how and why this socialisation occurs over such an extended time. If being socialized means being able to live in a group, then studying infant socialisation is needed to understand the maintenance of social groups (Fragaszy & Mitchell, 1974).

Most of our current knowledge remains limited to few studies that have addressed how sociality develops during ontogeny in non-human primates and other social mammals (e.g., Deputte, 2000; Ilany & Akcay, 2016; Jarrett et al., 2018; Kulik et al., 2015a, 2015b; Lonsdorf et al., 2014; Förster & Cords, 2005). Ilany and Akcay (2016) provide a good starting point for explaining how network structures in juveniles are generated and maintained by a process of inter-generational inheritance. Their approach treats social networks as the result of a dynamic process (Pinter-Wollman et al., 2014) that depends on environmental, individual, and structural effects (Ilany et al., 2015). Yet, it fails to consider changes in social bonds once these are established. Again, this notion of stability may be misleading as Jarrett et al. (2018) found that maternal networks were insufficiently stable to support the inheritance of social partners in juvenile vervet monkeys, *Chlorocebus pygerythrus*. This suggests that network flexibility, not stability, is what characterizes this population, and that juveniles must learn to cope with temporal shifts in network structure (Jarrett et al., 2018). This makes sense, as for long-lived individuals in stable social groups, demographic changes are recurrent, leading to social instability. This finding supports previous results from the same population, where female vervets were shown to possess the flexibility to shift patterns of social engagement in response to ecological and demographic conditions (Henzi et al., 2013; McFarland et al., 2014). Taken together, these results suggest that unpredictable variation in group size and structure may select for animals that are able to respond flexibly to circumstance and adjust affiliation networks accordingly (Chapman et al., 2016; Henzi & Barrett, 2007; Henzi et al., 2003). In other words, the socialisation process requires ongoing behavioural adjustment to achieve and sustain integration into an existing group (Deputte, 2000), where individuals choose partners in relation to the state of the local ‘market ’(Henzi et al., 2003; Noë & Hammerstein, 1994b, 1995b; Barrett et al., 1999). In turn, this means that relationships can be seen as highly informative, where the variance around a mean level of interaction between two individuals can be viewed as a contingent response to fluctuations in the supply and demand of the commodities on offer (Barrett & Henzi, 2006).

Whether or not social inheritance enables the emergence of offspring social networks, via the inheritance of their parents 'social connections, the close proximity to their parents plays an important role in juvenile social integration (Deputte, 2000). For instance, maternal style can have long-term on offspring social development, including social preferences, affiliative and aggressive behaviour (Maestripieri, 2018), while mothers can influence the development of sex-specific social behaviour (Thompson & Cords, 2020). Sex differences in bonding strength have appeared prior to sexual maturation (Cords et al., 2010; Jarrett et al., 2018; Lonsdorf et al., 2014; Nakamichi, 1989), where philopatric females have stronger social bonds than dispersing males (Andres et al., 2013; Cords et al., 2010; Frere et al., 2010; Kulik et al., 2015b; Nakamichi, 1989; Stumpf et al., 2009). Such sex differences are also found in play, with males playing more than females (Meredith, 2013). These early sex differences in social behaviour can be interpreted in light of the different life histories and reproductive strategies of males and females (Deputte, 2000). For instance, the intense grooming behaviour exhibited by young females may foreshadow their integration and acceptance into their social group whereas the structure of the grooming patterns of young males can be viewed as a prelude to emigration from the natal group (e.g., Jarrett et al., 2018; Kulik et al., 2015a, 2015b). These findings show that juveniles play an active role in their own social integration and adapt their social behaviour by growing into the social roles typical of their adult lives (Kulik et al., 2015b; Widdig et al., 2016). Kulik et al. (2015b) suggested that, at approximately two years of age, rhesus macaques experience a "social revolution", in which sex differences in social behaviour become stronger and individuals prepare for their sex-specific social roles (Kulik et al., 2015a; Nakamichi, 1989; Suomi, 2005). They proposed that it may be a “milestone” in the development of sociality in this species, from which point individuals “start behaving more similar to adults”.

As sex-specific social behaviours are an important aspect of adult behavioural competence, being linked to higher reproductive success, the juvenile period offers the possibility to look at the origins of social relationships, and more specifically, when sex-specific social behaviours emerge and how they develop through time. We hypothesize that these different developmental trajectories may lead to individual variation in behavioural flexibility. In turn, it may help explain how and why variation in sociality arises, and how this gives rise to variation in the fitness-related benefits of sociality.

1.6 A mechanism: the case of social niche construction

In this thesis, I adopt an approach that investigates behaviour in its broader social context. The “horizontal worldview” put forward by van Dijk and Withagen (2014) (HWV) captures this idea as it encourages us to look more closely at concrete situations in order to understand particular phenomena, rather than abstracting away to higher or lower levels of explanation, in a standard reductionist fashion. Wittgenstein (1969) attempted to rid his reader of the urge to overthink and intellectualise, by insisting they should look more closely at what is actually going on in the world. Adopting a horizontal attitude therefore forces us to acknowledge that animals are both constrained and offered opportunities by their broader physical and social environments. Consequently, it brings us closer to an understanding of the extent to which social life is controlled and constrained socially by larger social structures, and not just via an individual’s own inter-personal interactions. With this approach, I attempt to adopt the individual’s perspective to understand how it experiences its social environment.

Although variation in developmental trajectories is usually interpreted in terms of its potential influence on variation in adult social engagement and later fitness-related benefits (Barrickman et al., 2008), the actual processes by which integration is achieved are often left unspecified (but see Ilany and Akcay 2016). As already mentioned, juveniles are required not only to learn which relationships to form, but also how to cope with periods of change, by adapting their behaviours flexibly to situations (Borgeaud et al., 2017; Kaburu & Newton-Fisher, 2015), and by altering their own movement patterns to create favourable conditions for future interactions (Amici et al., 2008; Kohn et al., 2011).

This speaks directly to social niche construction (SNC), a domain within the field of niche construction theory (Odling-Smee et al., 2013). SNC is the process by which individuals influence the composition and dynamics of their own social environments (Odling-Smee et al., 2013), with a focus on the production of social structures that facilitate survival for their members (Heras-Escribano & de Pinedo-García, 2018). For instance, depending on their sex, young individuals may flexibly use a variety of behavioural strategies to interact with their social partners, possibly to best fit the sex-specific social roles that are typical of their adult lives (Nakamichi, 1989). These niches can also arise through social assortment, where individuals aggregate according to specific phenotypic similarities (Blumstein, 2013; Deputte, 2000). In this regard, the social niche specialization hypothesis derives from SNC (Bergmüller & Taborsky, 2010; Montiglio et al., 2013). It proposes that the presence of other group members causes individuals to behave differently from each other to reduce direct competition, thereby generating between-individual variation in behaviour (Wolf et al., 2008). Once individuals behave differently from one other, the presence of others increases the benefits of behaving predictably, thereby maintaining individual differences through positive feedback mechanisms (Montiglio et al., 2013; Wolf et al., 2011). In an evolutionary context, this view is of particular interest as niches shape the social conditions under which juveniles develop and live. Through SNC, organisms not only shape the nature of their world, but also in part determine the selection pressures to which they and their offspring are exposed. Practically speaking, focusing on the social niches of individuals allows one to examine the effects of social interactions at a meta-dyad level (Conradt & Roper, 2005), rather than being restricted to the local scale (i.e., dyadic level).

In this thesis, I focus on juveniles' socialisation and seek to understand how social relationships and sex-specific differences develop and evolve, while considering the wider social context of the interactions and associations across two different behaviours. To do so, I investigate SNC as a means for juveniles to make their immediate social environment more certain, hence facilitating the integration into their group. Putting this work into its broader context, I hope to get a better sense of social network emergence and maintenance, as well as a better understanding of how these processes might lead to later fitness-related benefits. The view proposed here sees social integration of juveniles as a result of a dynamic series of developmental processes where relationships are continually managed and renewed across contexts. This led me to develop and employ methods that can pick up these temporal dynamics. Constructing a dynamic time series of networks made me realize the many decisions that need to be taken related to the study of social dynamics, as well as the absence of a toolbox to help us out in this process. Consequently, I first built a R package that met my needs and provided guidelines to help researchers in their decision-making process. At the same time, when looking at juvenile social development, the need to rank individuals arose, which led me to build another R package addressing the question of appropriate ranking methodologies.

1.7 Methodological considerations

1.7.1 The case of SNA

At present, the use of both dynamic and multi-layer network approaches is not widespread. At the same time, anyone familiar with the field of behavioural ecology will have noticed the profusion of social network metrics that can be used to quantify and define sociality, the abundance of r packages, and the myriad decisions involved in addressing social dynamics. The improvements in our capacity to collect high-resolution data, coupled with rapidly improving computer software for analysis purposes, have been instrumental in the evolution and refinement of SNA and its application to animal societies. The slow uptake, then, is not that we are missing the necessary methods and tools. Rather, it seems to me that the rapid explosion of analytical methods has left researchers lagging behind as they try to understand and familiarise themselves with these new techniques and their applicability.

One of the most concrete examples of this is choosing a scale that is both biologically meaningful and contains enough data to construct a network representative of the group. Although this decision is central to the design of any longitudinal research study, it is often overlooked (Uddin et al., 2017). Furthermore, the very flexibility of SNA means that its application is not straightforward, even when using monolayer networks. Therefore, SNA requires researchers to pay careful attention to (i) the design of their longitudinal studies, (ii) how they construct and analyse their networks and what they represent, (iii) which metrics they use to capture the biological phenomenon of interest, (iv) the potential impact of missing or incorrect data, and so on (Evans et al., 2020; Farine & Whitehead, 2015; Farine, 2017; Uddin et al., 2017;

Whitehead, 2009). Put simply, there are numerous examples of the decision-making processes involved in the effective application of SNA, which constitute critical steps that should not be overlooked. This overall progress in SNA observed in the last decades has resulted in diverse R packages to render this tool more accessible to everyone and to facilitate its application (e.g., "igraph" (Csardi & Nepusz, 2006), "statnet" (Handcock et al., 2008), "ANT" (Sosa et al., 2020), visNetwork (Almende et al., 2019)). While these packages offer high data flexibility, no package offers an all-in-one toolbox for animal research. I will expand on this in Chapter 3, where I introduce a custom r package (netTS) to ease the construction and analysis of time-aggregated networks, notably in choosing the appropriate time scale.

1.7.2 The case of ranking methods

It was surprising to me that, when deciding which ranking method would be most suitable for my study, I could not find any good justification for why a given method was used in a particular study. In fact, dominance hierarchies, with their associated benefits and costs for individuals, are a key aspect of primate societies (Isbell, 1991; Schaik, 1983; Sterck et al., 1997; Wrangham, 1980). For instance, occupying a high-rank position in a dominance hierarchy can be tremendously beneficial with respect to both priority of resource access and fitness consequences (Holekamp & Strauss, 2016). The popularity of dominance hierarchies, and the need to represent them accurately, drove the development of a variety of methods for inferring dominance hierarchies from observational data (reviewed in Bayly et al., 2006; Briffa et al., 2013; De Vries, 1998). Owing to the immense proliferation and availability of dominance data, as well as their inherently dynamic nature, social ranks should be inferred in a robust and rigorous way. To do so, one needs to be able to choose the appropriate social ranking method for researchers' specific datasets. As no procedure was available, I developed a broad and dynamic tool with which to conduct a reliability assessment of available ranking methods, and which is also flexible enough to be applied to any dataset.

1.8 Outline of this thesis

Following this introductory chapter, I present an overview of the study species and population in Chapter 2. I provide detailed reports of specific methods and analyses used in the relevant chapters.

As mentioned earlier, there remain many analytical hurdles when implementing social network analysis. Chapter 3 presents an r package (netTS) to ameliorate this and offers three analytical steps for the construction and interpretation of time-aggregated networks.

Chapter 4 addresses the overwhelming array of ranking methods to choose from by offering a complementary approach that assesses the reliability of calculated dominance hierarchies. This approach provides researchers not only with a means of determining the most reliable method for their dataset but also allows them to assess how rank reliability changes among age–sex classes in a social group, and so tailor their choice of method to the specific attributes of their study system.

Chapter 5 presents findings on the process of network formation using data from three groups of wild vervet monkeys. I used a dynamic social network approach that allowed me to capture patterns of social change over time and to question whether juveniles followed Kohn's (2019) socialisation steps.

Chapter 6 follows on Chapter 5. Using the same approach, I investigated the formation of strong social ties, their composition, as well as the processes at play in their formation.

Chapter 7 forms a general discussion of my findings and allows me to re-contextualize my findings in the broader scope of sociality. It also frames my findings in light of their limitations and provides future directions.

CHAPTER 2: STUDY SPECIES AND POPULATION

In what follows, I present a general overview of the study site and study species. Data collection protocols are presented separately in each chapter, along with the specific statistical modelling techniques used for each analysis.

2.1 Study Species

2.1.1 Taxonomy and Distribution

Vervet monkeys (genus *Chlorocebus*; hereafter "vervets") are the second-most widespread and abundant species of the Cercopithecidae family and are considered to be a sister taxon to the guenons (*Cercopithecus*; Mertz et al., 2019). Six species compose this African genus, five of which are widely distributed (Groves, 2001). Vervets are semi-terrestrial and distributed across sub-Saharan Africa, including West Africa, northern Kenya and Ethiopia, and the South African temperate regions (Turner et al., 2019b).

My study species, *Chlorocebus pygerythrus*, has the most extensive latitudinal distribution of the genus and has been well studied in the wild (Turner et al., 2019a).

2.1.2 Ecology

Vervets are semi-terrestrial, territorial, and omnivorous. They feed on seeds, flowers, fruits, leaves, berries, gums, and insects. This dietary breadth underpins their broad distribution and allows them to occupy habitats that range from the margins of rain forest through to semi-desert (Pasternak et al., 2013). Vervets are also water-dependent and are, therefore, found along rivers. They are the most widely distributed African primate, after the baboons.

In my study population, *Vachellia karroo* leaves, seeds, and flowers are a primary and critical food source (Pasternak et al., 2013). Succulents and roots (particularly *Asparagus africanus*), however, are favored during the dry season when water is scarce or even absent (Pasternak et al., 2013).

2.1.3 Physical characteristics

2.1.3.1 Adults

Adult vervets have a silver-grey coat with white fur surrounding a black face, as well as black feet and hands. Vervet adult males have brightly coloured genitalia, with a red penis and blue scrotum. Compared to males, females do not experience an adolescent growth spurt (Turner et al., 1997). Males are both larger and heavier than females, typically weighing between 3.9 to 8.0 kg and averaging 5.9 kg at our study site (Pasternak et al., 2013). They have an average body length of 41 cm (Turner et al., 2019c). Females are approximately two-thirds the size of males, reaching masses of 3.4 to 5.3 kg, averaging around 3.3 kg at our study site (Pasternak et al., 2013).

On average, vervet males reach sexual maturity at five years of age (Horrocks, 1986), while females typically have their first infant between three and five years of age (Fairbanks & McGuire, 1984). Females have ovarian cycles that can be irregular during the non-breeding seasons (Else et al., 1986). Infanticide has not been observed, likely due to the lack of male reproductive coercion (Seyfarth, 1980).

Vervets are seasonal breeders, with the mating season typically falling between May and July in our region, and the birth season occurring between October and December. Gestation lasts between 163 to 165 days (Kavanagh et al., 2011; Seier et al., 2000) and inter-birth intervals vary between one to two years, dependent both on ecological conditions and whether the previous offspring survived (Lee, 1984, 1987; Varsanyi, 2021). As at other locations (Butynski, 1988), vervet females in our study population experience a moderately circumscribed birth season predominantly between October and December (Figure 2.1) (Blersch et al., 2022, under review).

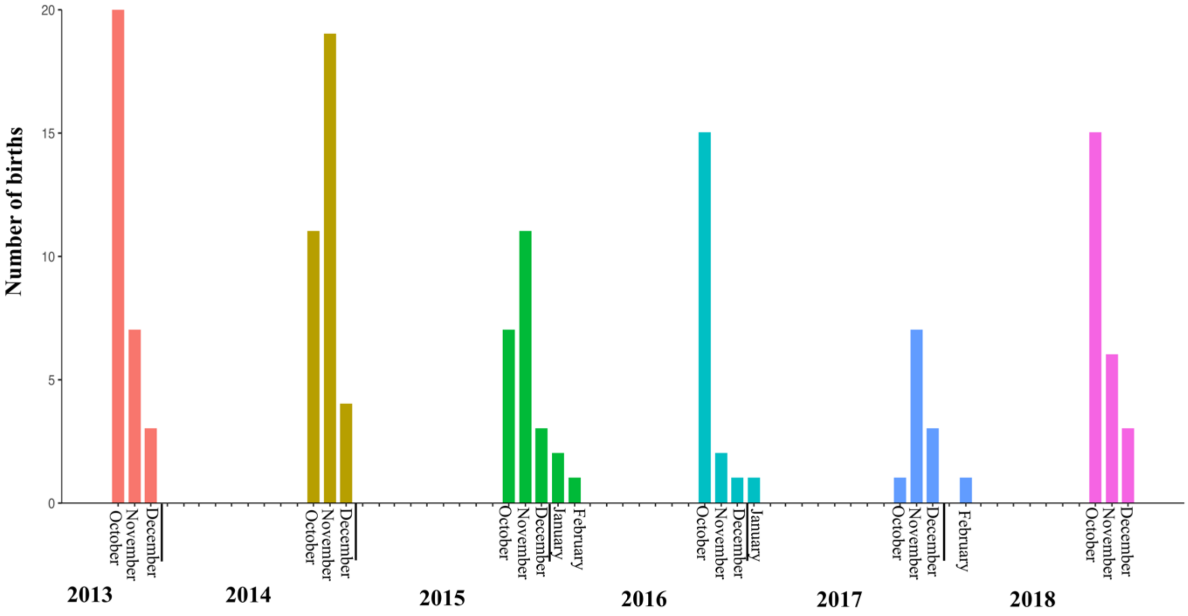

Figure 2.1 The distribution of births between October 2013 and December 2018, Cohort 2013 (red), Cohort 2014 (ochre), Cohort 2015 (green), Cohort 2016 (turquoise), Cohort 2017 (blue) and Cohort 2018 (pink).

2.1.3.2 Infants and juveniles

At birth, infants have black natal coats and pink faces (Figure 2.2). At one month of age, their faces begin to darken while their black coat gives way to the grey adult pelage at approximately three months of age (Lee, 1984, 1987; Seier, 1986). There is no sexual dimorphism in weight until 39 months of age (Lee, 1984, 1987; Seier, 1986), although growth rates can differ across birth cohorts as well as between wild and captive vervets (Jarrett et al., 2020). The juvenile period is said to begin with the cessation of suckling (Figure 2.3) and the emergence of independent foraging between five (Sashaw, 2012) and seven months (Figure 2.3) (Lee, 1987; Blersch et al., 2022, under review).

Figure 2.2 A female juvenile holds an infant, characterized by its natal pelt and pink face compared to the grey pelt and black face of the juvenile.

Figure 2.3 An infant suckling from its mother.

2.1.3.3 Age

Throughout this thesis, subjects are categorized as juveniles from the emergence of independent foraging between five (Sashaw, 2012) and seven months (Figure 2.3) (Lee, 1987); Blersch et al., 2022, under review) to sexual maturity (~3.5 years for females and 5 years for males (Jarrett et al., 2018; Wrangham et al., 1999). Past their first birth (or miscarriage), females were considered as adults, while males were considered adults past 5 years of age.

2.1.4 Social organisation

Vervets live in multi-male, multi-female troops, ranging in size between five to 76 individuals (Horrocks, 1986; Pasternak et al., 2013). The tolerance of other males within a troop is unusual in the African forest monkeys, which has been ascribed to the constraints on male migration patterns imposed by linear territories along rivers (Isbell et al., 2004). Females remain in their natal group (i.e., they are the philopatric sex), whereas males emigrate from their natal group at sexual maturity. Thereafter, they move roughly every 2.5 to 3 years (Henzi & Lucas, 1980; Young et al., 2019b), dependent upon their rank and integration into the female network (Young et al., 2019b). Dominance hierarchies are relatively stable in females, with daughters inheriting maternal rank—at least in small troops (Lee, 1983; Mertz et al., 2019). Males are co-dominant with females and have more variable dominance ranks over time (Mertz et al., 2019; Young et al., 2017).

The troops in our study population are much larger than the species ’average (Pasternak et al., 2013). This may be because group fission is constrained due to the large contrast in food productivity between the acacia woodland along the river, which the study troops inhabit, and the considerably lower productivity away from the river (Figure 2.4) (Pasternak et al., 2013). The size of these troops has been shown to have important consequences for social dynamics, principally by reducing the impact of dominance rank (Henzi et al., 2013; Josephs et al., 2016). In our population, female dominance hierarchies are relatively shallow (Henzi et al., 2013) compared to those in smaller groups elsewhere (Seyfarth, 1980).

Figure 2.4 An aerial view of the study site that encompasses the territories of the three study troops and illustrates the sharp distinction between the riparian acacia woodland and the dwarf shrub-land away from the river. Photo taken from an helicopter by Graham Pasternak in 2011.

2.2 Study site

The study site lies within the ~ 10,000. Samara Private Game Reserve in the Karoo, Eastern Cape, South Africa (32°22'S, 24°52'E). Research on the vervet population here has been conducted since 2008. This protected area is located in the semi-arid karoo biome and dominated by Acacia (*Vachellia karroo*) woodland centered on the Milk River. This river constitutes the only source of water for the study animals and flows intermittently. The study area undergoes large spatio-temporal fluctuations in both food and water availability, with severe, periodic droughts (McDougall et al., 2010; Young et al., 2019a).

The population is also subject to high predation from three species of territorial predators: caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*) and reintroduced cheetah

(*Acinonyx jubatus*). Aerial predation is less common in this study area, including two aerial predators: Verroux's eagle (*Aquila verreauxii*) and Verroux's eagle-owl (*Bubo lacteus*). The site has also three species of venomous snakes: puff adder (*Bitis arietans*), cape cobra (*Naja nivea*), and boomslang (*Dispholidus typus*). Although they are not predators of monkeys, puff adders (*Bitis arietans*) and cape cobra (*Naja nivea*) are known to be responsible for the deaths of vervet monkeys at the study site (see Figure 2.5). Other common mammals include ungulates such as kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella gazella*), red hartebeest (*Alcelaphus buselaphus*), duiker (*Sylvicapra grimmia*), springbok (*Antidorcas marsupialis*), eland (*Taurotragus oryx*), chacma baboons (*Papio ursinus*), cape buffalo (*Syncerus caffer*), white rhinoceros (*Ceratotherium simum*), aardvark (*Orycteropus afer*) and cape porcupine (*Hystrix africaeaustralis*). While baboons are known predators of vervets at other field sites (Enstam & Isbell, 2002), the vervets in our study population are not known to be predated by resident chacma baboons and do not alarm call when baboons are near (see Figure 2.6).

Figure 2.5 Juveniles vervet Monkeys and a cape cobra (*Naja nivea*) at the field site.

Figure 2.6 A Juvenile vervet monkey and chacma baboons (*Papio ursinus*) at the field site.

2.2.1 Climate

Climate data for the entire study period were available from an onsite weather station that provided information on daily ambient temperatures and rainfall. The area receives a declining average of 330 mm rain per annum. The field site's wet season is October to March, and the dry season lasts from April to September (Pasternak et al., 2013). The coldest month is July when snow falls on the surrounding mountains and nocturnal temperatures fall well below zero

(Mcfarland et al., 2015), while December and January are the hottest months, with maximum diurnal ambient temperatures rising to 46C.

2.2.2 Differential Resource availability

Marked intra- and inter-annual variation in rainfall and temperature underpin temporal shifts in habitat productivity. The Normalized Difference Vegetation Index (NDVI) was used in my analyses, not only because it is a good proxy for net primary productivity (Rasmussen, 1998; Winnie et al., 2008), but also because it has been shown to correlate strongly with food available to vervet monkeys specifically (Willems et al., 2009). NDVI estimates were obtained using MODIS NDVI data downloaded from NASA's Reverb|ECHO site (Didan, 2015). The Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) collect MODIS data with a return-to-site periodicity of 16 days (Didan, 2015). ArcGIS version 1.6.1 was then used to overlay the MODIS data onto the three territories, with each territory represented as a regular series of points 10-m apart. This led to the extraction of NDVI values from the MODIS rasters at each point. Area-weighted averages for each territory were generated for consecutive 33-day windows (16 days post and prior to the date of each MODIS raster) by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period (Figure 2.7) (Nord et al., 2021).

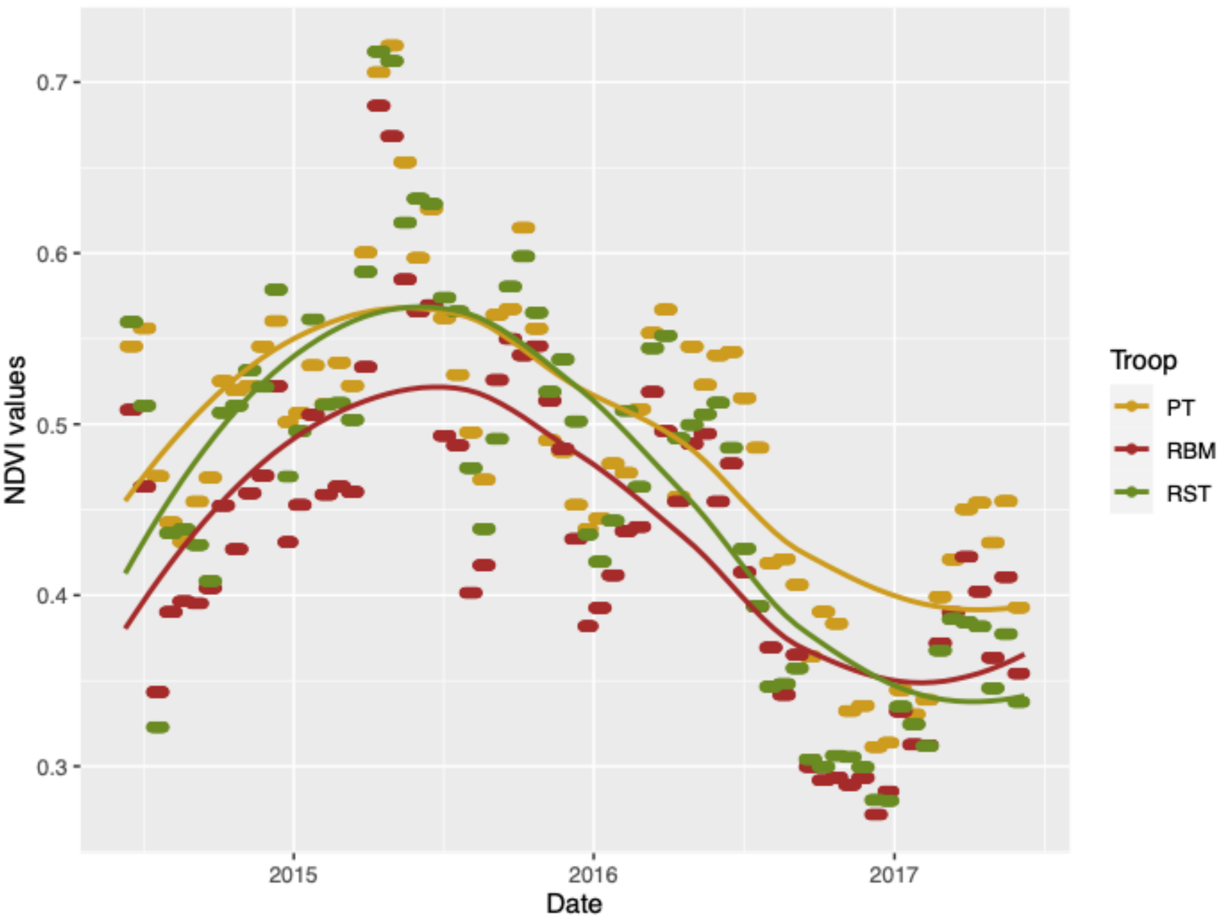

Figure 2.7 Plot of the NDVI values averaged within a 60-day window and used across the study period, by each troop. NDVI is an index value from 0 to 1.

2.3 Study period and troop composition

Data for this thesis were collected between June 2014 and July 2017, from three troops of vervet monkeys occupying adjacent and overlapping home ranges along the Milk River: Riverbend Mob (RBM), Picnic Troop (PT), and Riverside Troop (RST). These troops have been studied continuously since November 2008 (RST, RBM), and July 2012 (PT) as part of the on-going Samara Vervet Monkey Project. All individuals are uniquely identifiable from natural markings. Group size and composition varied throughout the study periods and across the three troops (Figure 2.7). The study subjects comprised three birth cohorts from the 2013, 2014 and 2015 birth seasons.

Figure 2.8 Variations in troop number and composition across years in (a) PT (b) RBM and (c) RST troops. The purple and orange lines show the fitted values of individual numbers for adult female and male respectively. The red and blue lines show the fitted values of individual numbers for juvenile female and male respectively. The grey bands represent the upper and lower 95% credible intervals. The dots show the raw data.

2.4 Study species suitability

Overall, vervet monkeys are an excellent model species for exploring questions regarding social integration (i.e., the development and maintenance of social networks). They have an extended juvenile period (Pereira & Altmann, 1985), are highly social and are easily observable. Furthermore, as vervet monkeys are seasonal breeders (i.e., most conceptions typically occur within the same 2- to 3-month period every year), this means that infants grow up with numerous same-age peers available as potential interaction partners. Consequently, every troop consists of several separate matrilines, each typically encompassing three or more generations of close female kin.

CHAPTER 3: CONSTRUCTING AND ANALYZING TIME-AGGREGATED NETWORKS: THE ROLE OF BOOTSTRAPPING, PERMUTATION, AND SIMULATION

This data chapter has been published in *Methods in Ecology and Evolution* (December 24th, 2019), under the title “Constructing and analyzing time-aggregated networks: The role of bootstrapping, permutation and simulation.” The authorship list for the published version is as below. Dr. Bonnell and I conceived the ideas and designed methodology. I collected the data. Dr. Bonnell analyzed the data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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3.1 Abstract

1. Animal social networks are often used to describe dynamic social systems, where individual behaviour generates network-level structures that subsequently influence individual-level behaviour. This interdependence between individual behaviour and group structuring is of central concern for questions concerning the evolution and development of social systems and collective animal behaviour more generally.

2. Various statistical methods exist for estimating network changes through time. One approach, time-aggregated networks, takes repeated snapshots of interactions within windows of time to generate a time series of networks. However, there remain many analytical hurdles when implementing the time-aggregated approach. To ameliorate this, we introduce an R package netTS that focuses on three analytical steps for analyzing time-aggregated networks: choosing

appropriate time scale using bootstrapping, comparing patterns to relevant null models using permutation, and finally building and interpreting statistical models using simulated data. We use simulated data to first highlight these steps, then use observed grooming data from a group of vervet monkeys as an applied example.

3.Our results suggest that the use of bootstrapping and permutation can accurately extract known patterns from simulated data. Using this approach with vervet data suggests that there is consistent social structuring, differing from what would be expected due to chance, and that some individuals are contributing to this structure more than others (i.e., keystone individuals).

4. We demonstrate that bootstrapping, permutation, and simulation can aid in constructing and interpreting time-aggregated networks. We suggest that the use of time-aggregated networks to quantify patterns of network change can be a useful tool alongside process-based approaches that seek mechanistic descriptions. Ultimately, by looking at both patterns and processes, dynamic networks can be used to better understand how individual behaviour generates social structures, and in turn how individual behaviour can be influenced by social structures, ultimately leading to a better understanding of the evolution of social behaviour.

3.2 Introduction

Understanding the dependence between individuals in social groups has been enhanced by the use of network approaches. A network approach deconstructs a social group into nodes and edges, representing, respectively, individuals and the relationship between individuals (Newman, 2010). This allows for the description of social dependence between two individuals (dyad scale), around the individual (ego scale), and at the entire group level (network scale). This approach has become a successful and common method in various research fields, with the result that many theoretical and empirical predictions are tied to measurements of networks (Chapman et al., 2016; Duboscq et al., 2016; Griffin & Nunn, 2012). In some cases, these theoretical and empirical concerns are temporal in nature, requiring some measure of how social networks change in time, i.e., viewing networks as dynamic rather than static (Aplin et al., 2015; Bonnell et al., 2019; Formica et al., 2016). For example, the magnitude of repeatability in social network position has direct implications for the selection of social phenotypes within a population (Aplin et al., 2015). Similarly, when populations experience demographic changes such as the birth of new individuals, the magnitude of a juvenile copying their mother's social partners can have important consequences for the long-term stability of a population's social structure (Ilany & Akcay, 2016; Jarrett et al., 2018). Thus, network measurements in time can have important implications (Farine, 2018).

One particularly advantageous outcome of switching from static to dynamic social networks is the ability to address questions of process in collective behaviour. For example, to understand how shifts in one individual's behaviour might cause a cascade of changes throughout a social group requires a dynamic network approach. A particular interest in collective behaviour is the feedback between individual- and group-level dynamics. Namely, how variation in individual-level behaviour creates group level structures, which in return influence further development of individual behaviour (Sumpter, 2010). By treating networks as dynamic, it becomes possible to identify and quantify the processes driving these individual-group feedbacks to gain a better understanding of how individual level variation develops and what are the consequences for group level behaviour. Interestingly, this particular focus on individual variation has some parallels with work in population dynamics that might prove useful in social network contexts (Benton et al., 2006).

Methodologically, time-ordered and time-aggregated network constructions have been introduced for analyzing dynamic networks (Blonder et al., 2012). On one hand, time-ordered networks are networks that retain the order of interactions. These network constructions have been shown to be especially valuable when interested in questions about flow on a network (e.g., information, disease), as the timing of individual interactions can have important implications for the transmission between distant individuals (Blonder & Dornhaus, 2011), though see Farine (2018) for a discussion about when accounting for timing of interactions might be more/less justified. On the other hand, time-aggregated networks are constructed by aggregating data within a period of time and can be useful for addressing questions regarding changes in network topology. Depending on the scale of aggregation, these time-aggregated networks lose the ability to directly query when two individuals interacted. However, they can provide information about how those interactions change between time-aggregated networks and therefore, can be very useful in measuring structural changes in networks through time. For example, time-aggregated networks have been used to compare how density of social networks changes between mating and birthing seasons (Brent et al., 2013).

There are a variety of software packages that enable the analysis of networks in time (Blonder et al., 2012; Fisher et al., 2017). In particular, the timeordered (Blonder & Dornhaus, 2011) package handles both time-ordered and time-aggregated network construction whereas the networkDynamic (Butts et al., 2014) one can be used to extract time-aggregated networks. Here we introduce a custom R package: netTS. Its purpose is to ease the construction and analysis of time-aggregated networks by: 1) facilitating window sizes choices by comparing i) how time-series extracted from time-aggregated networks change with window size, as well as ii) how uncertainty in network measures change with window-size, 2) contrasting the observed time series against null models using network permutations, and finally, 3) simulating network data to test, refine, and interpret statistical models used to analyse time-aggregated networks. A critical step when constructing time-aggregated networks is choosing the window size, as it defines the temporal scale at which networks are constructed and measured. Choosing a scale that is both biologically meaningful and contains enough data to construct a network that is representative of the group, can prove to be difficult. Similarly, comparing networks to a range of null network models is becoming standard practice to help identify and interpret structure in a network (Croft et al., 2011; Farine, 2017; Whitehead, 2008). Finally, simulations are becoming an essential part of good statistical practice and can be used to validate the use of a particular statistical tool (Gelman et al., 2013). The netTS package incorporates advances in these three areas to allow users to choose appropriate time scales, identify temporal structural changes, and to make informed inferences from statistical models.

In this paper, we first give an overview of analyzing time-aggregated networks using the netTS package with simulated data. We then use grooming data from a group of vervet monkeys (*Chlorocebus pygerythrus*) to provide an example of using time-aggregated data to address questions concerning the temporal dimensions of social structuring in animal populations. Here, comparing the results of simulations to empirical data can be a useful way of inferring candidate mechanisms generating social structure (Farine et al., 2014; Sumpter et al., 2012). Given that social structure is generated by individual-level behaviours, we investigated whether some individuals were disproportionately responsible for the maintenance of social structure through time, i.e., are there keystone individuals driving group structuring through their grooming interactions? Here we focus on quantifying the variation in influence of individual grooming behaviour on the social structure of the group through time. This example targets only part of the collective behaviour framework (i.e., individual-level behaviour → group-level structuring, not group-level structuring → individual-level behaviour) and provides an example of how the time-aggregated approach can be useful in studying collective animal behaviour more generally.

3.3 Methods

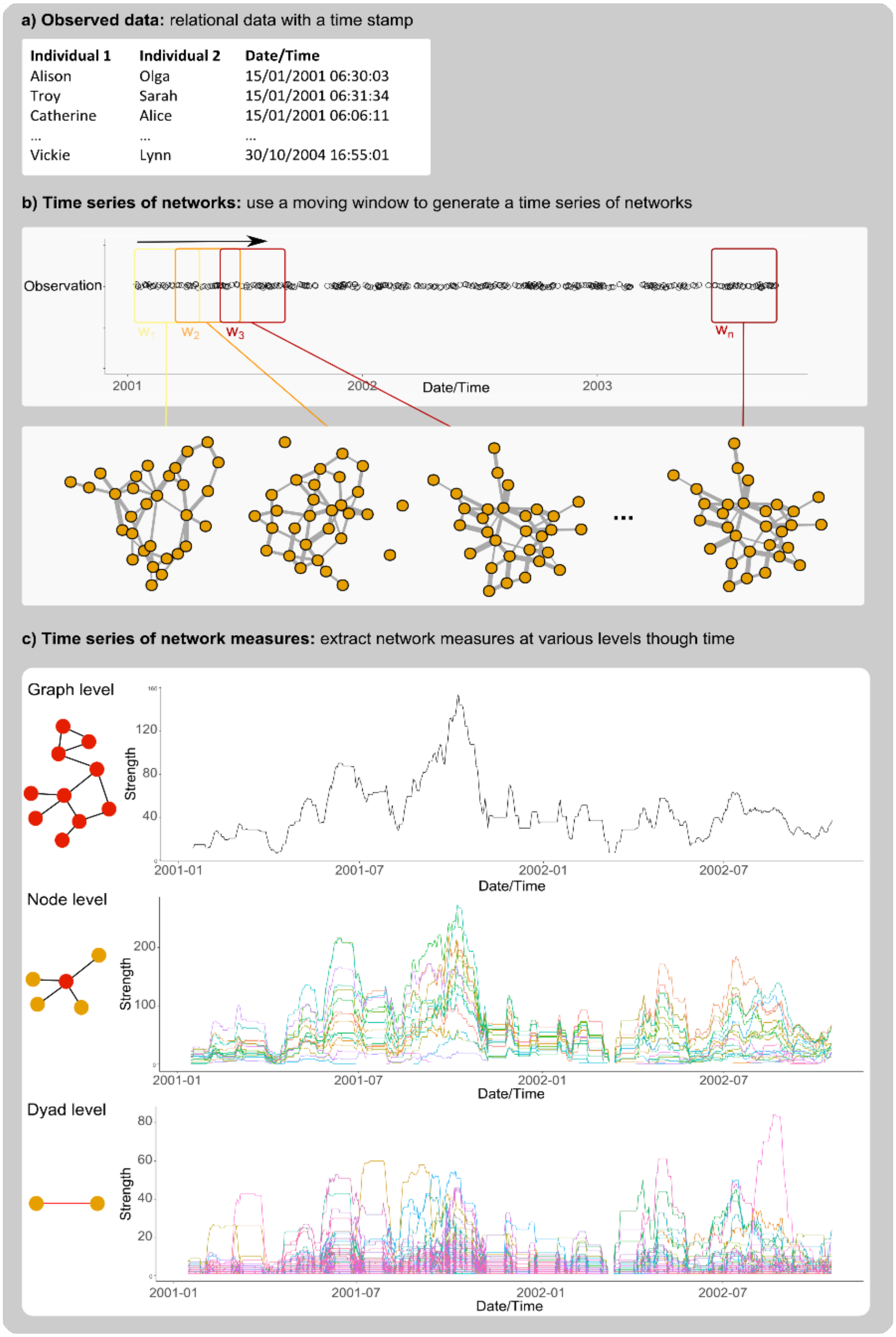
To introduce the netTS package, we first present the moving window approach for constructing time-aggregated networks from relational data. We then use simulated datasets to showcase three analytical steps to choose temporal scales and interpret results from the time-aggregated approach: 1) bootstrapping to choose lower limits to window size choices, 2) multi-scale time-series analysis to check for natural temporal scales, and finally 3) the use of permutation to interpret network measures extracted from these time aggregated networks. We perform these steps with two sets of simulated data: one in which there is no structure, and a second one with structure. This allows us to test whether the proposed methods can accurately detect (i) the presence of an underlying network structure and (ii) when there is none. The full package code can be found on github (github.com/tbonne/netTS), along with tutorials, and the code used in the analyses presented here.

After this introduction to the package using simulated data, we present an example using observed vervet grooming data. We first show how one can use bootstrapping and natural scales to help choose an appropriate temporal scale. We then show how network permutations can be used to identify network structures through time. Finally, we sought to quantify keystone individuals, i.e., individuals whose grooming behaviour has a larger impact on the overall network structure.

3.3.1 The Moving window approach to aggregation

Generally, when constructing social networks using time-aggregated networks to interrogate relational data, a careful consideration of scale is required, e.g., is it best to group data into daily/monthly/yearly networks (Blonder et al., 2012)? This package aims to help with this process using a moving window approach designed to work with any relational data accumulated through time. The main input to the netTS package is a data frame with the first two columns defining who is interacting, a third column with a date time stamp, and an optional weight column specifying the duration or magnitude of each interaction. Therefore, data collected by ad libitum sampling, focal follows, scan sampling, or gambit of the group can be used, though careful consideration of how to control for variation in sampling effort must be considered for each type of sampling methodology (see controlling for sampling effort below).

The moving window approach allows a user to define its size (e.g., windowsize = 1 month) and the amount to shift the window (e.g., windowshift = 1 day). This moving window subsets the relational data within a window and creates a network. It then shifts in time and repeats the process. By altering the size and shift of a moving window, it is possible to generate a time series of networks (Figure 1), which can be thought of as generating a multilayered network in which each network layer encodes the same type of interactions at different time points (Finn et al., 2019).



Individual 1	Individual 2	Date/Time
Alison	Olga	15/01/2001 06:30:03
Troy	Sarah	15/01/2001 06:31:34
Catherine	Alice	15/01/2001 06:06:11
...	...	...
Vickie	Lynn	30/10/2004 16:55:01

Figure 1 Overview of using a moving window approach to extract network measures over time: a) the relational input data, b) generate the time series of networks using a moving window approach, and c) extract network measures at the dyadic, node, and network scales.

3.3.2 Simulated data

To validate our proposed methods, we simulated interaction data following a scan sampling design. In these simulations, an observer will scan a group of individuals a number of times where each individual has the probability of interacting with another individual with probability A. Here we set the probability to 0.10 for all individuals. If during a scan an individual is to interact with another individual, it will choose from its neighbour based on a fixed underlying network. Here we simulate interactions with a fully connected network (i.e., everyone is as likely to groom everyone) and a network with a skewed degree distribution (i.e., everyone has a few grooming partners, and some have a lot). For the simulation with the skewed network, we additionally add a seasonal component to interaction probability, where there are seasonal fluctuations in probabilities in which individuals interact. The distance between peak interactions was set to 35 days with an increased interaction probability of 0.2. We provide the function used to simulate these data in the netTS package as the method sim.events.data (see vignette for more information).

3.3.2.1 Identifying a lower limit to window size

The ability to alter the window size introduces the possibility of multiple scales being chosen. The lower limit to window size choices can, to some extent, be specified by the fact that as window size gets smaller, less data is aggregated within each network and the network measures become progressively noisier, i.e., more dependent on the specifics of the remaining samples. This lower limit is likely to be a function of the rate of sampling and the biology of the behaviour under study (Farine, 2015).

To identify the lower limit of window size choices, for a particular dataset, we take advantage of a bootstrap approach on the event data used to create the networks. Applying this method, it is possible to take multiple bootstrap samples of the event data within a window, create a network with the bootstrapped sample, calculate a network measure, and then estimate the relative similarity between measures from the bootstrapped networks and the observed network (Costenbader & Valente, 2003; Farine & Strandburg-Peshkin, 2015; Lusseau et al., 2009). Highly similar estimates, and low variation in estimates, indicate that the network measure is robust to bootstrapped sampling, suggesting that the chosen window size is adequate to provide a good measurement. To test the efficacy of the bootstrapping approach, we provide a simulation test that suggests the relationship between bootstrapped networks and observed networks can provide useful information about the relationship between observed networks and a network constructed with all interactions (i.e., a complete network) (Figure S1).

Additionally, given that the bootstrap can only sample from the observed interactions, there is the possibility that missing interactions can drastically alter the network measure. In order to estimate the sensitivity of the network to missing data, we additionally estimate the effect of subsampling. To do so, we perform the bootstrapping procedure but on a subsampled portion of the observed data and compare the resulting bootstrapped networks to the measures in the observed network (Carter et al., 2019; Costenbader & Valente, 2003). This combination of bootstrapping and subsampling provides the user with the ability to assess uncertainty in a network measure under different window size choices. We implement this test in the check.windowsize function in netTS allowing users to experiment with potential window size choices. We further caution that there remains much work to be done in estimating network measure uncertainty (Farine & Strandburg-Peshkin, 2015).

This approach of using bootstrapping and subsampling is meant to test if the observed sample used to generate the network is sufficient to reliably capture network structure, i.e., if you had a slightly different observed sample, would the network structure come out roughly the same?

Applying this approach to the simulated datasets, we found that, for the unstructured simulated dataset, increasing the window sizes (even at a 60-day window), the similarity did not increase, and the effect of subsampling was comparably high (Figure 2a, c, e). Whereas for the structured dataset, increasing the window sizes led to higher similarity between bootstrapped samples and observed samples (Figure 2b, d, f). It also reduced the effects of subsampling. This suggests that using bootstrapping to estimate uncertainty can help distinguish between unstructured and structured networks and identify lower limit to possible window size choices.

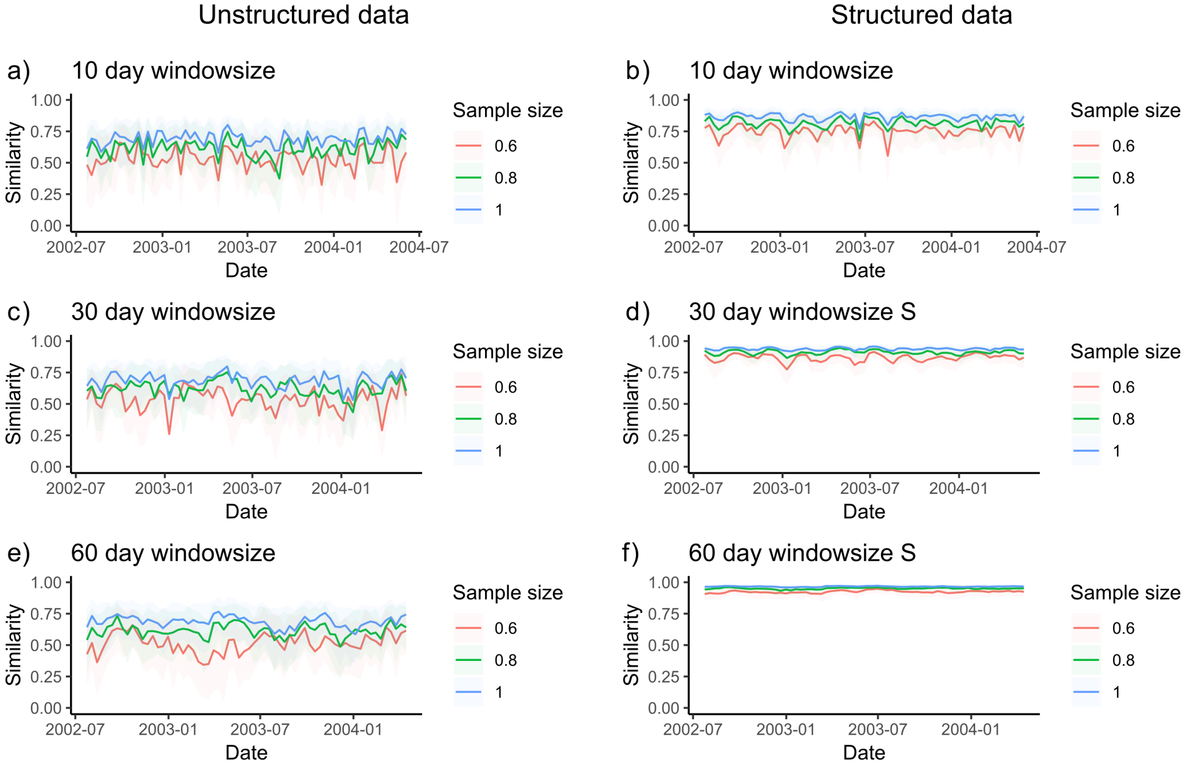


Figure 2 Estimating the lower bound of window size choice using bootstrapping and subsampling. Examples are shown for the unstructured (a, c, e) and structured (b, d, f) simulated datasets. Lines represent mean cosine similarity, shaded region the 95% quantiles, from 100 bootstrap comparisons between node degree in the observed and bootstrapped networks. Time series of observed networks were constructed using window size choices of 10, 30, and 60 days. To estimate the sensitivity to missing edges, this procedure was repeated using a random subsample of the original dataset (i.e., 1, 0.8, and 0.6 of the original data).

3.3.2.2 Choosing a window size

The choice of the upper limit to potential window sizes, apart from the maximum time scale of the dataset, has no *a prior* limit and will increasingly capture longer-term trends. In some cases, depending on the temporal dynamics of the systems of interest, "natural" scales can potentially exist (Caceres et al., 2011). To aid in looking for natural scales we introduce the use of sample entropy as an approach that works well with many types of time series data (Richman & Moorman, 2000). This measure is maximized when the time series is either completely random, or completely static, and minimized as the time series becomes more structured. Sample entropy is calculated by looking at sequences of values in a time series and comparing how many times each sequence of length n appears in the time series to how many times the sequence n+1 appears. The ratio between the two provides an estimate of predictability, e.g., if the first two values in the time series are 2.5 and 4.6, how many times do you find this sequence of 2, and if it is followed by the value 3.2, how many times do you find this sequence of 3 (i.e., n+1). By looking at how temporal scale alters this ratio, it is possible to identify potential natural scales, and provide a sense of how a particular network measure changes with temporal scale (Costa et al., 2002). The netTS package provides a function (check.timescale) to plot how sample entropy in a particular network time series measure changes with window size choices (i.e., scale). As the identification of temporal scales is an area of active research, we also provide the ability to input user defined functions to assess how temporal scale alters network time series measures (e.g., how does total coefficient of variation in the time series change with time scale?) (see vignette: choosing window size).

When we apply this approach to the simulated data, we see that in the case where there is no structure (full network) and where interaction probabilities remain constant, we find high sample entropy values (compared to the structured simulated dataset) with a shallow decrease in sample entropy as window size increases (Figure 3a). We also find large divergences between bootstrapped replicates. For the dataset with a structured network (skewed degree distribution and a seasonal change in interaction probabilities), we find lowest sample entropy at the true seasonal time scale as well as high agreement between bootstrapped replicates (Figure 3b).

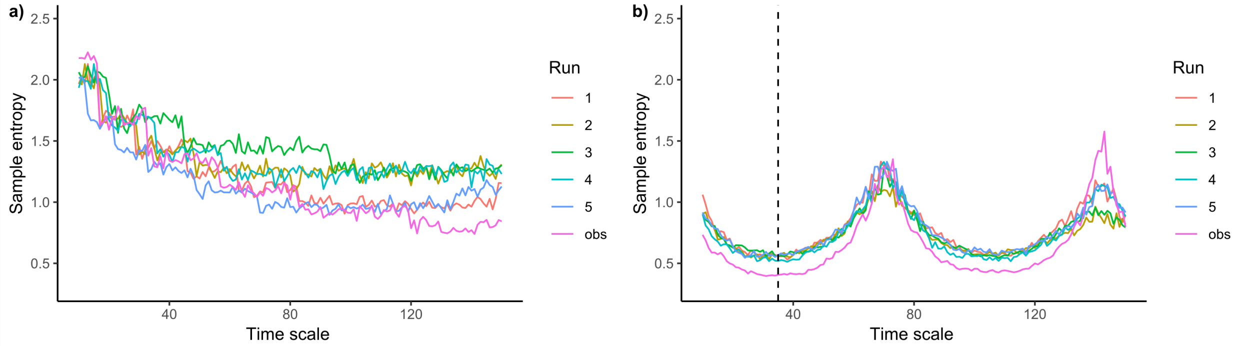


Figure 3 Sample entropy by window size for a) a simulated dataset constructed with no imposed temporal scale, b) a simulated dataset with a temporal scale imposed. The sample entropy from the observed data, along with 5 bootstrapped datasets, is calculated for each window size choice. The dashed line in b) indicates the imposed seasonal component in the simulated data.

Overall, the question of interest and knowledge of the study system are likely to play a large role in choosing the temporal scale to measure network change. In general, apart from attempting to identify one optimal window size, it is likely the case that the way a pattern of interest changes depending on the time scale chosen will itself be of great interest (Costa et al., 2002; Levin, 1992).

3.3.3 Extracting Network measurement through time

Once a window size has been selected and a time series of networks generated, it is possible to use network metrics at the scale of the network, node, or dyad (Newman, 2010). Although a few common metrics are built into the netTS package, the network measure required is a user-specified function. This function takes a network as input and returns a value, or vector of values in the case of node or dyadic measures. By using user-generated functions, the package can take advantage of the wide range of network measures available, without constraining users to a pre-specified list of options (see vignette: Introduction to netTS).

3.3.3.1 Controlling for sampling effort/time

Given the time series nature of the data, as well as the potential for variation in data collection methods through time, it is important to consider how changes in sampling effort might impact a potential measure (Davis et al., 2018; Franks et al., 2010). In some cases, the ability to use scaled or transformed measures, such as the simple-ratio index (SRI), can facilitate comparisons between networks in time (Farine & Whitehead, 2015). Another option, that keeps the measure on the observed scale, would be to directly control for sampling effort over time. This approach converts the observed social behaviour to a rate (e.g., interactions/hours of observation, or interactions/number of scans). For example, to construct an interaction network in Thronbills (genus Acanthiza), (Farine, 2015) divided the number of observed interactions between individuals by the time observed in the same flock. The netTS package offers the possibility to include a sampling effort function in order to help the user to control for a certain type of sampling effort. These functions take as input an event's data frame and returns a single value of effort. The netTS package provides three functions. The first approach sums the total time (effort.time), based on the first and last sample time of each day within a window. This method assumes equal sampling effort throughout the day, i.e., ad libitum data collection. The edges in network are divided by the time spent observing (number of interactions observed / number of hours observed). The second approach (effort.scan) uses a data frame, supplied by the user, containing the number of scans during sampling periods, e.g., number of scans per day. This approach is useful when observations are captured within set scanning periods and would be suitable for sampling regimes where periodic scans are used to collect data. Here, the edges in networks are divided by the number of scans within a window. Finally, the third effort function is designed to correct for variation in effort with focal data (effort.focal). This method requires a user supplied data frame with times and durations of focals. Each edge of the constructed network is divided by the amount of time it could have been observed, e.g., an interaction between A and B can only be observed when either A or B is the focal. In other words, if A and B are focalled for 10 and 5 minutes respectively, then 15 minutes is the total amount of time where A and B could have, potentially, been seen interacting. As sampling effort will vary by dataset and collection method, it is also possible to construct user defined effort functions to correct for sampling effort when estimating network measures (see vignette: controlling for sampling effort). Given our simulated data do not have variation in sampling effort, we present some examples using these methods below with our field data on vervet monkeys.

Because variation in sampling effort can have a large impact on the network structure, it needs to be considered carefully (Davis et al., 2018; Whitehead, 2008). Here we suggest the use of network indices (e.g., simple-ratio index) tailored in reducing variation in sampling effort, as well as the conversion of dyad weights to ratios by dividing interactions by sampling effort directly. We also propose the use of null network models, that can incorporate variation in sampling effort, to better distinguish what network structures might simply be a result of variation in sampling effort (Croft et al., 2011; Farine, 2017).

3.3.4 Interpreting measures through time using null models

Given the ability to compare how a network changes in time, it can also be useful to contrast how this changing network relates to a null model using network permutations. The exact specification of the null model, i.e., how it is constructed, can aid in understanding the structure of the observed network. For example, it is possible to construct a time series of centrality measures within a grooming network and look for trends over time. However, if we want to compare centrality measure to what might be expected if grooming partners are chosen at random, we would want to use a null model. The aim of the null model is to create replicated datasets in which the aspect that is of most interest to us, often who is observed with who, is randomized (Farine, 2017). Here, the choices of the null model can help refine how the observed pattern is different (Croft et al., 2011; Farine, 2017; Whitehead, 2008). You could decide to take all grooming events and randomly distribute them between nodes to generate a null model. Similarly, you could retain the fact that some individuals are more present in grooming events than others by permuting individuals between grooming events. You could then compare the observed network to those null models to make inferences about how it differs, or not. The way that the observed networks differ from the permuted networks and the specific choices of how permutations are carried out, can help highlight important structure in the observed networks. In netTS, by performing permutations for each time-aggregated network, it allows for estimations of how the network diverges from a null model through time (e.g., is it consistently different, or are there only certain times/seasons where there is a difference?). We provide some predefined permutation methods in netTS, but also allow for user-specified permutation functions that will take an event data frame as input and return a range of network measurement values (see vignette: Using network permutations).

With the simulated data, we show that using permutations can distinguish between the structured and unstructured datasets (Figure 4). The measures of eigenvector centrality and out-degree, for the unstructured simulated dataset, are well within the range expected due to randomized interactions (Figure 4c). However, in the case of the structured simulated dataset, we find that out-degree is well outside the range expected due to random, and for eigenvector centrality some values fall inside and outside the range expected due to chance interactions (Figure 4b, d). Given that the permutation used kept the number of times each individual was seen in an interaction, it then also retained the skewed degree distribution in the structured simulated dataset. The difference between the permuted and observed networks are then only driven by the difference in the arrangement of the edges beyond degree distribution. This, therefore, suggests only slightly more centralization than expected beyond what is expected given the skewed degree distribution.

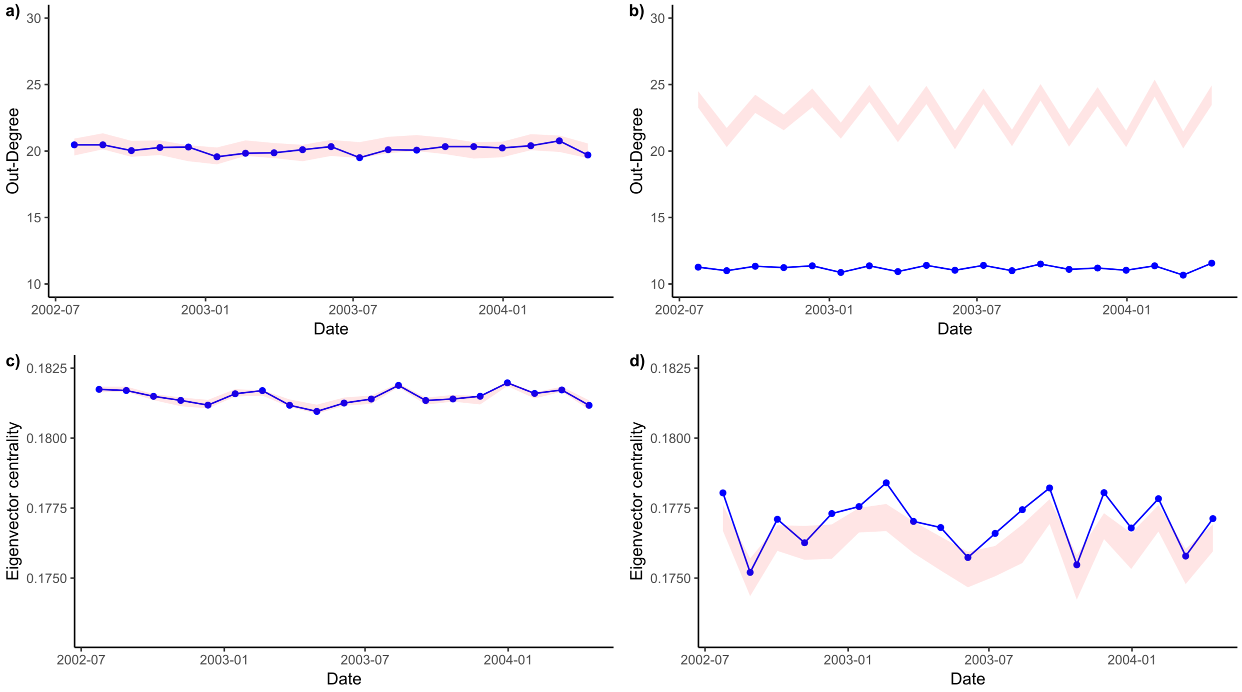


Figure 4 Eigenvector centrality extracted from networks generated using a, c) unstructured and b, d) structured simulated datasets. Permutations of individuals between simulated interactions were used to generate the range of eigenvector centrality values expected due to random interactions, while retaining individual differences in the amount of interactions.

3.4 Using netTS: an example of a primate social network

3.4.1 Input data

We use grooming data from a fully habituated group of vervet monkey in the Eastern Cape of South Africa (Josephs et al., 2016), e.g., Table 1. These gregarious primates occupy a semi-arid environment with large seasonal fluctuations of both temperature and rainfall, and similarly show seasonal breeding patterns (Lubbe et al., 2014; McFarland et al., 2014, 2015). These data were collected by scan samples taken twice every hour for 10 minutes, during 10-hour days, approximately 3-5 days per week between July 2015 and July 2016. The group consisted of 9-13 males and 11-16 females over the study period.

Table 1 Example data used as input for the netTS package.

from	**to**	**date**
<chr>	<chr>	<S3: POSIXct>
Laur	Malc	2015-07-01 12:32:19
Malc	Laur	2015-07-01 12:33:01
Ubun	Wall	6:08:26

3.4.2 Correct for changing sampling effort

Given that sampling effort can vary between time periods, it is important to control for it when comparing certain network measures over time, with some measures being more sensitive to sampling effort than others: e.g., node strength vs. node degree. Here, we demonstrate how controlling for the number of scans alters average strength of a network over time (Figure 5). All subsequent analyses use these corrected network measures.

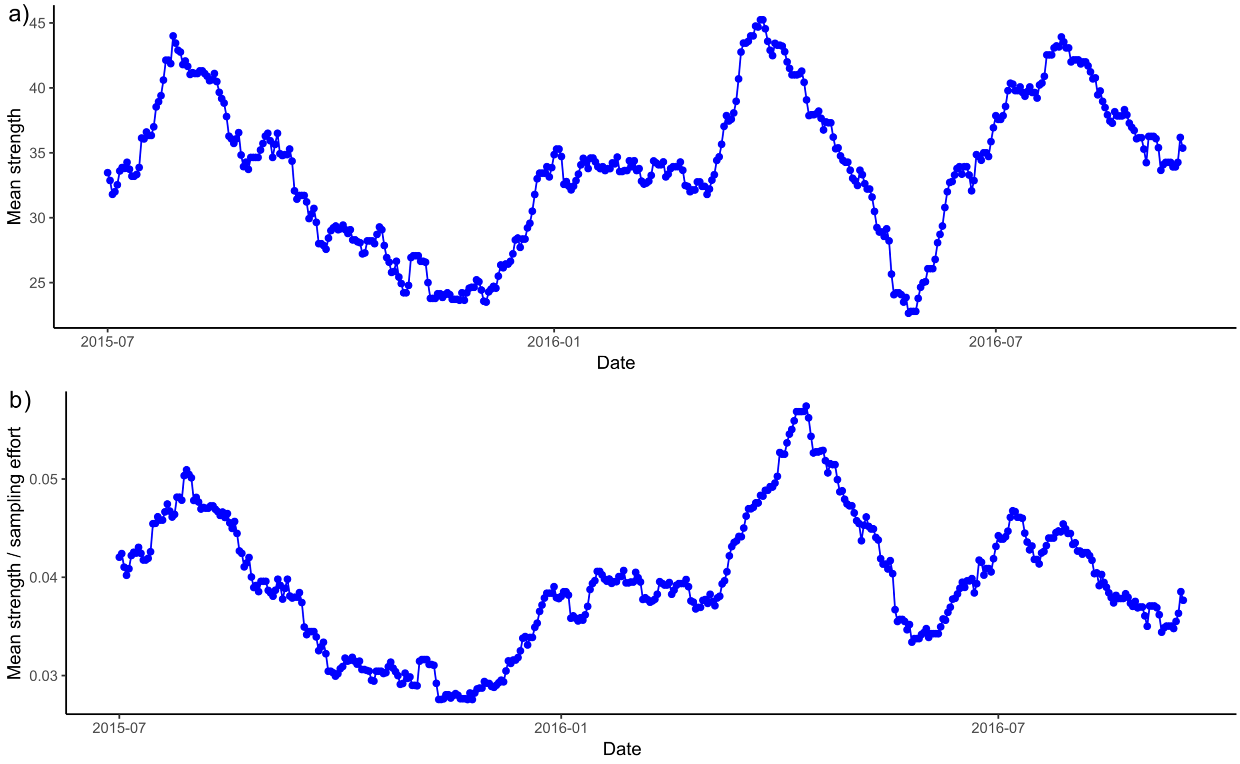


Figure 5 Mean network strength over time for a group of vervet monkeys: a) without correcting for sampling effort in the field, and b) after correcting for sampling effort.

3.4.3 Assess window size choice

We first use the bootstrap test to identify the lower end of possible window size choice (Figure 6). The results show that, given the temporal resolution of the vervet data network, measurement accuracy is reduced in window sizes below 30 days. By looking at estimates of similarity across the study period, it can also help to identify time periods where sampling effort was not adequate for a particular window size. For this vervet dataset, the consistently high similarity between the bootstrapped and observed networks, using a 60-day window, suggests that the window size results in robust networks.

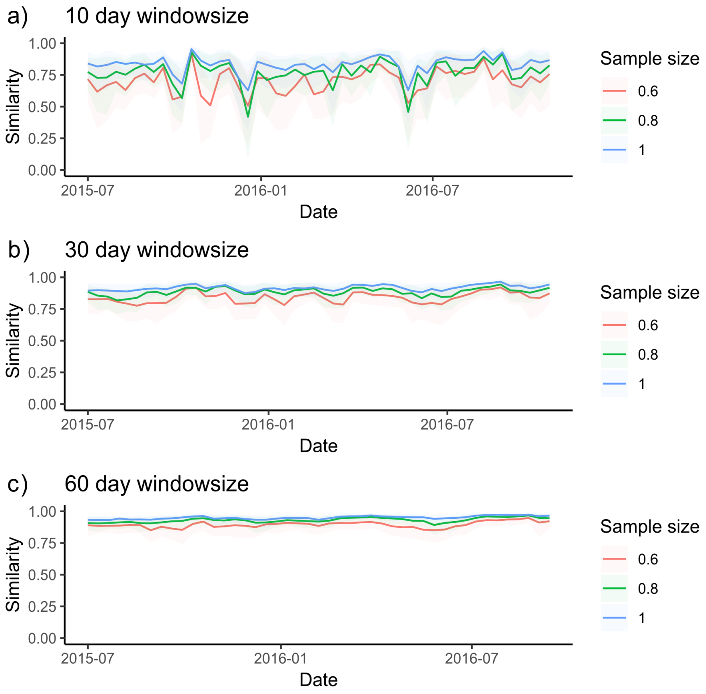


Figure 6 Results of the bootstrap test to quantify the uncertainty in networks constructed using a) 10 day, b) 30 day, and c) 60 day window sizes. For each window size, cosine similarity values between observed and bootstrapped estimates of node degree are presented for the full data and subsampled datasets to assess sensitivity of network structure to missing data. Higher similarity estimates and lower variability around these estimates, indicated by the shaded areas in b-e (95%CI), suggest more robust network measurements.

We then vary the window size from 10 days to 150 days to see how sample entropy changes (Figure 7). In this case, sample entropy showed a quick decrease similar to the shape of the unstructured simulated dataset, though with a lower entropy and higher agreement between bootstrap samples. We also found a smaller scale oscillation of 7 days, picking up that data was not collected on our study population on the weekends. Given the bootstrap and sample entropy results, we choose a window size of 63 days, meeting the bootstrap minimum, and accounting for the temporal effect of weekend in our data.

It is also important to note that, when looking at how a time series changes with temporal scale (i.e., window size), the results will depend on the particular network measure used to construct the time series, e.g., mean network strength/degree, or eigenvector centrality might show very different responses to changes in temporal scale. In this case, we used mean strength of the network due to our interest in how changes in individual network strength impacts group level structures.

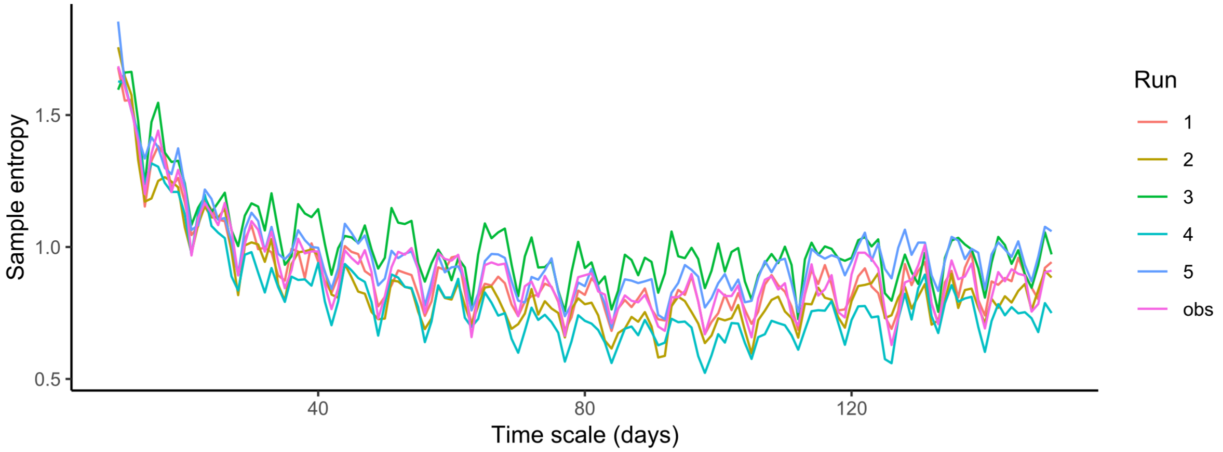


Figure 7 The relationship between window sizes used to create networks (i.e., temporal scale), and sample entropy of the resulting time series. Observed sample entropy measures are presented along with measures calculated on five bootstrapped samples from the observed data.

3.4.4 Assessing network structure through time

We used a permutation approach to assess the consistency of mean out-degree (the number of partners groomed) and mean eigenvector centrality of the network (magnitude to which the grooming interactions concentrate on a few well-connected individuals) (Figure 8).

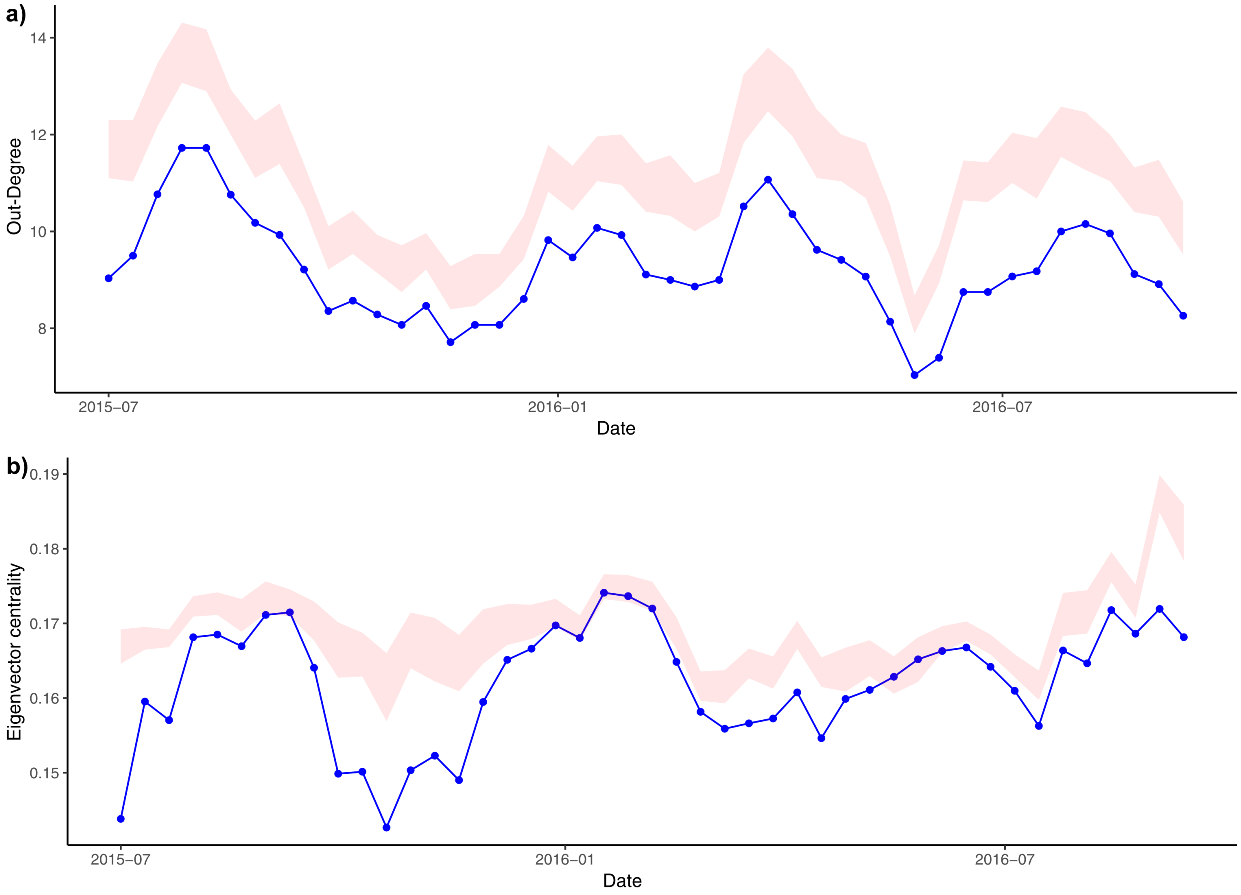


Figure 8 Permutation across time: a) mean out-degree of grooming, and b) mean eigenvector centrality. The observed values are presented as blue points, and the 95% quantiles generated through permutations are presented as a pink ribbon.

We can see from Figure 8 that, within the group, out-degree is consistently lower than expected with random grooming interactions, i.e., individuals are more selective with whom they groom compared to random. Whereas, in the case of mean eigenvector centrality, there is less differentiation between random and observed networks, with only occasional times when mean eigenvector centrality is not lower than expected by chance. In these examples, the null network had a higher mean out-degree and mean eigenvector centrality compared to the observed. It is also important to note that, in netTS, it is possible to compare networks to null network models, however there is no function at the moment to compare two networks directly to each other using permutation.

3.4.5 Identifying keystone individuals

To identify keystone individuals, we look to see how individual changes in out-grooming behaviour influenced the centrality of the group as a whole. Here, we are interested in answering the question: do some individuals influence the social structure of the group more than other individuals when they groom? If certain network structures have beneficial effects for individual fitness within a social group, are some individuals more responsible for the maintenance of this structure, and how does that relate to who benefits most from a particular social network structure (Alberts, 2019; Brent, 2015; Schülke et al., 2010)? An example of this is that eigenvector centrality has been shown to be a better predictor of offspring survival in female baboons than dyadic-level connections (Cheney et al., 2016).

With the netTS package, we extracted individual out-grooming strength and eigenvector centrality of the network over time. We then used a generalized additive mixed model to estimate how changes in individual out-grooming influenced the eigenvector centrality of the network. We allowed this effect to vary by individual by using a random slope for the effect of out-grooming. If this random slope turns out to be negligible, it would suggest that changes in out-grooming behaviour for all individuals has the same effect on mean eigenvector centrality. We also control for seasonal effects via a circular basis spline on day-of-year, and model dependence in the residuals using an AR1 process. We fit the model with the brms package following a Bayesian approach (Bürkner, 2017).

The model suggests that there are some differences between individuals in the effect of their grooming on centrality of the group (standard deviation in the effect of grooming: sd(grooming)

= 0.16, 95%CI: 0.10,0.24) (Table S1). Running the model with and without a random slope (ΔWAIC = -24.38, se = 15.26) suggests that there is some evidence for individuals that are associated with increases/decreases in centrality when their out-grooming increases, and points to potential keystone individuals (Figure 9).

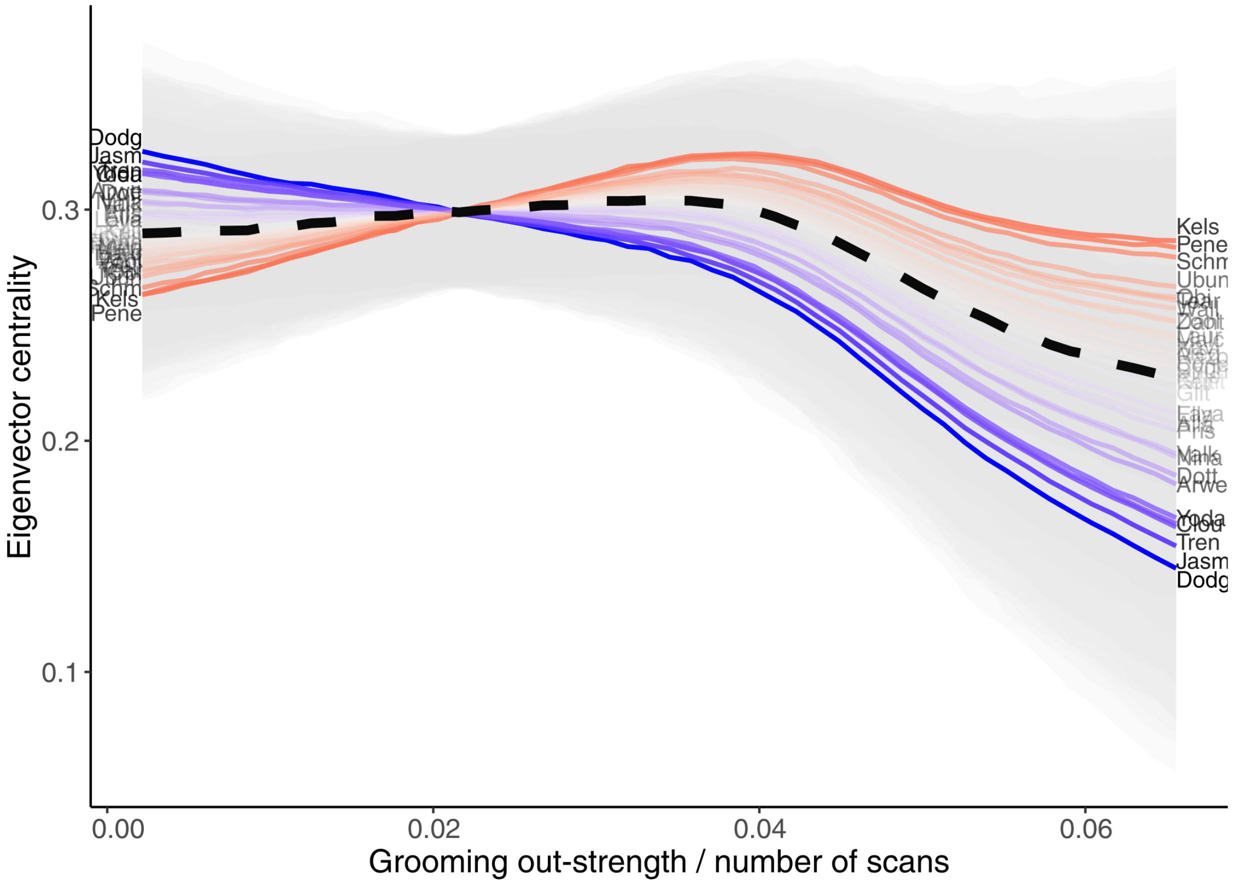


Figure 9 Model estimating how changes in out-strength by nodes influence the centrality of the network as a whole: a) overall mean effect of out-grooming on network eigenvector centrality, and b) individual level effect of out-grooming on network eigenvector centrality. Individual lines represent the effects of particular nodes (individuals) and are coloured based on their deviation away from the mean effect: i.e., blue is lower than the mean, and red is above the mean effect. Shading indicates the 95% credible intervals for each line. Each line is also given labels based on the name of the individual to aid in identifying those individuals having either a more positive or negative effect on eigenvector centrality.

To better interpret and make inferences from these results, we use the unstructured and structured simulated datasets. Running the same regression model on simulated data, with a fully connected grooming network, suggests that when individual grooming is not constrained, i.e., all individuals have equal probability of receiving grooming, the model found little difference in individual influence on group eigenvector centrality (sd(grooming) = 0.04, 95CI: 0.00, 0.08) (Table S2). However, in the case where individuals show constraints in their grooming behaviour (i.e., there was a skewed distribution), the model found differences in the effect of node out-strength on centrality of the group (sd(grooming) = 0.09, 95CI: 0.05, 0.14) (Table S3). Given these simulated data were constructed with a fixed network structure, and no between individual differences in grooming probability, the result suggests that certain positions within the network can have more of an impact on eigenvector centrality. In the case of the observed data, where the network structure is dynamic and there are individual differences in grooming, we see larger estimates of individual differences in their impacts on eigenvector centrality. This suggests that variation in individual contribution to group structuring is more prominent in the observed dataset, though more work would be needed to tease apart the role of individual differences in network position and interaction rates on group level structure. This example, however, does highlight that the use of simulated data can be used effectively to better interpret results from observed data.

3.5 Conclusions

Time-aggregated networks are a promising approach for quantifying patterns of structural change in animal social networks. Taking a dynamic view of social structure can address recent questions in the animal social network literature. For example, if certain network positions or characteristics provide fitness benefits (Alberts, 2019), a dynamic approach to networks can be used to quantify the consistency to which individuals maintain these positions/characteristics and, potentially, could reveal the mechanisms behind these processes (Ostner & Schülke, 2018). Similarly, in a more applied context, given social structuring has the potential to influence population dynamics (Alberts, 2019; Benton et al., 2006; Cantor et al., 2019), a dynamic approach might be used to better understand how environmental changes influences social structuring, providing further insights into population dynamics of social species in response to climate or landscape changes. The construction of time-aggregated networks, however, requires careful consideration of measurement and temporal scale. Similarly, the choice, parameterization, and interpretation of statistical models employed to analyse the resulting time-series of networks require careful inspection. We advocate for the use of bootstrap, permutation, and simulation to facilitate decision-making regarding these choices, and have introduced the netTS package for this purpose. We suggest that the patterns of change in social networks can be a used in combination with process-based approaches, e.g., stochastic actor-oriented networks, or relational event models, which seek mechanistic descriptions (Butts, 2008; Snijders et al., 2010). This combination of pattern and process is vital for understanding both the drivers behind social structuring and the subsequent consequences of these structures in social groups, leading to a better understanding of the dynamics of social structuring in animal populations.

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3.7 Supplementary material

Results from the keystone analysis:

Table S1 Parameter estimates for the keystone model predicting individual level out-grooming effects on group level eigenvector centrality. Due to the use of splines in this model, Figure 3 in the main text is provided to aid in the interpretation of the table. The delta WAIC is presented for the comparison between the full model, random intercept and slope, to the random intercept only model. Negative values for this delta WAIC suggest a better fit for the full model.

Parameter	**Estimate**	**lower-95%CI**	**upper-95%CI**
Intercept	-0.64	-0.81	-0.48
Sigma	0.21	0.21	0.22
Linear: out-grooming	-1.15	-2.56	0.36
sd(Intercept)	0.05	0	0.13
sd(out-grooming)	0.16	0.1	0.24
cor(Intercept, out-grooming)	-0.3	-0.99	0.82
Smooth: out-grooming	0.99	0.46	1.93
Smooth: Day of Year	0.95	0.57	1.67
ar[1]	0.98	0.98	0.99
R2 marginal	0.43	0.38	0.49
R2 conditional	0.45	0.45	0.50
ΔWAIC	-24.38 (se = 15.26)		

Table S2 Parameter estimates for predicting individual level out-grooming effects on group level eigenvector centrality using an unstructured simulated dataset, i.e., a fully connected grooming network. The delta WAIC is presented for the comparison between the full model, random intercept and slope, to the random intercept only model. Negative values for this delta WAIC suggest a better fit for the full model.

Parameter	Estimate	Lower 95%CI	Upper 95%CI
Intercept	0.02	-0.02	0.06
Sigma	0.43	0.42	0.43
Linear: out-grooming	-0.68	-2.22	0.97
sd(Intercept)	0.02	0.00	0.05
sd(out-grooming)	0.04	0.00	0.08
cor(Intercept, out-grooming)	0.06	-0.95	0.95
Smooth: out-grooming	0.85	0.34	1.85
Smooth: Day of Year	1.01	0.58	1.84
ar[1]	0.85	0.85	0.86
R2 marginal	0.33	0.30	0.35
R2 conditional	0.33	0.30	0.36
ΔWAIC	-2.34 (se = 4.02)		

Table S3 Parameter estimates for prediction of individual level out-grooming effects on group level eigenvector centrality using a structured simulated dataset, i.e., a skewed degree distribution grooming network. The delta WAIC is presented for the comparison between the full model, random intercept and slope, to the random intercept only model. Negative values for this delta WAIC suggest a better fit for the full model.

Parameter	Estimate	Lower 95%CI	Upper 95%CI
Intercept	0.03	-0.03	0.09
Sigma	0.35	0.34	0.35
Linear: out-grooming	0.81	-0.18	1.45
sd(Intercept)	0.02	0	0.07
sd(out-grooming)	0.09	0.05	0.14
cor(Intercept, out-grooming)	-0.11	-0.96	0.89
Smooth: out-grooming	0.12	0	0.41
Smooth: Day of Year	0.38	0.22	0.65

ar[1]	0.92	0.91	0.92
R2 marginal	0.23	0.19	0.28
R2 conditional	0.24	0.19	0.28
ΔWAIC	-22.55 (se = 9.99)		

Simulation test for the use of bootstrapping to measure network uncertainty:

Here we used simulated data to test if the sample of our observed sample (i.e., bootstrap) can provide an estimate of the adequacy of our observed sample compared to the "complete" set of interactions. To do so we first created a "complete" network representing all the interactions within a group, then sampled from these interactions to create an observed network. We then took 1000 bootstrap samples from this observed network and calculated similarity between the observed and bootstrap networks. We then varied the rate of sampling and plotted the relationship between the true similarity between our observed network and the complete network, and the similarity between the bootstrap and observed networks. We show that the similarity between the bootstrap and observed networks does provide information about the similarity between the observed network and the complete network. We also show that perhaps the variability in the bootstrap similarity is more informative than mean similarity, and that using node level values performs better than using full network comparisons (Figure S1).

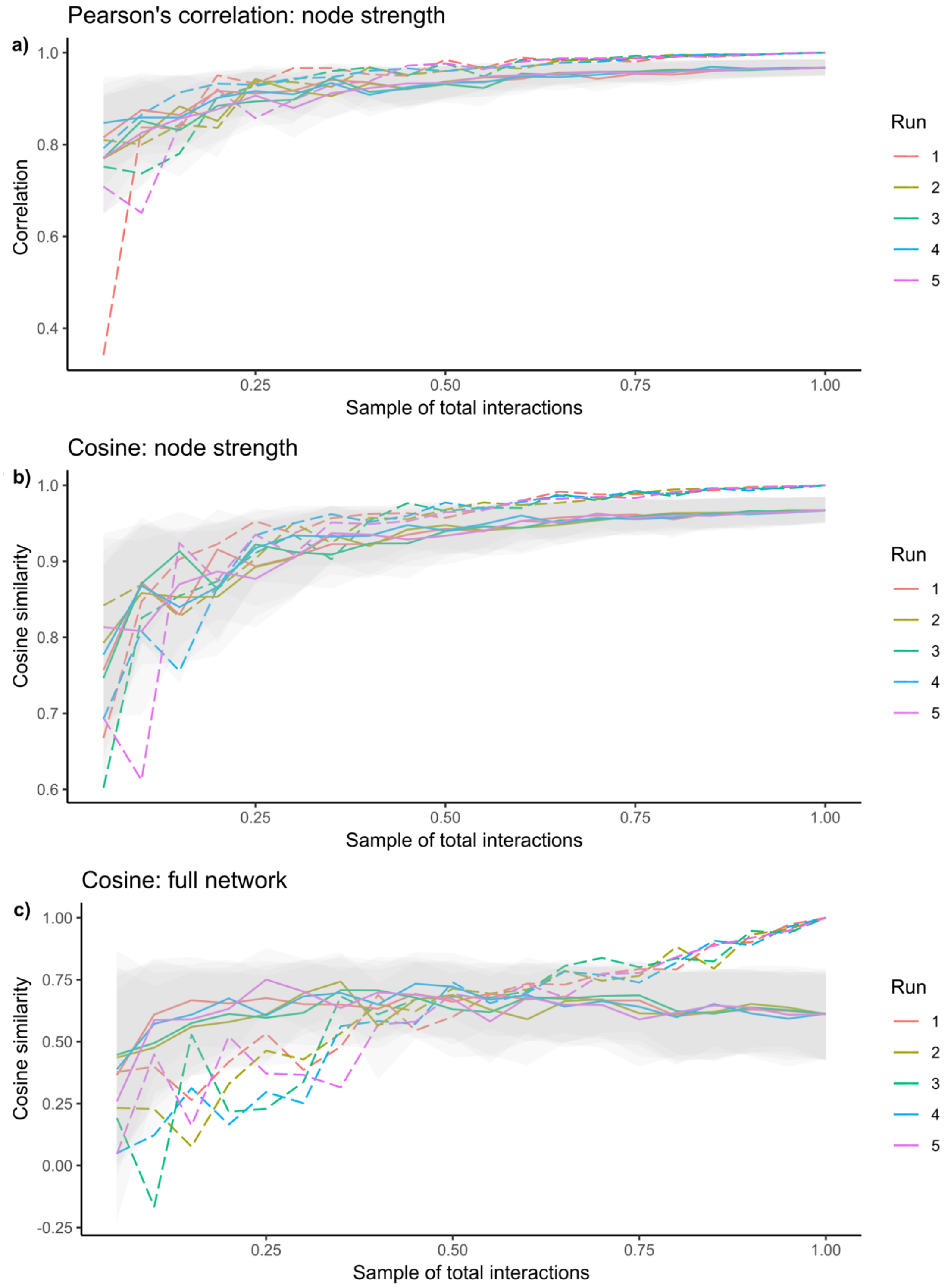

Figure S1 Performance of the bootstrap sampling method on estimating the relationship between an observed and complete network: i.e., can the bootstrapped networks help identify when the observed network is not representative of the complete network? Dashed lines indicate the relationship between the observed and complete networks. Solid lines represent the relationship between the bootstrapped networks and the observed network, and the grey shading represents the uncertainty in that relationship.

CHAPTER 4: COMPARING DOMINANCE HIERARCHY METHODS USING A DATA-SPLITTING APPROACH WITH REAL-WORLD DATA

This data chapter has been published in *Behavioral Ecology* (September 11th, 2020), under the title "Comparing dominance hierarchy methods using a data-splitting approach with real-world data." The authorship list for the published version is as below. I contributed to the study concept/design, data collection, data analysis and drafting the manuscript. Dr. Henzi and Dr. Barrett contributed to funding acquisition, supervision and the drafting and critical revision of the manuscript. Dr. Bonnell contributed to data analysis, supervision and helped draft the manuscript. All authors approved the final version of the manuscript.

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4.1 Abstract

The development of numerical methods for inferring social ranks has resulted in an overwhelming array of options to choose from. Previous work has established the validity of these methods through the use of simulated datasets, by determining whether a given ranking method can accurately reproduce the dominance hierarchy known to exist in the data. Here, we offer a complementary approach that assesses the reliability of calculated dominance hierarchies by asking whether the calculated rank order produced by a given method accurately predicts the outcome of a subsequent contest between two opponents. Our method uses a data-splitting "training-testing" approach, and we demonstrate its application to real-world data from wild vervet monkeys (*Chlorocebus pygerythrus*) collected over three years. We assessed the reliability

of seven methods plus six analytical variants. In our study system, all 13 methods tested performed well at predicting future aggressive outcomes, despite some differences in the inferred rank order produced. When we split the dataset with a 6-month training period and a variable testing dataset, all methods predicted aggressive outcomes correctly for the subsequent 10 months. Beyond this 10-month cut-off, the reliability of predictions decreased, reflecting shifts in the demographic composition of the group. We also demonstrate how a data-splitting approach provides researchers not only with a means of determining the most reliable method for their dataset, but also allows them to assess how rank reliability changes among age-sex classes in a social group, and so tailor their choice of method to the specific attributes of their study system.

4.2 Introduction

Dominance hierarchies are key to understanding social structure across many animal taxa. Recognition of their importance, and the need to represent them accurately, has driven the development of a variety of methods for inferring dominance hierarchies from observational data (Bayly et al., 2006; Briffa et al., 2013; De Vries, 1998). Given the array of options available, selecting the method that best fits a given dataset can thus prove challenging. So, how does one choose? One obvious possibility is to refer to the existing literature in order to assess which method is most commonly used for the particular study system or species on which one works, determine how and why such a choice was made, how it was justified, and then follow suit with one's own data. The flaw with this strategy, as we have discovered, is that there is wide variability in the methods used within and between study systems and species, and researchers rarely, if ever, provide any justification for their choice.

This is not to say that researchers have not assessed ranking methods in a systematic fashion. Indeed, there is a substantive literature that has focused on determining the validity of ranking methods. However, these studies do not provide all the resources needed to enable researchers to make a fully informed choice for their own datasets as they carry their own limitations, a point on which we now expand. In one set of studies, a number of ranking methods have been applied to an empirical dataset, and greater levels of agreement between methods have been taken to indicate that the methods are accurate and robust (Balasubramaniam et al., 2013; De Vries, 1998; Gammell et al., 2003; Neumann et al., 2011). Sánchez-Tójar et al. (2018) argue, however, that similar results across methods could also mean they suffer from a common bias, rather than necessarily providing an index of the methods ’robustness. As such, they do not necessarily offer guidance on which method should be selected: they could all be as bad as each other if common flaws cannot be identified.

Consequently, Sánchez-Tójar et al. (2018) have recommended the use of simulated data, where the dominance hierarchy is created by, and thus known to, the researchers. Validity can then be assessed by correlating the hierarchy produced by different ranking methods to the known hierarchy. Simulations can therefore test for and identify flaws in ranking methods and give researchers confidence that a method is actually measuring what it claims to be measuring. However, simulation studies make the implicit assumption that their results will apply equally to real-world empirical datasets. This can be misleading because simulated data are much cleaner and less noisy than real-world data. The latter will always contain a certain amount of noise, as well as a degree of uncertainty with respect to the outcomes of agonistic interactions, and both of these contribute to the underlying structure of the dataset. Furthermore, while most ranking methods focus almost exclusively on dyadic interactions, this does not preclude the possibility that contest outcomes are influenced by the presence of other individuals, whether through tacit or overt support (Bissonnette et al., 2015; Higham & Maestripieri, 2010). Again, this generates potential noise in real-world empirical datasets. Finally, in the real-world, one is forced to acknowledge that the true hierarchy can never be known. Thus, no matter how high the validity of a method tested on simulated data, it is impossible to determine whether an inferred hierarchy does, in fact, map onto the true hierarchy in an empirical real-world example.

Given this, we suggest that, in addition to simulation studies of validity, there is also value in assessing the reliability of different ranking methods when applied to real-world datasets. Specifically, one can use the hierarchy generated by a particular method to test whether it will correctly predict the outcome of future dyadic aggression between two opponents. This, we feel, is the closest one can get to determining if any given method produces reliable and, therefore, useful measures in the real world. Here, we offer a means by which researchers can compare different ranking methods and determine which offers the greatest reliability for their specific dataset. This will allow researchers to offer a clear justification for their choice of method, improve transparency and increase the rigour of behavioural research.

We base our argument for the value of reliability on the notion that dominance hierarchies reduce uncertainty about the outcomes of contests between group members (Beaulieu et al., 2014; Mendonça-Furtado et al., 2014), and the assumption that the state of the hierarchy at a given time will be predictive of future interactions (Drews, 1993; Hinde, 1976; Roney & Maestripieri, 2003; Rowell & Olson, 1983; Strauss & Holekamp, 2019). Here, "prediction" (Bernstein, 1981) alludes to the confidence with which the statistical asymmetry in dyadic contests predicts the outcome of any subsequent conflict within the same dyad. Thus, it follows that, if the inferred relative rank position of two animals can predict the outcome of a later aggressive interaction, then we have good evidence to suggest that a method is reliable.

To estimate a method's reliability, we developed a "data-splitting" approach. Splitting a dataset into two distinct components—typically referred to as the training and testing datasets—is a common technique in predictive modelling and machine learning (Dupuy & Simon, 2007; Kuhn & Johnson, 2019; Liu et al., 2016; Liu & Cocea, 2017). In machine learning, one of the main requirements is to build computational models with high predictive and generalization capabilities (Mitchell, 1997). When an appropriate model for data is not completely known, the data themselves can be used to select the appropriate model using data-splitting. Here, the training dataset is used to build a model (Faraway, 1998). Once trained, the predictive power of the model can be assessed by running it on the testing dataset (Dupuy & Simon, 2007; James et al., 2013; Liu & Cocea, 2017; Oghaz et al., 2017; R Ho, 2020; Siva, 2018). In our case, the model outputs are the dominance hierarchies (comprised of each individual rank, rating or score) produced by each ranking method. We then assess whether these outputs correctly predict the outcome of aggressive dyadic encounters in our testing dataset.

To demonstrate how data-splitting can be used with a real-world dataset, we make use of a three-year dataset of aggressive interactions in vervet monkeys (*Chlorocebus pygerythrus*), a gregarious primate species. We investigate the performance of seven alternative ranking methods. Each method's performance was assessed by determining whether individual ranks/ratings/scores obtained from the training dataset could successfully predict the outcome of the aggressive interactions that occurred in the testing dataset. Given the time period covered by our dataset and the possibility of large changes in rank structure over time, we were particularly interested in comparing the performance of ranking methods that are characterized as non-sequential (i.e., where interactions are aggregated over time), to those characterized as sequential (i.e., where the data are not aggregated and thus the sequencing of interactions is retained in the data). Given that, over time, changes in both demographic and ecological variables will give rise to changes in the dynamics of social groups, we predict that sequential approaches will perform better than non-sequential ones in our dataset (Goffe et al., 2018; Neumann et al., 2011; Williamson et al., 2016).

Finally, we highlight the use of the "data-splitting" approach as an opportunity to quantify how reliability decays within particular age-sex classes of opponents. Focusing first on the whole group, we look at the overall trend in reliability across time. Due to the likelihood of demographic and ecological change mentioned above, we expected to see an overall decay in reliability. We then go on to investigate reliability at the adult sex-specific dyad level. In vervet monkeys, females are the philopatric sex, and (often) inherit a rank position just below their mothers' (Fairbanks & McGuire, 1984). Thus, we predicted that reliability in predicted outcomes for females would remain stable through time. In contrast, we anticipated a decay in reliability at the adult male dyad-level due to migration between groups, which generates variation in male cohort composition, and hence greater rank instability. This analysis also allows us to determine whether some dyads are over-presented in the dataset, which could in turn have an impact on rank order computation and, hence on a method's reliability when applied to group as a whole.

It is important to note that our aim here is not to determine the most reliable ranking method in any absolute sense. We also acknowledge that the use of a single real-world dataset to assess the reliability of a method holds its own problems. As such, we recognize the necessity of repeating these analyses on other populations and/or species to determine which patterns generalize, and which are highly specific to a given dataset. However, the goal of this study is to demonstrate the value of a training-testing approach that will enable researchers to identify the most reliable method for their particular dataset. That is, we present a "proof of concept" to illustrate that our approach has value and make no claims for the generality of findings with respect to the relative performance of each specific method. However, we consider the training-testing approach itself to be widely applicable precisely because it is not tied to any specific data requirements (e.g., no minimum amount of data required or specific length of study period needed) or to any particular assumptions (e.g., regarding age-sex classes of individuals, linearity of the hierarchy, or the nature of the interactions included). Our method thus offers researchers a useful tool with which to conduct a convenient systematic reliability assessment of available methods. Adopting this approach will increase the reliability of the literature as a whole, by ensuring selected methods are offered with appropriate justification.

4.3 Methods

4.3.1 Study site and subjects

Data used for these analyses were collected between January 2015 and December 2017 as part of a long-term field project at the Samara Private Game Reserve, South Africa (32o22’S, 24o52’E). We used data from one of our three study groups (RBM). All animals were fully habituated and individually recognizable. The study group occupied semi-arid riverine woodland (Pasternak et al., 2013), and group composition varied across the study period (Males: 20-6, Females: 13-8; Juveniles: 33-9; Infants: 11-2).

4.3.2 Behavioural data collection

Agonistic behaviours, identities of participants and interaction outcomes were recorded ad libitum on all group members (i.e., across all sex and age categories). We wished to make use of the most diverse and complete dataset and chose to leave our dataset in its original form, hence we retained agonistic encounters with juveniles and infants as well as those that involved coalitions (i.e., where one or more animal comes to the aid of another against a common opponent). Only unknown outcomes were discarded. We decided on this approach as we wanted our dataset to include uncertainty and noise to ensure we would not artificially increase the reliability of a given method by training and testing on a circumscribed and clearly determined array of interactions. By training the ranking methods with a noisy dataset, we can get a better sense of how well they can generate a reliable set of ranks without any form of pre-screening of "acceptable" interactions. Agonistic behaviours included displacements, threats, chases and bites. The visibility of the habitat, together with the modal presence of more than one observer (Henzi et al., 2013; McFarland et al., 2014), means it is unlikely that there was any systematic bias in the recording of agonism. We recorded 11,323 agonistic interactions between 66 individuals across the 36-month period. The initial training dataset comprised 8,308 interactions, with the testing dataset accounting for the remaining 3,031 interactions. For more details on the training dataset structure, see Supplementary Material (S1).

4.3.3 Methods used to infer ranks and ratings

Among the tested ranking methods, it is possible to distinguish two families that differ in their overall approach (see Table 1). The first family is based on the sequence in which interactions occur (which we refer to here as sequential methods). It includes the Elo-rating method (Elo, 1978), as well as two of its variants: the Bayesian Inference (BI) approach (Goffe et al., 2018) and the modified Elo-rating (Newton-Fisher, 2017).

The second relies on interaction matrices and comprises the David's score method (David, 1987; Gammell et al., 2003), the Inconsistencies and Strength of Inconsistencies (I&SI) method (De Vries, 1998), and the Percolation and Conductance (P&C) method (Fujii et al., 2015). Finally, the randomized Elo-rating (Sánchez-Tójar et al., 2018) was also included to the non-sequential methods. Despite being derived from a sequential approach, the changes implemented mean that this method shares many common features with non-sequential methods. For a general introduction to each method's background, see Supplementary Material (S2).

As noted above, several different statistical packages and options are available for the David's score, thus we assessed 13 methods in all. Regarding the computation of David's scores, we used the functions offered within each package. These functions differed in their input and/or their way of dealing with draws (i.e., undecided interactions where there were no unambiguous winners and losers), hence potentially leading to differences in inferred scores.

We used R to conduct all rank-order estimations and subsequent analyses. Reliability was calculated using a custom package "rankReliability". This package provides researchers with the opportunity to estimate how reliable their inferred ranks are through time, while giving them the freedom to choose their preferred ranking-method, the dataset of their choice (e.g., including juveniles/polyadic interactions, keeping/excluding draws …), as well as how to split the data. The code can be found at https://github.com/tbonne/rankReliability.

Table 1 Summary of the different methods tested in this study

Method	Outcome	Analytical details
I&SI	Ordinal rank order	Package: compete Function: isi13 with nTries= 450
David's score	Individual overall success	Packages: compete, steepness & EloRating Indices: Pij and Dij
Percolation & Conductance	Rank order + dominance uncertainty	Package: Perc MaxLength= 2 and 4

Randomized Elo-rating	Individual overall success + the uncertainty around the estimates	Package: aniDom with n.rand= 1 000
Original Elo-rating	Individual overall success	Package: EloRating Initial scores: 1 000 and k=100
Modified Elo-rating	Individual overall success	Newton-Fisher (2017) code 4 categories of aggression intensity. Lowest starting at k= 200, with k increasing by 25 per aggression intensity
Bayesian Inference	Individual overall success, start ratings, the Elo-rating winning/losing shift coefficient (k) + the uncertainty around the estimates	Goffe et al., (2018) code

While the I&SI and P&C approaches produce ordinal ranks and David's score gives cardinal scores, the rest of the methods produce ratings as outputs. For simplicity, we refer to ranks, scores and ratings as outputs. The choices made regarding the analyses of each method are detailed in the Supplementary (S3).

4.3.4 Construction of training and testing datasets and comparison of methods

To assess the performance of each method we estimated i) the average percentage of future interactions correctly predicted, ii) the amount of data required to make reliable predictions, and iii) the rate of decay in prediction accuracy. The first measure of performance evaluates the overall ability of each method, while the second looks at the sensitivity to training sample size, and the third captures the temporal stability in each method's future predictions (i.e., does the accuracy of predicted outcomes decline through time and, if so, how fast).

4.3.4.1 Determining the method's average reliability: how do non-sequential and sequential methods compare?

Data splitting ratios often vary across studies, making it difficult to offer uniform guidelines on how data should be partitioned. Although some authors recommend using 70% of the data as the training set and 30% as the testing set (Liu & Cocea, 2017), others prefer a ratio of 75:25 (Oghaz et al., 2017) or 80:20 (Siva, 2018). Whatever the ratio chosen, there are two conditions that should be kept in mind when splitting the dataset: the training set must be large enough to estimate meaningful ranks, and the testing dataset must be long enough to estimate mean predictive performance. This excludes any extreme cuts, e.g., 99/01.

Here, we chose to use the first 80% (2.1.2015 – 25.4. 2017) of our data to train the methods, with testing undertaken on the remaining 20% (26.4.2017 – 31.12. 2017. Figure 1a) (Shah, 2017). This ensured that we always had a training dataset with a sufficient number of observations to infer reliable outputs. We also excluded from analysis any animals that were present only during the testing phase of the dataset, but retained those present only in the training dataset, as the latter are able to provide information about their opponents. For each method, we calculated dominance hierarchies from our training dataset. As the estimated outputs are measured on different scales (e.g., ratings, scores), we converted these to ordinal ranks and used these new outputs for the rest of our study.

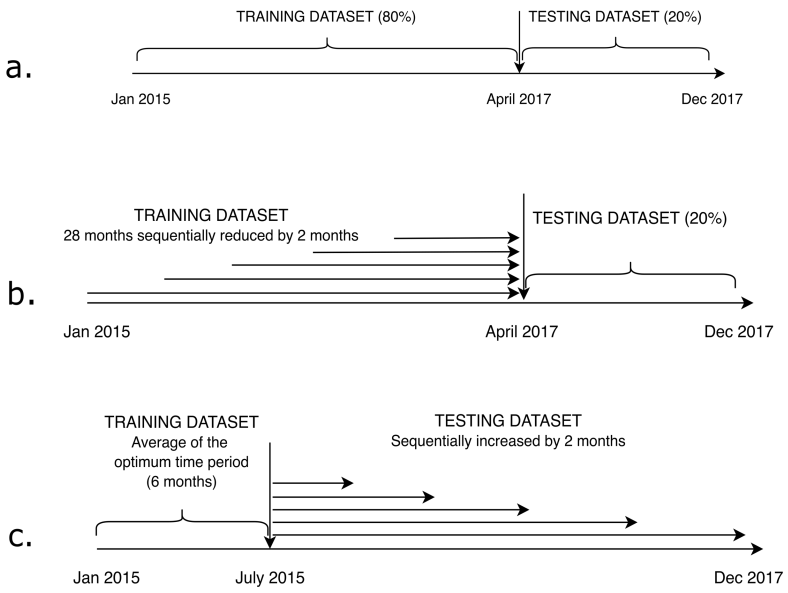

Figure 1 (a) Original approach used to assess methods ’reliability. (b) Modified approach to assess the length of time period required for inferring reliable ranks. (c) Modified approach to assess the time period over which aggressive outcomes can be correctly predicted.

The first step in our analysis was to compare the ranking structure of each method. To do so, we visualized the data using a hierarchical clustering approach, which assembled results according to their similarity. Initially, each method was assigned to its own cluster. The algorithm then proceeded, joining the two most similar clusters at each stage and continuing until there was just one single cluster. In this way, methods that were most similar to each other were combined into branches, which were then fused higher up in the clustering process. Euclidean distance was used to measure the dissimilarity between each pair of methods. The hclust R function (stats package) was used to generate this hierarchical clustering.

Following this initial comparison, rank orders were then used to assess how well they matched the outcome of dyadic aggressive interactions in the testing dataset (matched =1 or no match=0). In other words, did the winner of the interaction in the testing dataset have a higher inferred rank than the loser? In the case of tied interactions in the testing dataset, the outcome was correctly predicted only if both individuals had been assigned the same ordinal rank. The proportion of correctly predicted outcomes was then translated into a percentage to determine which methods achieved better results than others. Finally, we applied a multilevel Bernoulli model to investigate how these correctly predicted outcomes (matched = 1, not matched =0) varied across each ranking method. We then visualized the average percentage of correctly predicted outcomes for each method, along with the variance, using a violin plot.

4.3.4.2 Determining the optimal amount of data required for inferring reliable ranks

Our second aim was to estimate the amount of data needed to infer reliable outputs. To do so, we kept our testing dataset constant and modified the length of the training dataset. Specifically, we maintained the same end date for the training dataset, while varying its start date. Thus, as the training dataset decreased in size, only the most recent observations were included. Our original training dataset comprised 28 months, which we reduced sequentially by two months, until only two months were left (i.e., we truncated the dataset starting from January 2015 towards April 2017: Figure 1b).

At each reduction in size, we computed the methods 'output, converted them into ordinal ranks and assessed these against the interaction outcomes in the testing dataset. The same procedure outlined in section (i) was used to calculate the percentage of correctly predicted outcomes. These percentages were then plotted in order to determine the amount of data needed to predict reliable ranks (i.e., ranks that were used to predict the outcome of future interactions).

4.3.4.3 Determining the time period over which an inferred rank order can be used

To determine the length of time needed to correctly predict aggressive outcomes from obtained outputs, we performed the reverse procedure to that used above. That is, we gradually increased the size of our testing dataset and looked at its impact on the percentage of correctly predicted outcomes. Based on the results obtained in the previous analysis, we calculated the average optimal training dataset length across all methods. Using the average in this way meant that the training dataset could be kept constant, thus easing comparisons between the different methods. We used the remaining data as our testing dataset, and systematically varied its length. We began with the 2-month period that followed directly from the training phase (July-September 2015) and then sequentially increased the testing dataset by 2 months until the 30-month limit was reached in December 2017 (Figure 1c).

Using the ordinal ranks inferred from the training dataset, we looked to see whether they matched the observed outcomes for each testing dataset. The percentage of correctly predicted ranks was plotted as a function of the testing dataset length to give us an insight into the rate of decay of each method's reliability (i.e., over what period can we use a given set of inferred ranks without any loss of reliability).

4.3.5 Using the testing dataset to probe reliability changes

To look at reliability changes in predicted aggressive outcomes, we made use of our testing dataset and the I&SI method, as the latter produced the most reliable outcomes for our dataset. We used the optimal training dataset length (i.e., 6 months) based on the results of our previous analysis (ii). This ensured that we could compute reliable rank order while maximizing the size of the testing dataset (i.e., 30 months). Using the same approach as above, we looked to see whether the inferred ranks matched the observed outcomes in our testing dataset. We also determined whether the adult dyad participants were females or males for each observed outcome.

In this analysis, we first plotted the observed values of predicted outcomes at the group level to give a picture of the overall trend in reliability changes over the entire testing period. We then took our investigation down to the dyad level by plotting the observed values from the adult female-female and male-male dyads. We used the plotting function from the "rankReliability" package to plot the changes in outcome predictions over time at the group and sex-specific dyad level.

4.3.6 Ethical note

All protocols were non-invasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505).

4.4 Results

4.4.1 Determining the method's average reliability: how do non-sequential and sequential methods compare?

Our dendogram identified the extent to which the methods provided similar estimates of rank order in our study group (Figure 2a). The output from the BI approach, the modified and the original Elo-rating cluster was the most different from the others, followed by the I&SI. The blue cluster, comprising all the David's scores methods, was the most similar in its outputs, followed by the cluster including the P&C and the randomized Elo-rating methods. Overall, the non-sequential methods produced a set of rank orders that were more similar to each other than to those produced by the sequential methods.

We visualized the average percentage of correctly predicted outcomes in the testing dataset in Figure 2b. While the dendogram indicates how similar the methods were in their outputs (rank order), Figure 2b shows the variance in the percentage of correct predictions produced by each method. In other words, they give us a sense of the "confidence" in the rank outputs produced (i.e., how effective were they at predicting future aggressive outcomes?). If we look at the red cluster (BI, the original and modified Elo-rating), for example, we see that these methods produced similar outputs (Figure 2a) and yet they differed in their reliability (Figure 2b): the BI approach had a higher percentage of correct predictions than the modified Elo-rating. Another intriguing pattern is that the P&C/randomized Elo-rating (pink cluster) and the I&SI (green cluster) differed in their outputs (Figure 2a), but the randomized Elo-rating method's reliability was more similar to the I&SI than it was to the P&C methods (Figure 2b).

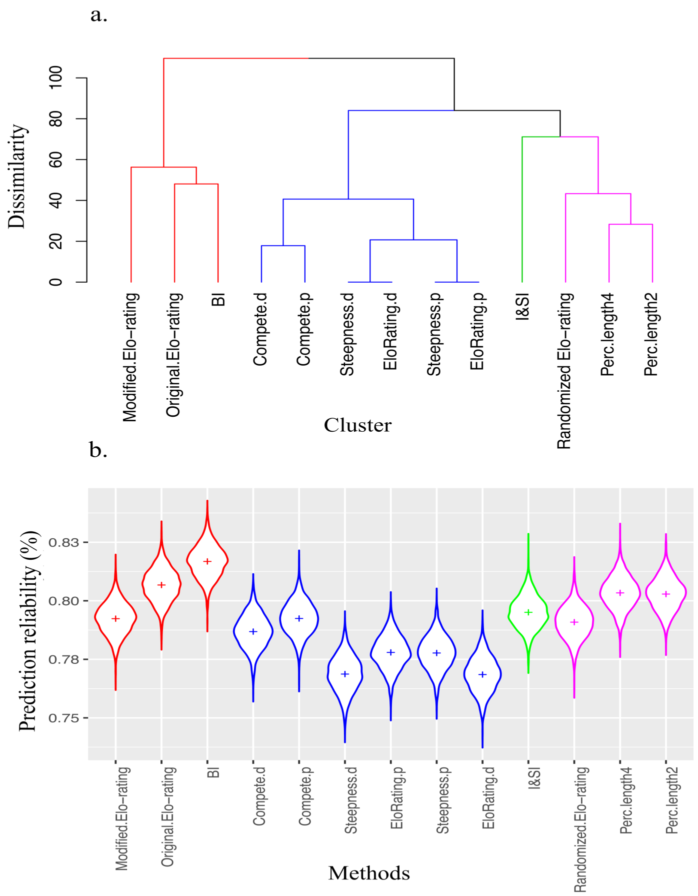

Figure 2 (a) Similarity between the rank orders produced by each method. The height of the split, on the vertical axis, indicates the similarity of rank order between two methods. The higher the split, the less similar the methods were in terms of their outputs. (b) Similarity of methods 'reliability. Distribution of the percentage of correctly predicted outcomes across the methods used. Each cross represents the average estimate of the percentage of correctly predicted outcomes. Each colour represents a dissimilarity cluster. Red, cluster represented the sequential approaches while pink, blue and green ones were non-sequential methods. Blue corresponded to the David's score variants.

The overall percentage of correctly predicted outcomes for each method is given in Table 2. These indicated that all methods did well in inferring reliable ranks (i.e., those that predicted future interaction outcomes). The BI method provided the best fit to the data, predicting 82.2% of aggressive outcomes, followed by the original Elo-rating method (81.0%). The two P&C variants (maxLength4 and maxLength2) produced an identical value of 80.6%, followed by the I&SI with

79.6%. The David's score obtained from the three different packages, and via the two different functions (Dij and Pij), were the lowest performing with values ranging from 76.4% to 79.3%, along with the modified and randomized Elo-rating with respectively a percentage of predicted outcomes of 79.2 and 79.1. The David's scores from the "EloRating" package and those from the "steepness" package (Pij and Dij function) gave the exact same percentage outcomes. Compared to Dij function, the Pij predicted a higher number of reliable outcomes across all three packages used. Moreover, the "compete" package had a higher efficiency than the "EloRating" and "steepness" packages (as the "EloRating" and "steepness" packages presented the same global percentage of reliability, as well as the same patterns throughout the rest of the analysis. We only use the "steepness" package in what follows from here). In general, and rather to our surprise, the family of sequential approaches was not more reliable with respect to predicting future aggressive outcomes. Taken together, these results showed that, despite these methods differing in their approach and the nature of their outputs, they all showed a high level of reliability when predicting the outcomes of future aggressive interactions.

Table 2 Percentage of correctly predicted aggressive outcomes over an 8-month testing dataset for our vervet monkey's troop (RBM).

Method	Package	Option	% prediction RBM
I&SI	Compete	isi13	79.6
	Compete	Dij	78.6

David’s scores		Pij	79.3
	Steepness/ EloRating	Dij	76.4
		Pij	77.5
Percolance & Conductance	Perc	maxLength4	80.6
		maxLength2	80.6
Elo-rating	EloRating	default	81.0
	Newton-Fisher’s code	K variation	79.2
Bayesian Inference	Goffe’s code	Rstan	82.2
Randomized elo-rating	aniDom	n.rands=1000	79.1

4.4.2 Determining the optimal amount of data required for inferring reliable ranks

We found that our original assumption was borne out: the reliability of predicted outcomes was not greatly affected by the length of the training dataset (Figures 3 and 4). The non-sequential approaches (Figure 3), however, did show more variation in the percentage of correctly predicted outcomes depending on the length of the training dataset. Despite this sensitivity, a maximum value for reliability could be found for each method. On average, these peaks occurred at 6 months, which we suggest represents the optimal length of time period needed to correctly predict future outcomes in this dataset. As the number of months in the training dataset increased, the non-sequential methods showed more of a decay in reliable prediction compared to the sequential methods (as one would expect). Moreover, the I&SI method displayed the highest percentage of correctly predicted outcomes when the training dataset spanned the period of 4 to 16 months.

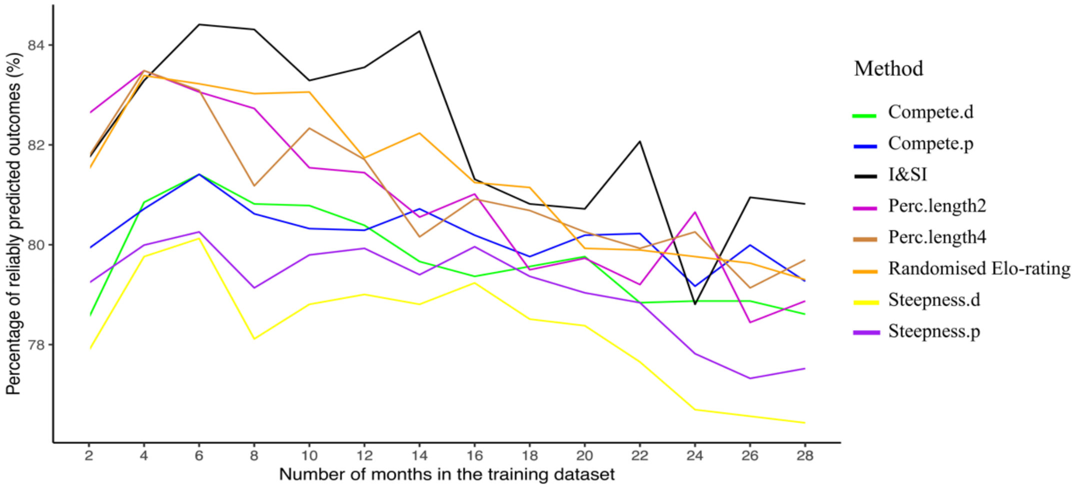

Figure 3 Variation of the percentage of outcome prediction with the non-sequential methods in function the number of months included in the training dataset.

Figure 4 presents the family of sequential approaches and shows that the length of the training dataset did not have any impact for two of the three methods: the original Elo-rating and the BI. In fact, both methods performed well regardless of the length of the training dataset. There is some evidence to suggest, however, that the original Elo-rating method and the BI approach produced slightly more reliable predictions once the training dataset exceeded four months, and 10 months respectively. As for the modified Elo-rating method, it shows a sensitivity to the amount of data in the training dataset. A first peak in reliable prediction appeared at training dataset lengths between four and 12 months. Beyond 12 months, reliability decreased and then stagnated as the training dataset length increased.

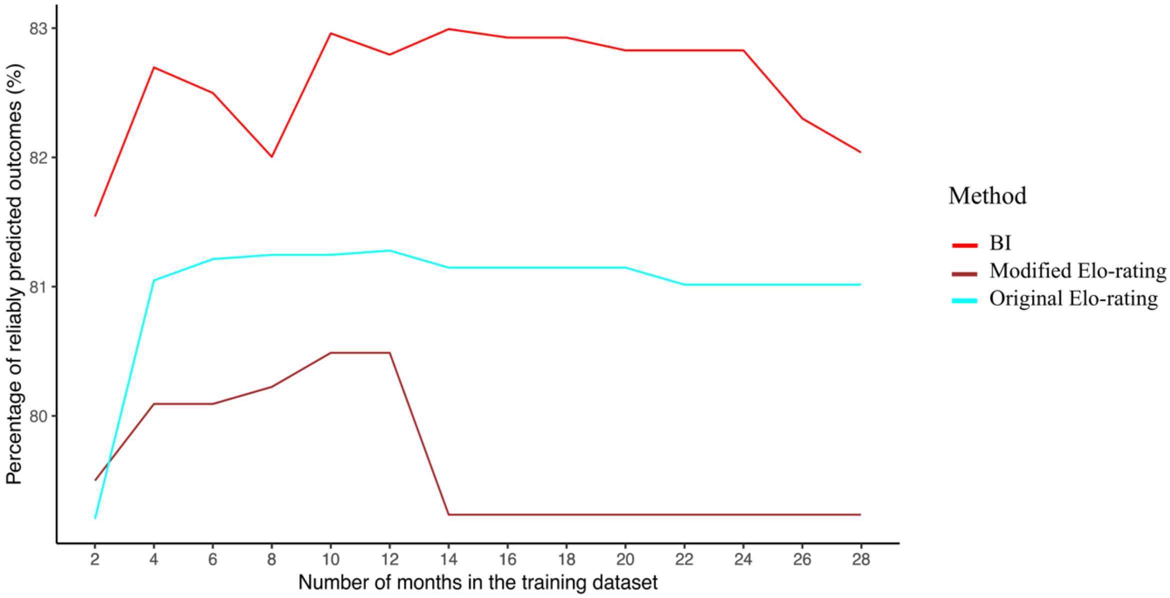

Figure 4 Variation of the percentage of outcome prediction with the sequential methods as a function the number of months included in the training dataset.

With the exception of P&C and randomized Elo-rating, all methods from the non-sequential approaches produced an optimal percentage of correct prediction with a 6-month training set. The sequential approaches reached saturation sooner at 4 months, although the BI approach showed a temporary decrease at 8 months. In our next analyses, we used a 6-month period for the training dataset as this represented the best compromise in terms of enabling comparison across all methods. Shortening the training set in this manner gave us a larger testing set of 30 months in total (2.5 years) to assess our third question.

4.4.3 Determining the time period over which an inferred rank order can be used

The percentage of correct predictions for each testing dataset length is plotted in Figure 5a-c. At first sight, all methods showed the same pattern. First, a decline in outcome predictability occurred at four months, which was then followed by a peak in prediction reliability, corresponding to a testing dataset of eight to 10 months in length (Figure 5a). Past 10 months, the reliability of predicted outcomes showed a constant and slow decay.

The I&SI, as well as the P&C approach, stood out as the methods that led to the highest percentage of correctly predicted outcomes over the whole testing dataset's length (Figure 5a), followed by the BI approach. The remaining methods were clustered with a lower percentage of correctly predicted outcomes throughout the testing dataset's length.

Moving away from the general pattern, Figure 5a highlights the differences between non-sequential and sequential approaches. Again, the latter were no more reliable than non-sequential approaches. However, they distinguished themselves in the sense that all the tested methods were good at correctly predicting outcomes (i.e., they clustered in the centre of the range of performance), whereas the non-sequential methods showed a much wider range of variation.

In order to examine these patterns in more detail, we separated the non-sequential and sequential approaches to enable the similarities and differences – between and within each family – to be seen more easily. With regard to the non-sequential approaches (Figure 5b), both the I&SI and P&C methods displayed a pattern of fluctuation, whereas David's score showed a smoother curve with a constant decrease in reliability once past a testing dataset of 2 months. The "compete" package appeared to perform better than the "steepness" package; both packages produced similar curves. The randomized Elo-rating also presented fluctuations and was the method showing the lowest reliability through time. Finally, the I&SI and P&C methods displayed a higher percentage of correctly predicted outcomes compared to the sequential methods throughout the whole testing dataset length, except for P&C with maxLength 2 past 26-months of the testing dataset.

With respect to sequential approaches (Figure 5c), the BI and the original Elo-rating displayed the general pattern described above. The modified Elo-rating showed the same pattern in prediction reliability until 12 months, where its percentage of correctly predicted outcomes started increasing with the length of the testing dataset.

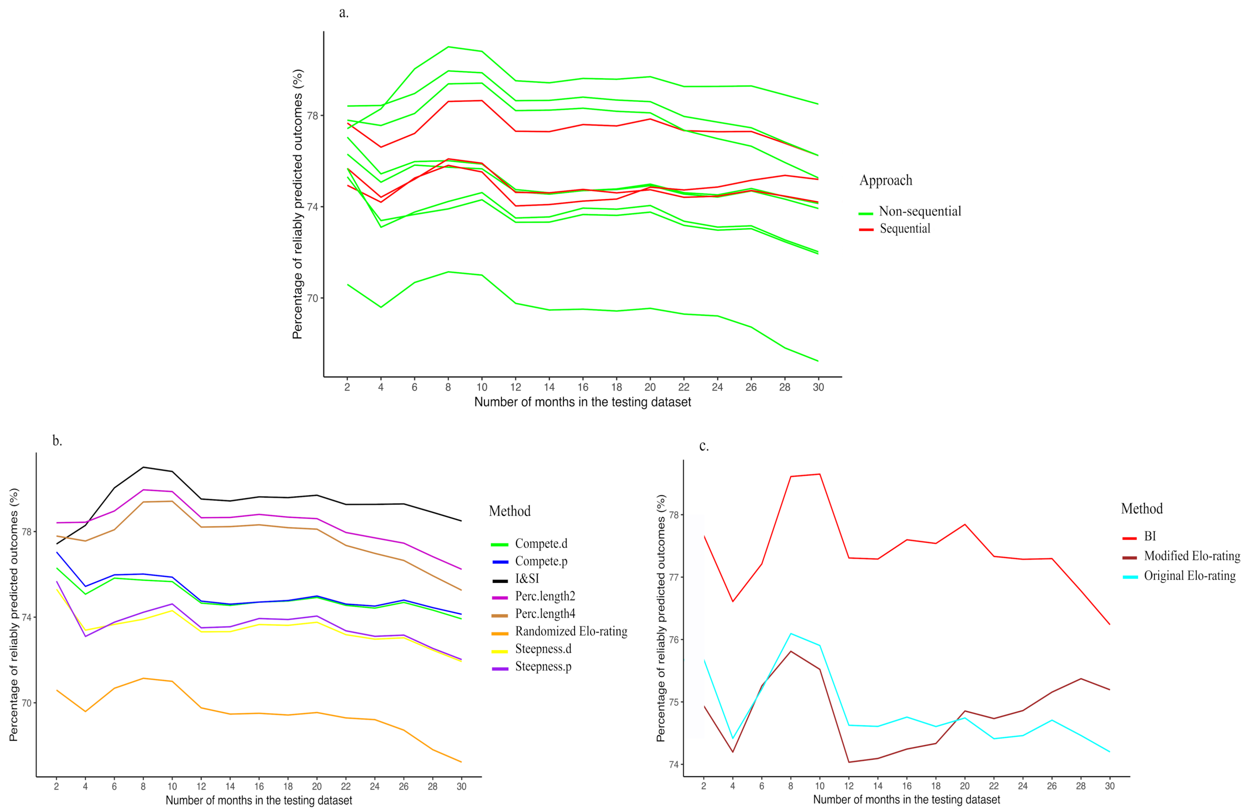

Figure 5 Variation of the percentage of correct predictions as a function of testing dataset length across (a) all methods, (b) sequential approaches only, (c) non-sequential approaches only.

4.4.4 Using the testing dataset to probe reliability changes

The reliability changes in the predicted outcomes of aggressive interactions over the 30-month testing dataset are plotted in Figure 6a-c. Looking at the global trend (Figure 6a), we found that our original assumption did not hold. Instead of a predicted decay in reliability of predicted outcomes, the overall reliability remained very stable across the 30 months.

In order to examine these reliability changes in more detail, we looked at the predicted outcome patterns at a finer scale: the adult sex-specific dyad level. We separated the adult female and adult male dyads to enable the patterns to be seen more easily (Figure 6b, c). With respect to the adult female dyads (Figure 6b), our assumption held: reliability remained stable throughout the whole testing dataset. Regarding the adult male dyads, a stable pattern in the reliability was observed for the first five months, followed by a peak in over the next three months (Figure 6c). Past this peak, reliability showed a quick decline.

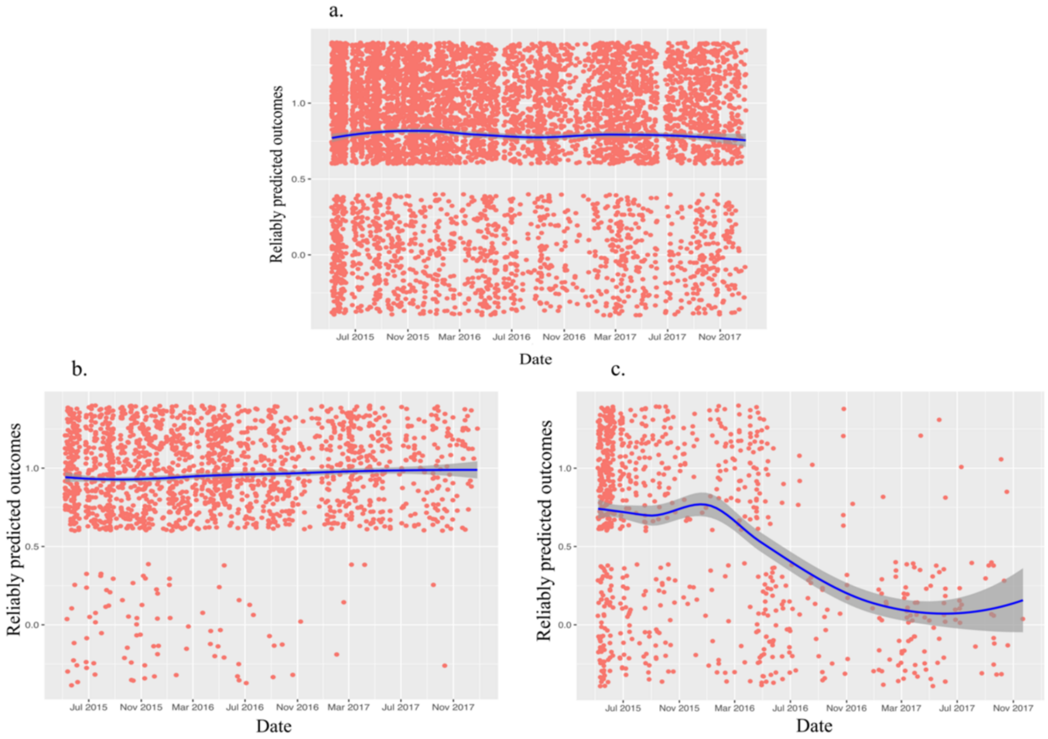

Figure 6 Variation of the fitted (line with 95% confidence interval) and observed (jittered points) values of outcome predictability (correct prediction =1, not correct =0) as a function of time at the (a) group-level, (b) adult female dyad-level, (c) adult male dyad-level.

4.5 Discussion

We have presented a training-testing procedure, and associated code, that will allow researchers to determine the most reliable method for calculating dominance ranks for their particular dataset. We used data from our own long-term study of vervet monkeys to demonstrate the utility of the method. Overall, we found that all methods tested performed well at correctly predicting future aggressive outcomes in our dataset, i.e., all methods were reliable. With respect to the impact of the length of the training dataset, all methods again displayed high reliability from the very start (i.e., with little to no training period), but all showed improvement as the length of the training period increased. With respect to the length of the testing dataset, we found that (with a fixed training period of 6 months), all methods could correctly predict aggressive outcomes for the subsequent 10 months. Finally, looking at changes in predicted outcomes over time, adult male dyads showed more variability than adult female dyads.

More specifically, our first analysis revealed that, despite some differences in obtained rank order, all methods succeeded at inferring reliable ranks. We suspect this may be because individuals whose ranks were inaccurately assigned were those that did not interact frequently; hence they did not appear often in the testing dataset, and so did not have an impact on the reliability of a given method. This finding goes against our prediction that sequential methods would perform better than non-sequential ones. Our prediction here was based on the assumption—built into the non-sequential family of methods—that all individuals represented in a matrix were co-resident at some point (i.e., all had the chance to interact). With an original training dataset of 28 months length, we predicted that this assumption would most likely be violated and hence lower the performance of non-sequential methods relative to sequential ones. Contrary to our prediction, the non-sequential family performed well at producing reliable ranks, suggesting that violation of this assumption was of minor significance. In this study, we analysed data from a species in which stable ranks tend to persist through time, and in which few rank reversals occur. This specific social dynamic may have enhanced the reliability of the non-sequential methods due to the large amounts of data included (i.e., more agonistic interactions to work with). If this were so, however, we would have expected to see poorer performance over shorter time frames (investigated in the second part of the analysis), and this was not the case.

In our second analysis, we found that only a short training period was necessary to infer reliable ranks across all methods. The sequential methods, however, were less sensitive to the amount of data present in the training dataset, and hence showed a constant efficiency regardless of the length of training, compared to the non-sequential approaches. This is not unexpected given that sequential approaches track rate variations continuously and update the ratings after each interaction. From the non-sequential perspective, the combination of high overall reliability with some temporal fluctuation suggested that, in our study species, individual position in the rank order shows a form of "regression to the mean". That is, individuals may experience very mild shifts in relative rank position up or down the hierarchy across time, but nevertheless occupy more or less the same "absolute" position. This, in turn, suggests that rank changes may reflect the ecological and demographic contexts in which they occur, rather than pointing to genuine changes in inherent power. We should also highlight that, when the training dataset did not exceed 22 months, it was the non-sequential I&SI and P&C methods that produced the highest percentage of correctly predicted outcomes.

Finally, the training-testing procedure gave us greater insight into the working of the randomized Elo-rating method. When applied to a short training dataset (i.e., 6 months), the sequence of interactions clearly did not matter, and the method's reliability was high. As the training dataset increased up to 28 months, however, there was a decline in reliability, which reflects the fact that, over this period, demographic change was inevitable, and the order of interactions may well have begun to exert an influence on the structure of the hierarchy. Given this outcome with our data (and assuming this holds true across other datasets), this suggests that the randomised Elo-rating method will indeed prove useful in determining when interaction order matters in a given dataset, as originally suggested by Sánchez-Tójar et al. (2018).

We also found that, with the exception of the randomized Elo-rating, all methods correctly predicted aggressive outcomes for at least 10 months. Past this threshold, however, reliability in prediction decreased as the testing dataset increased in length. The decay was rather shallow, however, and there was still high predictability in aggressive outcomes, indicating overall rank stability during the period covered by our sample. This is not to say, however, that rank predictability did not fluctuate as the length of the training period increased, and it was apparent that the degree of fluctuation was dependent on the method used. The sequential methods produced more fluctuations than the non-sequential methods. This is probably because the former are likely to catch small shifts in rating position as they constantly update, whereas the non-sequential methods are more likely to produce a rank order that captures the overall social dynamic. The fluctuations observed suggest that rank shifts were occurring in the study group during particular periods, and so another advantage of using a training-testing procedure is that it provides researchers with a way to home in on periods of rank instability, which may prove useful when attempting to answer questions relating to the effects of dominance on various behaviours and in relation to ecological variables.

It is important to note here that the intention behind the data-splitting approach was to enable a better understanding of rank structure within a particular dataset, not to determine which method was absolutely the most reliable. That is, the specific results we have presented here may not generalize to other datasets. Indeed, differences may well be expected because other species and populations will vary in their frequency of agonistic interactions, the steepness of their hierarchy and the (a)symmetry in aggressive outcomes. Shizuka & McDonald (2015), for example, have shown that differences in dominance hierarchy structure across animals may be a consequence of the study design (e.g., how many animals to observe and how much interaction data to collect). Hence, our goal was to show that a training-testing approach can be applied to any dataset to determine the most reliable ranking method, and thus we consider this approach to be useful in and of itself. Having said this, it will be interesting to see whether any commonalities do, in fact, emerge across different datasets. It is therefore necessary to repeat these analyses on other populations and other species to determine what patterns might be more general, and which are highly specific to a given dataset. At present, we can say that the data-splitting approach allows researchers to assess which method will work best for their dataset, given the size of their sample, and the length of time over which the study was conducted.

For the purposes of comparison across methods, we converted all model outputs to ordinal ranks. Although we agree with Strauss and Holekamp (2019) that such conversion is useful for identifying hierarchy dynamics, we consider this to be a limitation of our study. In fact, we did not consider how the magnitude of rank differences might affect reliability, nor did we consider any uncertainty around rank calculations. These components may very well matter, especially in species where a linear rank order may not be representative of the social hierarchy. This point also serves to highlight the true advantage of methods like the BI, randomized Elo-rating and the P&C approach, which enable researchers to look at the uncertainty around ranks, and thus gain a more complete understanding of the social hierarchy.

We also acknowledge that the use of empirical data does not allow us to distinguish between the two sources of error that could explain differences in the methods ’performance: (i) inadequacies of the method, and (ii) real biological change. Thus, to reiterate and emphasize the point made above, our findings are only valid with respect to our data and cannot be assumed to apply to other datasets. Within our dataset, however, we think it is safe to assume that variation in a method's reliability compared to others does, in fact, reflect something about the method itself. Given that we tested all methods on the same training/testing datasets, any potential biological changes within the dataset should have been detected by at least some of the methods. This, of course, is where the usefulness of simulated data comes into play, as simulation allows one to tease apart these two sources of error more effectively, as well as gaining some more general insights into each method (Sánchez-Tójar et al., 2018). Our suggestion here is that the most informative approach will involve comparing simulation studies of methods using constructed datasets with reliability studies of methods applied in real-world settings; in this way, we can determine whether methods that show high validity also show high reliability in real-world contexts. In fact, one of the latest studies to date (Strauss & Holekamp, 2019) used both simulated and empirical data from a long-term field study of spotted hyenas (*Crocuta crocuta*) to assess the performance of the modified and unmodified methods in inferring longitudinal hierarchies.

Finally, using the testing dataset to investigate reliability changes in predicted outcome, at the group and dyad level, allowed us to get a better understanding of social dynamics. Adult male dyads displayed most variation, which was not detectable at the group level, while the adult female dyads remained stable across the entire study period (30 months). Thus, the data-splitting approach can also help to achieve a better understanding of how dominance ranks vary within a given group over time in relation to factors like sex and age class. A multi-scale approach can thus provide a more comprehensive perspective on the temporal dynamics in outcome predictions, and hence the social ranks, through time. In other words, we consider that data-splitting provides researchers with an excellent tool to probe the social dynamics of their study species in more depth, rather than simply offering a means of determining the most reliable ranking method. It would be also interesting (and possible) to look at the outcomes of aggressive encounters that do not match the ranks assigned to each participant, when both were extracted on the same day. This would give us a better idea of the true degree of outcome unpredictability, allowing us to assess whether uncertainty in rank assignment is due to the nature of the aggressive interaction itself or whether it reflects something about the context in which it takes place.

In conclusion, a data-splitting approach gives researchers the power to tailor the selection of a dominance-ranking method to the particular nature of the dataset they are using. In addition, it provides insights into group dynamics, which can enable researchers to home in on regions of their dataset that will permit analyses into how and why rank shifts occur and discover the underlying causes of both rank stability and unpredictability across time.

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4.7 Supplementary material

Table S1 Details on the original training dataset structure.

Parameters	Training dataset
Total number of interactions	8308
Number of individuals excluded from testing dataset	4
Number of draws	307
Number of coalitions	1108
Number of counter-aggressions	2014
Number of aggressions lost by the aggressor	500
Number of Adult-Adult aggressive interactions	4658
Number of Adult-Juvenile aggressive interactions	2588
Number of Juvenile-Juvenile aggressive interactions	1062
Number of deaths	21
Number of individuals recruited into the group	6 new males and 30 new juveniles
Average monthly troop size	33.1 sd=3.5

S2: Methods' introduction and backgrounds

Among the tested ranking methods, it is possible to distinguish two families that differ in their overall approach. The first relies on interaction matrices and comprises the David's score method (David, 1987; Gammell et al., 2003), the Inconsistencies and Strength of Inconsistencies (I&SI) method (De Vries, 1998), and the Percolation and Conductance (P&C) method (Fujii et al., 2015). These methods use all observed interactions within a particular timeframe to determine average measures of dominance rank single quasi-static ranking. As a result, one cannot differentiate if the ranks obtained depend directly on the number of individuals present in the matrix itself. Thus, any observed fluctuation in ranks across time periods may simply be from the consequence of a demographic event, or from the variation in an animal's competitive abilities. Consequently, these methods cannot provide information about the mechanisms by which ranks either change or are maintained over time. As such, non-sequential methods are not always easy to apply to highly dynamic animal societies, or to sparse datasets (Neumann et al., 2011).

The second family is based on the sequence in which interactions occur (which we refer to here as sequential methods), with wins and losses continuously updated, giving rise to a rating for each individual. All these methods are based on the Elo-rating method used to rank chess players (Elo, 1978). As this approach involves a more dynamic assessment of the hierarchy over time, it can more easily accommodate changes in group-composition. The Elo-rating's variants are the modified Elo-rating (Newton-Fisher, 2017), the Bayesian Inference (BI) approach (Goffe et al., 2018) and the randomized Elo-rating (Sánchez-Tójar et al., 2018). All address various difficulties associated with the application of original Elo-rating to animal societies (Foerster et al., 2016; Goffe et al., 2018; Newton-Fisher, 2017; Sánchez-Tójar et al., 2018).

Newton-Fisher (2017) presents two developments of Neumann et al. (2011)'s R function to improve its efficiency: (i) the incorporation of prior history and (ii) the recognition of differing intensities of aggression in agonistic interactions (the "k" variable). When rating subjects, k is used to determine the degree to which each interaction influences the future rank trajectory of both winner and loser (Ibid.). Goffe et al. (2018) modification, by contrast, deals with limitations related to the "burn-in" period: the time needed to accumulate sufficient observations and thus enable the computation of reliable ratings (Albers & De Vries, 2001; Neumann et al., 2011). To do so, the authors use "partial pooling", an approach that rests on the assumption that all initial ratings are sampled from the same distribution with a shared variation parameter, σ. Finally, Sánchez-Tójar et al. (2018) suggested a modification to the original Elo-rating whereby they randomized the order in which interactions occurred. This was based on the assumption that, in societies with a stable social structure, the sequence of interactions will be less relevant to the determination of ranks than in systems where social structure is more volatile. Despite being derived from a sequential approach, the changes implemented mean that this method shares many common features with non-sequential methods. For this reason, the randomized Elo-rating is presented as being part of the non-sequential family.

- **Inconsistencies and Strength of Inconsistencies method (I&SI):** (De Vries, 1998)

The dominance matrix is reorganized iteratively to minimize (1) number of inconsistencies (I) and (2) strength of inconsistencies (SI). The output is ordinal rank order.

Because this method is matrix-based, the obtained ranks depend directly on the number of individuals present in the matrix itself. Static methods implicitly assume stable dyadic relationships in order to generate a meaningful result.

Finally, it seeks to find a nearly linear, hence it is most appropriate if the assumption of linearity is statistically supported (De Vries, 1995, 1998), that is, if the degree of linearity in the set of dominance relationships is significantly higher than expected on the basis of random relationships (Schmid & De Vries, 2013). However, dominance hierarchies with linear structures have now appeared to be less prevalent in animal groups than was once assumed (Douglas et al., 2017).

- **David's score:** (David, 1987; Gammell et al., 2003)
  It is a matrix-based approach in which the relative strength of opponents is taken into account. Static methods implicitly assume stable dyadic relationships in order to generate a meaningful result and the obtained ranks depend directly on the number of individuals present in the matrix itself.

It seeks to provide a suitable measure of individual overall success, determined by weighting each dyadic success measure by the un-weighted estimate of the opponent's overall success and from which a rank order can be derived directly. Here, the outputs are non-integer indices of success.Every dyadic interaction is independent of every other dyadic interaction. The paired comparison paradigm (David, 1988) requires that the number of records for each dyad should roughly be the same.

- **Percolation and Conductance (P&C):** (Fujii et al., 2015)
  Given that dominance relations do not always fulfil the criteria for linearity (Signe & Van Schaik, 2000; van Hooff & Wensing, 1987), this network-based method permits nonlinear structure to emerge via estimates of network directional consistency in the flow of dominance interactions, and the detection of blocks of dominance ambiguity that are indicative of nonlinear segments of a hierarchy. This technique uses paths within the agonistic network to generate an individual's probability of winning against all other individuals. It measures the consistency of information flow through the network (Fushing et al., 2011). In other words, it combines information from direct win/loss interactions and from indirect pathways to create a matrix of probabilities. The network transitivity determines how much to weigh the indirect 'wins' from these pathways.

It still relies on interaction matrices. Static methods implicitly assume stable dyadic relationships in order to generate a meaningful result.

It makes the assumption that we have independence among the collection of conflict outcome data. Non-overlapping dominance paths independently provide degrees of stochastic transitive dominance potential.

- **Elo-rating:** (Elo, 1978; Neumann et al., 2011)
  Elo-ratings are based on the sequence in which interactions occur, with ratings continuously updated. It enables the rating process to continue despite changes in group-composition. No matter whether the critical linearity assumption is satisfied or not, this approach always provides a ranking sequence. That is to say, it becomes extremely convenient because of its easy application, even though the resultant ranking sequence might be poorly supported by the data (Shev et al., 2012).

It seeks to provide a suitable measure of individual overall success (non-integer indices), from which a rank order can be derived directly. It makes the assumption that all agonistic interactions entered into the model are equivalent in their potential influence on rank trajectories. In rating subjects, the variable k is used to determine the degree to which each interaction influences the future rank trajectory of both winner and loser. In other words, it determines the number of rating points that an individual gains or loses after a single encounter (Neumann et al., 2011). Newton-Fisher (2017) argues that holding k constant makes the implicit assumption that, as long as a clear winner and loser can be identified, variation in the intensity of aggression does not influence social dominance rank or rank trajectories.

In the absence of any knowledge of prior dominance relationships, the method assigns all individuals the same initial Elo-rating score, which is then updated as interactions are added across the observation period. Consequently, a "burn-in" period is necessary so that sufficient observations can accumulate and enable the modelled rankings to catch up with the computation of reliable ratings of dominance relationships (Albers & De Vries, 2001; Neumann et al., 2011). Both Albers & De Vries (2001) and Neumann et al. (2011) are vague about how long this process might take, probably because the duration of the burn-in will vary with the frequency of agonistic interactions (Newton-Fisher, 2017).

- **Modified Elo-rating:** (Newton-Fisher, 2017)
  This method brings two developments: (i) the incorporation of prior history and (ii) the recognition of differing intensities of aggression in agonistic interactions.

- **Bayesian Inference approach (BI):** (Goffe et al., 2018)
  This approach facilitates the estimation of initial ratings, as well as the value of k. It estimates both the most probable rank order as well as the posterior probability of that order. It uses "partial pooling", which rests on the assumption that all initial ratings are sampled from the same distribution with a shared variation parameter σ.

- **Randomized Elo-rating:** (Sánchez-Tójar et al., 2018)
  This method is based on randomizing the order in which interactions occur. It makes the assumption that if the individual dominance ranks are relatively stable over time, the sequence in which interactions occur shouldn't affect the inferred ranks.

S3: Analysis details

The following sections explain in more detail the choices made regarding the analyses for each method.

The I&SI method

It is recommended to find the matrix with the lowest SI associated with a certain number of iterations (nTries). To do so, we performed an optimization to find the nTries that best fit our data. We used the DEoptim package (Mullen et al., 2011). The DEoptim function searches for the global optimum of the objective function (fn) between lower and upper bounds on each parameter to be optimized. It is important to emphasize that the result of DEoptim is a random variable, i.e., different results may be obtained when the algorithm is run repeatedly with the same settings. In our case, the function fn with the highest percentage of accurately predicted outcomes was kept, along with the optimized parameter corresponding to the number of iterations (nTries). We assigned to this parameter the lower bound of 50 and the upper bound of 1000.

Once the optimal parameter value had been extracted, individual ranks were calculated using the latest function version "isi13" from the R package "compete".

The use of this optimization led us to modify our training/testing approach into a training/validation/testing one. Specifically, we divided the original 80% training dataset in two datasets, commonly called training and validation. The training dataset (i.e., the first 80%) was used to attribute the nTries value, leading to the calculation of individual ranks based on this value (Figure 5). The remaining 20%, the validation dataset, allowed us to see how well these ranks did in predicting the aggressive outcomes. Depending on the percentage of accurately predicted outcomes, the nTries value was updated accordingly in the training dataset. Once the optimized nTries value was obtained, it was used to calculate the ranks from the entire, original 80% training dataset. The testing dataset then allowed us to test the efficiency of the calculated ranks in predicting future aggressive outcomes. Here nTries= 449 was chosen.

David's Score

This approach proposes two alternative indices to compute David's scores: Pij and Dij. Pij represents the winning proportion of individual i against j, which leads to a matrix of observed win proportions as an output. For the Dij index, a matrix is obtained where the observed proportion of wins (Pij) is corrected for the chance occurrence of this observed outcome. Balasubramaniam et al. (2013) argued that Pij might be a better choice for species with high levels of directional asymmetry (i.e., despotic species), whereas Dij may be a better choice for species with low levels of directional asymmetry (i.e., tolerant species). We compared both these indices. Furthermore, the David's score method can be calculated with the aid of three different R packages. The decision was made to include them all in the analysis, producing two calculated scores per package. This allowed us to assess whether the calculated ratings were the same across all packages and if not, which package led to the highest percentage of accurate predictions.

Percolation and Conductance

The parameter maxLength helps find all indirect pathways of a particular length and then update the conflict matrix. Examining information gained through indirect pathways provides information that can be used to decide on the appropriate maxLength for a dataset. To assist with this decision, the Perc package offers a transitivity function as a way to estimate an alpha value, which is used to weight the information from the indirect pathways to give an indication of the extent to which we can trust information from indirect pathways. Greater transitivity is associated with assigning higher weight to information from indirect pathways (Fushing et al., 2011). We tested MaxLengths of 2 and 4.

Elo-rating method

In the original method, k is held constant, and all individuals receive the same elo-rating at the initiation of the burn-in period. Elo-ratings were calculated with 1000 as the initial value and k set to 100 (Neumann et al., 2011).

Derivations of the Elo-rating methods

Modified Elo-rating (k variation)

In this method, each dominance interaction is classified according to the most intense level of aggression displayed by the winner (Newton-Fisher, 2017). This being required, we excluded behaviours recorded as "unknown" from the analyses and distinguished among non-aggressive, stationary, active and physical threats. This classification is based on our inter-troop encounter protocol (Barrett, L. & Henzi, S.P., unpublished data). Non-aggressive behaviours included supplants (i.e., where the aggressor takes the victim's place) and displacements (i.e., when one animal submissively moved away when approached within 10 meters). Any aggressive behaviour that did not include a forward movement was considered a stationary threat, such as lunge, facial and vocal threats. Active aggression involved ongoing forward movement (i.e., chase or charge) but where no physical contact was made with the target of aggression. Physical aggression was scored in instances where body contact was made (e.g., a bite or slap). We assigned a different K value to each of these categories, using the default value of 200 (Neumann et al., 2011) for the most commonly observed form of aggression (i.e., the non-aggressive interactions of displace and supplant) and scaling up in multiples of 25 to distinguish varying intensities. This led to the creation of a modified training data set and its detailed composition is given in Table 3.

Table S2 Modified training data set for the modified Elo-rating method (Newton-Fisher, 2017).

	Modified training data set				
Aggression Number	Total	Physical	Active	Stationary	Non-aggressive
RBM Troop	8083	886	1644	1625	3934
K value	-	300	250	225	200

Bayesian inference (BI) approach

We implemented this method using Goffe et al. (2018) code (with no additional analytical choices or justification required).

Randomized Elo-rating

By randomizing the order of observed interactions, this approach allows the creation of K replicated datasets, where K corresponds to the number of randomisations performed. In this study we were only interested in obtaining the final scores (return.as.ranks =TRUE). The function returns a NxK matrix that gives the final scores for each individual (rows) after each randomisation of the order. In order to use the information contained in all the iterations, we extracted the mean ratings for each individual.

We followed the same procedure as Sánchez-Tójar et al. (2018) and randomized the order in which interactions occurred 1000 times.

CHAPTER 5: NETWORK FORMATION DURING SOCIAL INTEGRATION IN JUVENILE VERVET MONKEYS

This data chapter has been published in *Animal Behaviour* (September 7th, 2022), under the title "Network formation during social integration in juvenile vervet monkeys." The authorship list for the published version is as below. I contributed to the study concept/design, data collection, data analysis and drafting the manuscript. Dr. Henzi and Dr. Barrett contributed to funding acquisition, supervision and the drafting and critical revision of the manuscript. Dr. Bonnell contributed to data analysis, supervision and helped draft the manuscript. Dr. Dostie contributed to data extraction. All authors approved the final version of the manuscript.

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5.1 Abstract

Understanding the development of social relationships, or the process of socialization, can provide insights into the processes by which social network structures emerge and vary across species. In this analysis, we investigated the process of network formation from a developmental perspective using data from three groups of wild vervet monkeys, *Chlorocebus pygerythrus*. We used a dynamic social network approach that allowed us to capture patterns of social change over time. Specifically, we considered the temporal dynamics of two separate interaction networks, spatial and grooming associations, and investigated these patterns between the sexes. We used these data to test predictions derived from a developmental framework on relationship formation put forward by Kohn (2019, *Animal Behaviour*, 154, 1–6). We found that females and males differed in their grooming patterns but were similar in their spatial associations. Furthermore,

spatial proximity ego-networks showed seasonal patterns, whereas grooming ego-networks did not. When all relevant centrality measures were considered in concert, we found evidence to suggest that a distinctive network structure forms across the course of development, with ego-networks composed of few strong ties and many weak ties, regardless of behaviour and sex. However, these networks were not produced according to the processes described by Kohn (2019), perhaps because Kohn's framework is concerned mainly with network composition and not structure. Overall, our results provide evidence for social niche construction across development, with the formation of a core social 'bubble' of strong ties that can provide a consistent and predictable immediate social environment. More broadly, these patterns suggest that network formation is a process of ongoing adjustment to the social environment, and not an attempt to meet an optimal end goal.

5.2 Introduction

Social network analysis provides a powerful quantitative framework for measuring individual social phenotypes and social structure (Wey et al., 2013). A particular topic of interest has been the identification of the costs and benefits associated with different social network positions, and how these might link to fitness (Croft et al., 2016; Sih et al., 2009; Wey et al., 2008). Such efforts have produced evidence suggesting that the structure of networks, and individuals' position within them, can influence both adult and offspring longevity as well as offspring survival (Brent, 2015; Cheney et al., 2016; McFarland et al., 2017; Ostner & Schülke, 2018; Snyder-Mackler et al., 2020). At the same time, however, we still lack a comprehensive theory to explain how different network structures are generated and maintained, and why network diversity varies within and between species (Ilany & Akçay, 2016).

Initial efforts to construct such a theory have been made by Ilany and Akçay (2016), who investigated whether the emergence of network structure could be explained by a process of intergenerational inheritance, where offspring acquire network connections from their parents (Ilany & Akçay, 2016). Proximately, this can be explained as a consequence of newborns staying close to their mothers, which leads them to interact initially, and primarily, with their mother's social partners (Deputte, 2000). These initial associations come to constitute the core of the developing infant's own social network (i.e. ego-network). There is evidence for this kind of network inheritance among taxa that form stable social groups and that contain multiple generations (Goldenberg et al., 2016; Ilany et al., 2020; Ward & Hart, 2003; Whitehouse & Lubin, 2005). Such patterns raise the possibility that social inheritance is a general mechanism for network maintenance among group-living species. However, in wild vervet monkeys, *Chlorocebus pygerythrus,* Jarrett et al. (2018) found that, although there was some evidence for network inheritance by juveniles, the adult grooming network could not be replicated by the inheritance of maternal contacts alone. This appeared to be a consequence of two factors. First, maternal networks were insufficiently stable to support the inheritance of social partners and thereby to recreate the overall network (see also Schino et al., 2004, for *Macaca*). That is, maternal network composition seemed to represent a moving target for offspring, such that matching was unavoidably imprecise. Second, simulations showed that a greater number of associations with nonmaternal contacts was needed to replicate the global network, suggesting that the formation of bonds with age cohort peers and other immatures, in addition to bonds with adults, were key to network formation, maintenance and variation over time. Functionally, it makes intuitive sense for juveniles to develop advantageous connections with peers who share a similar life expectancy and a greater probability of continued presence in the group, and not rely on contacts with older individuals alone. If this interpretation is accurate, we might anticipate that juveniles will actively structure their interactions to achieve a network containing both inherited contacts and connections formed independently of the mother.

In this regard, Kohn (2019) proposed that juvenile social relationships develop according to three temporally structured phases: exploration, pruning and consolidation. That is, as juveniles explore their social environment, their social connections go through an initial period of overproduction, followed by attrition and then consolidation. This process is argued to allow juveniles to converge on species-typical relationships first, by exploring many potential social connections in the group, and second, by responding to contingent behavioural feedback from others to guide the formation of longer-lasting relationships (Deputte, 2000). Thus, juveniles should initially explore their social environment widely and then become more selective in their choice of social partners over time (Ward & Webster, 2016). Furthermore, species sex differences have been found to appear prior to sexual maturation (Cords et al., 2010; Jarrett et al., 2018; Lonsdorf et al., 2014; Nakamichi, 1989), whereby the philopatric females have stronger social bonds than dispersing males (Andres et al., 2013; Cords et al., 2010; Frere et al., 2010; Kulik et al., 2015; Nakamichi, 1989). These early sex differences in social behaviour can be interpreted in light of the different life histories and reproductive strategies of males and females (Deputte, 2000). Therefore, Kohn's developmental steps may allow us to detect the emergence of behavioural sex differences and to track their development through time.

Kohn's (2019) mechanistic framework speaks directly to the idea of social niche construction (SNC). SNC describes the way in which individuals, singly or collectively, influence the composition and dynamics of their social environments (Laland et al., 2016). While this definition of SNC is consistent across the literature, the definition of the "social niche" itself varies considerably (Saltz et al., 2016). Authors have defined social niches (both explicitly and implicitly) as social groups, social environments and/or patterns of social interactions

(Bergmüller & Taborsky, 2010; Flack et al., 2006; Kohn et al., 2011; Ryan, 2011) that can be stable (Kohn et al., 2011), and which exert an influence on individual's phenotype and/or fitness (Bergmüller & Taborsky, 2010; Laskowski & Bell, 2014; Montiglio et al., 2013; Ryan, 2011; Saltz et al., 2016). This imprecision is reflected in the lack of empirical attempts to characterize social niches in concrete, empirical terms (but see Kohn et al., 2011). One possible solution is to characterize a social niche using social networks. For instance, Flack et al. (2006) suggested that social niches could be represented graphically as the local connections of an individual's network (ego-network) in multiple, overlapping social networks ('interaction networks', in Barrett et al., 2012). In other words, the different types of social interactions that characterize an individual's engagement with others constitute the components of a social niche. These components can each be represented as individual social interaction networks (Barrett et al., 2012). Here, we begin an exploration of social niche formation via an investigation of two social niche components. More specifically, we use a dynamic social network approach that allows us to capture the processes of exploration, pruning and consolidation at the individual level.

To do so, we consider the temporal dynamics of two separate interaction networks, spatial association and allogrooming, in three groups of wild vervet monkeys. Spatial association and grooming represent two key components of an individual's social niche, as both offer the means by which animals can exert control over the individuals found in their immediate vicinity. These components also provide a useful contrast, as grooming generally requires mutual attraction between partners, whereas spatial proximity can often be achieved unilaterally. In addition, we compare these patterns between the sexes, as the development of enduring social relationships should be more advantageous for females, who remain in their natal group for life, than for males, who are the migrating sex.

Regarding both spatial and grooming associations, and following Kohn (2019), we predicted that juvenile social interactions would translate into large (high network degree) and dense (high network strength) ego-networks during the exploration phase (Fig. 1a). As this phase is expected to be characterized by a lack of structure and stability in juveniles' ego-networks, we also predicted that social interactions would be distributed equally among the focal animal's partners (low skewness), and that networks should lack a consistent composition (low cosine similarity). During the pruning (Fig. 1b), and consolidation (Fig. 1c) phases, juveniles should develop and strengthen preferred social interactions. Consequently, we predicted a decline in individual ego-network size and density, followed by a stabilization of the network at this new size and strength distribution. Simultaneously, we expected social interactions to become increasingly concentrated on fewer partners that remained consistent over time. That is, we predicted an increase in skewness and cosine similarity across the developmental period, followed by a stabilization at this new level. Although we predicted that spatial and grooming associations would display the same patterns across time, we expected them to differ in magnitude in ways that would reflect the level of control an individual could exert over its associates. That is, grooming behaviour is more precisely targeted toward specific individuals, whereas spatial associations combine such active elements with more passive forms of association, where individuals demonstrate mere tolerance of others rather than choice. Consequently, we expected spatial ego-networks to be larger and more dense than grooming networks, and we predicted that spatial ego-network structure and stability would be lower than for grooming ego-networks. In addition to a test of Kohn's (2019) framework, then, our study aimed to demonstrate the general utility of social network analysis for characterizing aspects of social niche formation.

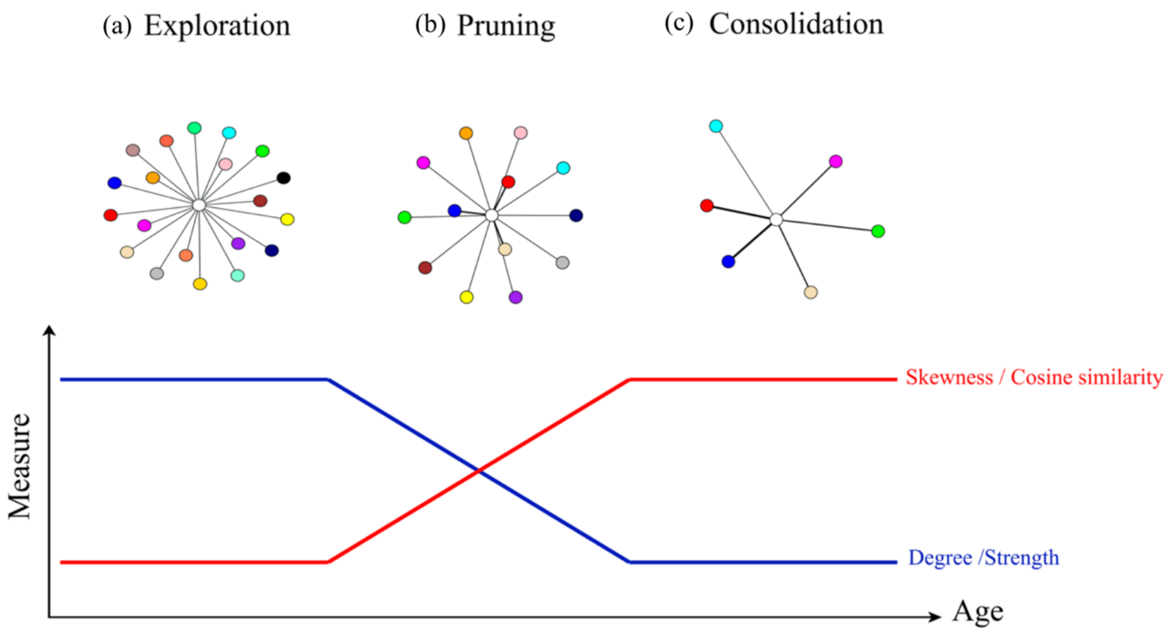


Figure 1 Kohn's (2019) phases of socialisation translated into ego-networks, associated with the predictions for degree, strength, skewness and cosine similarity during juveniles' development. 1a. Exploration - degree/strength are predicted to be high and skewness/cosine similarity should be low; 1b. Pruning - degree/strength are predicted to decline and skewness/cosine similarity increase; 1c. Consolidation - degree/strength are predicted to be low and skewness/cosine similarity are high.

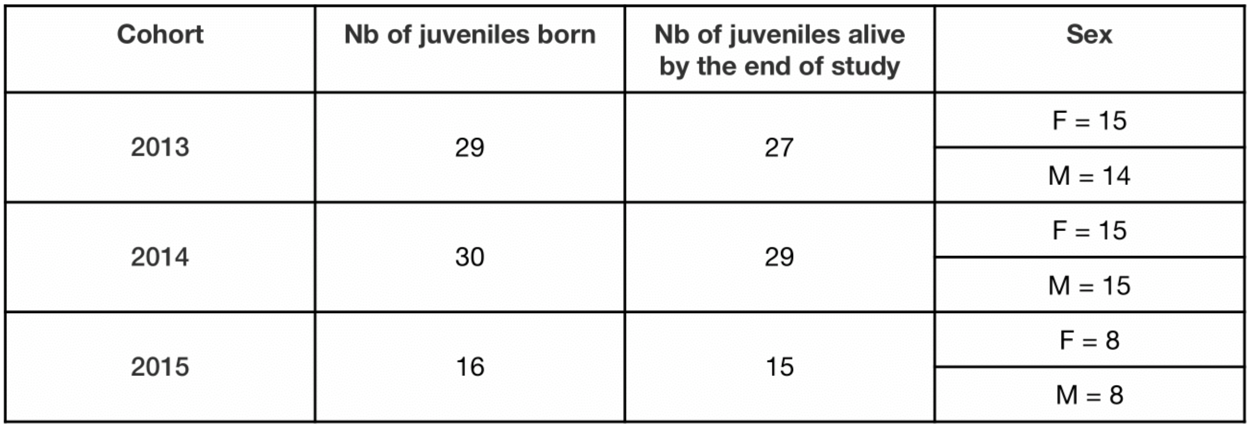
5.3 Methods

5.3.1 Study population and subjects

The data used for this study were collected between June 2014 and June 2017 from three troops of vervet monkeys occupying adjacent and overlapping home ranges in the Samara Private Game Reserve in the semi-arid Karoo biome, Eastern Cape, South Africa (Pasternak et al., 2013). The three study groups (mean ± SD group size: PT group: = 39 ± 8; RBM group: 49 ± 6; RST group: 57 ± 7) were fully habituated, and all animals were individually identifiable from natural markings. Vervets live in multi-male, multi-female troops, ranging in size between five and ~ 75 individuals (Horrocks, 1986; Pasternak et al., 2013). The troops in our study population are much larger than the species' average (Pasternak et al., 2013). It is possible that group fission is constrained because there is a large contrast in food productivity between the acacia woodland along the river, within which the study troops inhabit, and the considerably lower productivity away from the river (Pasternak et al., 2013). On average, vervet males reach sexual maturity at 5 years of age (Horrocks, 1986) and females typically have their first infant between 3 and 5 years of age (Fairbanks & McGuire, 1984). Females are philopatric, whereas males emigrate from their natal group at sexual maturity. Thereafter, they move roughly every 2.5–3 years (Cheney et al., 1988; Henzi & Lucas, 1980), dependent upon their rank and integration into the female network (Young et al., 2019b).

Vervets are seasonal breeders who give birth to a single offspring. Birth season occurs during the rainy months of the austral spring (Butynski, 1988), i.e. between October and December. The study subjects comprised three birth cohorts from the 2013, 2014 and 2015 birth seasons. The number of juveniles, as well as the representation of each sex varied across cohorts and years (see Table 1).

Table 1 Size of cohorts at birth and at end of the study, as well as their composition.



Cohort	Nb of juveniles born	Nb of juveniles alive by the end of study	Sex
2013	29	27	F = 15
			M = 14
2014	30	29	F = 15
			M = 15
2015	16	15	F = 8
			M = 8

5.3.2 Data collection

We began data collection when all cohort members were nutritionally independent of their mothers and classified as juveniles (Jarrett et al., 2018), which corresponded to an age of approximately 7 months (± 1 months) for the 2013 and 2014 cohorts. Data collection started later for the 2015 cohort, around 11 months (± 1 months), due to logistical reasons. Each troop was followed on foot by one or more researchers on each 10 h study day, 3–5 days a week (PT: 583 days; RBM: 601 days; RST: 613 days). We used electronic hand-held data loggers and commercial software to record data from all visible animals using scan samples conducted every 30 min (see Young et al., 2017, for more detail). Each scan was conducted over a period of 10 min, and we collected data on each animal's activity (feeding, moving, resting and grooming) and all spatial associates within 3 m. When animals were recorded as grooming, we noted the identity of their partners. For agonistic interactions, data were collected ad libitum, with the identity of the individuals involved recorded, along with the direction of the aggression and the outcome of the encounter (i.e. methods follow Young et al., 2017).

5.3.3 Ethical Note

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505).

5.3.4 Data extraction

Grooming and spatial data were treated separately in our analyses. Using the 'netTS' package (Bonnell & Vilette, 2020) in R version 3.5.2 (R Core Team, 2017), both data sets were aggregated over a 60-day window that was then shifted successively by 30 days (see Supplementary material S1 for sampling effort). We estimated the convergence of our measures in both the grooming and spatial proximity networks, using the 'check.windowsize' function of the 'netTS' (Bonnell & Vilette, 2020) package in R and 1000 iterations. The 'check.windowsize' function also allowed us to measure the sensitivity of this subsampling. We found high similar estimates (i.e. converged) and low variation in estimates (i.e. robust to subsampling) using a 60-

day window for degree, strength, and grooming cosine similarity. This means that the chosen window size was able to provide good measures. The estimates were not as robust for skewness and spatial cosine similarity, suggesting the potential for noise in our predicted patterns. Although skewness measures showed a relatively larger amount of noise, a window size of 60 days (2 months) appeared to be a good compromise between desired temporal aggregation and noise in our estimated network measures (Supplementary Figs. S2.1, S2.2). Within each window, spatial association and grooming interactions were aggregated to construct weighted, nondirected networks at the node level (i.e. ego-networks). In other words, each juvenile present within the window had an ego-network created that consisted of its direct connections. The age in days of each juvenile was registered at the start of each time block, as were the number of scans and the mean size of each troop. Applying a temporal dynamic approach allowed us to detect the points at which potential patterns emerged.

To extract ordinal ranks, we used the Percolation and Conductance (P&C) method (Fujii et al., 2015) from the 'Perc' package in R. We chose this method following the training-testing procedure described in Vilette et al. (2020), and included agonistic interactions between all individuals (males, females and juveniles). We used a 4-month burn-in period, specific to each troop, and calculated ordinal ranks for each juvenile within each 60-day window, across the entire study period.

5.3.5 Social Network structure

To capture Kohn's (2019) phases, we extracted the following four measures of network centrality. (1) Degree, which is the sum of each node's connections. This captures the number of partners a focal subject has and indicates the extent of its connectedness to other nodes (Farine & Whitehead, 2015). (2) Strength, which is the sum of each node's connections weighted by the frequency of the interaction with other nodes. An individual with high strength is either weakly associated with many other group members and/or strongly associated with a few group members (Farine & Whitehead, 2015). (3) Skewness, which measures the extent to which the distribution of the edge weights distribution is symmetrical. Positive (right-skewed) values identify individuals that are weakly associated (low strength/weak ties) with many group members (high degree), while having strong associations (high strength/strong ties) with only a small subset (low degree). Negative (left-skewed) values indicate juveniles that are disproportionately placing effort into many partners (degree) with whom they associate very frequently (strength). A skewness of zero indicates that animals are distributing their effort equally across all partners (see Supplementary Fig. S3). To capture the distribution accurately, we calculated skewness only when the number of partners was greater than two. (4) Cosine similarity is used to measure the extent to which the patterning of values in two vectors (a, b) is similar (Newman, 2010). Here, cosine similarity assesses the similarity of the edge weights between two consecutive ego-networks, with values that range between 0 and 1. An individual whose social partners (ego-network) change markedly between time t and $t + 1$ will have a low cosine similarity, whereas individuals whose social partners are similar at t and $t + 1$ will be associated with a high cosine similarity. More details on calculating cosine values are given in the Supplementary material (see Cosine Similarity Measure S4).

5.3.6 Environmental conditions

As food availability may well contribute to the structuring of juvenile associations, we measured troop level estimates of resource availability using the Normalized Difference Vegetation Index (NDVI) (Willems et al., 2009). NDVI data were collected from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images using Google Earth

Engine (Gorelick et al., 2017). The satellites Aqua and Terra (this is the MODIS constellation) collect electromagnetic reflectance from the surface of the earth. NASA uses these two parts of the spectrum to calculate NDVI for any given point on the Earth every 16 days, so the NDVI raster is a derived bitmap image that is created from data collected by the satellite. In this study, area-weighted averages for each territory were generated for consecutive 33-day windows (16 days following and prior to the date of each MODIS raster) by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period (see Young et al., 2019a, for details of the data extraction procedures). NDVI scores, which range between -1 and 1, are higher in more photosynthetically active areas, and are therefore considered to indicate increased plant food availability.

5.3.7 Statistical analyses

We analysed our data within a Bayesian framework, using the 'brms' package (Bürkner, 2017) in R version 3.5.2 (R Core Team, 2017). We used hierarchical generalized additive mixed models (HGAM), which allow the relationships between the explanatory variables and the response to be described by smooth curves (Pedersen et al., 2019). This approach is useful as it does not assume a fixed trend but, instead, estimates a nonlinear trend without a theoretically prespecified shape. In other words, a smooth curve gives the opportunity for nonlinear trends, if any, to emerge, hence giving further freedom for the model to fit the data. We ran all models with four chains and 1000 iterations after specifying weakly informative priors (normal (0,1)). We performed prior predictive checks to ensure that these priors did not drive the patterns obtained from our predictions (see Supplementary material, Prior Predictive Checks Compared to the Predicted Patterns, Fig. S5). Model diagnostics confirmed MCMC convergence, with all $\hat{R}<1.1$

(Gelman & Shalizi, 2012). We used the 'posterior predictive check' (pp_check function) from the 'bayesplot' package (Gabry et al., 2019) to determine the quality of the model fit to the data.

For each measure of network centrality (strength, degree, skewness) and temporal partner consistency (cosine similarity), we constructed two models: one for grooming and one for spatial associations, generating a total of eight models. For all eight models, the model structure was constant. Our data set structure consisted of repeated measures within individual, mother, cohort and troop identity, as well as sex. As such, we let the effect of age vary by these five grouping variables, using factor smooths (Pedersen et al., 2019). We also allowed the effect of ordinal rank to vary by individual, using a factor smooth. Factor smooths implicitly incorporate group-specific intercepts. That is, it creates an estimate for each level of the grouping variable, but only estimates one smoothing parameter for all groups of this grouping variable. Put simply, these grouping variables deviate from the mean and hence vary in their pattern. We expected each grouping variable to vary in its ability to maintain a certain network structure as juveniles aged. Each of these interactions was added as a single smooth. We controlled for variability in environmental conditions by including NDVI as single smooth to the model. Additionally, a single smooth for troop number was included to address variation in troop size, along with one for age, to account for developmental variation. Continuous variables were scaled and mean-centred (see Supplementary material S6 for model structure). Apart from the number of spatial partners (i.e. spatial degree), a Poisson model was run for all our count variables (three in total). As dispersion issues are common with Poisson models, we ran an analysis of residuals from the models to detect any dispersion issues ('DHARMa' Package). We addressed dispersion issues present in our three models by running models with a negative binomial distribution. When this approach did not remove the dispersion issue, hurdle models were run (Hilbe, 2017). To determine which model to report in the main text, we used three approaches in concert: (1)

Models were compared using leave-one-out cross-validation ('LOO'; Vehtari et al., 2016) with the 'loo_compare' function of 'brms'; (2) We looked at the magnitude of the dispersion, from the analysis of residuals; (3) We used the posterior predictive checks. Once the model that fitted best our data set was found, we compared its estimates with the estimates of our simpler original Poisson model. This was used to assess whether the influence of the dispersion issue affected our results. As this was not the case for any of our three models, we report the simpler Poisson models in the main text and provide the necessary details regarding the other models in the Supplementary material (Figs. S8–S10). As such, when considering the influence of age and sex on the number of partners, we constructed a binomial for spatial associations as the maximum number of spatial partners was known. That is, we used a binomial model (Hilbe, 2017) with troop size as the number of trials to model the number of partners. We specified a Poisson distribution for the number of grooming partners, as well as the frequency of spatial and grooming associations. Finally, for all models run with a Poisson distribution (degree and strength), the log of the total number of observation sessions within the aggregated sample period was included as an offset in the model to account for differences in observation effort. When using the distribution of edge weights (skewness) as our response variable, we constructed a skew-normal model for spatial and grooming associations, as the response values were all positive with a skewed distribution. For both types of interaction, a zero-one inflated beta model was constructed to look at partner preference (cosine similarity), due to the presence of a large proportion of zeros. All the model summary tables are presented in the Supplementary material (Figs. S7–S14), accompanied by Dharma nonparametric dispersion tests and posterior predictive distribution plots, when required.

Given the nature of the statistical models, as well as the inclusion of interaction effects, direct interpretation of model estimates is not straightforward from a summary table. To aid interpretation, we generated whole model predictions using the ‘fitted()’ function, from the ‘brms’ package, to extract the fitted values of our models. Variables that were not of direct interest were fixed to their mean (e.g. troop size, NDVI, rank), while predictions were made for the variables of interest (i.e. age and sex). These predictions were then used to construct predictive posterior plots with the ‘ggplot2’ package (Wickham, 2009). These plots allowed us to see how males and females differed in their response to the average effect of our response variables. Given their interpretative familiarity, we specified the 95% credible intervals (CI) in our plots to assess whether the sexes differed meaningfully in the structure of the revealed patterns. That is, we considered whether the CIs for females and males overlapped completely (i.e. no detectable difference between the sexes) or not at all (i.e. a meaningful quantitative difference between the sexes). The raw data, plotted with the predicted patterns, are presented in the Supplementary material (Figs. S15–S16), and are excluded here to make the patterns easier to see. Model main effects are presented as summary statistics (Tables S7–S14 in supplementary material) for posterior means, standard errors, 95% CIs, along with conditional R2 values for each model, estimated using the ‘bayes_R2’ function (Gelman & Shalizi, 2012).

5.4 Results

5.4.1 Social network structures

5.4.1.1 Spatial ego-network structure

Neither degree nor strength displayed the predicted pattern of high initial values followed by a decline and levelling off (Fig. 2a, b). Instead, both sexes displayed an overall decline in the number of partners as they aged. This overall pattern was interspersed with a more dramatic drop in the number of partners at around 2.5 years of age, followed by an increase in both sexes, with males showing a more precipitous drop and greater subsequent increase than females. Predictions were estimated with a mean troop size fixed at 48 individuals, revealing that at a very young age, both sexes were spatially associated with almost the whole troop (mean degree = ~ 44). For strength, the general trend, for both sexes, was a cyclical pattern of peaks and troughs that aligned with the annual birth season, with higher strength during the birth season, accompanied by an overall and constant decrease (Fig. 2b). Despite the general similarity in the pattern shown, female strength values were higher than those of males throughout the developmental period. As might be expected, given these results, neither skewness nor cosine similarity showed the predicted increase over time. Instead, both sexes displayed fluctuating positive skewness values across birth seasons (Fig. 2c), with a more nuanced increase for the third birth season. During the second birth season, females displayed much higher skewness values than males. Spatial cosine similarity values declined over time for both sexes, with the deceleration being more pronounced for males (Fig. 2d). Nevertheless, both sexes sustained high cosine values overall. Lastly, this overall decrease was interspersed with a slight increase in cosine similarity values during the second birth season.

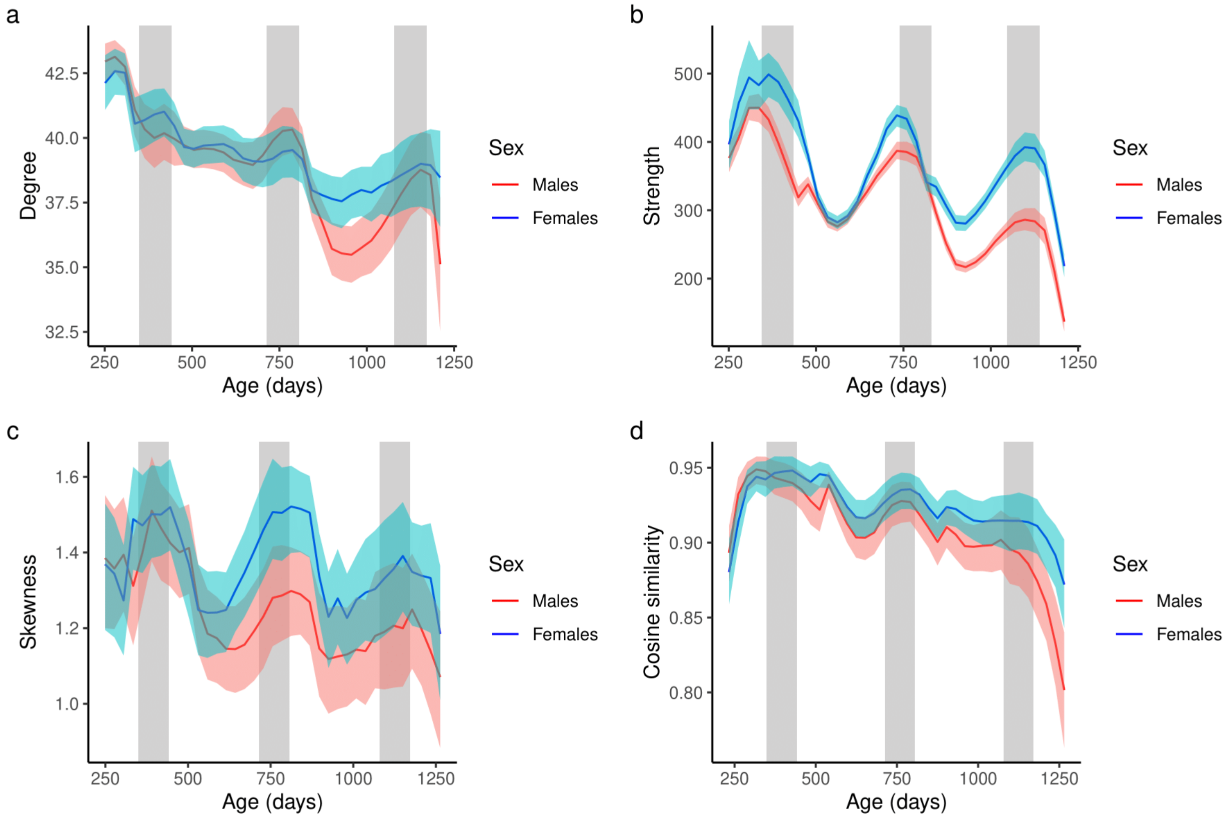


Figure 2 Variation in the (a) degree (b) strength (c) skewness and (d) cosine similarity of spatial associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were estimated with mean troop size fixed at 48 individuals.

5.4.1.2 Grooming network structure

Again, observed patterns did not support our predictions. Rather, the mean number of grooming partners steadily increased over time for both sexes. The increase was, however, slower for males, with the result that divergence between the sexes also increased over time (Fig. 3a). There was an increase in grooming strength observed in females, before settling down following the first birth season. A peak in strength was then observed between the second and third birth season. This overall increase in strength was not mirrored by males, where strength declined with age (Fig. 3b). Yet, the same peak was observed, to a lesser magnitude, between the second and third birth season. The sexes thus displayed meaningfully different patterns in their grooming associations. With respect to skewness, females showed a fluctuating positive pattern over time, which reached a somewhat bumpy plateau between ~ 1.5 and 2.5 years of age, followed by a decrease (Fig. 3c). This pattern was mirrored by males, although at a distinctively lower level. In the case of cosine similarity in grooming, both sexes began with high mean cosine values, followed by a consistent decline in partner similarity as they grew older (Fig. 3d), with the decrease being somewhat more pronounced for males.

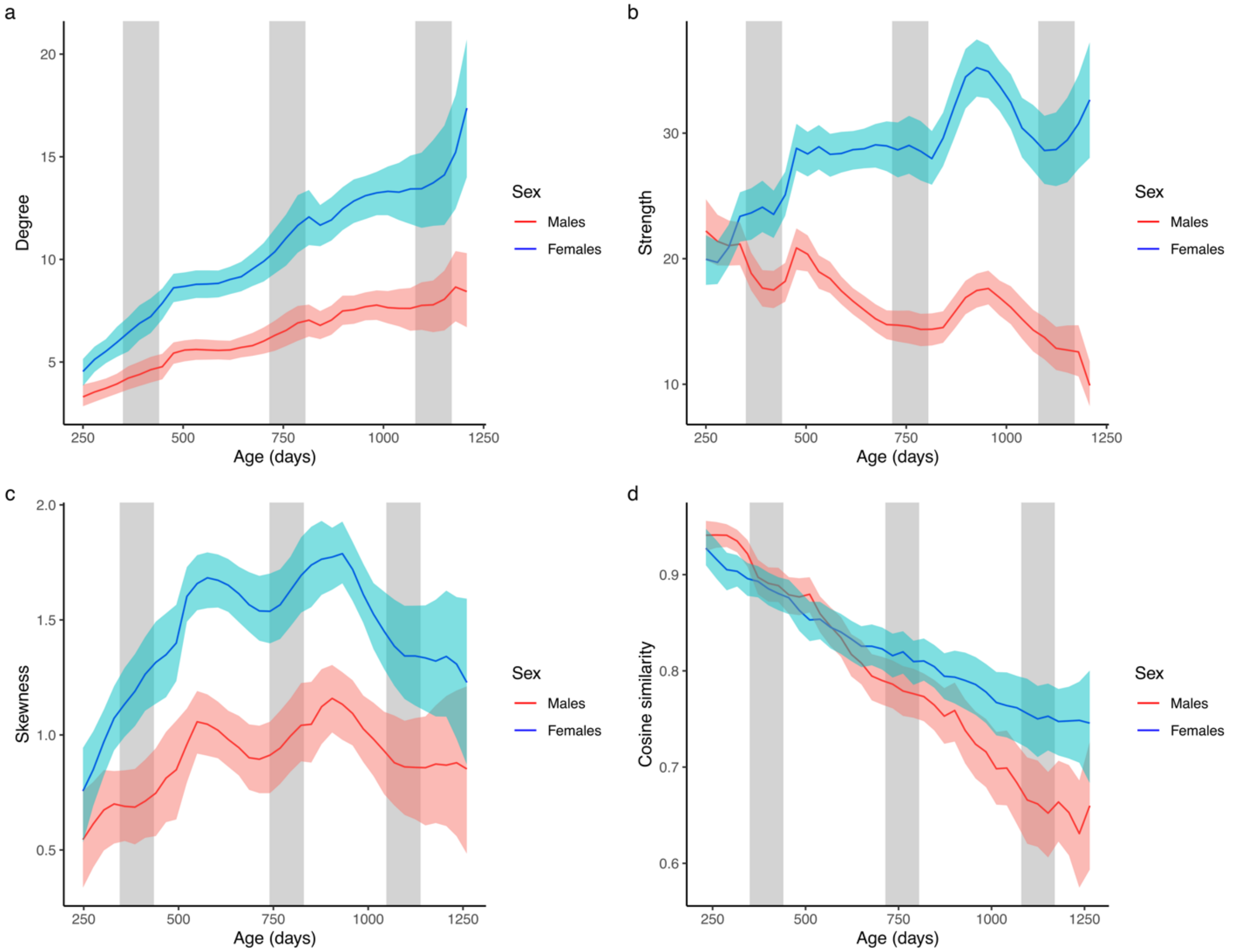


Figure 3 Variation in (a) degree (b) strength (c) skewness and (d) cosine of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were calculated with a mean troop size fixed at 49 individuals.

5.5 Discussion

Taken together, our results did not show convincing evidence for the developmental patterns of social engagement predicted by Kohn (2019). That is, for both spatial proximity and grooming networks, the high initial observed values of degree and strength were not followed by a period of consistent decline that eventually reached a plateau, representing the formation of a stable network comprising a subset of similar contacts.

If we consider spatial proximity first, we found that, for both sexes, although it underwent an overall decline, degree nevertheless remained high across development, and did so despite a dramatic drop observed around the 2.5-year mark. In the case of strength, both sexes showed a striking cyclical pattern corresponding to the annual birth season, with an overall decline in strength across time. We also did not find the patterns expected for skewness and cosine similarity. Instead, values for both skewness and cosine similarity were high initially and remained so over time. However, this is not to suggest there was no variation at all. In the case of skewness, there was again evidence for a cyclical pattern corresponding to each birth season, but at a lower magnitude during the third. For cosine similarity, although we found a decline over time, the magnitude of this shift was small, and values remained high across the entire period.

In social network terms, these results suggest that, for both sexes, spatial ego-networks became smaller and also diminished in density (i.e. juveniles were less frequently in proximity to other individuals). The skewness measure suggested that these ego-networks were composed of numerous weak ties and a few strong ones, with the strong ties remaining similar through time (which accounts for the sustained high cosine values). In other words, individuals were not distributing their effort equally. This finding comes as a surprise for two reasons. First, we initially assumed that individuals would find it harder to structure their spatial interactions consistently. Second, given the observed seasonal variations in the frequency of interactions, we would have expected to observe a loss of structure at some point (i.e. the distribution no longer being positively skewed). This suggests that the arrival of a new cohort of newborns into the group led to changes in size, composition and dynamics of the group, to which juvenile interactions were sensitive. Previous work has shown that attraction to newborns may promote close spatial associations with mothers (Silk, 1999, 2009; Silk et al., 2003), leading spatial social structure topologies to become more centralized. This is indeed what we observed with spatial associations, where the upward shifts in strength during the birth season (Fig. 2b) combined with the positive fluctuations in skewness (Fig. 3c), suggest that these associations become centred on a subset of individuals at this time (i.e. the surplus of effort put on fewer strong ties increases the contrast between weak and very strong ties, leading to an increase in skewness). Future studies might helpfully investigate whether the birth of a new infant draws juveniles back to their mothers and her associates, and also how strength and skewness relate to each another. In other words, it would be useful to address whether the increase in frequency of associations leads juveniles to focus more tightly on a subset of their partners (increase in skewness) or whether is it the change in their ego-network structure (high skewness) that allows them to then increase their association frequency.

If we now turn to grooming patterns, although we also found distinctive patterns across time, once again these did not conform to Kohn's (2019) developmental model. We found that juvenile females were characterized by low degree at the beginning of the study period followed by a consistent increase in the number of partners (from around five partners at the beginning of the period up to 15 partners at the end) and their frequency of interaction over time. This raises issues concerning time budget constraints and social coordination. Among cercopithecines, adult females can groom across the entire female cohort (i.e. the total number of females in the group) as long as this cohort remains below some threshold size (e.g. seven for female mountain baboons, *Papio cynocephalus ursinus*: Henzi et al., 1997; five to six for vervet monkeys: Henzi et al., 2013). Above this level, grooming cliques become smaller due to problems that arise with respect to social coordination. As such, the large grooming cliques acquired by juvenile females seem anomalous. However, the increase in grooming partners was also accompanied by an increase in positive skewness values until 2.5 years of age. This suggests that the average female frequently groomed a small subset of partners (strong ties), while the remainder of her partners were groomed infrequently (weak ties). Furthermore, throughout the first 2.5 years, the contrast between weak and strong ties increased, suggesting that juvenile females were not forced to reduce or cap the number of partners in their grooming cliques, but instead underwent a shift in how they distributed their grooming within their networks as degree increased. Around 2.5 years of age, however, a decrease in skewness was observed, although values remained positive. This decrease was accompanied by an increase in degree, which suggests that the contrast between strong and weak ties became less stark. That is, some compromises may take place on strong partners, rather than on the number of partners, where juveniles invest less in their strong ties. Therefore, it would be interesting to further investigate how degree and skewness respond in relation to variation in troop size.

In contrast to the female pattern, males showed a much shallower rise in degree over time, along with a decrease in the frequency of interactions (Fig. 3a, b). Males also showed generally high skewness values, with an increase across the first 2.5 years, while their values were nevertheless consistently lower than those for females (Fig. 3c). Thus, although male ego-networks showed the same structure of weak and strong ties, this was not as pronounced as it was for females. Males were, however, similar to females with respect to cosine estimates, again showing a constant decline in partner similarity over time (Fig. 3d). Taken together, these patterns suggest that males were less strongly integrated into grooming networks than females

(Fig. 3a, b)—a pattern also found in previous studies (Blaszczyk, 2018; Cords et al., 2010; Jarrett et al., 2018). This sex difference may arise because males migrate at sexually maturity and are less likely to invest in the development of enduring social relationships.

Although we have treated spatial proximity and grooming as two separate components of the animals' social niche, examining these patterns in concert can help our understanding of the process by which juveniles build their niches. First and foremost, spatial proximity ego-networks showed seasonal patterns, whereas grooming ego-networks did not. As predicted, juveniles associated more frequently with spatial partners than with grooming partners (Figs. 2, 3b) and they associated with more spatial partners (Figs. 2, 3a) than they did grooming partners. One possible interpretation, then, is that juveniles have different interaction styles (passive versus active) across behavioural contexts. It may be that, for juveniles, regulating who is within 3m of them may be challenging. A grooming interaction, in contrast, involves two willing partners, allowing a more active, controlled choice of association, in terms of the effort invested and the partners targeted. Against our predictions, however, spatial proximity associations showed higher partner stability and revealed ego-networks composed of many weak ties and few strong ties. One possible explanation here is that spatial ego-networks may be less robust to large-scale changes at the level of the group, such as the arrival of the birth season, where the sudden influx of multiple newborns may lead juveniles to be in proximity to others more frequently due to the increased attention received by their mothers and new siblings. In contrast, grooming interactions are less likely to be affected by such large-scale shifts in group dynamics because juveniles can control partner choice. However, they may be more likely to respond to smaller-scale, more continuous fluctuations, such as shifts in time budget demands with increasing troop size. Indeed, adult patterns of grooming in our population respond to contingent ecological and demographic conditions in just this way (Henzi et al., 2013; Young et al., 2019a).

Although our patterns did not resemble those predicted by Kohn (2019), a common pattern was observed in the structure of the networks (i.e. social niche components) for both sexes. This finding, we believe, allows us to explain why Kohn's (2019) model apparently does not describe social integration in our population. Our data suggest that individuals' ego-networks are composed of many weak ties and few strong ties. While the focus of many network studies often falls on the identity and traits of the individuals (the "who") that comprise an ego-network, we suggest that, in this case, it is the structure of the network itself that is of developmental relevance (the "how"). Kohn's (2019) model is largely focused on the "who", where the third and final step is based on the establishment of preferred relationships. What our findings suggest is that juveniles are also building a network of a particular structure, as well as establishing preferred relationships. We interpret the formation of this subset of strong ties as a way to create a more secure social space for an individual, which we can characterize as a "social bubble". Having found this additional "level" of structure, it raises the possibility that, by considering the overall ego-network, we have focused on the wrong level, and that it is within the layer of strong ties that Kohn's (2019) proposed phases operate. Taking a closer look at social bubble formation and composition over time is therefore warranted, as it seems likely that this sets the social conditions to which juveniles are exposed (see Kohn et al., 2022). For example, in terms of spatial proximity, an animal that is broadly spatially integrated, with numerous weak ties, may ensure enhanced protection against predators, while a more consistent social bubble of strong ties may guarantee protection against potential conspecific competitors. In a grooming setting, infrequent grooming partners may translate into more opportunistic grooming that serves immediate goals (Barrett & Henzi, 2006), while a social bubble of frequent grooming ties, perhaps with kin, may serve other fitness-related goals (Josephs et al., 2016; Silk et al., 2006).

Therefore, our findings point to the necessity of better understanding the relative role of strong and weak ties in predicting primate fitness, as suggested in other recent work (Ellis et al., 2019; Ostner & Schülke, 2018; Schülke et al., 2022).

Finally, another component likely to have had an impact on our observed patterns is the chosen timescale. Kohn did not explicitly consider temporal dynamics and did not give details of the period over which these phases were believed to occur, and many possible timescales are possible, from days to weeks to, as we have considered here, years. With regard to social integration in our population, questions about its duration and whether individuals all integrate at the same pace remain unanswered. It is possible that Kohn's (2019) three phases may, in concert, operate over a shorter timescale than we have considered here. It is also possible that each phase may have its own particular duration, and that this may vary individually. For example, in species where juveniles can explore their social group without being socially at risk (e.g. where there is no infanticide), it may be that the exploration phase takes longer than the other two phases. In addition, as relationships in a social group represent a dynamic negotiation between dyads in response to ecological factors and other aspect of group dynamics, it is also possible that Kohn's (2019) phases may recur, at least to some degree, each time the social group undergoes a change in size and composition. That is, such changes may disrupt and relaunch the network formation process, resulting in a series of network formation cycles, rather than a singular, clean, linear progression. Investigating individual variation may therefore help us understand the pace at which juveniles integrate into the group, and hence the appropriate time frame needed to cover the entire process of integration

Overall, consideration of developmental social dynamics has allowed us to get a more detailed appreciation of how social networks and social niches are constructed over time. One obvious point to make is that both spatial proximity and grooming patterns did not reveal any shift, either gradual or sudden, that marked the end of the juvenile period and the emergence of an adult pattern. This contrasted with gross sex differences in patterning, where a clear differentiation between male and female social engagement became increasingly apparent. This suggests that the former pattern does not simply reflect a methodological failure to detect a pattern that was, in fact, there. Consequently, our findings do not indicate any kind of "social revolution" occurring at a key point in development as suggested for other species (Kulik et al., 2015), whereby a typical juvenile form of engagement is discarded in order to commence the daily business of adulthood. The early and distinct behavioural sex differences found in our population also suggest that the migrating males and philopatric females may adopt different social strategies as soon as they become independent of their mothers and do not arise as a result of sexual maturity. It seems much more likely that, as we have seen, there are no large-scale shifts in social engagement, but rather continuous multiple small adjustments that result in the formation of a beneficial network structure. Thus, ongoing social dynamics may promote only short-term stability that can be expected to shift over time, and juveniles form the network structures that serve them best for the time being (i.e. they are not engaging in suboptimal patterns of engagement as part of the process of working towards a more beneficial end-goal). That is, being able to coordinate activities and sustain proximity with specific partners calls for individuals to be able to flexibly adjust to temporal shifts in their social network structure throughout the developmental period. Hence, it seems reasonable to consider the possibility that social integration, in general, may be a process of ongoing continual adjustment achieved through SNC among highly social species. In turn, SNC offers a mechanism by which individuals can form the network structures that best serve their needs given the ecological and social conditions they face. Here, SNC apparently enables young animals to embed themselves in more secure ego-network structures (social bubbles), while retaining the benefits of broader integration in the group through the presence of weak social ties (McFarland et al., 2017).

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5.7 Supplementary material

S1: Sampling effort across our study period, by troop

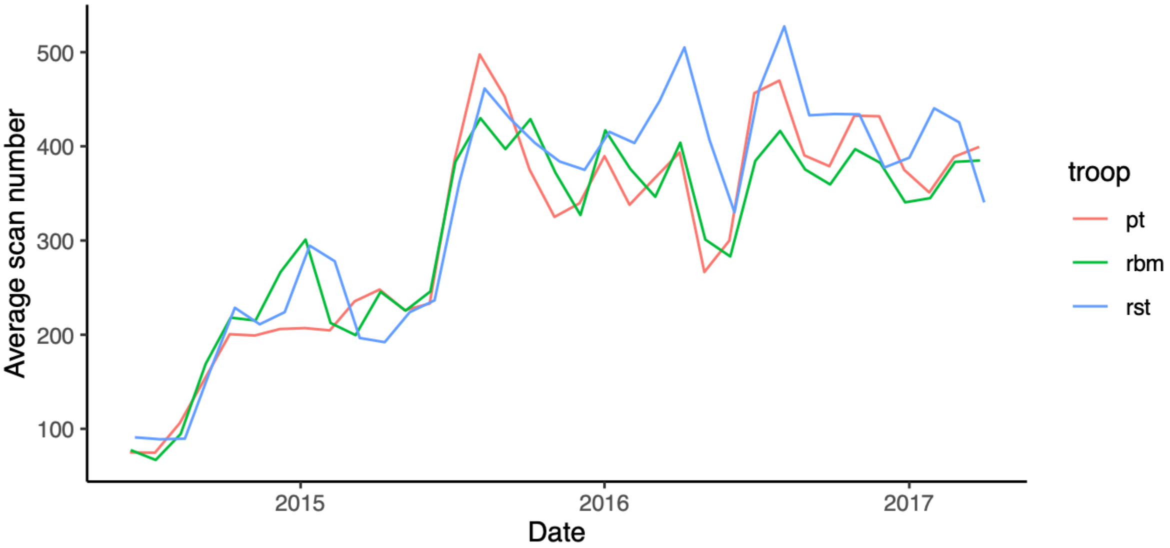


Figure S1 Variation in the average number of scans per window, by troop.

S2: Determining Stability and Robustness of Network Window Size

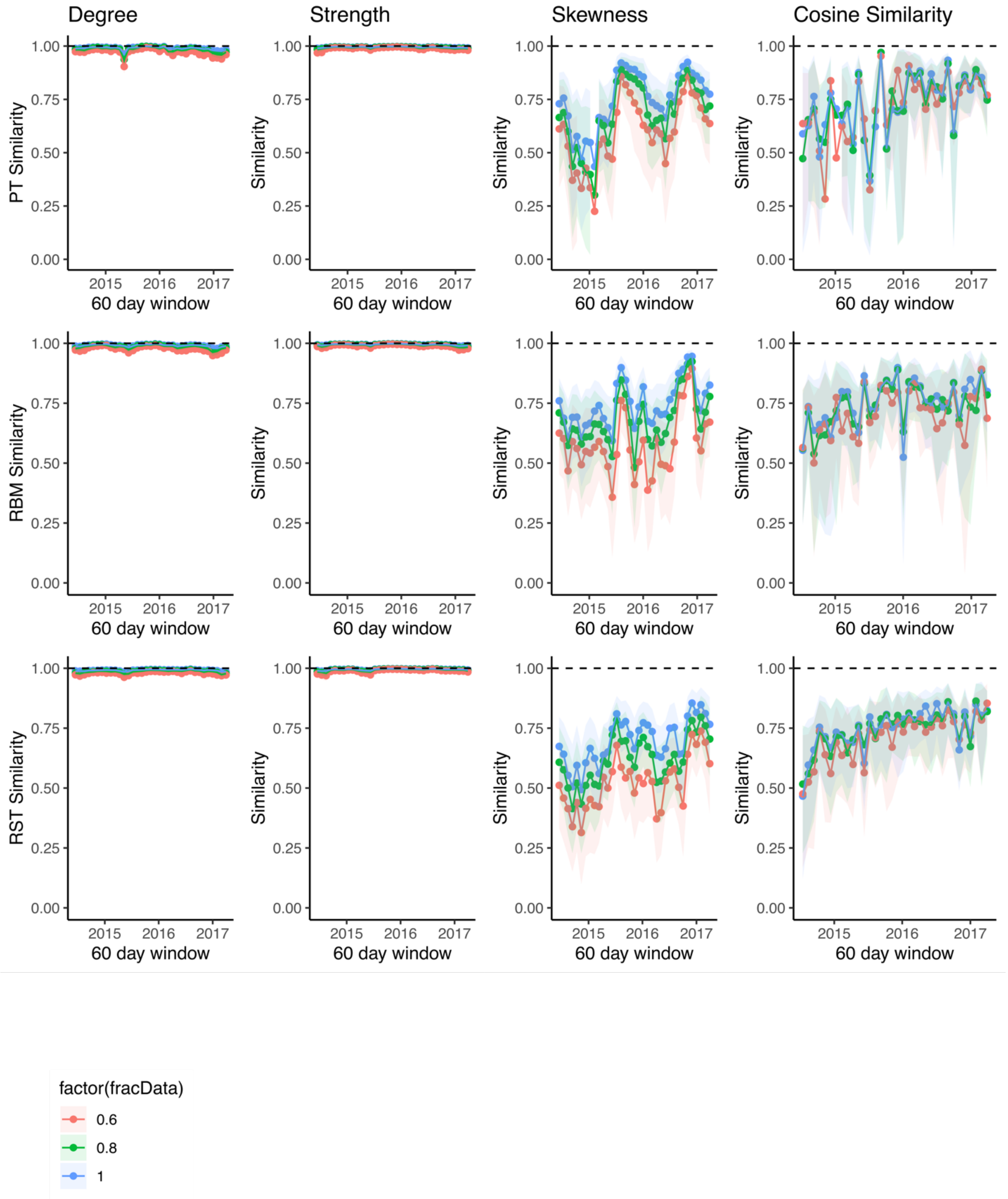


Figure S2.1 Results of estimating the lower bound of window size choice using bootstrapping and subsampling for the spatial proximity networks across 60-day sampling windows for each troop (rows) and each of our measures (columns). The y-axis is the correlation between the network level measures of nodes in the observed and bootstrapped networks. The lines and points represent the mean cosine similarity, while the shaded areas represent the 95% CI calculated from 1000 bootstrapped samples. Cosine similarities were estimated for subsamples of the data: 100%, 80%, and 60% to quantify the influence of potential missing data on network measures.

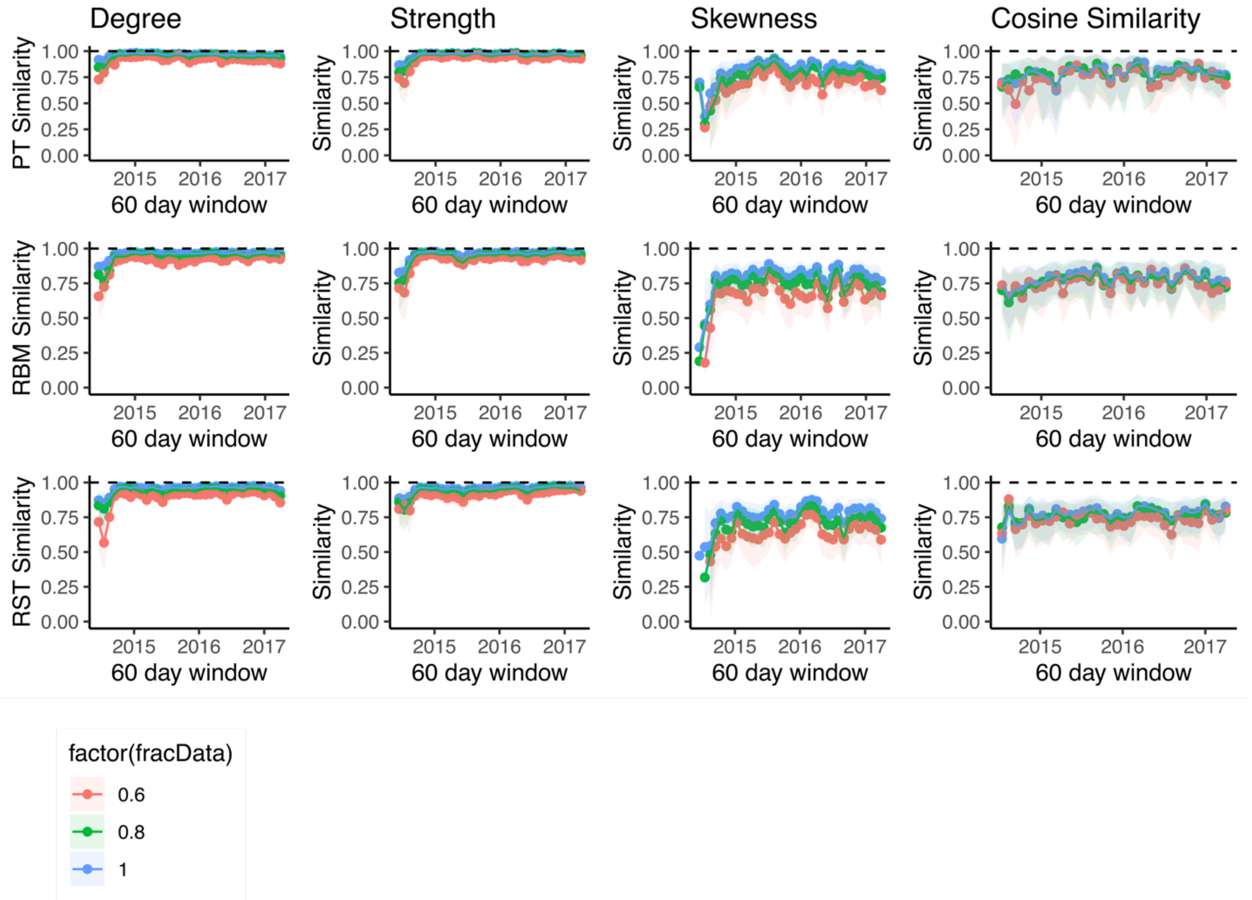


Figure S2.2 Results of estimating the lower bound of window size choice using bootstrapping and subsampling for the grooming networks across 60-day sampling windows for each troop (rows) and each of our measures (columns). The y-axis is the correlation between the network level measures of nodes in the observed and bootstrapped networks. The lines and points represent the mean cosine similarity, while the shaded areas represent the 95% CI calculated from 1000 bootstrapped samples. Cosine similarities were estimated for subsamples of the data: 100%, 80%, and 60% to quantify the influence of potential missing data on network measures.

S3: Skewness measure

Skewness is a measure of the lack of symmetry observed in a distribution. Here, we are looking at the weight distribution.

Positive values for the skewness indicate right skewed data, which means that the right tail is long relative to the left tail (Figure S3.1). The mean (red) of positive skewed data is greater than the median (green). More concretely for us, a positive skewness means that most of the weight distribution is on low values while the tail of the distribution is on higher values. This means that a juvenile with a positive skewness is predominantly associated with many partners (high degree) infrequently (low strength). The rest of their associations concentrates on a subset of few partners (low degree), but at high frequency (high strength).

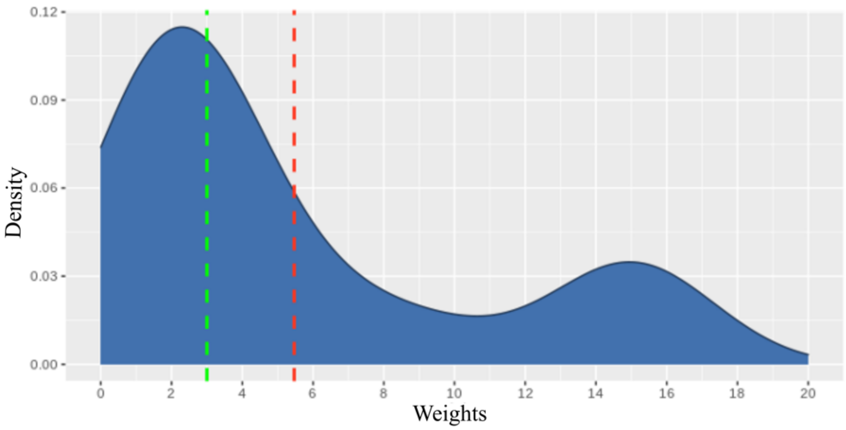


Figure S3.1 Distribution of weights with a positive skewness. The mean is represented in red. The median is in green.

The skewness for a normal distribution is zero (Figure S3.2). In this scenario, juveniles distribute their effort equally among their partners.

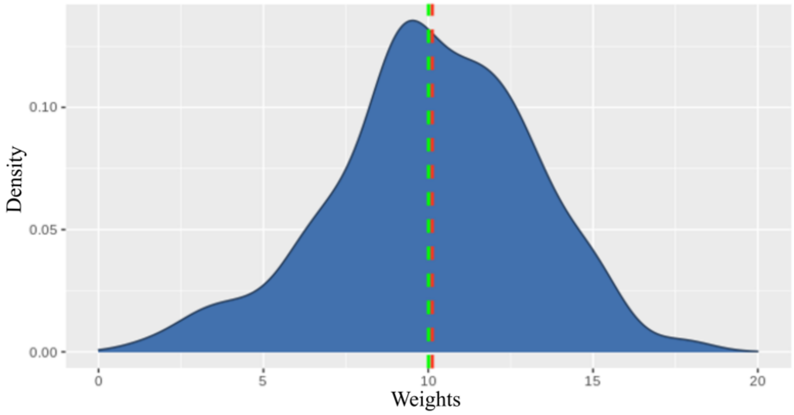


Figure S3.2 Distribution of weights with a null skewness. The mean is represented in red. The median is in green.

Negative values for skewness indicate data that are skewed left, meaning that the left tail is long relative to the right tail (Figure S3.3). In a negative skewed distribution, the median is greater than the mean. Concretely, a juvenile with a negative skewness is distributing predominantly its effort into a high number of partners (degree) with whom they associate very frequently (strength). The rest of the juvenile's effort goes into a few partners (low degree) with which the focal barely interacts (low strength).

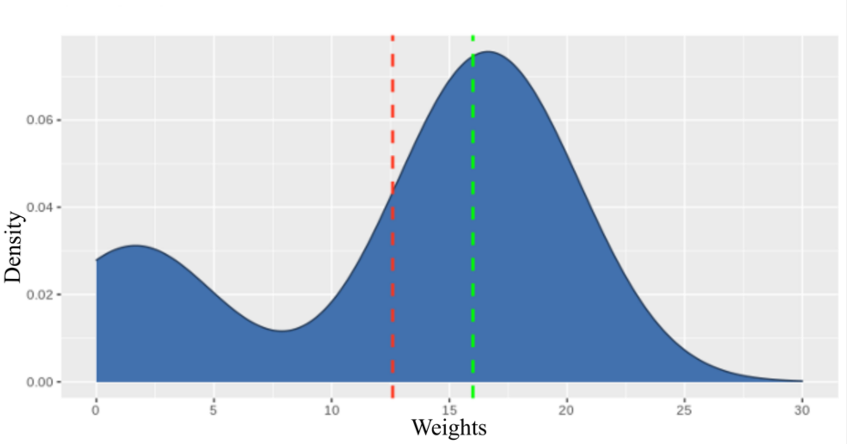


Figure S3.3 Distribution of weights with a negative skewness. The mean is represented in red. The median is in green.

Note that without a distribution (e.g., less than 3 weights measures, and hence three partners), the measure cannot capture the distribution (= undefined skew). Therefore, skewness was only inferred when the number of partners (degree) was above 2.

<u>S4</u>: Cosine similarity measure

Cosine similarity assesses the extent to which the patterning of values in two vectors (a, b) is similar, making it appropriate for differing sample sizes (Newman, 2010). This metric is a measurement of orientation/style, not one of magnitude like Euclidean distance, and is expressed as the cosine of the angle between two vectors.

$$cos\theta = \frac{a.b}{\| a \| \| b \|}$$

In our case, a vector is a suite of weights, each weight corresponding to the number of times a distinct dyad (the focal and its partner) was seen interacting. Cosine similarity offers the possibility to center the variable (i.e.., the suite of weights) by subtracting the mean of the variable to every value of the variable.

When doing so, cosine similarity becomes the equivalent of the Pearson correlation. When not centred, the measure is called cosine similarity.

Regarding the Pearson correlation, the values range from −1 to 1. A value of exactly 1 implies the juvenile's partners between time t and time t+1 are exactly the same. Graphically speaking, in this case, all data points lying on a line. The correlation sign is determined by the slope of the

line. A value of 0 implies that there is no linear dependency between the partners at time t and time t+1. A value of -1 would tell us that we see the opposite relationship observed at time t. Cosine similarity, however, looks at the angle between two vectors of points, and not the slope. If the direction is similar (low angle), then the two vectors are similar. If the two vectors point in opposite direction (large angle), then they are dissimilar. In our case, the cosine similarity values range between 0 and 1 as frequencies of interactions can't be negative.
As correlation estimates similarity based on how weights have changed relative to other grooming partners, while cosine estimates similarity assesses similarity based on how direction of weights of all the partners have shifted overall. As such, we chose not to center our variable and used cosine similarity measure.

S5: Prior predictive checks compared to the predicted patterns

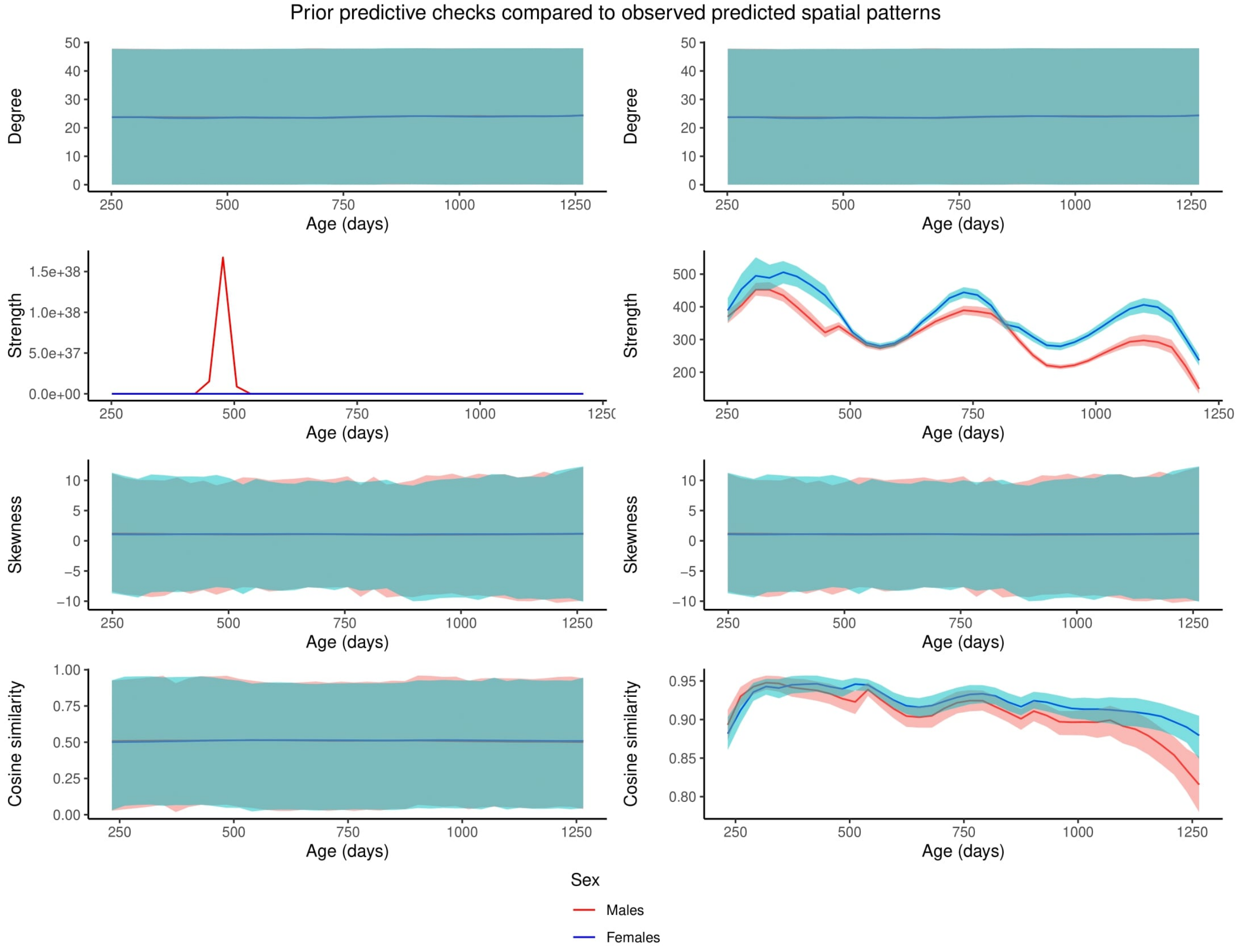


Figure S5.1 Comparison between prior predictive checks (on the left) and the predicted variation in the degree, strength, skewness, and cosine similarity of spatial associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Predictions were estimated with mean troop size fixed at 48 individuals.

Looking at the prior predictive checks for strength, we see a pattern for age. This is common when using models with splines and weakly informative priors entered on zero. However, when comparing the prior predictive checks with their respective observed variation through age, they are different, which tells us that the way the model updates from those priors is not being impacted by our priors. For degree, skewness and cosine similarity, there are no patterns for age, which means that our data are driving the observed patterns and not our priors.

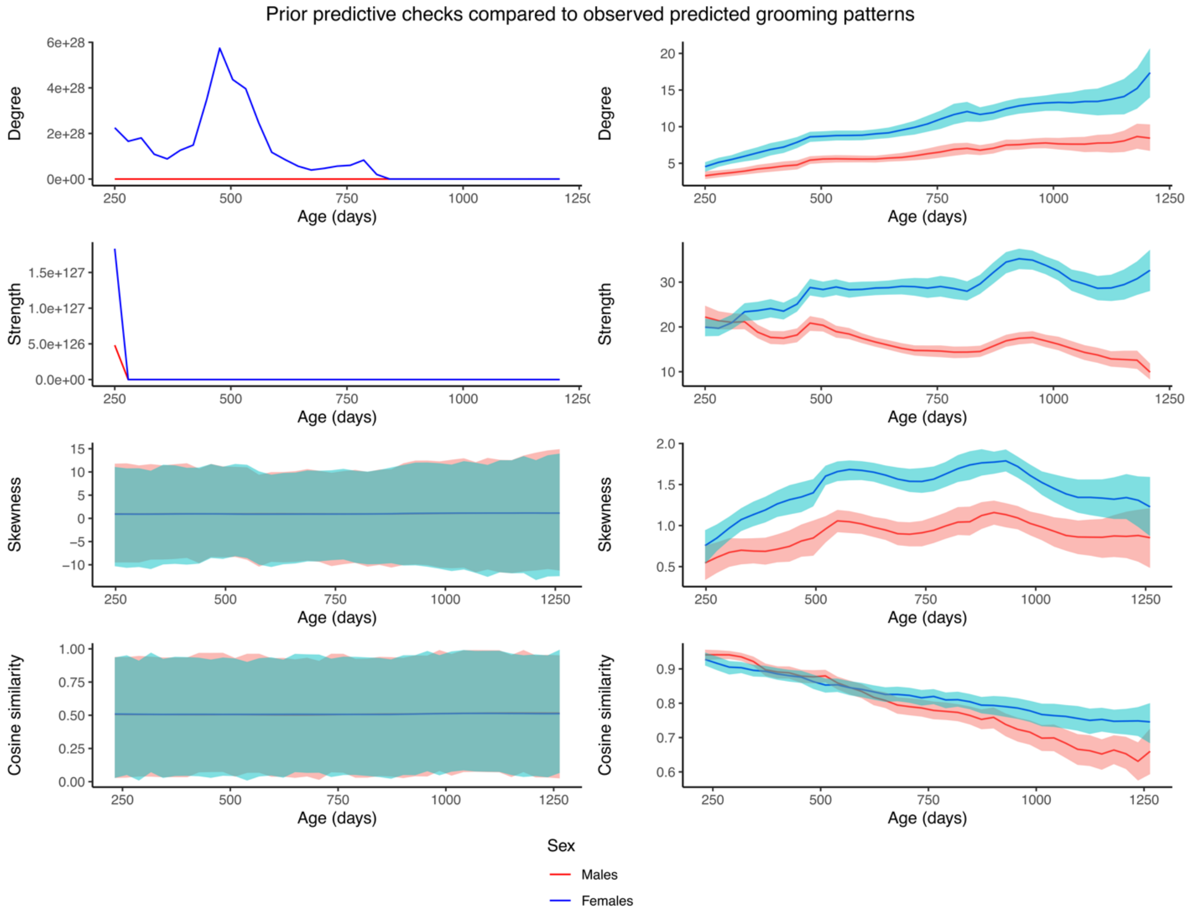


Figure S5.2 Comparison between prior predictive checks (on the left) and the predicted variation in the degree, strength, skewness, and cosine similarity of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Predictions were estimated with mean troop size fixed at 49 individuals.

Looking at the prior predictive checks for degree, we see a pattern for age in females, and none for males. The same goes for strength, with our prior predictive check, where we see a pattern at a very young age for females, and a slight indication of a pattern for males. Again, this common to see when using models with splines and weakly informative priors centred on zero. However, when comparing the prior predictive checks with their respective observed variation through age, they are different, which tells us that the way the model updates from those priors is not being impacted by our priors. For both skewness and cosine similarity, there are no patterns for age, which means that our data are driving the observed patterns and not our priors.

In a second phase, we showed that our model results were not sensitive to the priors, by changing our weakly informative priors (normal (0,1)) to more informative ones (normal (0, 0.1) and then normal (-4, 4)). By restricting the range of values that the outcome is likely to take, we sought to see whether the results of our models would change. Here, we focused on the three count variables that had originally showed prior predictive checks that revealed that the models predicted a wide range of values (i.e., grooming degree, spatial and grooming strength).

When constraining our priors (normal (0, 0.1)), we observe prior predictive checks (on the left) and the predicted variation in the spatial strength, grooming degree and grooming strength by age and sex for juvenile vervets (Figure S5.3). When comparing the model results using weakly and informative priors, we see no difference in our results.

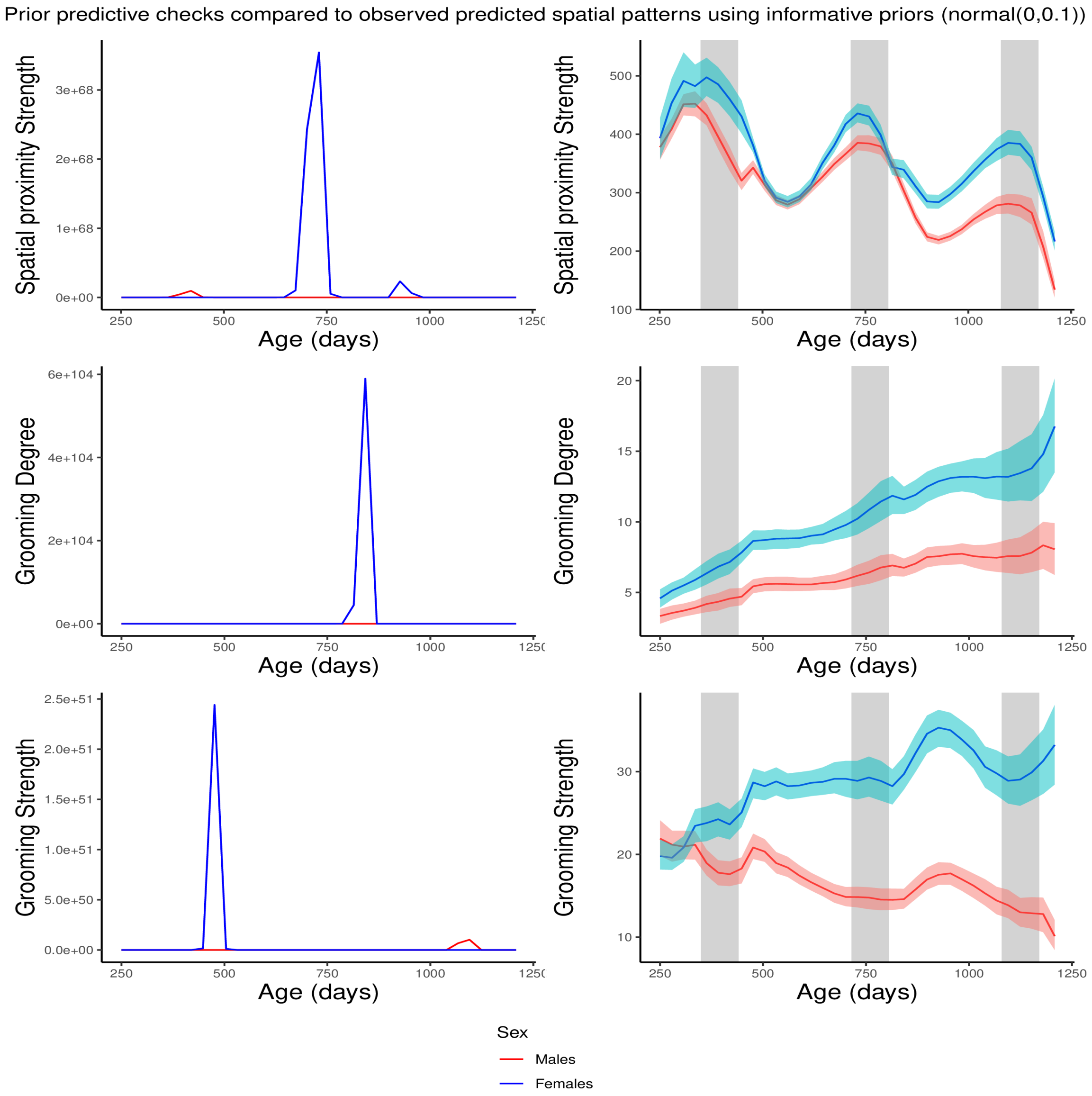


Figure S5.3 Comparison between prior predictive checks (on the left) and the predicted variation in the degree, strength, skewness, and cosine similarity of grooming associations by age and sex for juvenile vervets using normal (0, 0.1) priors. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Predictions were estimated with mean troop size fixed at 49 individuals.

Finally, when using priors even more constrained (normal (-4, 4)), we still observe the same results (Figure S5.4). As such, we feel confident that our models are not sensitive to our choice of priors.

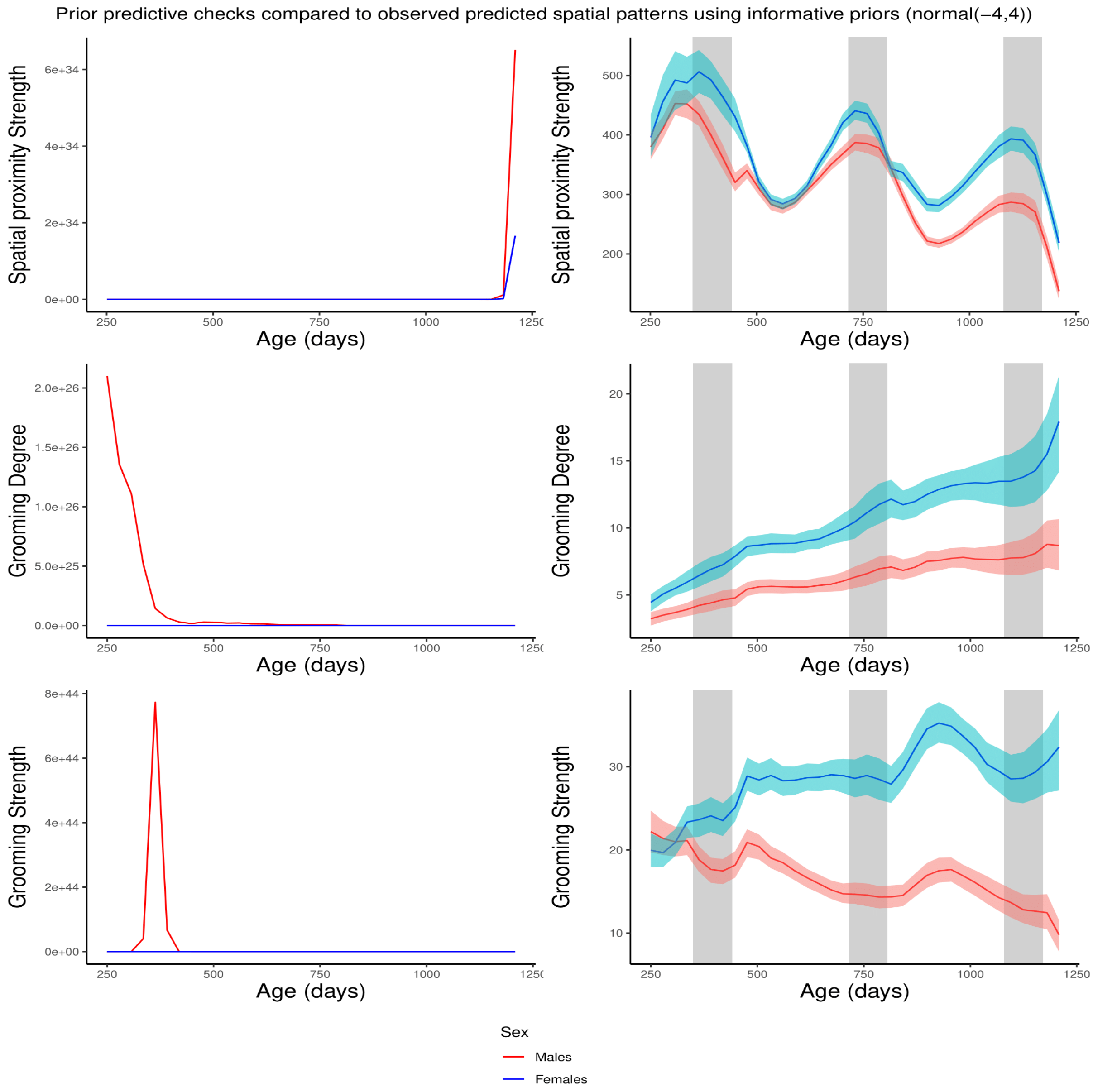


Figure S5.4 Comparison between prior predictive checks (on the left) and the predicted variation in the degree, strength, skewness, and cosine similarity of grooming associations by age and sex for juvenile vervets using normal (-4, 4) priors. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Predictions were estimated with mean troop size fixed at 49 individuals.

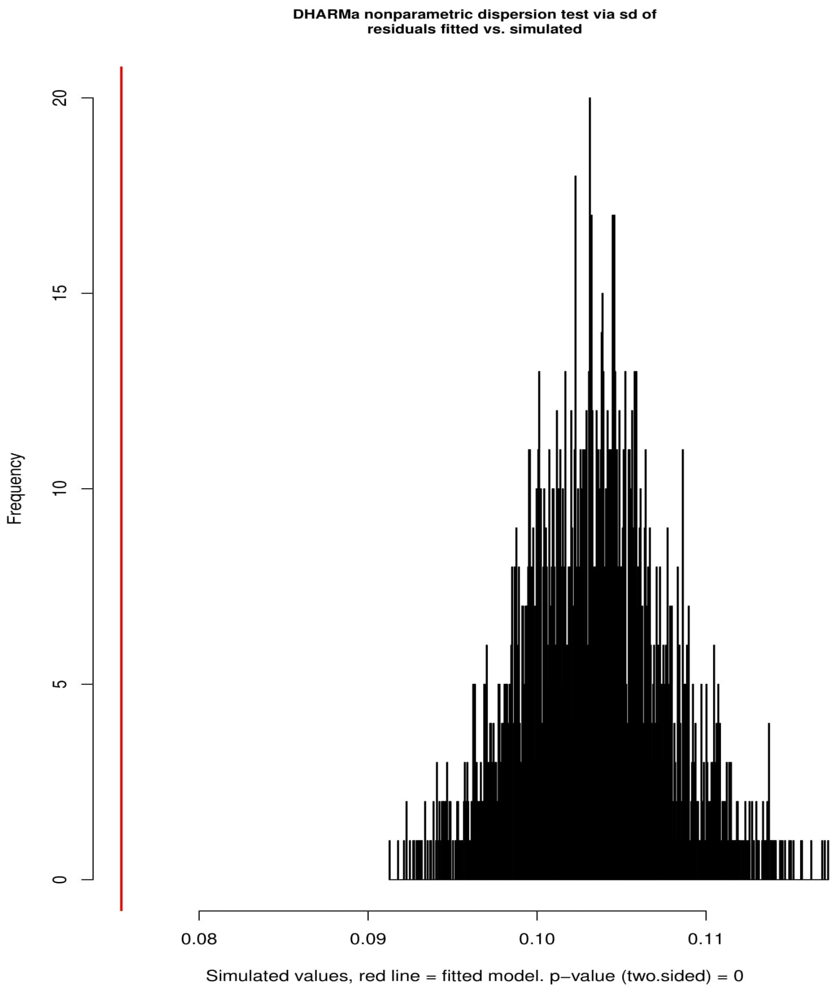
S6: models’ structures

Summary of the model parameters used in hierarchical generalized additive models (HGAMs) to assess the influence of age and sex factors and our response variables. All independent variables and interactions had a smooth term around them. All continuous predictor variables were mean-centered and standardized by two standard deviations to allow for effect size comparisons across continuous and dichotomous variables (Gelman 2008).

Interaction type	Response variable	Fixed effects	Interactions	Distribution
Spatial proximity	Degree	Age Scan.nb NDVI	Age by juvenile ID Age by cohort ID Age by sex Age by troop ID Age by mother ID Rank by ID	Binomial
	Strength	Age NDVI Troop.nb	Same as above	Poisson
	Skewness	Age Scan.nb NDVI Troop.nb	Same as above	Skew-normal
	Cosine similarity	Age Scan.nb NDVI Troop.nb	Same as above	Zero-one-inflated beta
Grooming	Degree	Age NDVI Troop.nb	Same as above	Poisson
	Strength	Age NDVI Troop.nb	Same as above	Poisson
	Skewness	Age Scan.nb NDVI Troop.nb	Same as above	Skew-normal
	Cosine similarity	Age Scan.nb NDVI Troop.nb	Same as above	Zero-one-inflated beta

S7: Degree in spatial proximity associations

S7.1 Under-Dispersion in the Binomial Model for the number of spatial partners

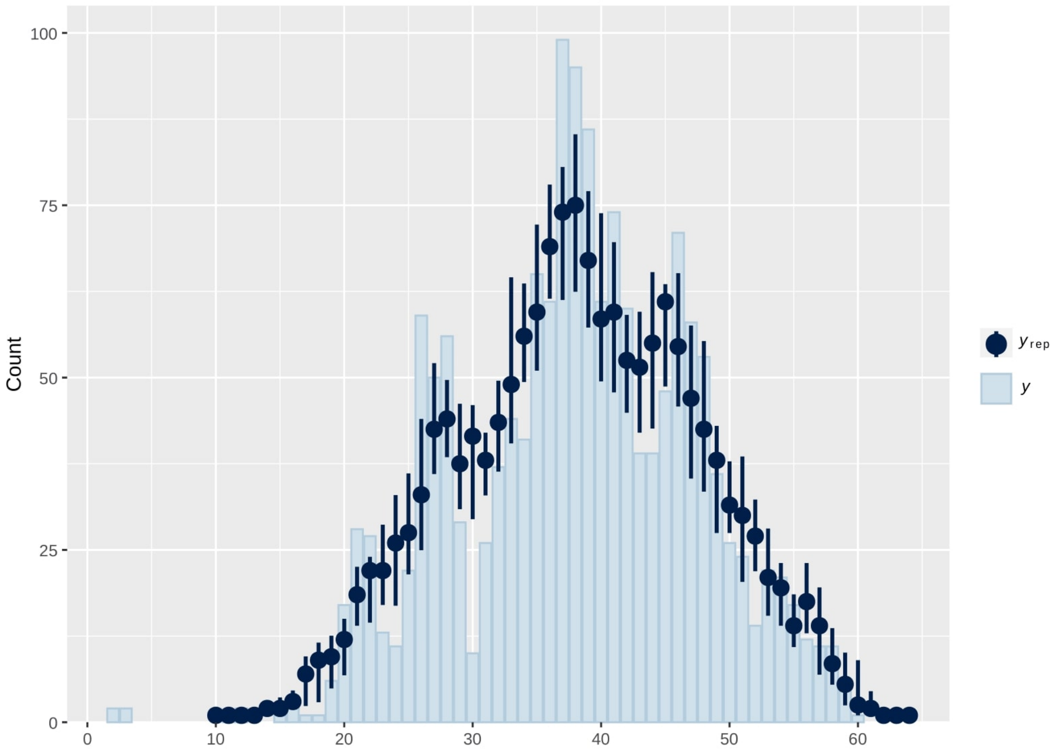


S7.2. Summary table of the Binomial Model for the number of spatial partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in spatial associations, using a binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

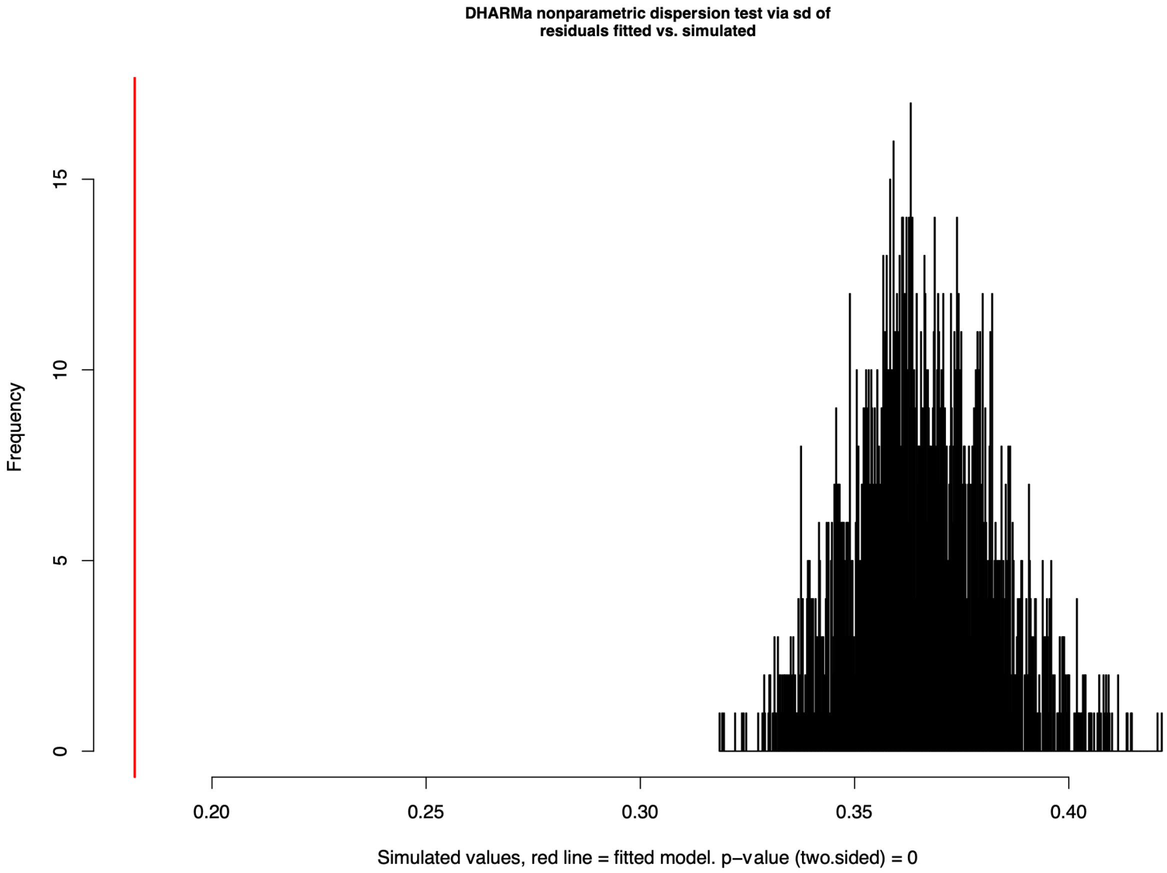
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	1.60	0.50	0.51	2.50
	s(age)	-0.35	0.90	-2.09	1.30
	s(scan.nb)	0.88	0.80	-0.74	2.40
	s(NDVI)	-0.15	0.57	-1.50	0.88
Smooth Terms	sds(age)	0.84	0.70	0.03	2.53
	sds(age ID1)	0.85	0.10	0.64	1.03
	sds(age ID2)	0.43	0.32	0.02	1.18
	sds(age cohort1)	1.86	0.38	1.27	2.75
	sds(age cohort2)	2.05	1.82	0.07	6.67
	sds(age troop1)	1.68	0.30	1.19	2.37
	sds(age troop2)	3.72	1.91	1.52	8.65
	sds(age mumID1)	0.26	0.18	0.01	0.64
	sds(age mumID2)	1.47	0.74	0.18	2.94
	sds(scan.nb)	2.18	0.63	1.25	3.65
	sds(age sex1)	0.32	0.21	0.01	0.79
	sds(age sex2)	1.28	1.41	0.04	5.39
	sds(NDVI)	0.40	0.44	0.01	1.67
	sds(rank ID1)	0.52	0.07	0.40	0.66
	sds(rank ID2)	0.40	0.30	0.02	1.14
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.91	0.00	0.90	0.91

S7.3. Comparing the observed outcome variable (degree) to datasets simulated from the posterior predictive distribution of the number of spatial partners model, using a Binomial distribution



S8: Degree in grooming associations

S81.1. Under-dispersion in the Poisson Model for the number of grooming partners

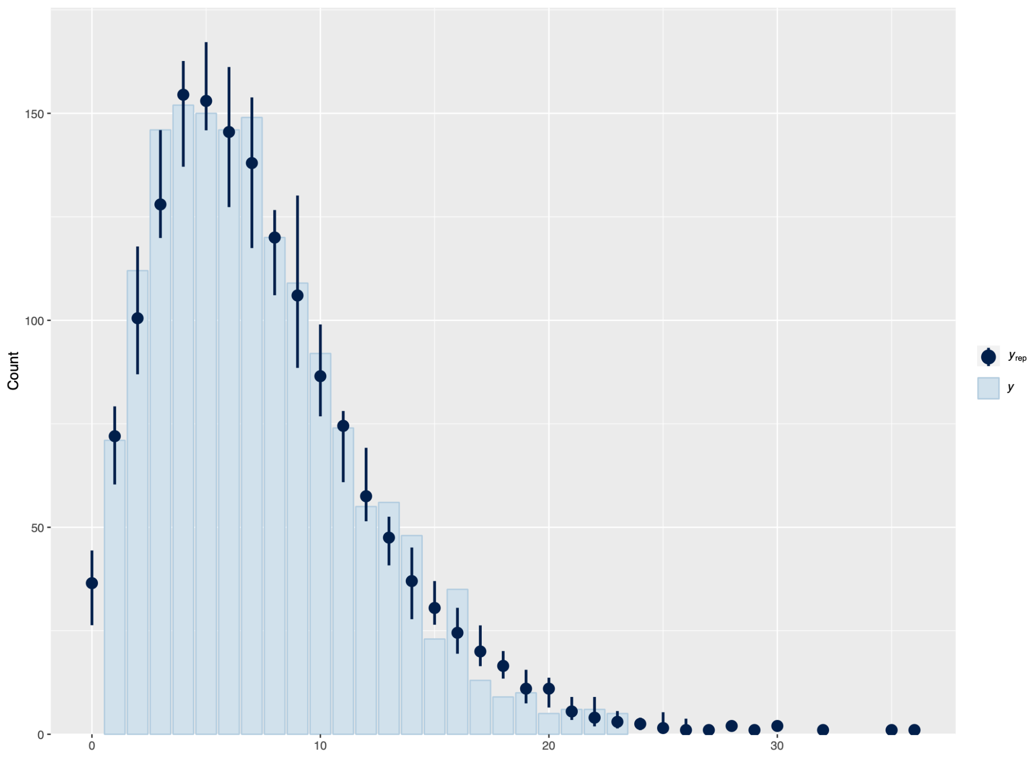


S8.1.2. Summary table of the Poisson Model for the number of grooming partners

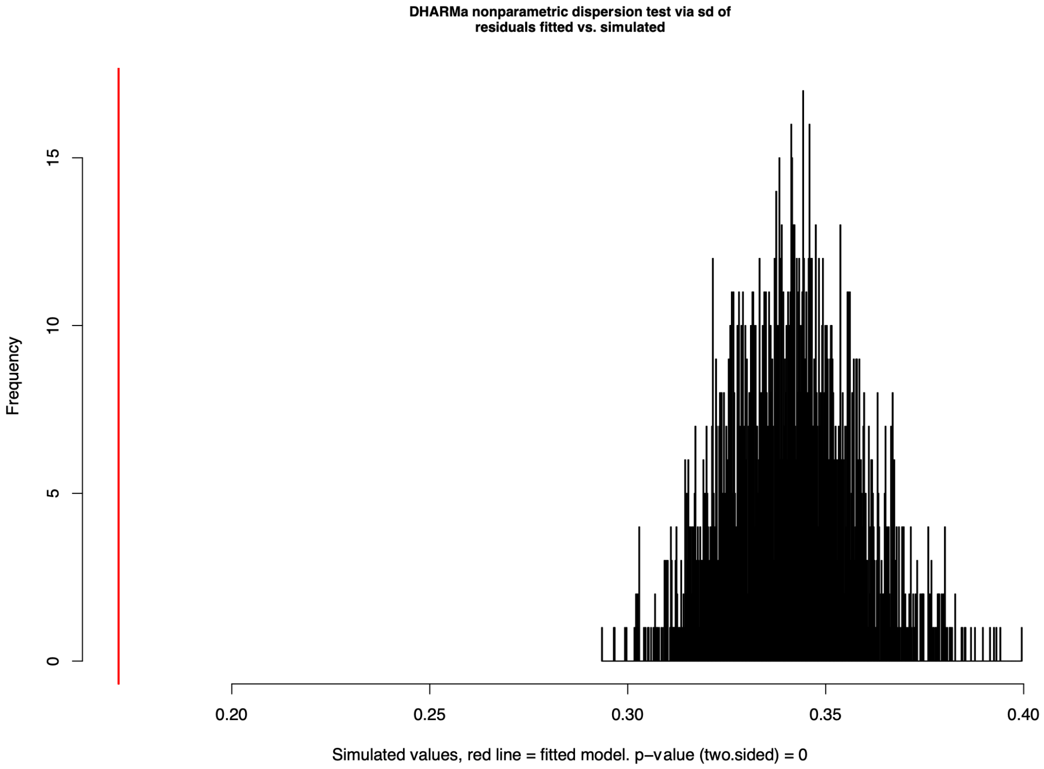
Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in grooming associations, using a poisson distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)-1

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-4.04	0.43	-4.92	-3.18
	s(age)	1.27	0.80	-0.42	2.69
	s(NDVI)	0.14	0.55	-1.02	1.18
	s(troop.nb)	-0.42	0.54	-1.58	0.53
Smooth Terms	sds(age)	0.55	0.52	0.02	1.96
	sds(age ID1)	0.43	0.09	0.24	0.58
	sds(age ID2)	0.54	0.34	0.03	1.24
	sds(age cohort1)	0.74	0.22	0.40	1.22
	sds(age cohort2)	1.61	1.38	0.06	5.29
	sds(age troop1)	0.18	0.11	0.01	0.42
	sds(age troop2)	1.91	1.28	0.51	5.27
	sds(age mumID1)	0.18	0.11	0.01	0.41
	sds(age mumID2)	0.83	0.36	0.13	1.54
	sds(age sex1)	0.18	0.11	0.01	0.44
	sds(age sex2)	3.27	2.13	1.08	8.80
	sds(NDVI)	0.39	0.25	0.07	1.02
	sds(troop.nb)	0.41	0.35	0.02	1.31
	sds(rank ID1)	0.06	0.04	0.00	0.16
	sds(rank ID2)	0.48	0.31	0.02	1.15
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.76	0.01	0.74	0.78

S8.1.3. Comparing the observed outcome variable (degree) to datasets simulated from the posterior predictive distribution of the number of grooming partners model, using a Poisson distribution



S8.2.1. Under-dispersion in the Negative Binomial Model for the number of grooming partners

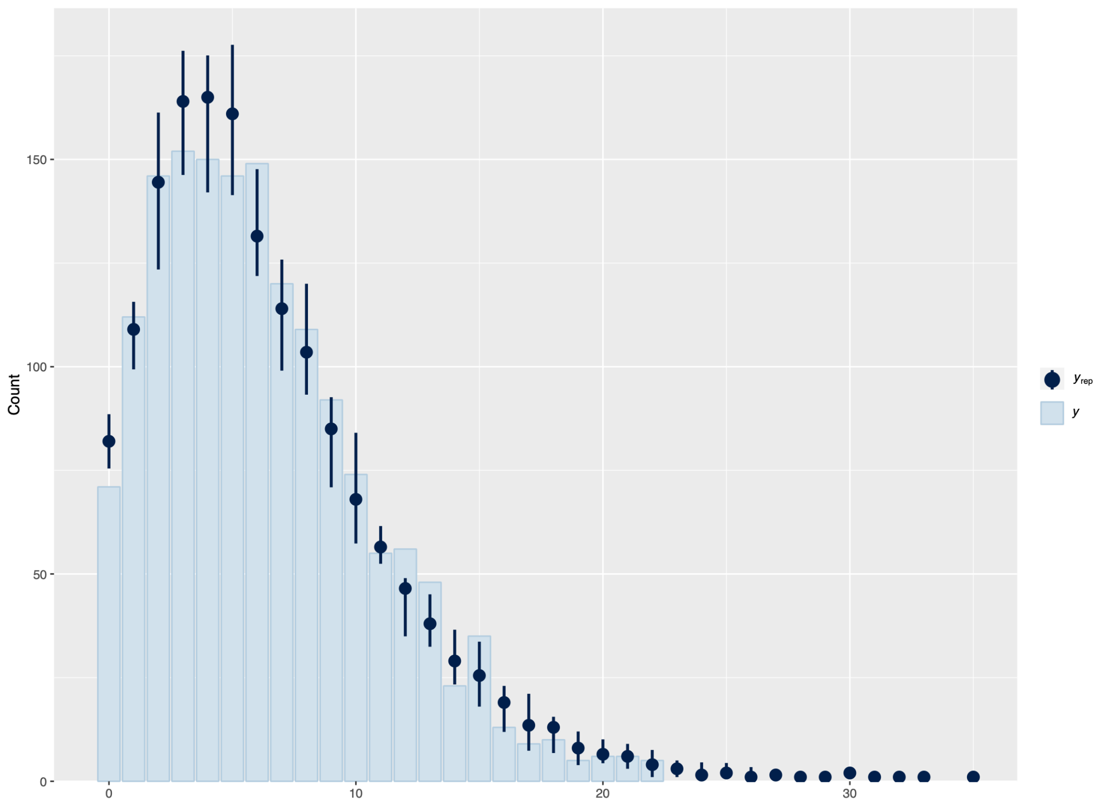


S8.2.2. Summary table of the Negative Binomial Model for the number of grooming partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in grooming associations, using a negative binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

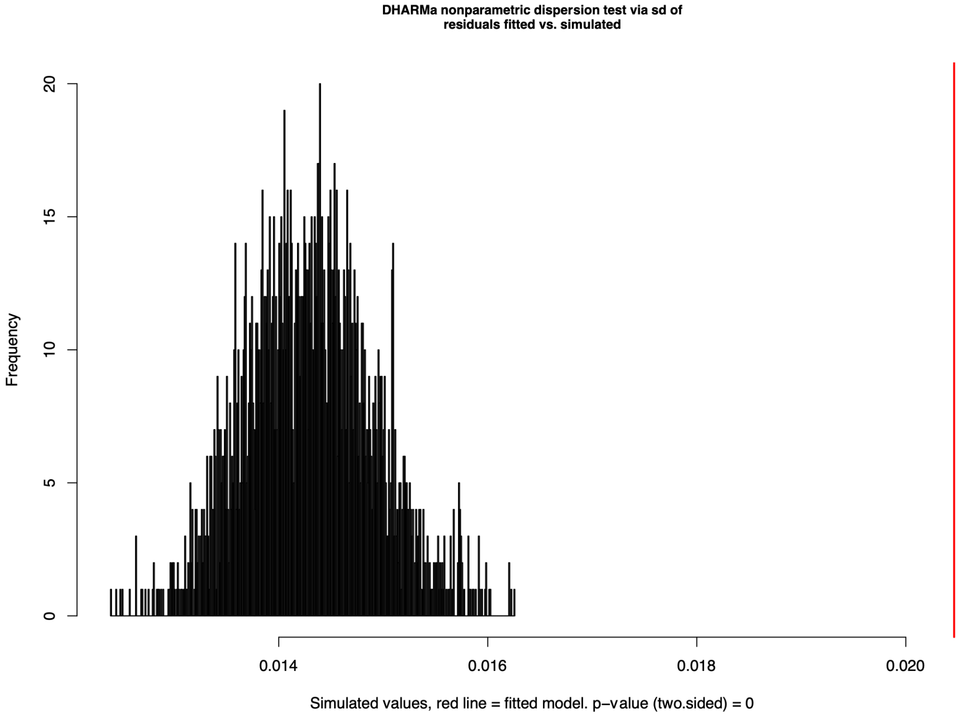
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-4.32	0.45	-5.22	-3.39
	s(age)	1.62	0.89	-0.15	3.35
	s(NDVI)	0.01	0.56	-1.14	1.11
	s(troop.nb)	-0.25	0.54	-1.39	0.80
Smooth Terms	sds(age)	1.15	0.72	0.12	2.85
	sds(age ID1)	0.62	0.10	0.41	0.81
	sds(age ID2)	0.57	0.38	0.03	1.42
	sds(age cohort1)	0.57	0.31	0.07	1.23
	sds(age cohort2)	1.16	1.21	0.03	4.38
	sds(age troop1)	0.28	0.18	0.02	0.72
	sds(age troop2)	2.23	1.39	0.59	5.95
	sds(age mumID1)	0.28	0.16	0.01	0.59
	sds(age mumID2)	1.13	0.47	0.14	2.02
	sds(age sex1)	0.18	0.17	0.01	0.60
	sds(age sex2)	3.67	2.09	1.33	9.56
	sds(NDVI)	0.40	0.26	0.08	1.08
	sds(troop.nb)	0.50	0.44	0.02	1.67
	sds(rank ID1)	0.07	0.05	0.00	0.20
	sds(rank ID2)	0.52	0.35	0.02	1.31
Family-specific Parameters	Shape	405.62	143.81	199.78	737.86
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.77	0.01	0.75	0.79

S8.2.3. Comparing the observed outcome variable (degree) to datasets simulated from the posterior predictive distribution of the number of grooming partners model, using a negative binomial distribution



S9: Strength in spatial proximity associations

S9.1.1. Over-dispersion in the Poisson Model for the frequency of spatial interactions

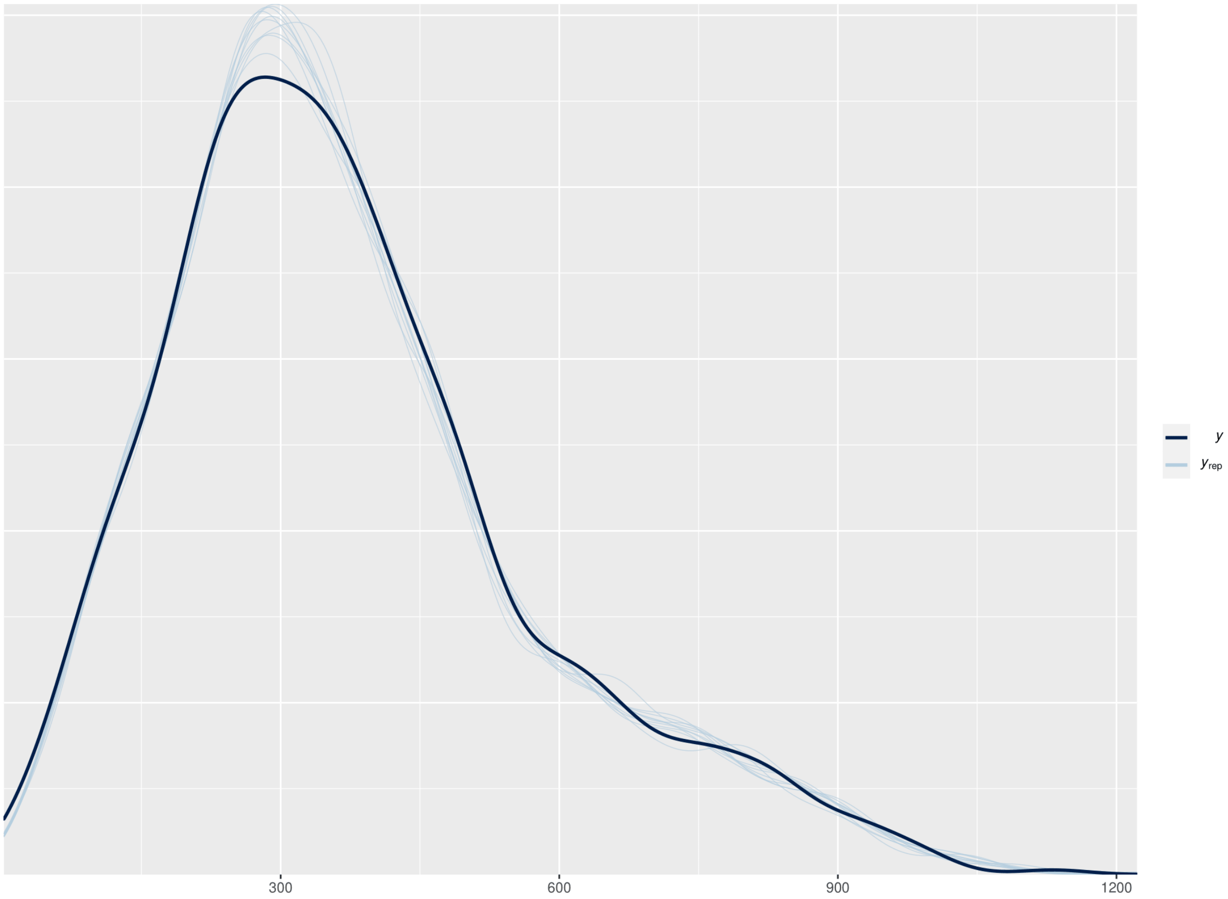


S9.1.2. Summary table of the Poisson Model for the frequency of spatial interactions

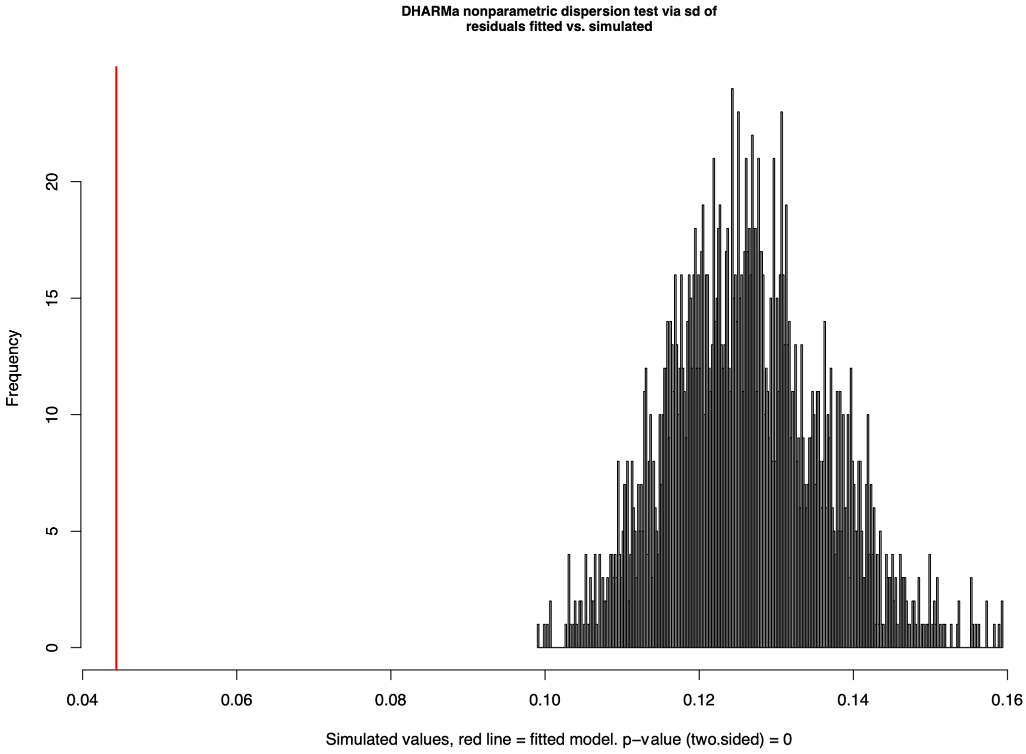
Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the frequency of interactions (strength) in spatial associations, using a Poisson distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	0.45	0.71	-0.82	1.95
	s(age)	1.32	0.36	0.67	2.05
	s(NDVI)	2.10	0.27	1.59	2.68
	s(troop.nb)	0.45	0.71	-0.82	1.95
Smooth Terms	sds(age)	14.12	3.54	8.59	22.12
	sds(age ID1)	1.47	0.09	1.32	1.68
	sds(age ID2)	0.81	0.50	0.08	1.81
	sds(age cohort1)	6.63	1.71	3.77	10.56
	sds(age cohort2)	9.07	6.52	0.36	25.34
	sds(age troop1)	3.01	0.93	1.75	5.95
	sds(age troop2)	1.37	1.29	0.05	4.61
	sds(age mumID1)	1.81	0.18	1.51	2.23
	sds(age mumID2)	1.94	0.49	1.05	2.91
	sds(age sex1)	0.16	0.13	0.00	0.48
	sds(age sex2)	2.58	2.60	0.27	9.46
	sds(NDVI)	0.93	0.25	0.57	1.49
	sds(troop.nb)	0.63	0.19	0.35	1.08
	sds(rank ID1)	0.54	0.04	0.47	0.62
	sds(rank ID2)	0.88	0.54	0.05	2.05
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.98	0.00	0.97	0.98

S9.1.3. Comparing the observed outcome variable (strength) to datasets simulated from the posterior predictive distribution of the spatial interaction frequency model, using a Poisson distribution



S9.2.1. Under-dispersion in the Hurdle Model for the frequency of spatial interactions, using a Negative Binomial distribution

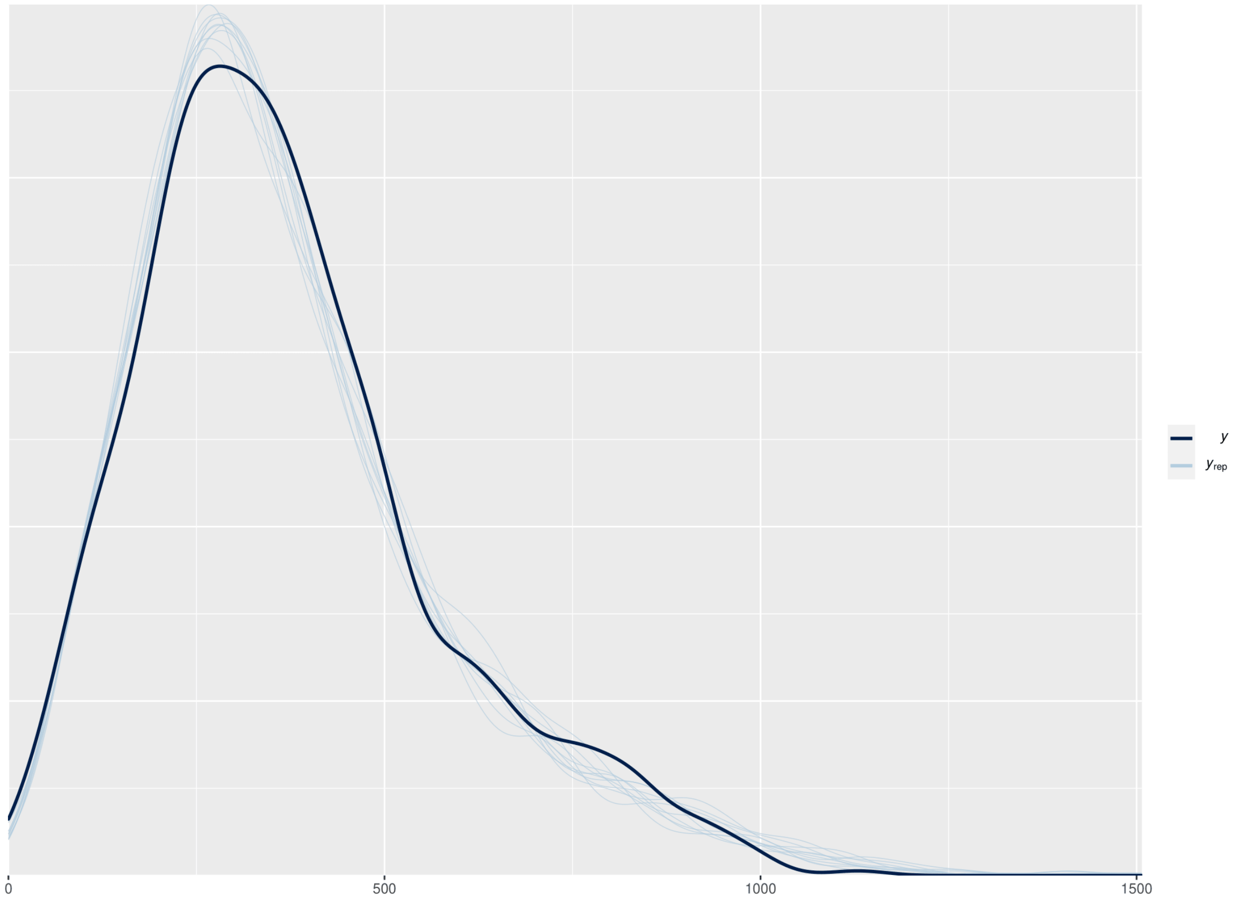


S9.2.2. Summary table of the Hurdle Model for the frequency of spatial interactions, using a Negative Binomial distribution

Summary statistics of a Bayesian hierarchical generalized additive mixed hurdle model (HGAM) for the frequency of interactions (strength) in spatial associations, using a Negative Binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter). Estimates are on the logit scale for the hurdle portion of the model (hu; probability of application)

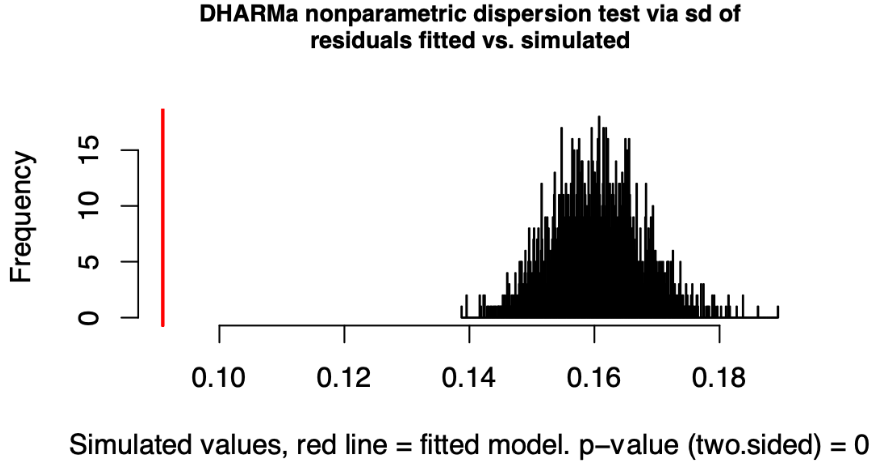
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	0.00	0.43	-0.81	1.00
	hu_Intercept	-0.66	2.35	-6.38	3.00
	s(age)	0.49	0.83	-1.20	2.10
	s(NDVI)	0.36	0.57	-0.78	1.51
	s(troop.nb)	1.05	0.57	0.06	2.23
	hu s(age)	188.33	189.10	9.69	715.22
	hu s(NDVI)	144.92	147.50	10.70	607.41
	hu s(troop.nb)	49.73	67.92	-12.62	263.74
Smooth Terms	sds(age)	3.85	1.30	1.79	6.77
	sds(age ID1)	0.66	0.07	0.53	0.81
	sds(age ID2)	0.32	0.24	0.01	0.89
	sds(age cohort1)	0.72	0.30	0.30	1.45
	sds(age cohort2)	2.21	1.81	0.11	6.98
	sds(age troop1)	0.71	0.20	0.41	1.22
	sds(age troop2)	3.09	1.74	1.05	7.20
	sds(age mumID1)	0.68	0.09	0.50	0.85
	sds(age mumID2)	2.99	0.69	1.78	4.40
	sds(age sex1)	0.11	0.10	0.00	0.35
	sds(age sex2)	1.75	1.54	0.11	5.78
	sds(NDVI)	1.07	0.40	0.48	2.00
	sds(troop.nb)	0.54	0.35	0.14	1.44
	sds(rank ID1)	0.07	0.04	0.00	0.17
	sds(rank ID2)	0.28	0.21	0.01	0.75
	sds(hu_age)	2.75	2.95	0.10	9.89
	sds(hu_age ID1)	4.23	6.82	0.10	18.41
	sds(hu_age ID2)	3.01	3.74	0.10	11.65
	sds(hu_age cohort1)	2.73	3.49	0.08	9.95
	sds(hu_age cohort2)	272.29	396.11	0.22	1303.94
	sds(hu_age troop1)	2.56	2.53	0.09	9.31
	sds(hu_age troop2)	2.79	3.72	0.07	10.57
	sds(hu_age mumID1)	4.57	7.40	0.11	21.37
	sds(hu_age mumI2)	3.12	5.03	0.09	12.44
	sds(hu_age sex1)	2.76	3.02	0.07	10.87
	sds(hu_age sex2)	111.10	259.84	0.14	862.71
	sds(hu_NDVI)	2.63	2.76	0.10	8.89
	sds(hu_troop.nb)	2.64	2.97	0.10	9.45
	sds(hu_rank ID1)	3.36	3.86	0.08	13.60
	sds(hu_rank ID2)	3.05	3.72	0.08	12.17
Family-specific Parameters	Shape	44.83	2.78	39.71	50.50
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.93	0.00	0.92	0.94

S9.2.3. Comparing the observed outcome variable (strength) to datasets simulated from the posterior predictive distribution of the spatial interaction frequency hurdle model, using a Negative Binomial distribution



<u>S10</u>: Strength in grooming associations

S10.1. Under-dispersion in the Poisson Model for the frequency of grooming interactions

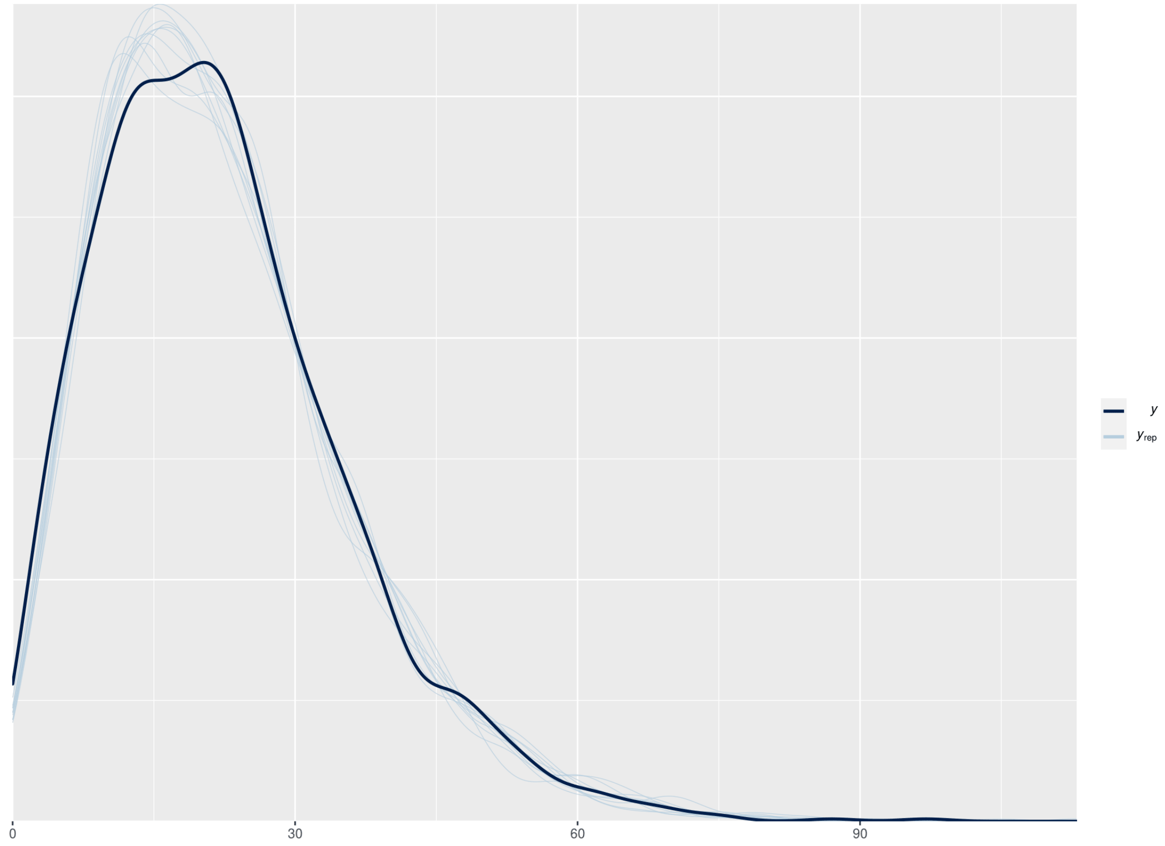


S10.2. Summary table of the Poisson Model for the frequency of grooming interactions

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the frequency of interactions (strength) in grooming associations, using a Poisson distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-2.86	0.47	-3.73	-1.86
	s(age)	-0.10	0.72	-1.53	1.31
	s(NDVI)	-0.23	0.56	-1.18	1.01
	s(troop.nb)	0.47	0.52	-0.38	1.63
Smooth Terms	sds(age)	0.44	0.41	0.02	1.49
	sds(age ID1)	1.28	0.10	1.07	1.45
	sds(age ID2)	0.71	0.50	0.04	1.85
	sds(age cohort1)	0.61	0.23	0.24	1.15
	sds(age cohort2)	1.30	1.24	0.04	4.47
	sds(age troop1)	0.50	0.14	0.25	0.81
	sds(age troop2)	2.47	1.85	0.57	6.66
	sds(age mumID1)	0.42	0.23	0.03	0.83
	sds(age mumID2)	2.06	0.72	0.38	3.49
	sds(age sex1)	0.32	0.15	0.06	0.66
	sds(age sex2)	3.07	2.13	0.88	8.73
	sds(NDVI)	0.43	0.29	0.08	1.16
	sds(troop.nb)	0.41	0.37	0.03	1.44
	sds(rank ID1)	0.14	0.07	0.01	0.27
	sds(rank ID2)	0.64	0.47	0.03	1.76
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.88	0.00	0.87	0.88

S10.3. Comparing the observed outcome variable (strength) to datasets simulated from the posterior predictive distribution of the grooming interaction frequency model, using a Poisson distribution



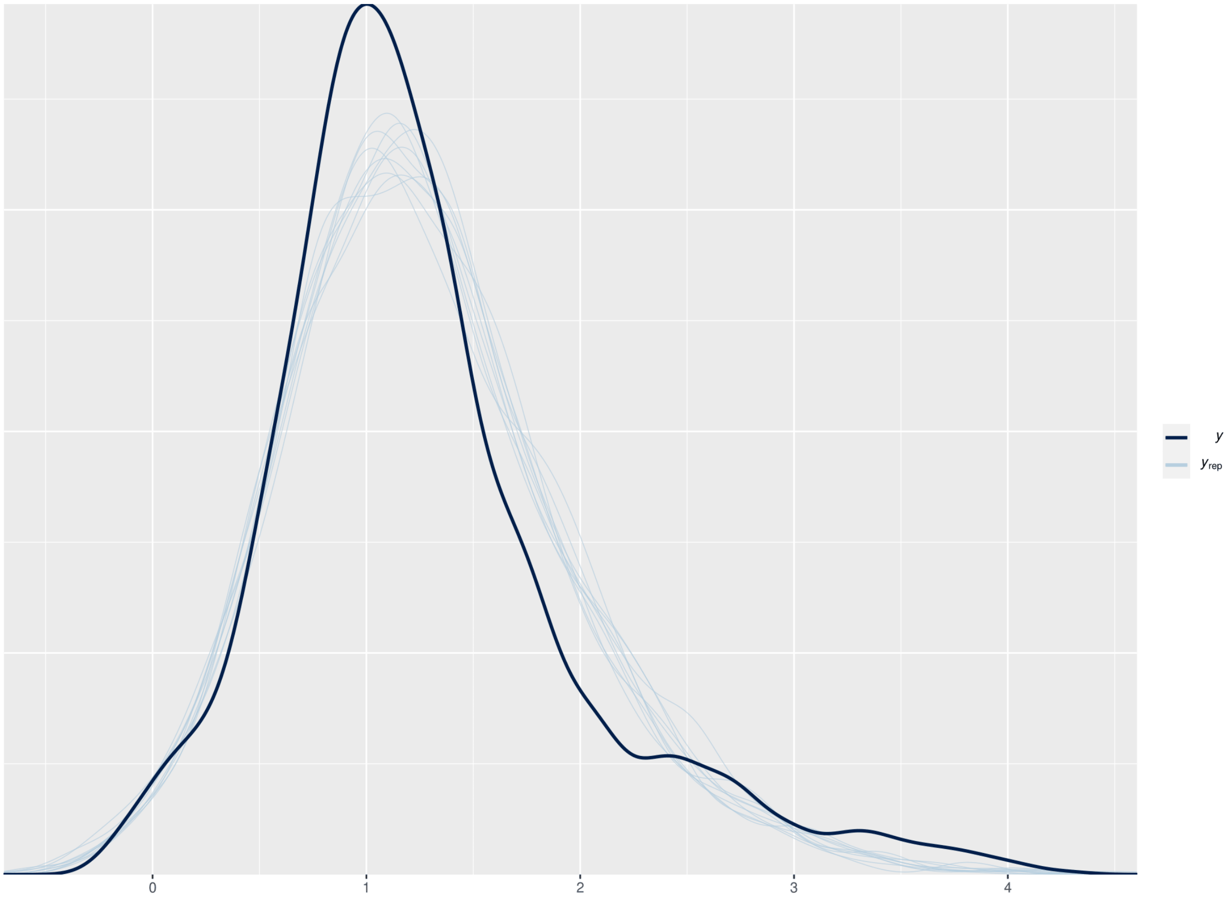
<u>S11</u>: Skewness in spatial proximity associations

S11.1. Summary table of the Skew-Normal Model for the distribution in frequency of spatial interactions

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the distribution of edge weights (skewness) in spatial associations, using a skew-normal distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	1.49	0.26	0.94	2.05
	s(age)	-0.10	0.76	-1.58	1.39
	s(scan.nb)	-0.06	0.53	-1.25	0.94
	s(NDVI)	-0.90	0.79	-2.37	0.73
	s(troop.nb)	-0.07	0.64	-1.44	1.07
Smooth Terms	sds(age)	0.47	0.42	0.02	1.57
	sds(age ID1)	1.26	0.10	1.08	1.46
	sds(age ID2)	0.62	0.44	0.03	1.63
	sds(age cohort1)	0.97	0.27	0.54	1.60
	sds(age cohort2)	1.51	1.35	0.05	5.00
	sds(age troop1)	0.36	0.15	0.07	0.68
	sds(age troop2)	0.87	0.90	0.03	3.25
	sds(age mumID1)	0.27	0.19	0.01	0.67
	sds(age mumID2)	1.78	0.47	0.82	2.70
	sds(scan.nb)	0.48	0.39	0.03	1.46
	sds(age sex1)	0.18	0.13	0.01	0.52
	sds(age sex2)	1.32	1.41	0.04	5.08
	sds(NDVI)	1.33	0.56	0.61	2.72
	sds(troop.nb)	0.71	0.45	0.16	1.86
	sds(rank ID1)	0.18	0.10	0.01	0.37
	sds(rank ID2)	0.63	0.46	0.02	1.68
Family-specific Parameters	Sigma	0.41	0.01	0.39	0.43
	Alpha	5.25	1.04	3.67	7.73
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.60	0.02	0.57	0.63

S11.2. Comparing the observed outcome variable (skewness) to datasets simulated from the posterior predictive distribution of the distribution in frequency of spatial interactions model, using a skew-normal distribution



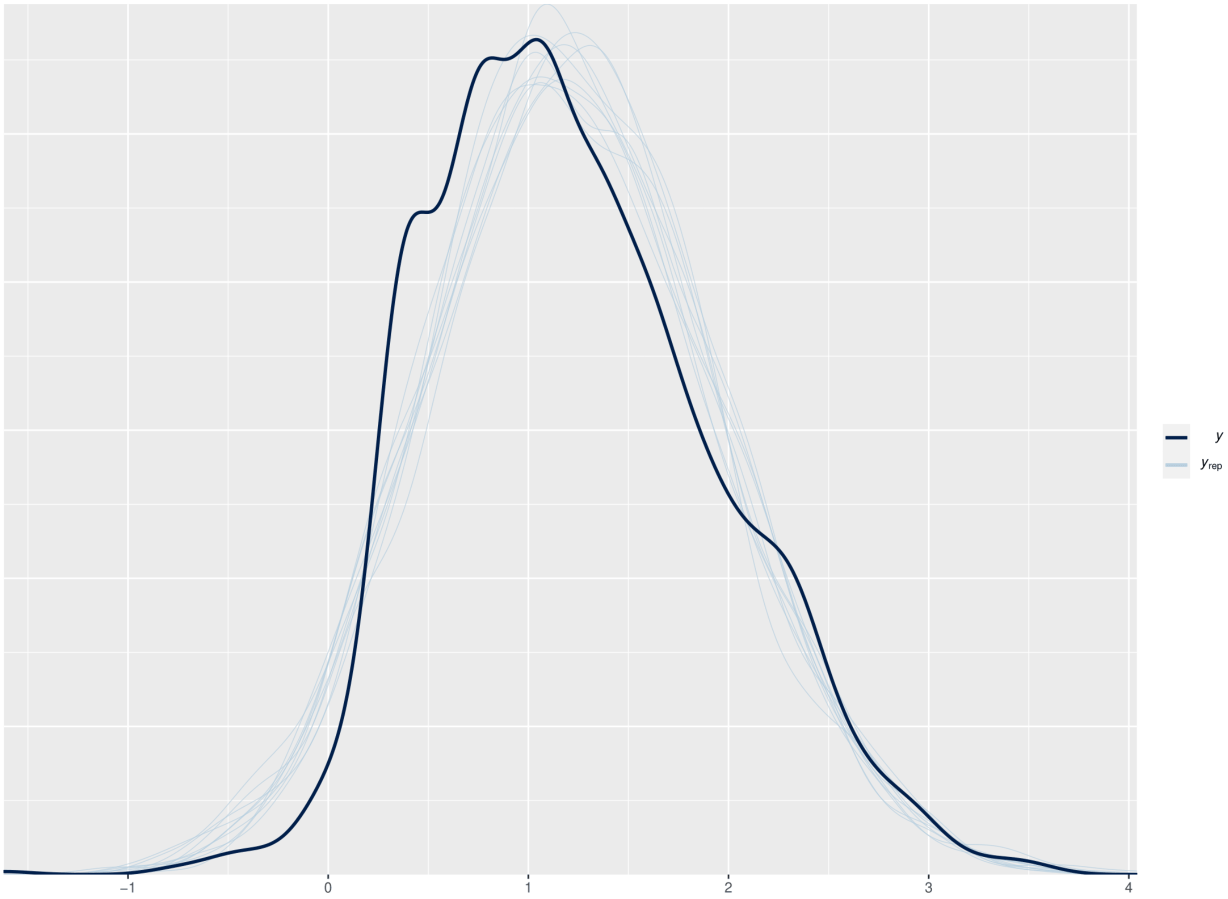
S12: Skewness in grooming associations

S12.1 Summary table of the Skew-Normal Model for the distribution in frequency of grooming interactions

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the distribution of edge weights (skewness) in grooming associations, using a skew-normal distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	1.01	0.43	0.14	1.86
	s(age)	0.67	0.80	-0.95	2.19
	s(scan.nb)	0.78	0.76	-0.96	1.93
	s(NDVI)	-0.44	0.53	-1.46	0.71
	s(troop.nb)	-0.05	0.45	-1.05	0.78
Smooth Terms	sds(age)	0.85	0.66	0.04	2.56
	sds(age ID1)	0.96	0.11	0.74	1.18
	sds(age ID2)	0.48	0.33	0.02	1.22
	sds(age cohort1)	0.58	0.31	0.06	1.23
	sds(age cohort2)	1.42	1.26	0.06	4.69
	sds(age troop1)	0.26	0.20	0.01	0.73
	sds(age troop2)	0.91	0.94	0.03	3.56
	sds(age mumID1)	0.23	0.15	0.01	0.55
	sds(age mumID2)	0.46	0.34	0.01	1.25
	sds(scan.nb)	0.43	0.37	0.02	1.37
	sds(age sex1)	0.40	0.25	0.04	0.97
	sds(age sex2)	2.93	2.06	0.71	8.58
	sds(NDVI)	0.32	0.28	0.01	1.05
	sds(troop.nb)	0.23	0.24	0.01	0.86
	sds(rank ID1)	0.14	0.10	0.01	0.36
	sds(rank ID2)	0.42	0.31	0.01	1.15
Family-specific Parameters	Sigma	0.49	0.01	0.46	0.51
	Alpha	-0.03	0.58	-1.06	1.03
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.52	0.02	0.49	0.56

S12.2. Comparing the observed outcome variable (skewness) to datasets simulated from the posterior predictive distribution of the distribution in frequency of grooming interactions model, using a skew-normal distribution



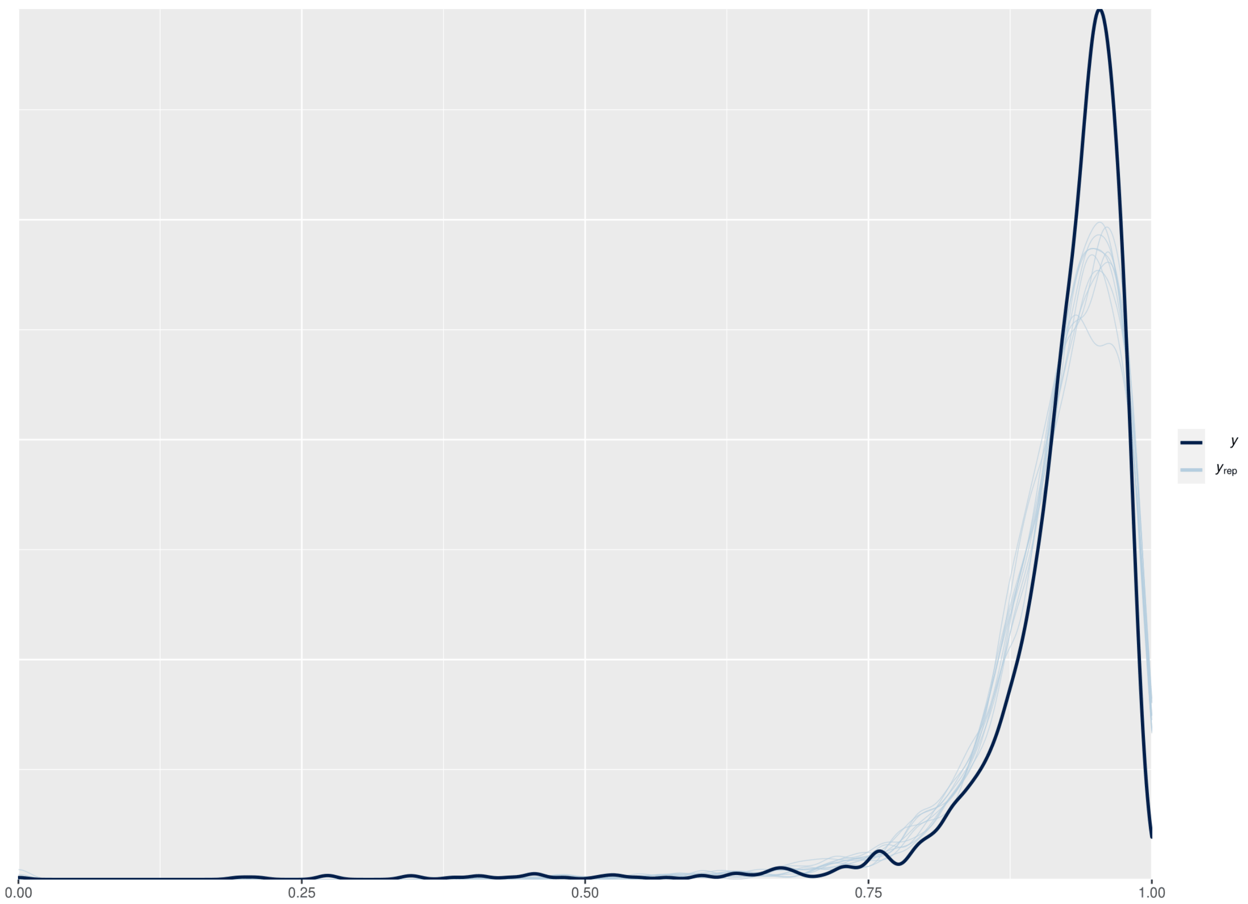
<u>S13</u>: Cosine similarity in spatial associations

S13.1 Summary table of the zero one inflated Beta Model for the similarity in spatial partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity in spatial partners (cosine), using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	2.43	0.55	1.29	3.44
	s(age)	0.53	0.93	-1.21	2.34
	s(scan.nb)	1.60	0.85	-0.11	3.26
	s(NDVI)	-0.46	0.88	-2.23	1.26
	s(troop.nb)	-0.27	0.74	-1.31	1.44
Smooth Terms	sds(age)	4.09	1.74	1.24	7.99
	sds(age ID1)	0.63	0.08	0.46	0.79
	sds(age ID2)	0.58	0.38	0.03	1.39
	sds(age cohort1)	1.74	0.57	0.82	3.03
	sds(age cohort2)	4.59	2.70	0.78	11.43
	sds(age troop1)	0.47	0.21	0.11	0.95
	sds(age troop2)	1.05	1.01	0.04	3.64
	sds(age mumID1)	0.17	0.12	0.01	0.45
	sds(age mumID2)	0.66	0.43	0.04	1.61
	sds(scan.nb)	2.09	0.69	1.06	3.79
	sds(age sex1)	0.49	0.28	0.08	1.16
	sds(age sex2)	2.21	1.99	0.26	7.22
	sds(NDVI)	2.08	0.79	0.95	3.88
	sds(troop.nb)	0.47	0.57	0.01	2.16
	sds(rank ID1)	0.73	0.10	0.53	0.94
	sds(rank ID2)	0.49	0.35	0.02	1.31
Family-specific Parameters	Phi	52.81	2.44	48.28	57.87
	Zoi	0.00	0.00	0.00	0.01
	Coi	0.67	0.18	0.30	0.95
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.53	0.02	0.49	0.58

S13.2. Comparing the observed outcome variable (cosine similarity) to datasets simulated from the posterior predictive distribution of the similarity in spatial partner model, using a zero-one-inflated beta distribution



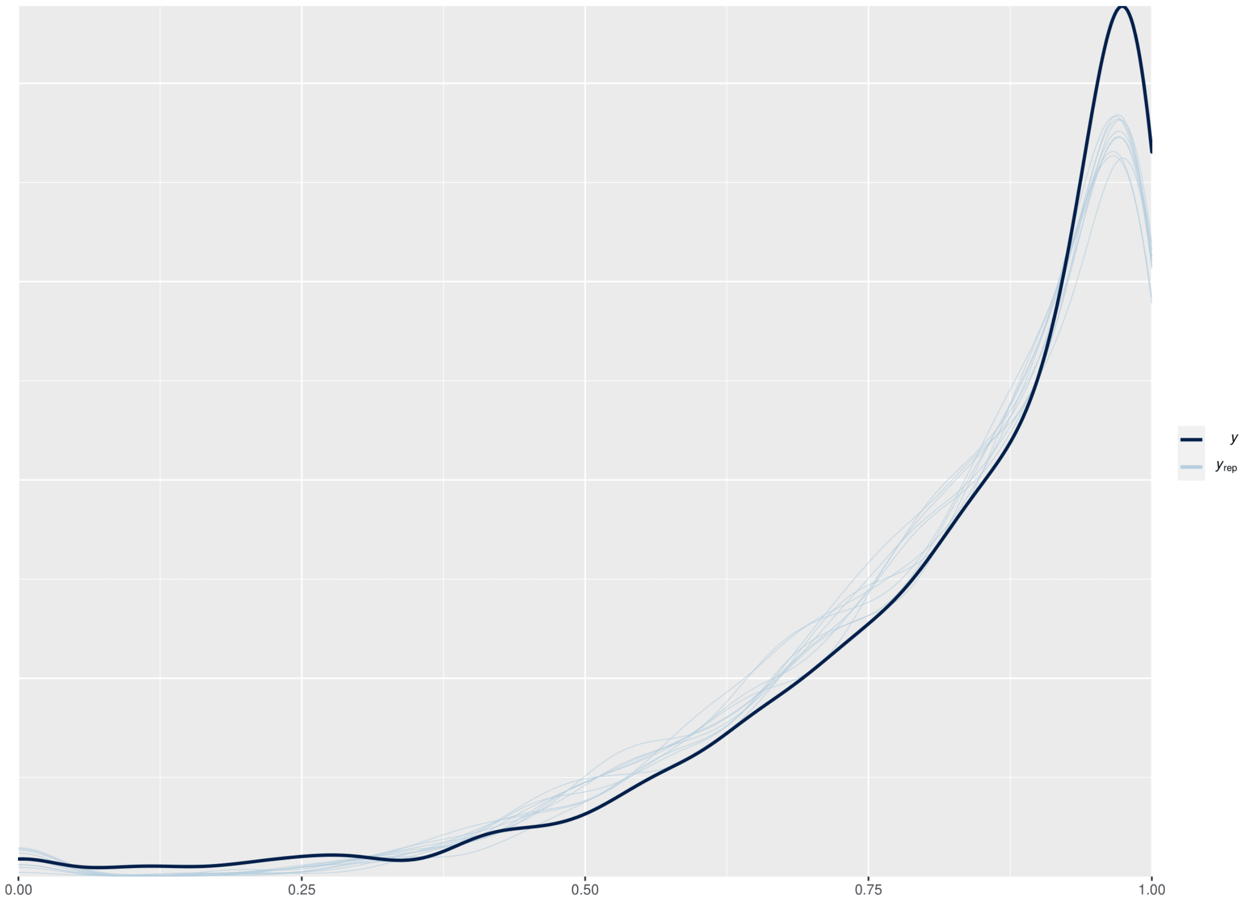
S14: Cosine similarity in grooming associations

S14.1 Summary table of the zero one inflated Beta Model for the similarity in grooming partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity in grooming partners (cosine), using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	1.90	0.31	1.27	2.56
	s(age)	-1.09	0.96	-2.91	0.85
	s(scan.nb)	1.64	0.58	0.23	2.55
	s(NDVI)	0.23	0.58	-0.83	1.46
	s(troop.nb)	-0.09	0.72	-1.34	1.45
Smooth Terms	sds(age)	1.00	0.62	0.11	2.49
	sds(age ID1)	1.43	0.20	1.04	1.83
	sds(age ID2)	0.82	0.61	0.04	2.32
	sds(age cohort1)	0.38	0.30	0.01	1.09
	sds(age cohort2)	1.24	1.26	0.04	4.53
	sds(age troop1)	0.57	0.34	0.03	1.31
	sds(age troop2)	1.46	1.31	0.06	4.75
	sds(age mumID1)	0.60	0.33	0.02	1.19
	sds(age mumID2)	2.74	0.77	0.97	4.20
	sds(scan.nb)	0.31	0.38	0.01	1.29
	sds(age sex1)	0.44	0.24	0.05	0.96
	sds(age sex2)	1.50	1.53	0.06	5.43
	sds(NDVI)	0.38	0.38	0.01	1.36
	sds(troop.nb)	0.83	0.91	0.02	3.49
	sds(rank ID1)	0.47	0.20	0.05	0.83
	sds(rank ID2)	0.84	0.59	0.04	2.26
Family-specific Parameters	Phi	9.99	0.46	9.12	10.93
	Zoi	0.03	0.00	0.02	0.03
	Coi	0.71	0.07	0.57	0.83
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.43	0.02	0.40	0.46

S14.2. Comparing the observed outcome variable (cosine similarity) to datasets simulated from the posterior predictive distribution of the similarity in grooming partner model, using a zero-one-inflated beta distribution



<u>S15</u>: Raw data from spatial interactions plotted with predicted patterns

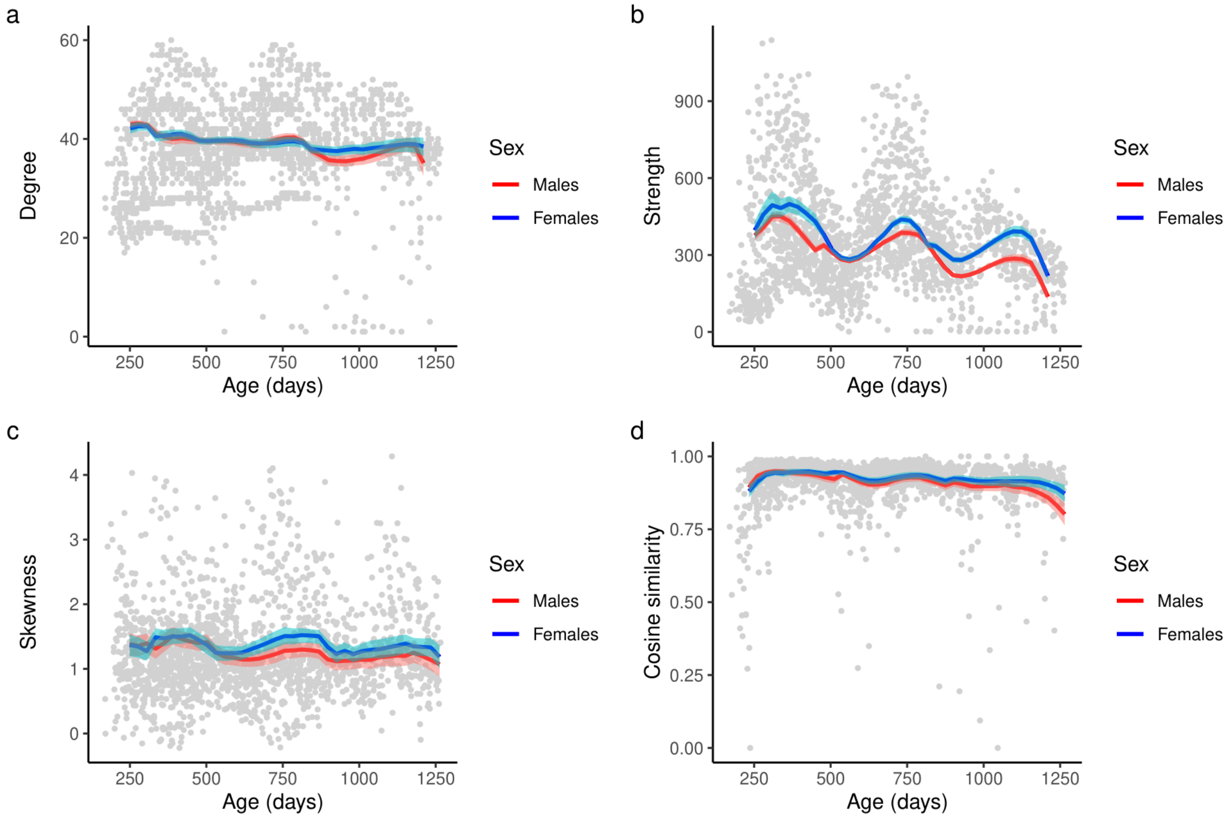


Figure S15 Variation in the (a) degree (b) strength (c) skewness and (d) cosine similarity of spatial associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). The grey dots show the raw data. Predictions were estimated with mean troop size fixed at 48 individuals.

<u>S16</u>: Raw data from grooming interactions plotted with predicted patterns

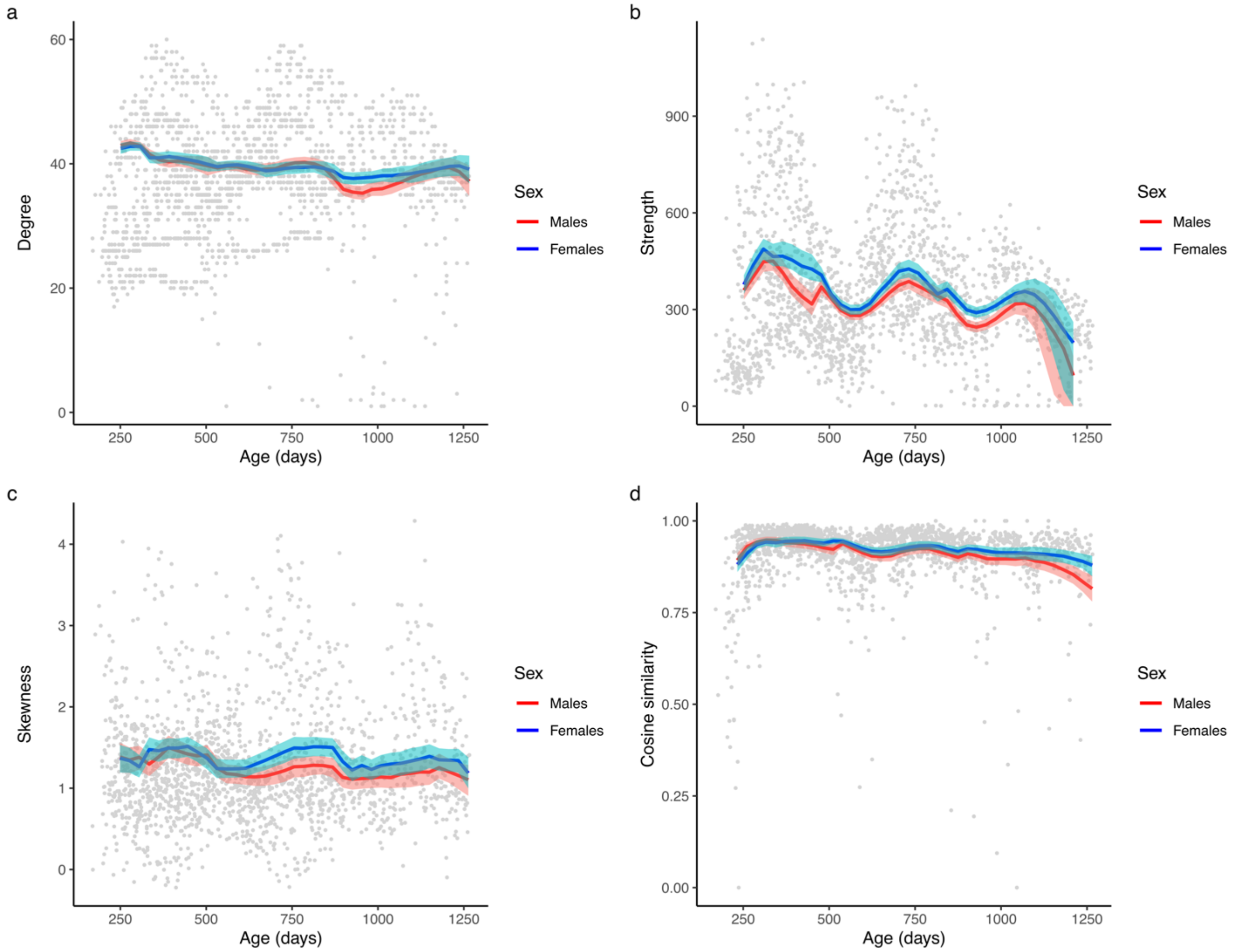


Figure S16 Variation in the (a) degree (b) strength (c) skewness and (d) cosine similarity of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). The grey dots show the raw data. Predictions were estimated with mean troop size fixed at 49 individuals.

CHAPTER 6: INSIGHTS INTO STRONG TIES FORMATION, COMPOSITION AND PROCESSES AT PLAY IN JUVENILE VERVET MONKEYS

This data chapter has been submitted in *Animal Behaviour* (September 30th, 2022), under the title "Insights into strong ties formation, composition and processes at play in juvenile vervet monkeys." The authorship list for the published version is as below. I contributed to the study concept/design, data collection, data analysis and drafting the manuscript. Dr. Henzi and Dr. Barrett contributed to funding acquisition, supervision and the drafting and critical revision of the manuscript. Dr. Bonnell contributed to data analysis, supervision and helped draft the manuscript. Dr. Dostie contributed to data extraction. All authors approved the final version of the manuscript.

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6.1 Abstract

Understanding the development of social relationships can provide insights into the processes by which social network structures emerge and vary across species. In this analysis, we follow up on a previous analysis where Kohn's (2019) model of social relationship formation was tested on three groups of wild juvenile vervet monkeys, in grooming and spatial behaviours. While developmental patterns did not conform to the exploration, pruning and consolidation phases identified by Kohn (2019), it revealed the formation of a core social "bubble" of strong ties across social development. Here, we ask whether Kohn's phases rather apply only to the strong ties that constitute the females' and males' social bubbles. Both bubble composition and

formation are also investigated to understand the influence of social bubbles on juveniles ' development as well as the role of maternal behaviour in this process. Once again, spatial and grooming social bubbles did not develop following Kohn's (2019) framework, nor did the potential processes at play in their formation. Spatial bubbles were composed mostly of juveniles with an increase in rate of associations with family members during birth seasons. Grooming bubbles, on the contrary, displayed a stable composition through time, with their mothers making up the entirety of their bubbles. Lastly, we found that a mother and her offspring's weak ties remained similar as juveniles developed.

Overall, our results suggest that the particular structure and composition seen in social bubbles emerges as a result of the type of the behaviour under consideration (grooming or spatial proximity) and group demography. Considering the processes at play, juveniles did not groom their spatial associates but distributed their grooming toward specific partners. Lastly, maternal grooming network instability provided juveniles with enough time to interact with mother's grooming partners, but not long enough for these relationships to be consolidated.

6.2 Introduction

Richard Alexander (1990) famously stated that juvenile primates have two main functions: "to get to the adult stage without dying, and to become the best possible adult". With respect to the latter, many authors have suggested that juveniles become good adults by using their extended developmental period to acquire the social knowledge needed to navigate their social groups, negotiate their social environments, and establish and sustain fitness-enhancing social relationships (Archie et al., 2014a; Bray et al., 2021; Cameron et al., 2009; Cheney et al., 2016; Deputte, 2000; Fairbanks, 2002; Feldblum et al., 2021; Frere et al., 2010; Schülke et al., 2010; Silk et al., 2003, 2009, 2010a; Stanton & Mann, 2012). In this regard, sex differences in social engagement also become relevant, given that these have been shown to develop prior to sexual maturation (Cords et al., 2010; Jarrett et al., 2018; Lonsdorf et al., 2014; Nakamichi, 1989), and vary with social structure. For example, where females are philopatric and males disperse at maturity, young females develop stronger social bonds than do males (spatial and grooming associations: Kulik et al., 2015; grooming associations: Cords et al., 2010; spatial associations: Frère et al., 2010; Stumpf et al., 2009; maternal association: Andres et al., 2013; Nakamichi 1989). Males, conversely, play more than females do (Kulik et al., 2015; Meredith, 2013).

Although such findings support the idea that social relationships are established in the juvenile period and prepare animals for their sex-specific social roles (Kulik et al., 2015; Nakamichi, 1989; Suomi, 2005), we still lack a detailed understanding of the processes by which early life social engagement leads to the establishment of enduring social relationships (Kohn, 2019). Recent studies have argued for the importance of: (i) parents' social connections (Ilany & Akçay, 2016), (ii) siblings' social influence (Kohn et al., 2022), and (iii) the structure of juveniles' ego-networks (Vilette et al., in press). Yet, an empirical assessment of Ilany and Akçay's (2016) model by Jarrett et al. (2018) found only limited evidence for social inheritance of maternal bonds in vervet monkeys (*Chlorocebus pygerythrus*)—that is, there was relatively little overlap between mother and offspring grooming partners. Jarrett et al. (2018) suggested that the mismatch between maternal and offspring grooming social bonds could be accounted for by the fact that juveniles are exposed to, and must learn to cope with, temporal shifts in maternal network structure. In other words, their findings indicated that maternal social networks represent too much of a moving target for offspring to match effectively, as well as suggesting that, in order to replicate and sustain the group-level network structure over time, juvenile animals should seek to form bonds with non-maternal associates. Thus, the stability of mothers' networks, combined with the demography of social groups, will regulate the availability of potential partners into which juveniles can invest their social effort. In turn, this investment will lead to the strengthening of certain social relationships with other individuals (Kohn, 2019; Schülke et al., 2010; Silk et al., 2003, 2006b), and to variation in the structure of both ego and global networks across time and between groups.

Social effort is known to vary across, and within, social relationships, leading to the notion of strong and weak ties (or relationships). Weak ties are characterized by interactions that are infrequent, while strong ties represent frequent and sustained levels of social interaction. Differentiating between social ties in this way is important as females with stronger social relationships have been shown to experience fitness-related benefits such as increased longevity (Archie et al., 2014b; Silk et al., 2010b), enhanced likelihood of surviving extreme events (Lehmann et al., 2015; McFarland & Majolo, 2013), enhanced infant survival (wild baboons: Silk et al., 2003, 2009) and increased individual reproductive performance (Kulik et al., 2012; Schülke et al., 2010). By the same token, however, some studies have also shown that there are advantages to having a wide range of partners. For instance, the number of weak bonds a female possessed predicted infant 12-month survival and infant longevity in baboons (McFarland et al., 2017), while vervet monkey females that invested in grooming a wider array of partners were at lower risk of predation (Josephs et al., 2016) and less susceptible to nocturnal hypothermia (Mcfarland et al., 2015).

Weak and strong ties qualitatively characterize the two ends of the relationship spectrum, where both can deliver fitness-related benefits, and where the relative merits of each are likely to be contingent on particular demographic and ecological conditions, which may shift over time. This means that juveniles would benefit from having both strong and weak associations at their disposal. Whereas strong social ties might soften the impact of stressful interactions with novel individuals (Kohn et al., 2022), weak ties may aid in predator avoidance or thermoregulation (Josephs et al., 2016; Mcfarland et al., 2015; Ostner & Schülke, 2018). In line with this, we have found that, through social niche construction, juvenile vervet monkeys embed themselves in secure ego-network structures composed of strong ties, while retaining the benefits of broader integration in the group through the presence of weak social ties (Vilette et al., in press). As expected, sex differences emerged early on (~ 8 months), with females putting more effort into grooming interactions and maintaining a tighter subset of strong grooming partners than did males. This sex difference may have foreshadowed females' integration and acceptance into their social group, whereas males grooming patterns may be viewed as a prelude to emigration from their natal group. In other words, during their juvenile period, females and males may adapt their social behaviour in ways that enable them to grow into the social style typical of their adult lives (Kulik et al., 2015; Widdig et al., 2016).

The formation of these ego-network structures, however, did not conform to Kohn's (2019) proposed model of social relationship formation, whereby individuals explore their social environment forming many social connections in the group, and then subsequently prune and consolidate a sub-set of these connections, leading individuals to maintain preferred connections with certain partners (Kohn, 2019). Rather, these ego-network structures—a core of strong ties constituting a "social bubble", and a periphery of weaker ties—were formed early and remained fairly stable over time (Vilette et al., in press). One explanation for why this should be is that the exploration, pruning and consolidation phases apply only to the formation of the social bubble of strong ties, and not to the overall ego-network. Here, we consider this possibility and investigate Kohn's (2019) socialisation steps at the social bubble level.

We then go on to consider the composition of social bubbles and their formation in order to investigate whether these bubbles are likely to provide social benefits to juveniles. In Spectacled parrotlets (*Forpus conspicillatus*), for example, juveniles form strong relationships with siblings immediately after fledgling, which then offers them a stable social position during their transition from the family group to the wider flock (Wanker et al., 1996). Kohn (2022) also found similar evidence in Gouldian finches (*Erythrura gouldiae*). In vervets, we hypothesize that a social bubble provides individuals with the chance to hone their social strategies in the context of a secure environment, as well as reducing the number of unpredictable, and potentially more risky, social encounters. That is, a stable bubble represents a low-risk network of predictable partners that buffer juveniles from potentially stressful situations. For example, in terms of proximity, an animal with a more consistent social bubble of strong spatial ties may increase protection against unfamiliar conspecific competitors (Kohn et al., 2022). In a grooming setting, a social bubble may allow individuals to have lower glucocorticoid levels (Crockford et al., 2008). As socialisation is heavily influenced by the availability of social partners and group composition, the specific characteristics of available group members can have a significant effect on the social development of infants (Deputte & Quris, 1997; Pereira & Leigh, 2003; Rosenblum & Coe, 1977). Therefore, a social bubble is likely to set the social conditions to which juveniles are exposed (Kohn et al., 2022). This raises the prospect that useful insights may be gained into the socialisation process by investigating the composition and stability of social bubbles over time, and how this relates to the nature of the social environment and reflects individual social preferences (Snyder-Mackler et al., 2020).

In what follows, we investigate social bubble formation in male and female juvenile vervet monkeys in both the spatial and grooming domains. These provide a useful contrast, as grooming generally requires mutual attraction between partners—and therefore more active social engagement, in the effort invested and the partners targeted—whereas spatial proximity can often be achieved unilaterally, as a more passive social engagement that requires animals to be merely tolerant of each other. Our analysis is comprised of three parts. The first part investigates Kohn's (2019) socialisation steps at the social bubble level. To do so, we study the spatial and grooming social bubble structures by looking at their size, the effort invested in them and the similarity in partners through time. In a second part, we then examine composition of bubbles in order to assess the proportion of group members to which juveniles are exposed over their development, and how varied their exposure is to both kin and non-kin adults and juveniles. Taken together, these two first parts address the question of whether social bubbles provide a stable and predictable social environment for juveniles during their development.

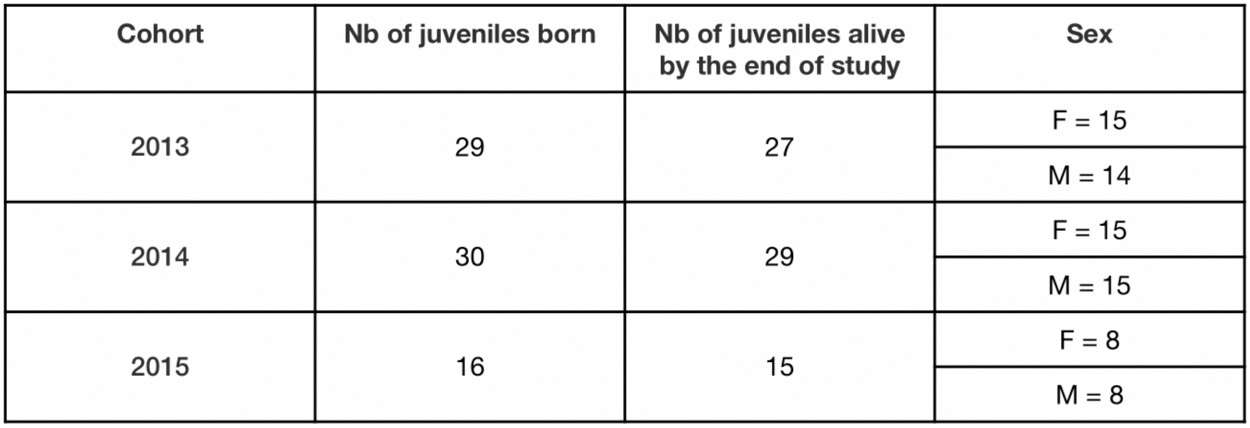
The last part of our analysis considers the processes at play in the formation of social bubbles. We address two main issues. (3a) As spatial and grooming bubbles are confounded to some degree (Henzi et al., 2013), we ask how the grooming bubble compares to the spatial bubble. To do so, we seek to see whether juveniles develop distinct spatial and grooming bubbles following Kohn's (2019) socialisation steps. (3b) We reconsider Jarrett et al. (2018) and Ilany and Akçay's (2016) findings by investigating the similarity between the grooming partners of mothers and offspring. Based on Jarrett et al.'s (2018) findings, we expect maternal networks to represent a moving target (i.e., to shift in composition over time) hindering the ability of offspring to prune and consolidate strong relationships with maternal contacts and hence being part of their own social bubbles. This instability, however, may lead mothers' grooming associates to be found outside of juveniles' social bubbles (i.e., they will comprise juveniles' weak ties). We therefore assess the extent to which a mother's weaker grooming ties overlap with her offspring's weaker grooming ties.

6.3 Methods

6.3.1 Study population and subjects

Data were collected between June 2014 and June 2017 from three troops of vervet monkeys occupying adjacent and overlapping home ranges in the Samara Private Game Reserve in the semi-arid Karoo biome, Eastern Cape, South Africa (Pasternak et al., 2013). The three study groups (PT: x-bar = 39 ± 8 SD; RBM: x-bar= 49 ± 6 SD; RST: x-bar = 57 ± 7 SD) were fully habituated from 2008 for RST and RBM and from 2012 for PT. All animals were individually identifiable from natural markings. The study subjects comprised three birth cohorts from the 2013, 2014 and 2015 birth seasons. The number of juveniles, as well as the number of each sex varied across cohorts and years (see Table 1).

Table 1 Size of cohorts at birth and at end of the study, as well as their composition.



Cohort	Nb of juveniles born	Nb of juveniles alive by the end of study	Sex
2013	29	27	F = 15
			M = 14
2014	30	29	F = 15
			M = 15
2015	16	15	F = 8
			M = 8

6.3.2 Data collection

We began data collection when all cohort members were nutritionally independent of their mothers and classified as juveniles (Jarrett et al., 2018), which corresponded to an age of approximately 7 months (+/- 1 months) for the 2013 and 2014 cohorts. Data collection began later for the 2015 cohort, at around 11 months (+/- 1 months), due to logistical reasons. Each troop was followed on foot by one or more researchers on each 10-h study day, 3 to 5 days a week (PT: 583 days; RBM: 601 days; RST: 613 days). We used electronic data loggers and commercial software to record data from all visible animals, using scan samples conducted every 30 minutes (Young et al., 2017). Each scan sample lasted 10 minutes, during which we collected data on each animal's activity (feeding, moving, resting and grooming) and the identity of all its neighbours within 3m. When animals were recorded as grooming, we noted the identity of their partners. Agonistic data were collected *ad libitum*, with the identities of the participants and the initiator, and the outcome (winner/loser) recorded (Young et al., 2017).

6.3.3 Ethical Note

All protocols were non-invasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505).

6.3.4 Data extraction

Grooming and spatial data were treated separately in our analyses. Using the 'netTS' package (Bonnell & Vilette, 2020) in R version 3.5.2 (Team, 2017), both datasets were aggregated over a 60-day window that was then shifted successively by 30 days. We used this period in line with our previous analyses. However, we used the 'check.windowsize' function, specifying 1000 iterations, of the 'netTS' package to estimate the convergence of our measures in both the grooming and spatial proximity networks. The 'check.windowsize' function also allowed us to measure the sensitivity of this subsampling. With spatial associations, we found highly similar estimates (i.e., convergence) and low variation in estimates of degree and strength using a 60-day window. This means that the chosen window size was robust to subsampling and able to provide good measures. The estimates were not as robust for cosine similarity, suggesting the potential for noise in our predicted patterns. With grooming associations, degree, strength and cosine similarity showed lower estimates and higher variations. Although grooming associations showed a relatively larger amount of noise, a window size of 60 days nevertheless appeared to offer a good and usable compromise (Supplementary S1). Within each window, spatial association and grooming interactions were separately aggregated to construct weighted, non-directed networks at the node level (i.e., ego-networks). In other words, each juvenile present within the window had a grooming and a spatial ego-network that consisted of its direct connections. The age in days of each juvenile was registered at the start of each time block, as were the number of scans and the mean size of each troop. Applying a temporal dynamic approach allowed us to detect the points at which potential patterns emerged.

To extract ordinal ranks, we used the Percolation and Conductance (P&C) method (Fujii et al., 2015) from the 'Perc' package in R. We chose this method following the training-testing approach (Vilette et al., 2020), as it presented the best trade-off between the optimal amount of data required to infer reliable ranks and how good this method was at inferring reliable ranks. Therefore, we used a 4-month burn-in period, specific to each troop, and calculated ordinal ranks for each juvenile within each 60-day window, across the entire study period. We included agonistic interactions between all individuals (males, females, juveniles).

6.3.5 Strong ties extraction

To extract strong ties, it is common practice to select a user-determined number of social bonds (Schülke et al., 2020; Silk et al., 2006a). This approach means that all individuals are, in essence, arbitrarily allocated a certain number of strong bonds (i.e., partners with whom they interact most frequently) regardless of the actual frequency of interactions (i.e., the choices here are not based on any biologically or statistically principled criteria) (Schülke et al., 2010; Silk et al., 2010b). Furthermore, restricting the analysis to a predetermined number of bonds eliminates the possibility of examining variability in the number of bonds formed by individuals. To address this issue, some studies have simply used higher than average composite sociality index (CSI) scores and lower than average CSI scores to identify strong and weakly bonded partners as a continuous measure (Mcfarland et al., 2015; Silk et al., 2006b). Others have used several thresholds to identify a strong tie from observational data alone and counted the number of strong ties with strength above (1) the 0.9 percentile, (2) the 3rd quartile, and (3) the mean value (Schülke et al., 2022). Yet, this approach also fails to consider the distribution of the data itself and more specifically, whether a clear distinction between weak and strong ties exists (i.e., whether there is a skewed distribution). In our analyses, we therefore developed an algorithm to model the distribution of edge weights on the assumption that, if strong ties (relatively large edge weights) were present, then the distribution of edge weights would be skewed. The code can be found at https://github.com/ChloeVilette/strong_ties_algo.

For each juvenile our model-based function proceeded as follows:

1 - The weight distribution was extracted for a given time period, representing the total number of times the focal animal was recorded as interacting with each of its partners.

2 – We ran two models (weights ~1), using the 'brms' package (Bürkner, 2017), specifying a skewed-normal and a normal distribution respectively. The priors for the mean weight (i.e., intercept) were adjusted in order to reflect the observed weak ties distribution (normal (1,2) and normal (1,1) for the skewed-normal and normal distribution respectively) and can be tailored to

what is thought to be weak ties based on prior information. We also specified priors (normal (0,10) and normal (0,1) for the skewed-normal and normal distribution respectively) on the sigma parameter, which defines the range of weak tie values around the mean weight. Lastly, we also set a weakly informative prior with mean 0 and standard deviation 4 on the magnitude of skew in the data: i.e., alpha. To then check which distribution fitted the extracted weight distribution better, we compared the skewed-normal and normal distribution models using leave-one-out cross-validation (Vehtari et al., 2016), which computed a formal difference score between the two models, with the 'loo_compare' function of 'brms'. The presence of small sample sizes (i.e., when an individual has only 1 or 2 partners), however, meant that the information present in the weight distribution alone was inadequate, leading to a very small and unreliable difference between a skewed and a normal distribution. To address this, we used a parameter "min_diff" to indicate how much evidence we were willing to accept in the difference score, computed using the leave-one-out cross-validation, between models with a skewed and a normal distribution in ties. This min_diff parameter constrained the algorithm to select only models for which there was strong evidence of a skewed distribution. It was set to a different value, based on the studied behaviour, in order to make the selection of strong ties more conservative (see below).

3.a - If a skewed distribution fit the data better, the largest weight within the distribution was classified as a strong tie. To search for the number of strong ties, we ran a model predicting weight using the classification of strong or weak tie. This model fitting approach compared, again using loo, possible classifications of strong versus weak ties, starting with the largest weight being the only one classified as a strong tie, followed by the strongest and second strongest being strong ties, and so on. Once model comparison had found the best model, we used that classification of strong versus weak ties to define our strong and weak ties.

3.b - If the normal distribution was a better fit to the focal' animal's weight distribution, then no strong ties were recorded.

Overall, this algorithm follows the logic of a semi-supervised classification where some small bit of information (1-priors about what a weak tie looks like, and 2-those strong ties should result in a skewed distribution) is then used to help perform unsupervised classification. To assess our algorithm's accuracy, we performed two tests. In the first, we simulated a normal distribution (i.e., no strong ties present) and recorded how many false positives (i.e., strong ties) our function detected. The second test consisted of adding one strong tie to a normal distribution. We then inferred how many times that strong tie was detected (i.e., true positives). Both tests were conducted on varying sample sizes (N = 2-50 interactions), with each sample size tested ten times. These simulations helped us tune our priors and the "min_diff" parameter to get the best results on simulated data before applying it to our real data. Using these two tests, we compared our built function to commonly used methods for the extraction of strong ties, such as counts of strong ties (strength > 0.9 percentile) and strength of strong ties (top 3* ties of individual) (see Supplementary S2). As our function was more reliable in detecting strong ties, we proceeded to extract the strong ties present in our data using this model-based approach. While this algorithm performed better than measures previously used, it still needs work as some flaws remain. For instance, by setting our "min_diff" parameter to 5 it enables the algorithm to distinguish between strong and weak ties. Yet, the higher this parameter is set, the bigger the difference between a weak and strong tie must be when the sample size is small (e.g., with this weight distribution (1, 3,15) no strong tie was detected). This was an issue in this analysis as the sample size between spatial and grooming behaviour differed (average interaction per individual across the study period: x-bar_spatial = 33.03 ± 11.43 SD; x-bar_grooming= 10.87 ± 2.91 SD). Therefore, we set the “min_diff” parameter differently based on the studied behaviour. That is, when extracting strong ties in spatial associations, we set “min_diff” to 5 as the sample size per individual was higher than the grooming interactions where the parameter was lowered to 2. Doing so allowed us to make the extraction of strong ties more conservative, based on the behaviour under analysis.

Using these isolated strong ties, spatial and grooming networks were created, where nodes corresponded the focal individual’s partner ID, while edges indicated the number of times the two individuals were recorded interacting, as well as the nature of the interaction (spatial or grooming). From these networks, we extracted the following measures.

6.3.6 Social Bubble Structure

We extracted three measures to capture the size, overall social engagement, and partner similarity in social bubbles. 1. Degree, which is the sum of each node’s strong connections. It captures the number of strong ties a focal subject has and therefore indicates the size of a social bubble. 2. Strength, which is the sum of each node’s connections weighted by the frequency of the interaction with other nodes. This measure specifies the overall effort invested in these strong ties. 3. Cosine similarity, which is used to estimate similarity in the patterning of values in two vectors (Jarrett et al., 2018; Newman, 2010; Vilette et al., in press,). Here, we used the measure to assess the similarity of the edge weights between two consecutive ego-networks, with values that range between 0 and 1. An individual whose social bubble (strong ties) changes markedly between time(t) and t+1 will have a low cosine similarity, whereas individuals whose social bubbles are similar at t and t+1 will show high cosine similarity. More details on calculating cosine values are given in the supplementary material (S3).

6.3.7 Social Bubble Composition

To investigate social bubble composition, two measures were extracted. 1. Rate of association with adults, which varies between 0 and 1. After their first birth (~ 3.5 years), females were considered to be adults, while males were considered adults at above 5 years of age. 2. Rate of association with family members, composed of the mother and any siblings. This measure also varies between 0 and 1.

6.3.8 Processes at play - Social bubbles comparison

To investigate the similarity between strong ties in juveniles' spatial and grooming networks at time t, we used cosine similarity as a multi-layer network measure. That is, spatial and grooming networks were compared at the individual level, within each two-month time-aggregated window. We applied the same reasoning for the similarity between ties outside of the mother's and offspring's total grooming bubbles, where the mother's and the offspring's grooming ego-networks were compared at time t. When comparing the mother's and offspring' grooming partners, the mother-offspring dyad was taken so that the mother did not appear as the juvenile's tie and the juvenile did not appear as its mother's partner.

6.3.9 Environmental conditions

As food availability contributes to the structuring of social associations (Bonnell et al., 2022), we measured troop-level estimates of resource availability using the Normalized Difference Vegetation Index (Willems et al., 2009). Area-weighted NDVI averages for each territory were generated for consecutive 33-day windows (16 days post and prior to the date of each MODIS raster) by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period (Young et al., 2019). NDVI scores, which range between -1 and 1, are higher in more photosynthetically active areas, and are therefore considered to indicate increased plant food availability.

6.3.10 Statistical Analyses

We analyzed our data within a Bayesian framework, using the ‘brms’ package (Bürkner, 2017) in R version 3.5.2 (R-Core-Team, 2017). We used hierarchical generalized additive mixed models (HGAM), which allow the relationships between the explanatory variables and the response to be described by smooth curves (Pedersen et al., 2019). This approach is useful as it does not assume a fixed trend but, instead, estimates a non-linear trend without a theoretically pre-specified shape. In other words, a smooth curve gives the opportunity for non-linear trends, if any, to emerge, hence giving further freedom for the model to fit the data. We ran all models with four chains and 1,000 iterations after specifying weakly informative priors (normal (0,1)). We performed prior predictive checks to ensure that these priors did not drive the patterns obtained from our predictions (see supplementary material S4). Model diagnostics confirmed MCMC convergence, with all $\hat{R}<1.1$ (Gelman & Shalizi, 2012). We used the ‘posterior predictive check’ (pp_check function) from the ‘bayesplot’ package (Gabry et al., 2019) to determine the quality of the model fits to the data.

Regarding the first part of our analyses, we constructed two models for each of our measures (cosine similarity, degree, strength and our two rates of association): one for grooming and one for spatial associations. This generated 10 models. For the second part of our analysis, a model was run for each of our two cosine similarity measures. For all 12 models, the model structure was constant (see supplementary material S5 for model structure). Our dataset structure consisted of repeated measures for individual, mother, cohort and troop identities, as well as for sex. We therefore let the effect of age vary by these five grouping variables, using factor smooths

(Pedersen et al., 2019). We also allowed the effect of ordinal rank to vary by individual, using a factor smooth. Factor smooths implicitly incorporate group-specific intercepts. That is, they create an estimate for each level of the grouping variable, but only estimate one smoothing parameter for all groups of this grouping variable. Put simply, these grouping variables deviate from the mean and hence vary in their pattern. We expected each grouping variable to vary in its ability to maintain a certain network structure as juveniles aged. Each of these interactions was added as a single smooth. We controlled for variability in environmental conditions by including NDVI as single smooth to the model. Additionally, a single smooth for troop number was included to address variation in troop size, along with one for age, to account for developmental variation.

Continuous variables were scaled and mean centred. For the count variables (i.e., spatial/grooming degree and strength), a Poisson model was run, with the log of the total number of observation sessions within the aggregated sample period included as an offset variable to account for differences in observation effort. As dispersion issues are common with Poisson models, we ran an analysis of residuals from the models ('DHARMa' Package). We addressed dispersion issues present in our models by running models with a negative binomial distribution. When this approach did not remove the dispersion issue, hurdle models were run (Hilbe, 2017). To determine which model to report in the main text, we used three approaches in concert: 1. Models were compared using leave-one-out cross-validation (Vehtari et al., 2016) with the 'loo_compare' function of 'brms'; 2. We looked at the magnitude of the dispersion, from the analysis of residuals; 3. We used the posterior predictive checks. We then compared the estimates of the best models with the estimates of our simpler, original Poisson models. This was used to assess whether the influence of the dispersion issue affected our results. With our grooming/ spatial degree and spatial strength models, the dispersion issue was influential, hence weare reporting the results from our negative binomial model in the main text for these three variables. With respect to our grooming strength model, the dispersion issue did not affect our results. As such, we report the simpler Poisson models in the main text and provide the necessary details regarding the other model in the supplementary material (S9).

When using the rates of association with adults and family members as our response variables, we constructed zero-one inflated beta models for spatial and grooming associations, as the response values varied between zero and one. We also used a zero-one inflated beta model when we looked at spatial and grooming partner similarity as well as when we investigated the similarity between grooming and spatial strong partners. A zero-one inflated beta model was also run when comparing ties outside of the mother's and offspring's grooming bubbles. All the model summary tables are presented in the supplementary materials (S6-S17), accompanied by Dharma nonparametric dispersion tests and posterior predictive distribution plots, when required.

Given the nature of the statistical models, as well as the inclusion of interaction effects, using a summary table on its own to interpret model estimates is not straightforward. We therefore generated whole model predictions using the fitted() function, from the 'brms' package, to extract the fitted values of our models. Variables that were not of direct interest were fixed to their mean (e.g., troop size, NDVI, rank), while predictions were made for the variables of interest (i.e., age and sex). These predictions were then used to construct predictive posterior plots with the 'ggplot2' package (Wickham, 2009). These plots allowed us to see how males and females differed in their response to the average effect of our response variables. Given their interpretative familiarity, we specified the 95% credible intervals (CI) in our plots to assess whether the sexes differed meaningfully in the structure of the revealed patterns. That is, we considered whether the CIs for females and males overlapped completely (i.e., no detectable difference between the sexes) or not at all (i.e., a meaningful quantitative difference between the sexes). Model main effects are presented as summary statistics (Table S6-S17 in supplementary material) for posterior means, 95% CIs, along with conditional R^2 values for each model, estimated using the 'bayes_R2' function (Gelman et al., 2019).

6.4 Results

6.4.1 Social Bubble Structure

6.4.1.1 Spatial ego-network structure

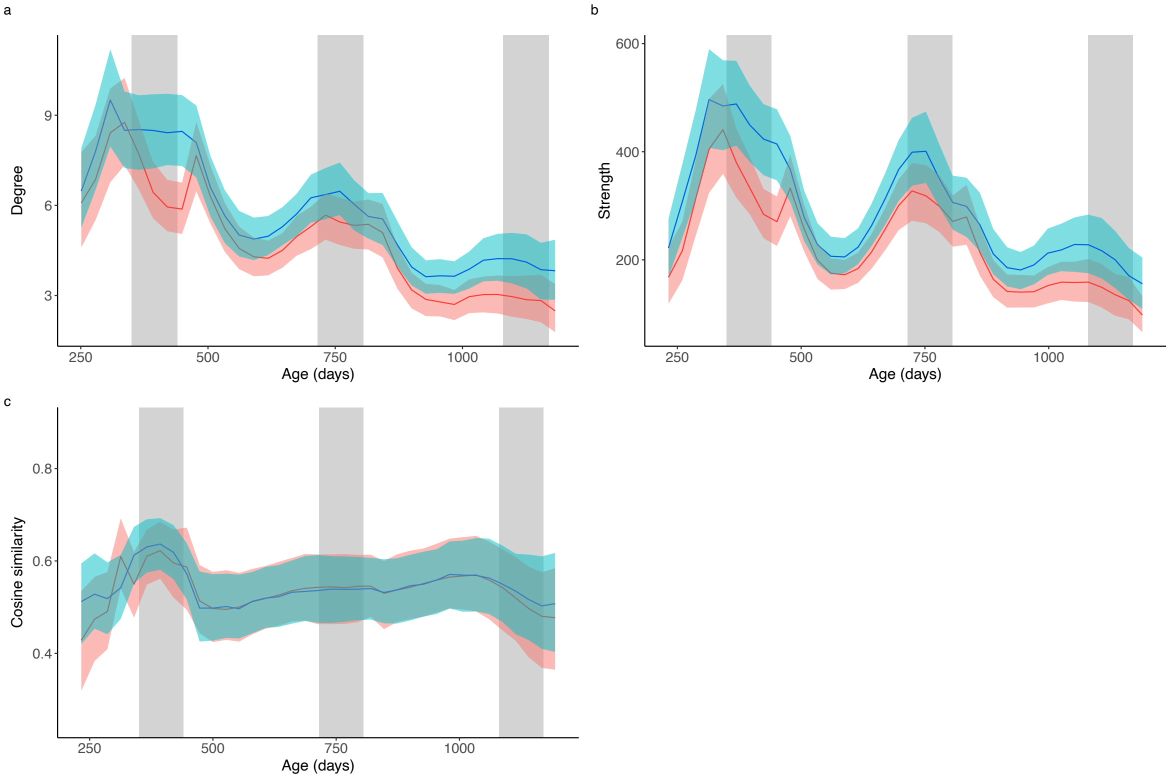


Figure 1 Variation in the (a) degree (b) strength and (c) cosine similarity of spatial associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were estimated with mean troop size fixed at 48 individuals.

As they aged, both sexes displayed a general decline in the number of partners within their spatial social bubble (Fig. 1a). There were, nevertheless, fluctuations, with slight temporary increases that aligned with each annual birth season. There were no sustained sex differences.

Although more pronounced, the same overall pattern was observed for mean strength (Fig. 1b). Finally, for both sexes, the observed pattern in the similarity of spatial partners present within juveniles' social bubbles was one of overall stability, although values were quite low. There was, however, a peak that aligned with the first birth season (Fig. 1c).

6.4.1.2 Grooming ego-network structure

With respect to the number of grooming partners (degree) in their social bubble (Fig. 2a), both sexes showed a pattern of stable, but low values, with increasing uncertainty in the estimates of the mean over time. In contrast, mean strength declined over time, although birth season seemed to exert a clear effect in one year (Fig. 2b). Finally, both sexes displayed a consistent pattern of very high values in the similarity of their grooming partners within their social bubble over time (Fig. 2c).

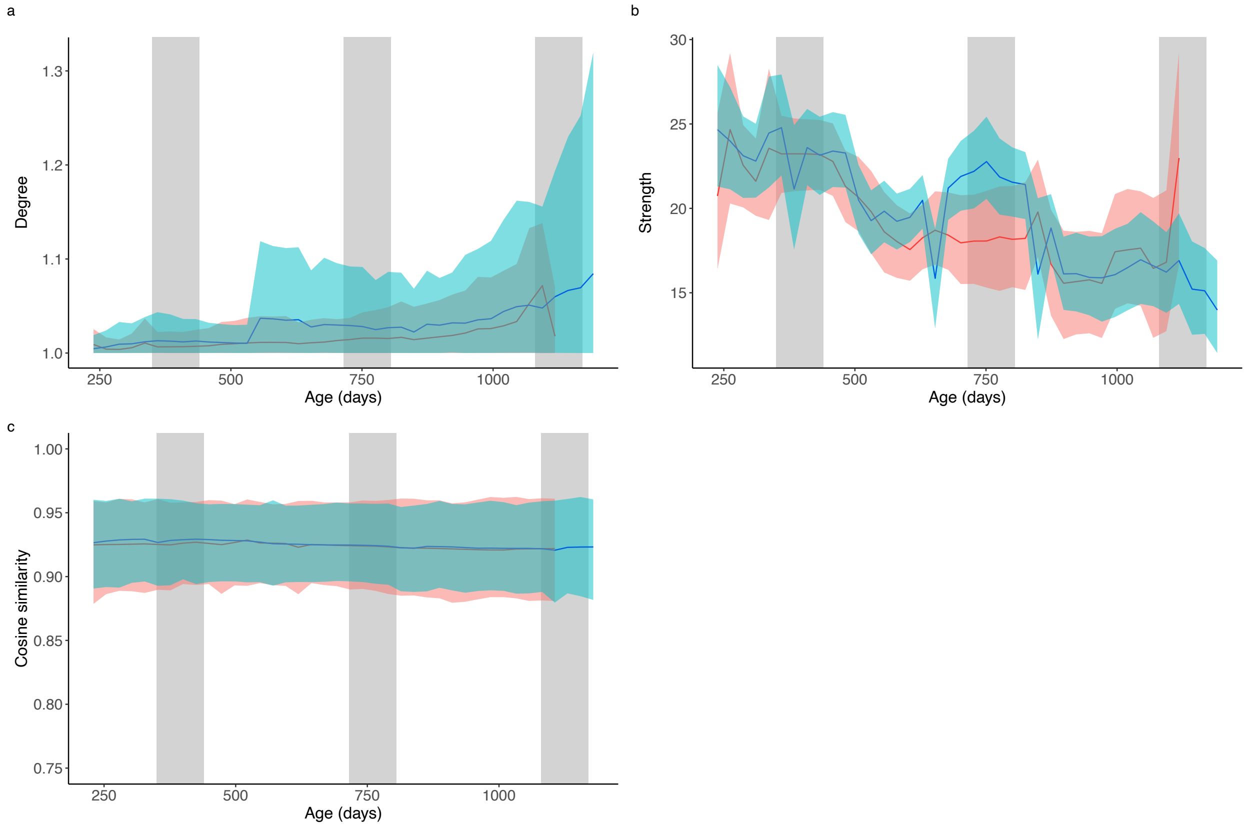


Figure 2 Variation in the (a) degree (b) strength and (c) cosine similarity of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were estimated with mean troop size fixed at 46 individuals.

6.4.2 Social Bubble Composition

6.4.2.1 Spatial Social Bubble Composition

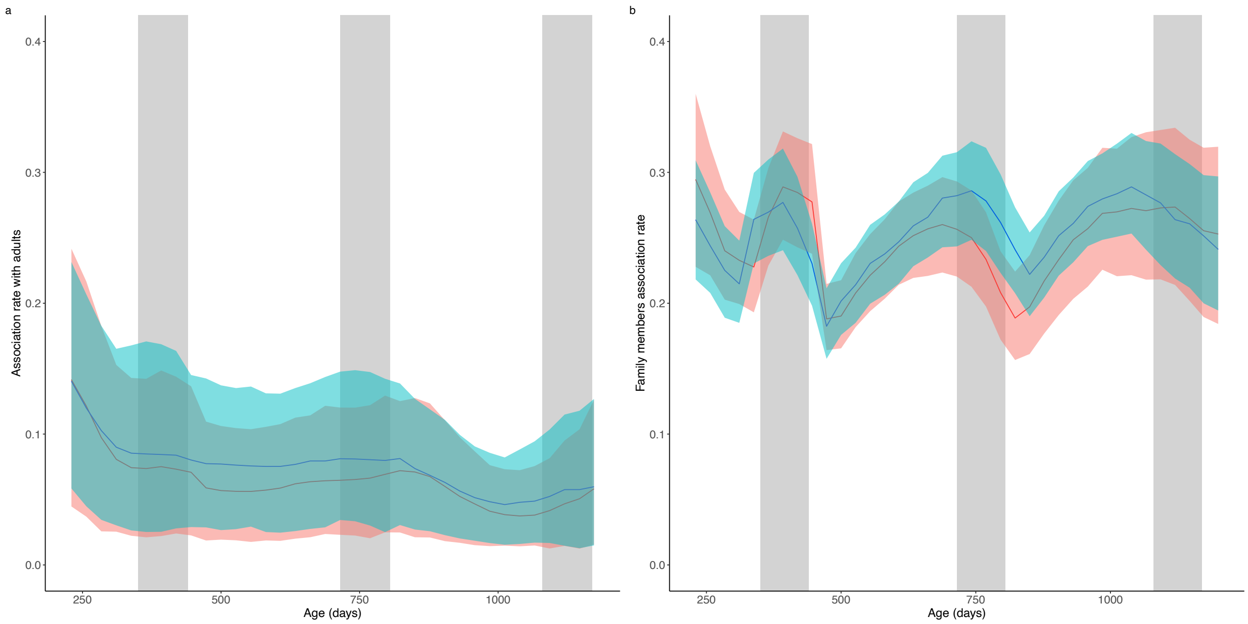


Figure 3 Variation in the (a) rate of spatial associations with adults and (b) rate of spatial associations with family members by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

For spatial association with adults over time, both sexes displayed a pattern of stable, but low, association over time (Fig. 3a). With respect to the rate of spatial association with kin, the general trend, for both sexes, was a cyclical pattern of peaks and troughs that aligned with the annual birth season, with rates increasing during the birth season (Fig. 3b).

6.4.2.2 Grooming Social Bubble Composition

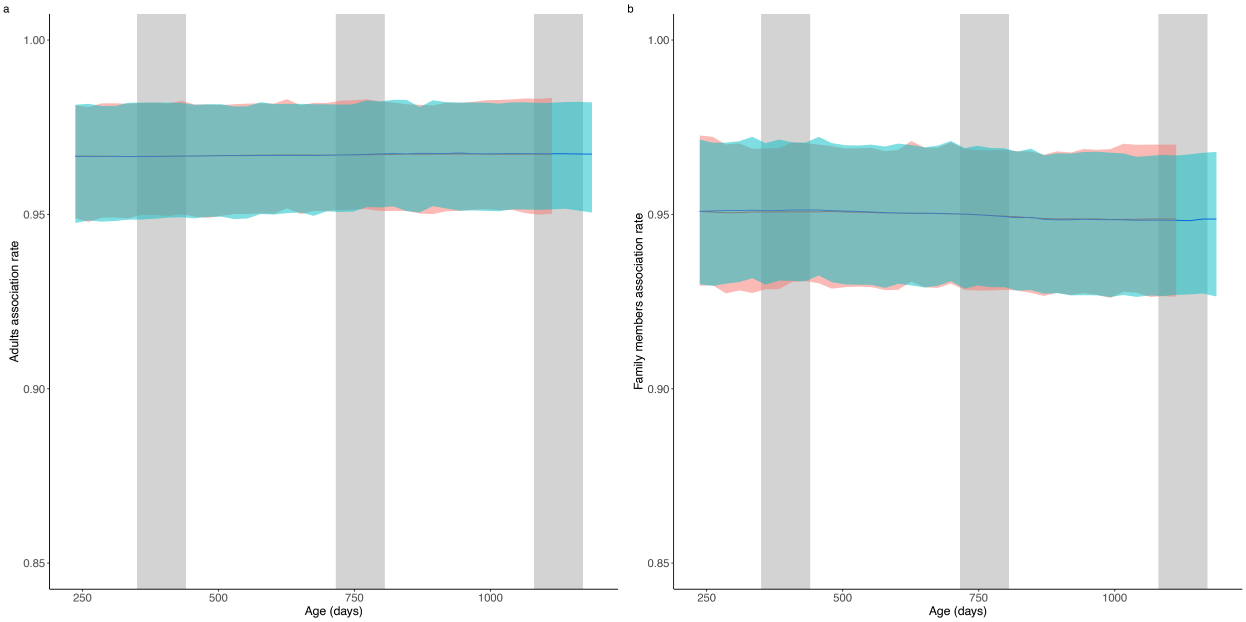


Figure 4 Variation in the (a) rate of grooming associations with adults and (b) rate of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

Both sexes displayed very consistent and high levels in their grooming association rates with adults (Fig. 4a) and family members (Fig. 4b) over time, with association rates with adults being slightly higher than with family members.

6.4.3 Processes at play - Social bubbles comparison

6.4.3.1 Comparison between spatial and grooming social bubbles

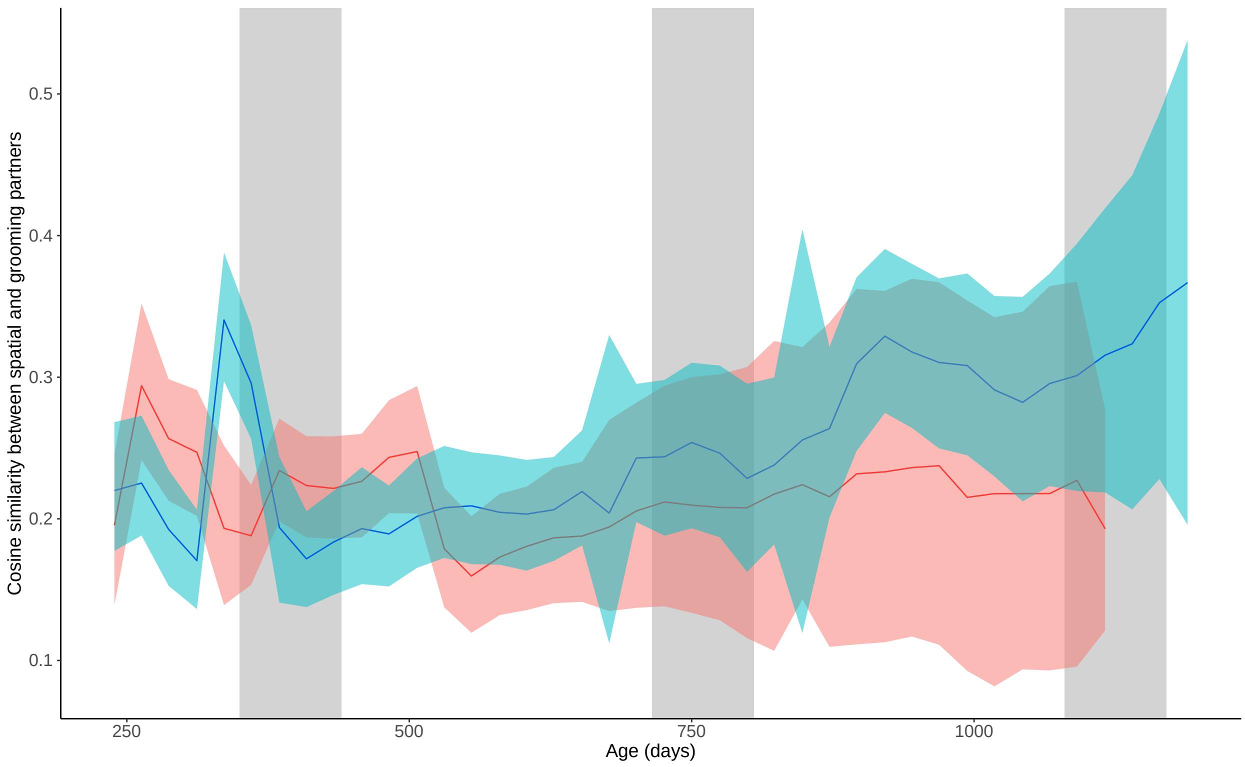


Figure 5 Variation in mean cosine similarity between spatial and grooming partners by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

Although spatial-grooming cosine similarity was generally low, there was a slight increase over time for females, whereas the general trend for males was a pattern of slightly fluctuating low values (Fig. 5).

6.4.3.2 Comparison between the mother's and the offspring's ties outside of the grooming bubble

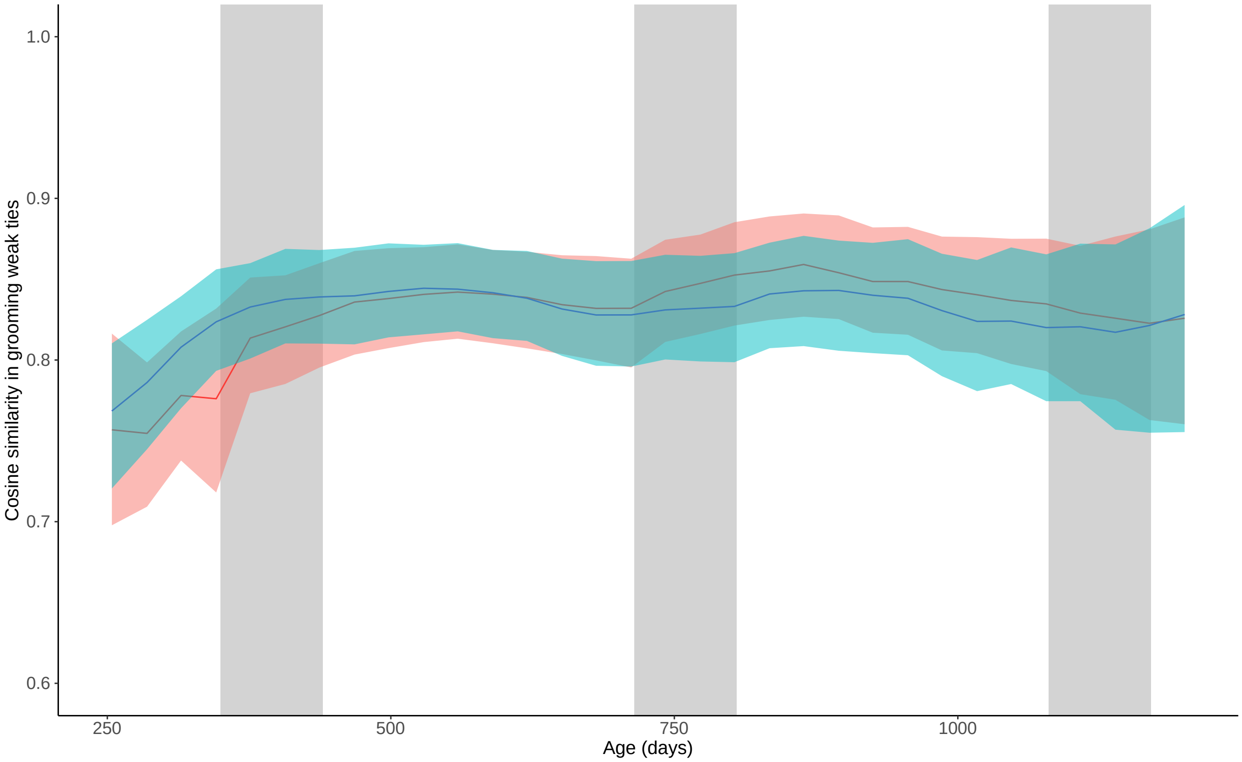


Figure 6 Variation in mean cosine similarity between mothers' and their offspring' weak grooming ties by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

The similarity between the grooming ties outside the bubbles of the mothers' and juveniles', for both sexes, showed a fairly stable pattern of high values in cosine similarity.

6.5 Discussion

Contrary to our prediction, we found that the structure of spatial proximity bubbles did not develop following Kohn's (2019) socialisation steps. In the case of degree, spatial bubbles showed an overall decline with age (Fig. 1a), interspersed with two bumpy periods during the birth season, between each decrease. Strength displayed the same pattern, although this was more pronounced and was of greater magnitude (Fig. 1b). Cosine similarity was low and quite stable over time for both sexes (Fig. 1c). Taken together, these results suggest that, for both sexes, juveniles' spatial bubble became more concentrated, in terms of size and social engagement, focusing on fewer changing partners they more strongly associate with. While the patterns displayed did not follow our predictions, the end result compares with Kohn's (2019) socialisation phases, where juveniles narrowed and strengthened certain social relationships. Yet, an important distinction here is that Kohn's (2019) framework was couched in terms of network composition (i.e., that exploration, pruning and consolidation was conducted with respect to particular individuals). In our case, juveniles do not appear to go through a process of pruning and consolidation with particular consistent partners; rather, they seem to prune and consolidate the social bubble structure itself.

With regard to grooming social bubble structure, our patterns did not conform to Kohn's (2019) framework either. Instead, the number of grooming partners (degree) remained very low and stable across development, while the overall effort invested in grooming (i.e., strength) decreased (Fig. 2a, b). Lastly, for both sexes, similarity in grooming partners remained very high and stable over time (Fig. 2c). As such, we see that, for both sexes, the majority of their social effort is placed into a single strong grooming partner, and that this effort diminishes over time. That is, juveniles maintain a single and consistent unique strong tie, without having to maintain their initial high grooming frequency with this partner. Focusing on female juveniles, we suspect that reducing grooming investment in this strong tie gives them time to invest in ties outside of their grooming bubble, as demonstrated by the increase both in grooming frequency and in the number of grooming partners in our previous analyses (i.e., female juveniles went from grooming 5 to ~15 individuals) (Vilette et al., in press). For males, by contrast, our current and previous analysis suggest they are less engaged and more scattered in terms of grooming effort and their overall number of grooming partners, where they went from 5 to 7 partners and engaged in less grooming through time (Vilette et al., in press). By reducing overall grooming investment, they may increase the time available to engage in other kinds of social behaviour (e.g., locomotor or social play), which may be more beneficial to their development in other respects.

As predicted, juveniles associated with more spatial partners (Fig. 1a and 2a) and showed less partner stability (Fig. 1c) than they did with their grooming partners (Fig. 2c). While this aligns with our previous study and the idea that juveniles have different interaction styles (passive versus active) across behavioural contexts, a more focused and stable grooming bubble may provide juveniles with the safety needed to explore their social environment and learn how to navigate it. In other words, by having a stable and predictable grooming partner to return to, juveniles may be able to spatially associate more freely with partners and begin to build their own ego-networks made of weak and strong ties. This directly speaks to the importance of having a secure attachment for the social development of immatures (Bowlby et al., 1989).

If we now turn to the composition of spatial and grooming social bubbles, we find opposing results. Rates of spatial association with adults and family members showed fluctuating patterns, with family members showing a cyclical pattern of peaks that aligned with the yearly birth season (Fig. 3a, b). Although we predicted a mix of individuals within spatial bubbles, we found instead that, for both sexes, young vervets mostly associated with other juveniles. The absence of association with adults reveals that the structuring of spatial interactions is unlikely to result from a passive consequence of spatial association patterns mediated by kinship (here, the mother), shown in adult vervets (Josephs et al., 2016). In other words, juveniles appear to be building their own spatial networks' structure rather than integrating into existent adult networks. One possible explanation is that associating with immatures may provide juveniles with other kind of social engagement (e.g., play) and/or with partners that have similar time budgets. Regarding association rates with adults and family members (Fig. 4a, b), both sexes showed very high and constant patterns through time. Taken together, this means that juveniles have very small but stable grooming bubbles, composed, almost exclusively, of adults and family members (that is, their mothers), supporting previous studies (Silk et al., 2006a, 2006b).

When we consider the structure and composition of spatial proximity and grooming bubbles in concert, the clearest contrast between them, in addition to size, is seasonal variation: spatial bubbles revealed clear seasonal patterns, whereas grooming bubbles did not. The observed sensitivity to changes in group composition for spatial behaviour was also seen in our earlier analysis (Vilette et al., in press), which did not distinguish between weak and strong ties. Focusing on the birth season, the upward shifts in association rate with family members, combined with the positive fluctuations in strength and degree, suggest that juveniles' spatial bubble structure is sensitive to the arrival of newborns. Here, the increase in number of strong partners and the effort they place into them is reflected in the increase in association rate with family members. Whether the observed fluctuations result from an active or passive process remains, however, to be determined. For instance, the increases in size and social effort may reflect an active choice by juveniles seeking proximity near specific individuals, whereas it could also manifest as a passive consequence of the social group becoming more centralized during birth season, and hence juveniles being more spatially engaged. With regard to the increase in rate of association with family members, previous work has shown that attraction to newborns promotes close spatial associations with mothers (Fairbanks, 1990; Johnson et al., 1980; Silk et al., 2003, 2009; Silk, 1999), an attraction that could also result from an active or a passive process. The absence of seasonal variation in grooming bubbles may indicate that juveniles control their choice of partners, and/or that this choice results from the mother herself, who controls her grooming. Investigating the direction of interactions further will allow us to distinguish who controls social engagement and how it is distributed among different partners.

That is, whether juveniles are actively shaping their social bubbles or whether the secure attachment provided by their mother is enough for them to be more passive in the process of their socialisation. Furthermore, one way to get a better understanding of the mechanisms at play would be to see how the different components of the juvenile social bubble (i.e., its size, social engagement, composition and stability) drives one another (e.g., does the increase in bubble size lead to an increase in social engagement, or vice versa?). Answering these questions would give us a better sense of whether juveniles are rehearsing or if they are already living the life of an adult monkey.

Lastly, despite displaying fluctuating patterns in their structure, spatial social bubbles are consistently composed of a particular class of individuals (here, immatures), implying that the structure itself may allow juveniles to associate with peers who share similar time budgets. With regard to grooming social bubbles, the absence of sex differences within strong ties, and the fact that only juveniles' mothers composed their grooming bubbles, suggests that sex-specific social variability may arise within their weak ties, rather than the strong tie of their social bubble. Overall, the difference observed between spatial and grooming bubbles suggests that the particular structure seen in social bubbles emerges as a result of the nature of the behaviour under consideration (grooming or spatial proximity) and group demography. The socialisation process of juveniles can therefore be seen as a continuous ongoing process of behavioural adjustment by which animals achieve and sustain integration into an existing group (Deputte, 2000).

Considering the potential processes at play in the formation of social bubbles, we again did not find the predicted pattern where spatial and grooming bubbles overlap at first and then slowly become more distinct. Instead, the similarity in these spatial and grooming bubbles remained consistently low over the juvenile period (Fig. 5). This was not surprising, considering that we observed a spatial bubble made of non-related juveniles (Fig. 3a, b) and a grooming bubble composed of the juvenile's mothers (Fig. 4a, b). This corroborates Henzi et al.'s (2013) observation that adult vervet monkey females did not simply groom their spatial associates but distributed their grooming more actively toward specific partners. Future analyses might well consider whether the grooming bubble shapes the structure of the spatial bubble, or vice versa. In asking about the similarity of ties outside of mother's and offspring's grooming bubbles, we investigated whether juveniles acquired the same partners as their mothers among their weak ties. We found that juveniles showed a continuous stable pattern of high similarity (Fig. 6), suggesting that a mother and her offspring's weak ties remained similar as juveniles developed. In other words, maternal grooming network instability may not allow immatures to develop strong ties with their mother's grooming partners. They may, however, have enough to time to interact with their mother's partners, even if these relationships cannot be consolidated. While mothers clearly play a role in juveniles' social bubble formation and more broadly, in their social integration, future work investigating the size and composition of the mother's grooming bubbles through time will give us a better idea of the social bubble structuring process and the extent to which juveniles' and adults' bubbles differ.

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6.7 Supplementary material

S1: Determining Stability and Robustness of Network Window Size

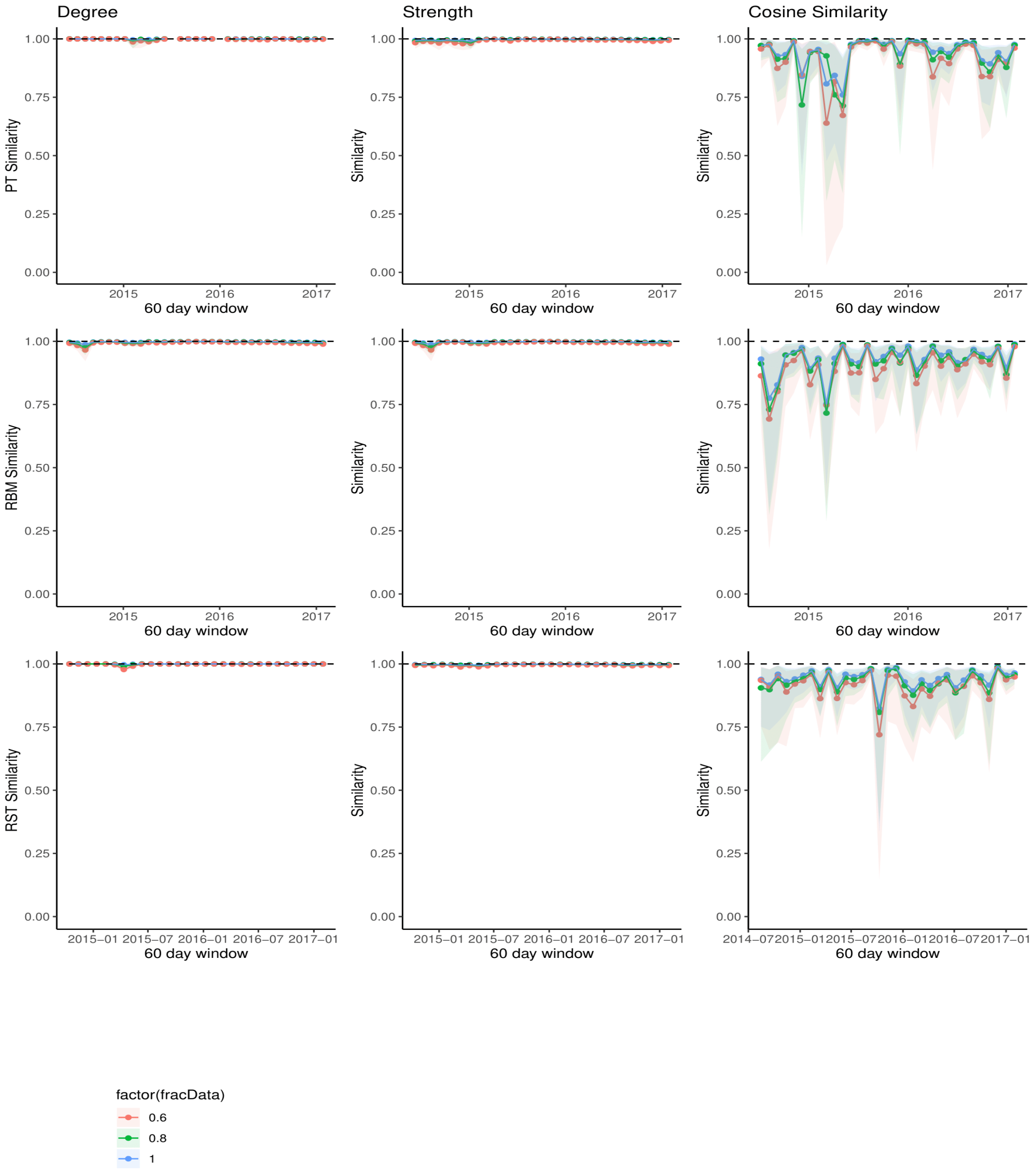


Figure S1.1 Results of estimating the lower bound of window size choice using bootstrapping and subsampling for the spatial proximity networks across 60-day sampling windows for each troop (rows) and each of our measures (columns). The y-axis is the correlation between the network level measures of nodes in the observed and bootstrapped networks. The lines and points represent the mean cosine similarity, while the shaded areas represent the 95% CI calculated from 1000 bootstrapped samples. Cosine similarities were estimated for subsamples of the data: 100%, 80%, and 60% to quantify the influence of potential missing data on network measures.

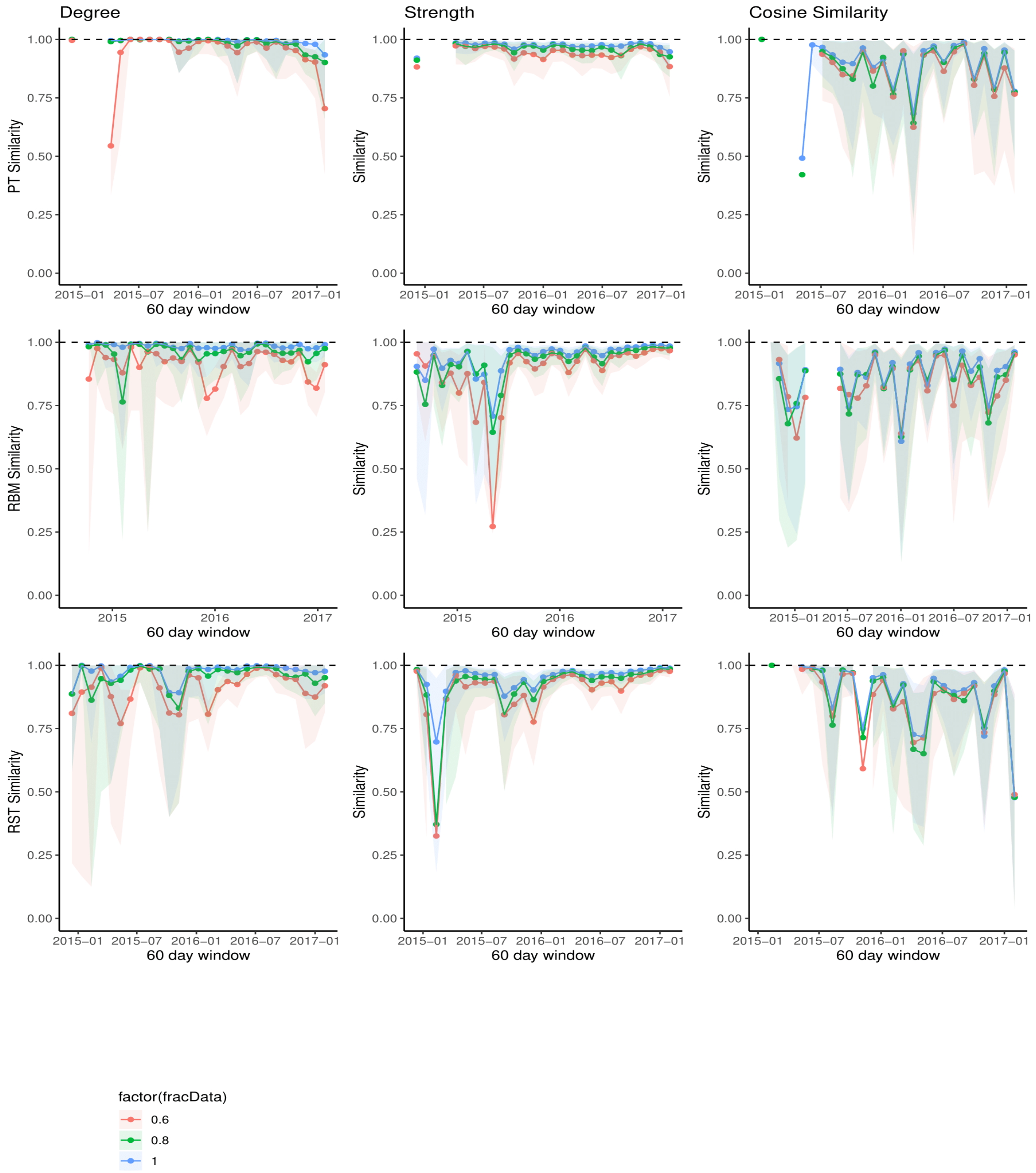


Figure S1.2 Results of estimating the lower bound of window size choice using bootstrapping and subsampling for the grooming networks across 60-day sampling windows for each troop (rows) and each of our measures (columns). The y-axis is the correlation between the network level measures of nodes in the observed and bootstrapped networks. The lines and points represent the mean cosine similarity, while the shaded areas represent the 95% CI calculated from

1000 bootstrapped samples. Cosine similarities were estimated for subsamples of the data: 100%, 80%, and 60% to quantify the influence of potential missing data on network measures.

S2: Strong tie algorithm

The figure below (Fig. S2.1) shows the rate of false positives detected using three different approaches and different sample sizes. Here, a normal distribution of varying size was simulated. This way, it was known that no strong ties were present in the distribution. The left column focuses on small sample sizes ranging from 2 to 10 interactions, whereas the right column represents bigger samples ranging from 15 to 50 interactions. These columns seek to reflect the sample size we have between grooming (less interactions) and spatial behaviour. As such, with small sample size (left column) the "min_diff" parameter was set to 2, whereas it was set to 5 for with bigger sample size (right column). Each line represents a different used approach. The first approach used is the count of strong ties where strength is superior to the 0.9 percentile. We see that this approach performs very well on small sample sizes where no false positives are detected. When the sample size gets bigger, however, the approach consistently detects false positives.

The second approach extracts the top 3 strongest ties present in the sample. Regardless of the sample size, this approach continuously detects strong ties, which is not surprising given its definition.

Lastly, the third approach that we offer in this analysis performs well at not detecting false positives regardless of the sample size.

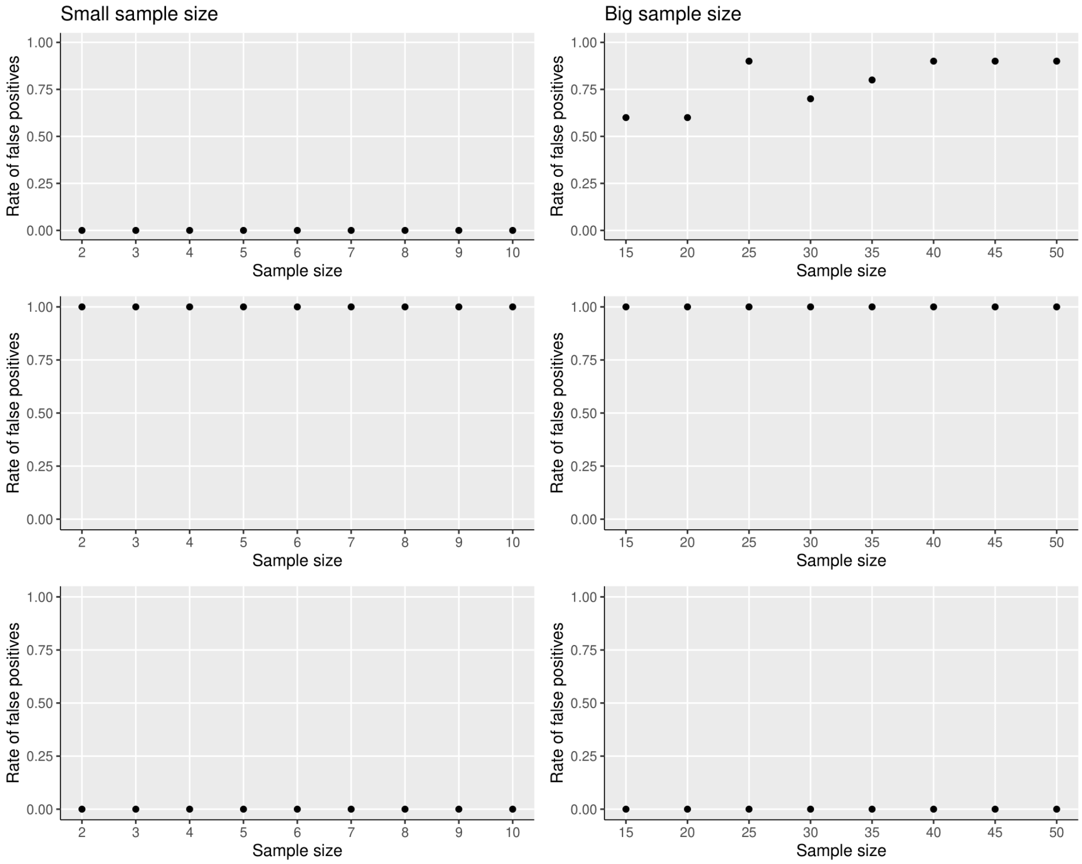


Figure S2.1 Performance at detecting false positives of the strength >0.9 percentile, top 3 ties approaches and our model-based function on small and big sample sizes.

The figure below (Fig. S2.2) assesses how well the three approaches detect the presence of one strong tie. Here a normal distribution was simulated, and a strong tie added to it. The layout of the figure follows the previous one with column representing small and big sample sizes whereas lines correspond to the different tested approaches. Overall, the first approach fails at detecting the strong tie across the varying sample sizes. The second approach automatically detects three strong ties instead of one, hence failing throughout the different sample sizes. Lastly the model-based approach shows high rate of detection when the sample size is small and an increasing success rate as the sample size gets larger (15 interactions and more).

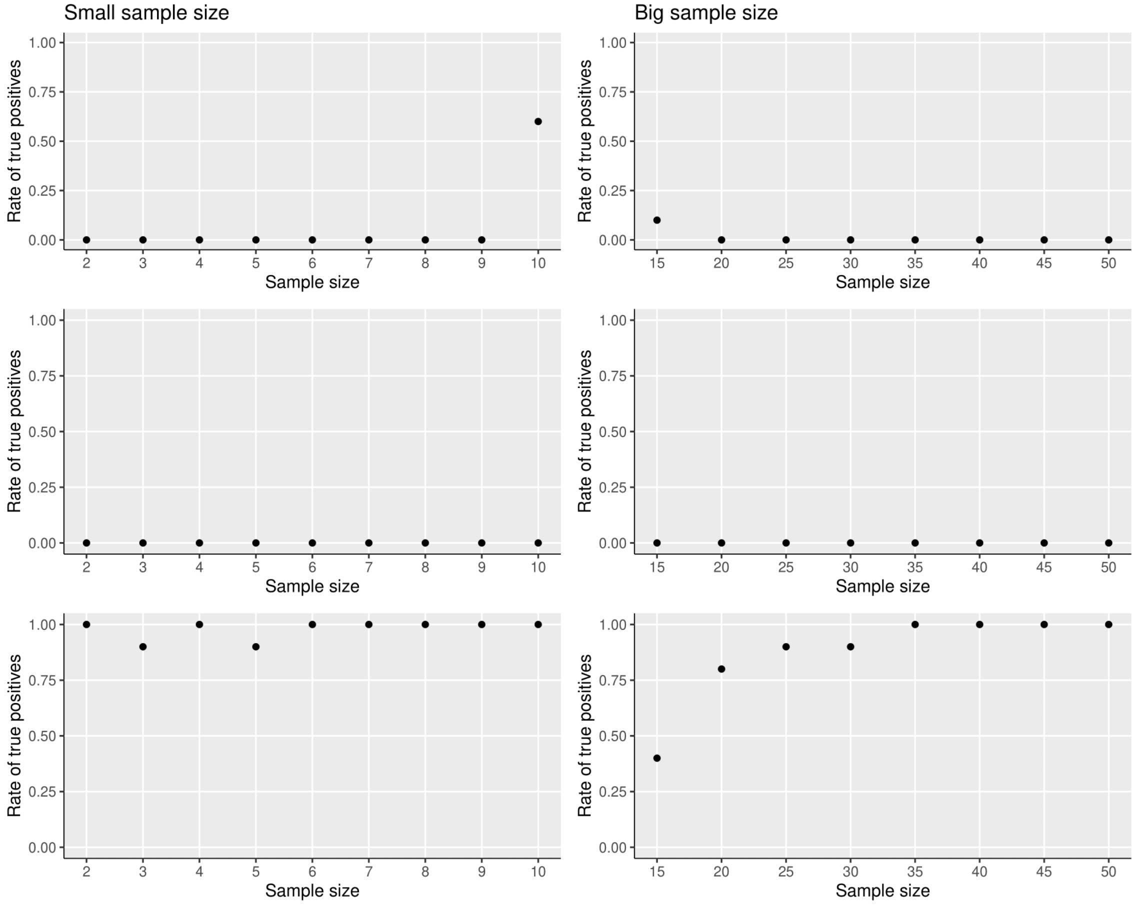


Figure S2.2 Performance at detecting true positives of the strength >0.9 percentile, top 3 ties approaches and our model-based function on small and big sample sizes.

<u>S3</u>: Cosine similarity measure

Cosine similarity assesses the extent to which the patterning of values in two vectors (a, b) is similar, making it appropriate for differing sample sizes (Newman, 2010). This metric is a measurement of orientation/style, not one of magnitude like Euclidean distance, and is expressed as the cosine of the angle between two vectors.

$$cos\theta = \frac{a.b}{\parallel a \parallel \parallel b \parallel}$$

In our case, a vector is a suite of weights, each weight corresponding to the number of times a distinct dyad (the focal and its partner) was seen interacting. Cosine similarity offers the possibility to center the variable (i.e.., the suite of weights) by subtracting the mean of the variable to every value of the variable.

When doing so, cosine similarity becomes the equivalent of the Pearson correlation. When not centred, the measure is called cosine similarity.

Regarding the Pearson correlation, the values range from −1 to 1. A value of exactly 1 implies the juvenile's partners between time t and time t+1 are exactly the same. Graphically speaking, in this case, all data points lying on a line. The correlation sign is determined by the slope of the line. A value of 0 implies that there is no linear dependency between the partners at time t and time t+1. A value of -1 would tell us that we see the opposite relationship observed at time t. Cosine similarity, however, looks at the angle between two vectors of points, and not the slope. If the direction is similar (low angle), then the two vectors are similar. If the two vectors point in opposite direction (large angle), then they are dissimilar. In our case, the cosine similarity values range between 0 and 1 as frequencies of interactions can't be negative.

As correlation estimates similarity based on how weights have changed relative to other grooming partners, while cosine estimates similarity assesses similarity based on how direction of weights of all the partners have shifted overall. As such, we chose not to center our variable and used cosine similarity measure.

<u>S4</u>: Prior predictive checks compared to the predicted patterns

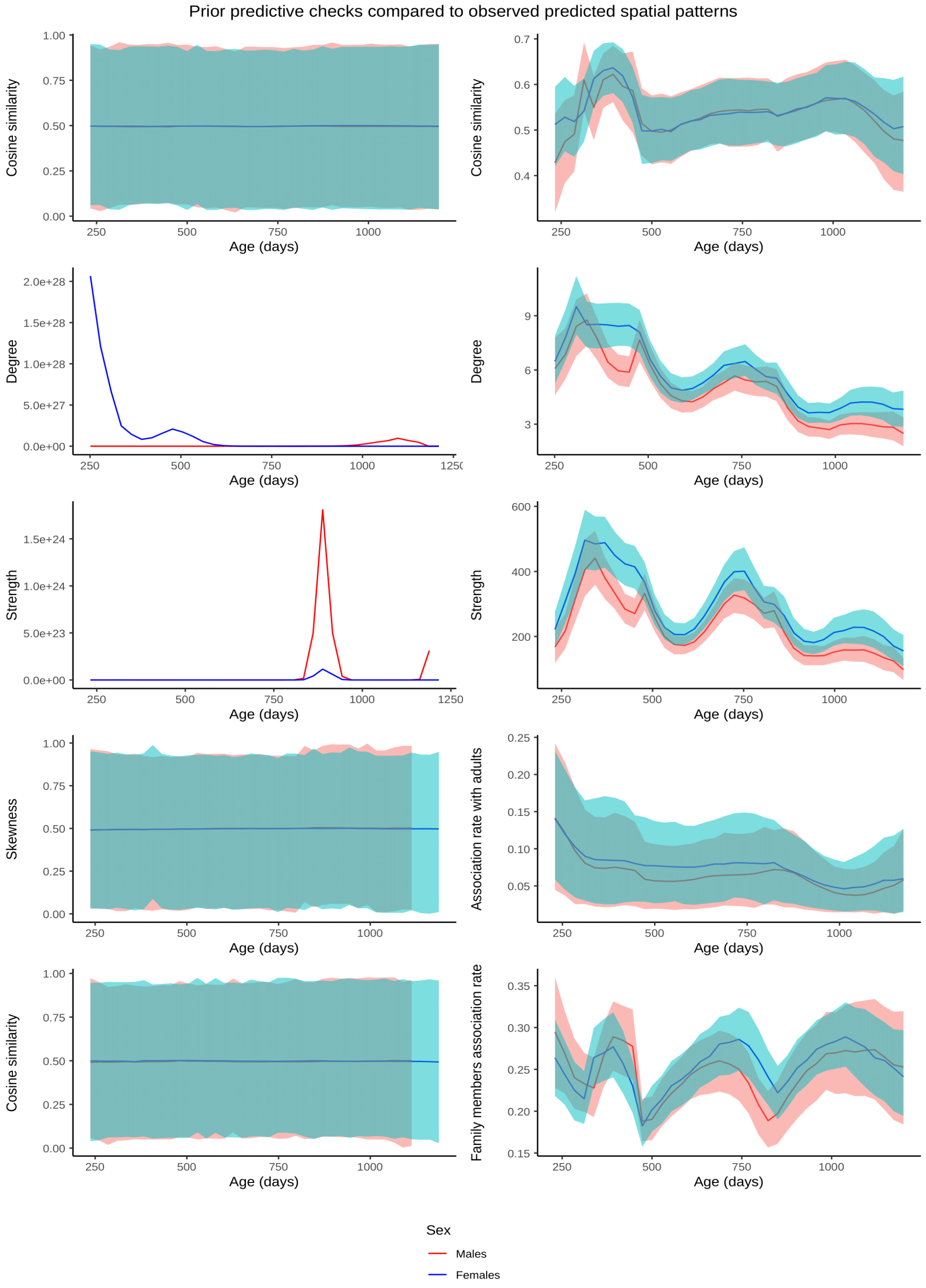


Figure S4.1 Comparison between prior predictive checks (on the left) and the predicted variation in the cosine similarity, degree, strength, and association rates with adults and family members of spatial associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands).

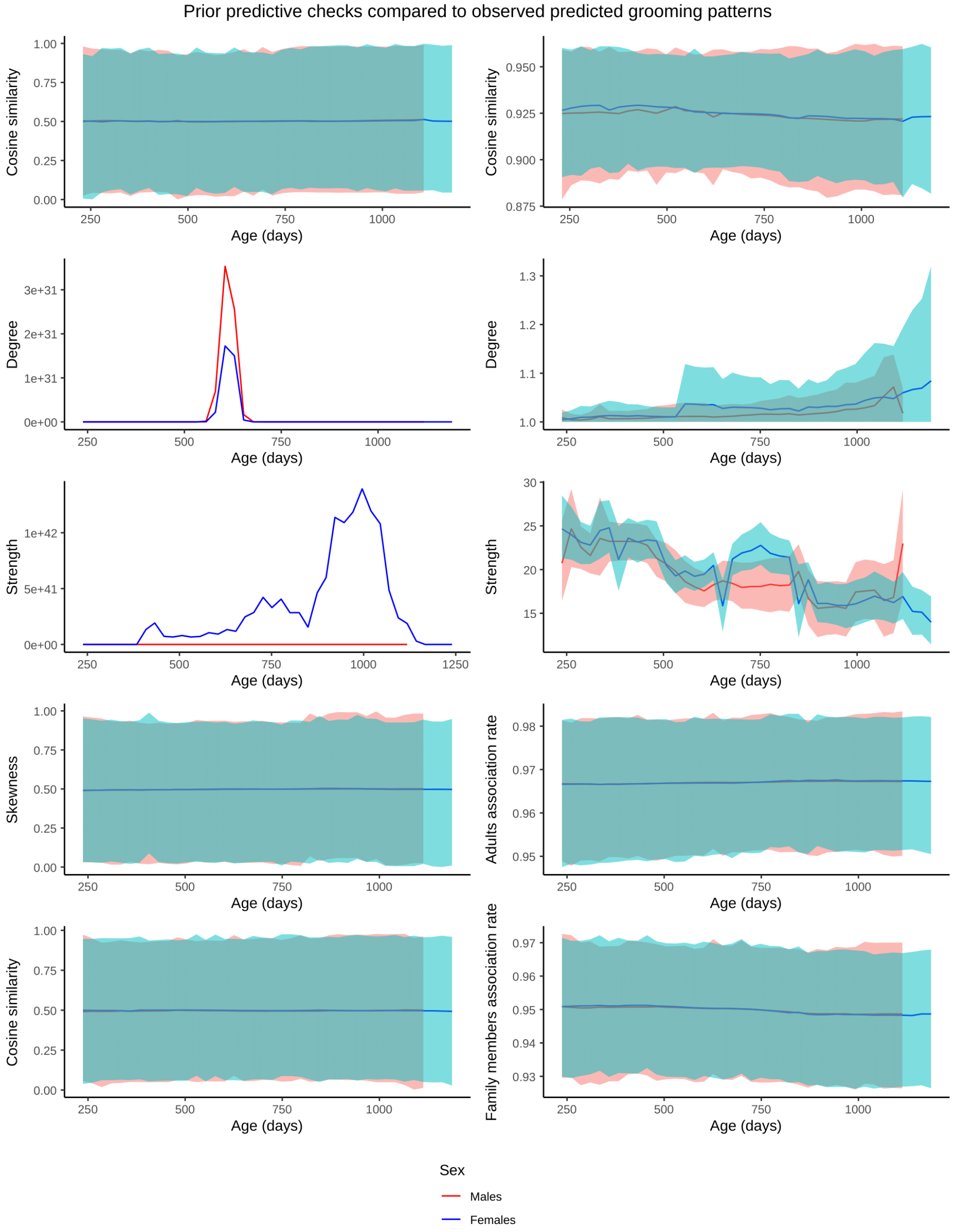


Figure S4.2 Comparison between prior predictive checks (on the left) and the predicted variation in the cosine similarity, degree, strength, and association rates with adults and family members of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands).

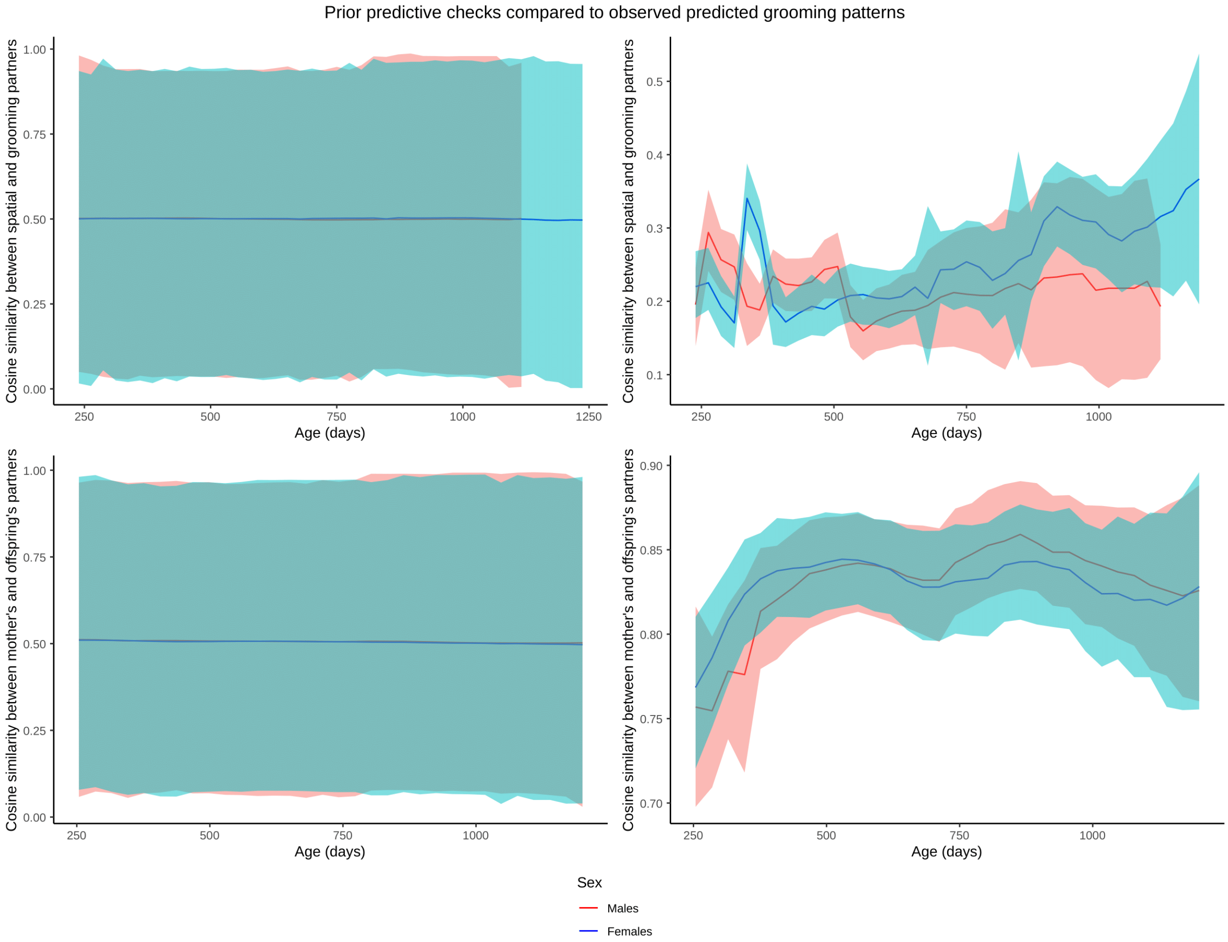


Figure S4.3 Comparison between prior predictive checks (on the left) and the predicted variation in the cosine similarity between spatial and grooming partners, as well as cosine similarity between mother's and offspring's weak grooming partners by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male respectively, with upper and lower 95% credible intervals (bands).

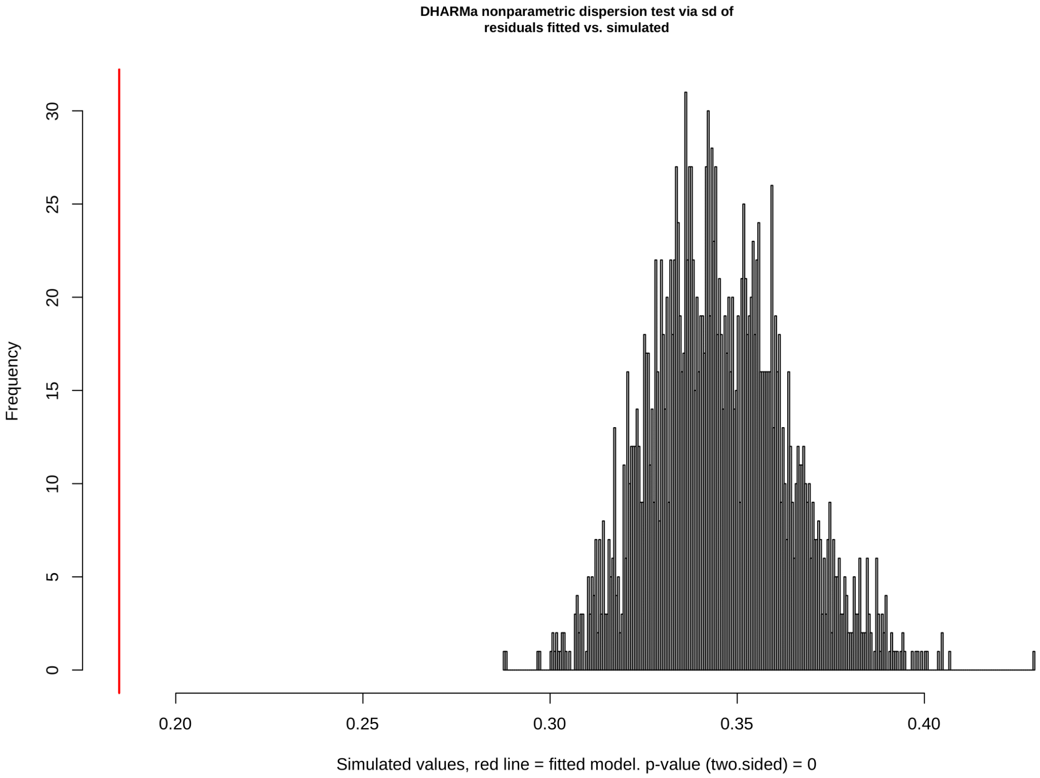
S5: models' structures

Summary of the model parameters used in hierarchical generalized additive models (HGAMs) to assess the influence of age and sex factors and our response variables. All independent variables and interactions had a smooth term around them. All continuous predictor variables were mean-centered and standardized by two standard deviations to allow for effect size comparisons across continuous and dichotomous variables (Gelman 2008).

Interaction type	Response variable	Fixed effects	Interactions	Distribution
Spatial proximity	Cosine similarity	Age Scan.nb NDVI Troop.nb	Age by juvenile ID Age by cohort ID Age by sex Age by troop ID Age by mother ID Rank by ID	Zero-one-inflated beta
	Degree	Same as above	Same as above	Negative Binomial
	Strength	Same as above	Same as above	Negative Binomial
	Association rate with adults	Same as above	Same as above	Zero-one-inflated beta
	Association rate with family members	Same as above	Same as above	Zero-one-inflated beta
Grooming	Cosine similarity	Age Scan.nb NDVI Troop.nb	Age by juvenile ID Age by cohort ID Age by sex Age by troop ID Age by mother ID Rank by ID	Zero-one-inflated beta
	Degree	Same as above	Same as above	Negative Binomial
	Strength	Same as above	Same as above	Hurdle Poisson
	Association rate with adults	Same as above	Same as above	Zero-one-inflated beta
	Association rate with family members	Same as above	Same as above	Zero-one-inflated beta
Spatial/Grooming comparison	Cosine similarity	Same as above	Same as above	Zero-one-inflated beta
Mother/Offspring comparison	Cosine similarity	Same as above	Same as above	Zero-one-inflated beta

S6: Degree in spatial proximity associations

S6.1. Under-dispersion in the Negative Binomial Model for the number of spatial partners

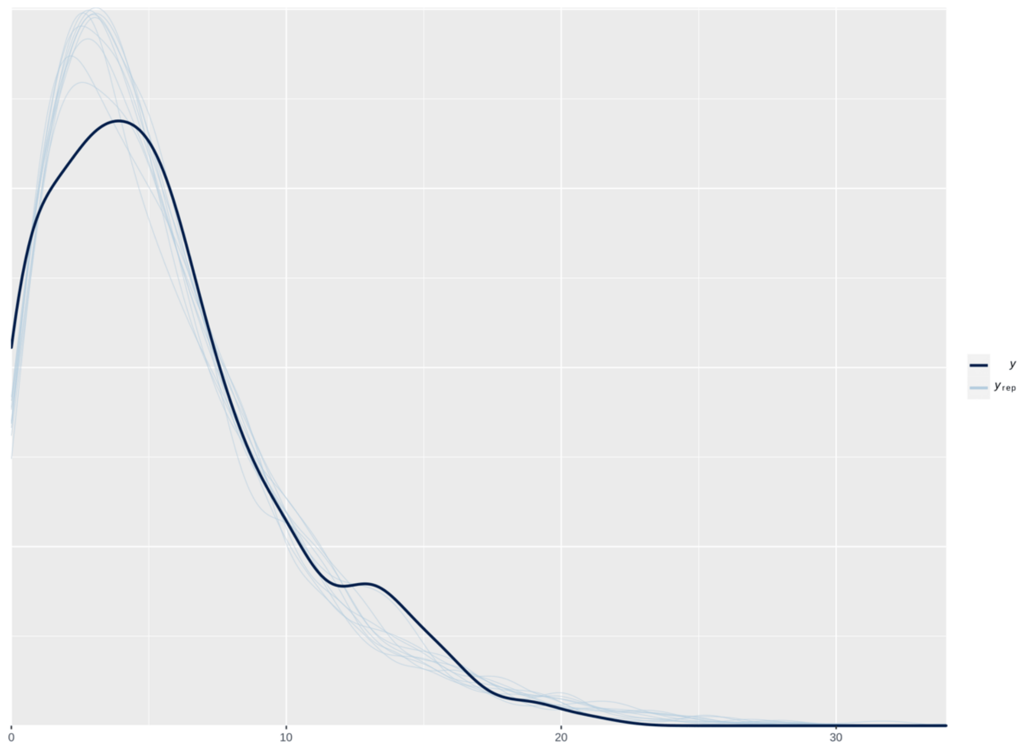


S6.2. Summary table of the Negative Binomial Model for the number of spatial partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in spatial associations, using a Negative Binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

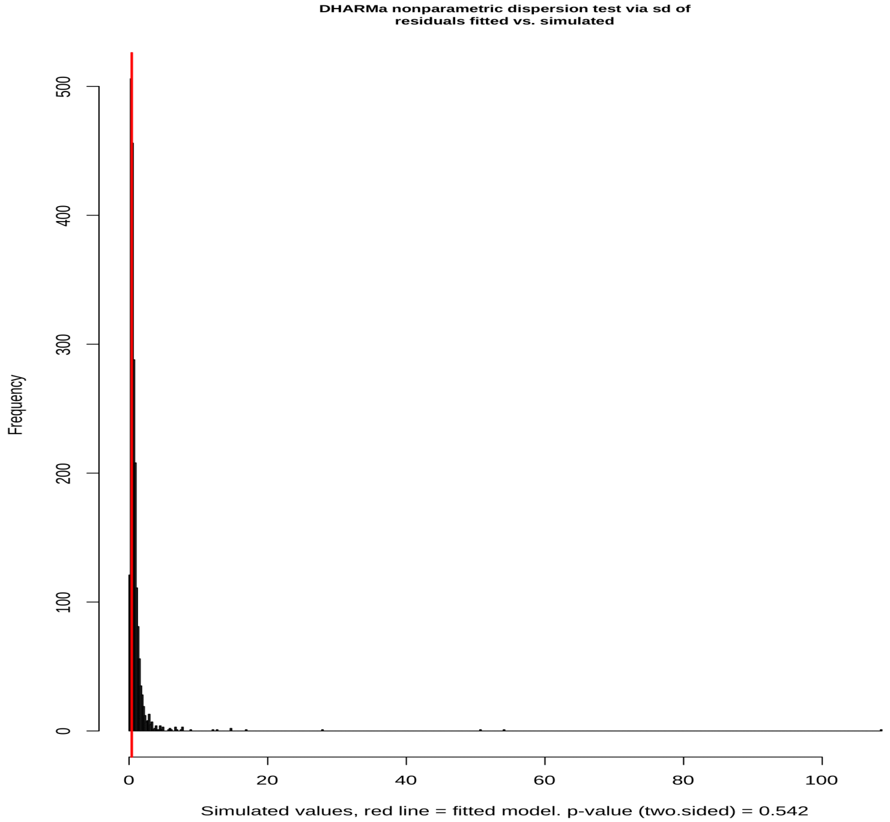
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-4.49	0.47	-5.42	-3.56
	s(age)	0.55	0.99	-1.30	2.46
	s(NDVI)	0.41	0.67	-0.81	1.79
	s(troop.nb)	0.02	0.83	-1.64	1.61
Smooth Terms	sds(age)	2.04	1.42	0.14	5.39
	sds(age ID1)	1.21	0.14	0.94	1.47
	sds(age ID2)	1.04	0.70	0.06	2.53
	sds(age cohort1)	1.97	0.50	1.17	3.15
	sds(age cohort2)	2.15	1.78	0.08	6.58
	sds(age troop1)	0.93	0.27	0.50	1.52
	sds(age troop2)	1.14	1.13	0.03	4.23
	sds(age mumID1)	0.41	0.26	0.03	0.93
	sds(age mumID2)	1.64	0.77	0.11	3.09
	sds(age sex1)	0.20	0.17	0.01	0.64
	sds(age sex2)	2.54	1.82	0.41	7.77
	sds(NDVI)	0.57	0.52	0.02	1.96
	sds(troop.nb)	1.82	0.70	0.72	3.48
	sds(rank ID1)	0.13	0.09	0.00	0.33
	sds(rank ID2)	1.03	0.67	0.04	2.43
Family-specific Parameters	Shape	273.51	128.23	109.83	598.95
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.75	0.01	0.73	0.77

S6.3. Comparing the observed outcome variable (degree) to datasets simulated from the posterior predictive distribution of the number of spatial partners model, using a Negative Binomial distribution



S7: Degree in grooming associations

S7.1. Under-dispersion in the Negative Binomial Model for the number of grooming partners

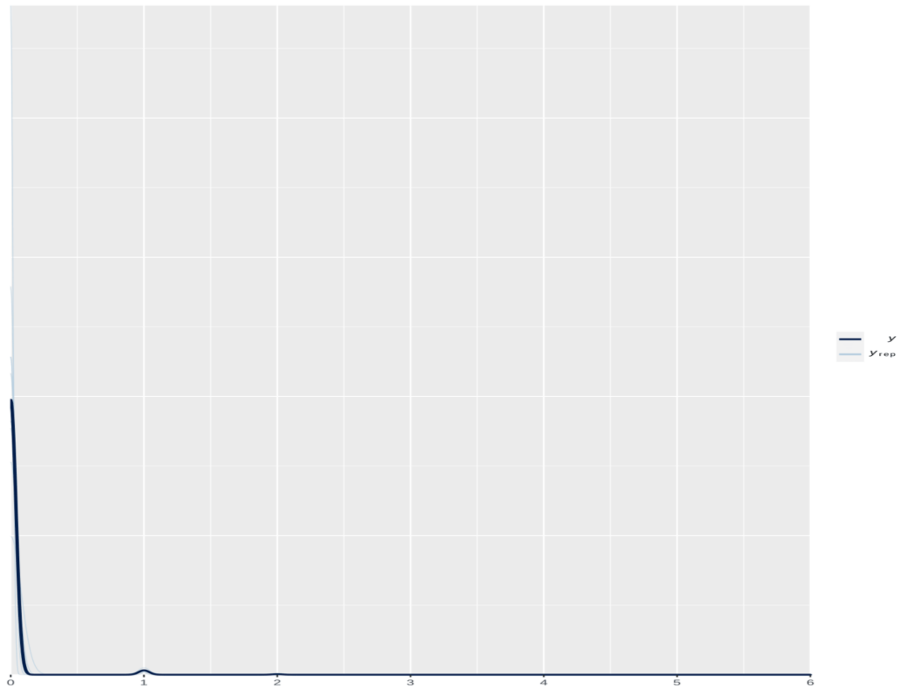


S7.2. Summary table of the Negative Binomial Model for the number of grooming partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in grooming associations, using a negative binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline “wiggliness” (spline variance parameter)

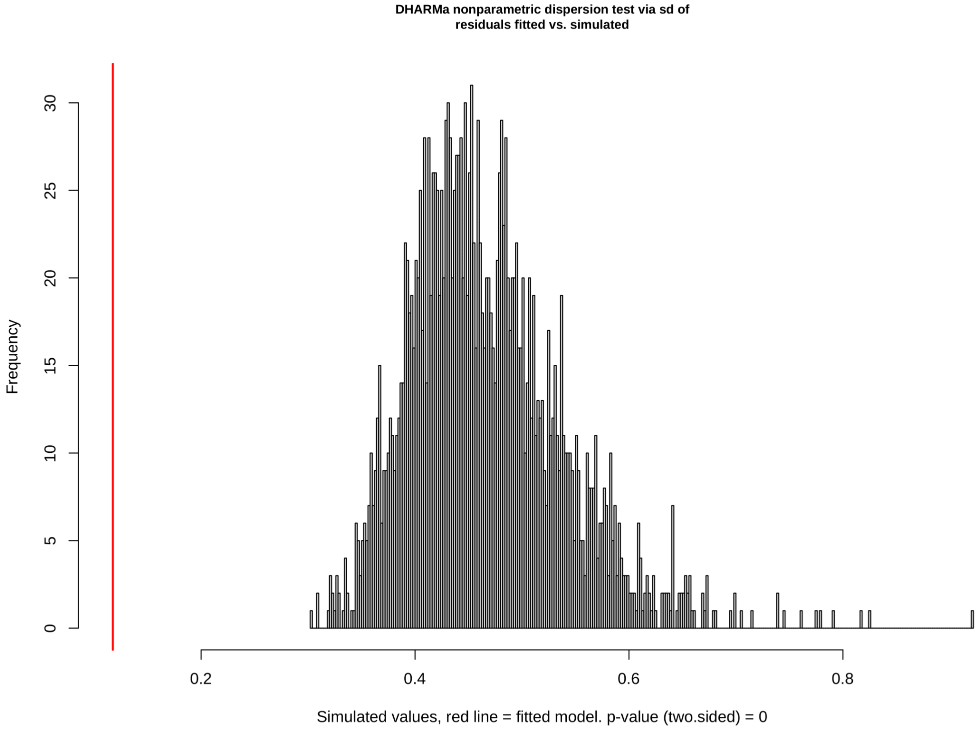
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-12.67	1.50	-16.18	-10.04
	s(age)	0.07	0.98	-1.81	1.94
	s(NDVI)	0.18	0.97	-1.68	2.03
	s(troop.nb)	-0.13	0.95	-1.98	1.67
Smooth Terms	sds(age)	1.73	1.61	0.06	5.63
	sds(age ID1)	2.61	1.95	0.12	7.08
	sds(age ID2)	2.92	2.87	0.12	10.69
	sds(age cohort1)	2.33	1.88	0.09	7.07
	sds(age cohort2)	3.97	5.17	0.11	15.99
	sds(age troop1)	2.20	1.83	0.09	6.63
	sds(age troop2)	2.37	2.49	0.07	8.47
	sds(age mumID1)	2.57	1.99	0.14	7.55
	sds(age mumID2)	2.95	2.99	0.10	11.03
	sds(age sex1)	1.58	1.39	0.07	5.29
	sds(age sex2)	2.75	2.94	0.10	10.79
	sds(NDVI)	1.71	1.53	0.08	5.37
	sds(troop.nb)	1.51	1.46	0.05	4.95
	sds(rank ID1)	2.28	1.69	0.08	6.26
	sds(rank ID2)	2.94	2.90	0.09	11.15
Family-specific Parameters	Shape	25.62	42.81	0.38	157.91
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.38	0.18	0.06	0.67

S7.3. Comparing the observed outcome variable (degree) to datasets simulated from the posterior predictive distribution of the number of grooming partners model, using a Negative Binomial distribution



S8: Strength in spatial proximity associations

S8.1. Under-dispersion in the Negative Binomial Model for the frequency of spatial interactions

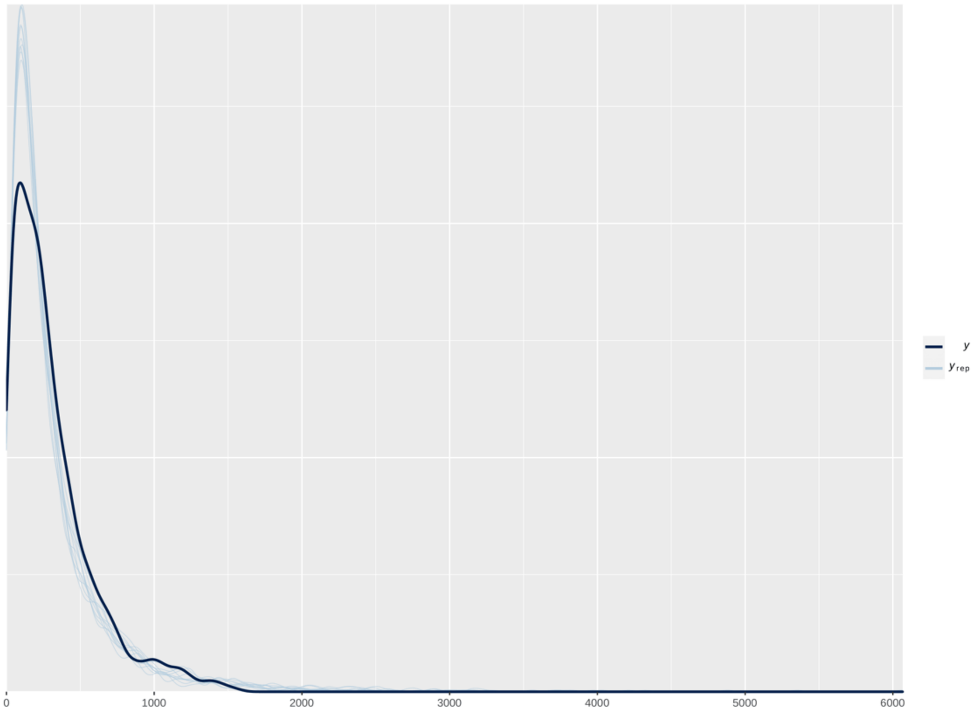


S8.2. Summary table of the Negative Binomial Model for the frequency of spatial interactions

Summary statistics of a Bayesian hierarchical generalized additive mixed hurdle model (HGAM) for the frequency of interactions (strength) in spatial associations, using a Negative Binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline “wiggliness” (spline variance parameter).

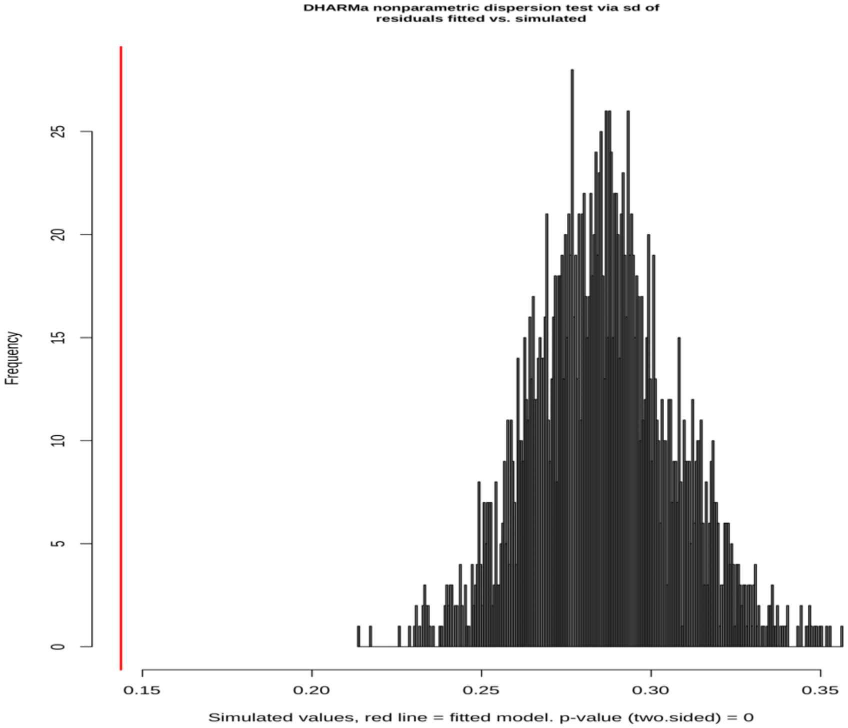
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-0.60	0.57	-1.70	0.55
	hu_Intercept	0.42	0.94	-1.41	2.21
	s(age)	0.30	0.70	-0.95	1.78
	s(NDVI)	0.67	0.75	-0.78	2.20
	s(troop.nb)	-0.60	0.57	-1.70	0.55
Smooth Terms	sds(age)	4.22	2.28	0.56	9.37
	sds(age ID1)	1.46	0.18	1.13	1.82
	sds(age ID2)	0.97	0.66	0.04	2.44
	sds(age cohort1)	2.64	0.69	1.52	4.21
	sds(age cohort2)	2.39	2.05	0.09	7.68
	sds(age troop1)	1.22	0.34	0.69	1.99
	sds(age troop2)	1.52	1.39	0.07	5.09
	sds(age mumID1)	0.53	0.30	0.03	1.09
	sds(age mumID2)	2.00	0.78	0.15	3.41
	sds(age sex1)	0.21	0.20	0.01	0.74
	sds(age sex2)	2.59	1.88	0.48	7.37
	sds(NDVI)	0.53	0.53	0.02	1.94
	sds(troop.nb)	0.87	0.53	0.22	2.22
	sds(rank ID1)	0.15	0.11	0.01	0.40
	sds(rank ID2)	0.94	0.65	0.03	2.43
Family-specific Parameters	Shape	3.51	0.18	3.18	3.85
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.77	0.01	0.74	0.79

S8.3. Comparing the observed outcome variable (strength) to datasets simulated from the posterior predictive distribution of the spatial interaction frequency model, using a Negative Binomial distribution



<u>S9</u>: Strength in grooming associations

S9.1.1. Under-dispersion in the Poisson Model for the frequency of grooming interactions

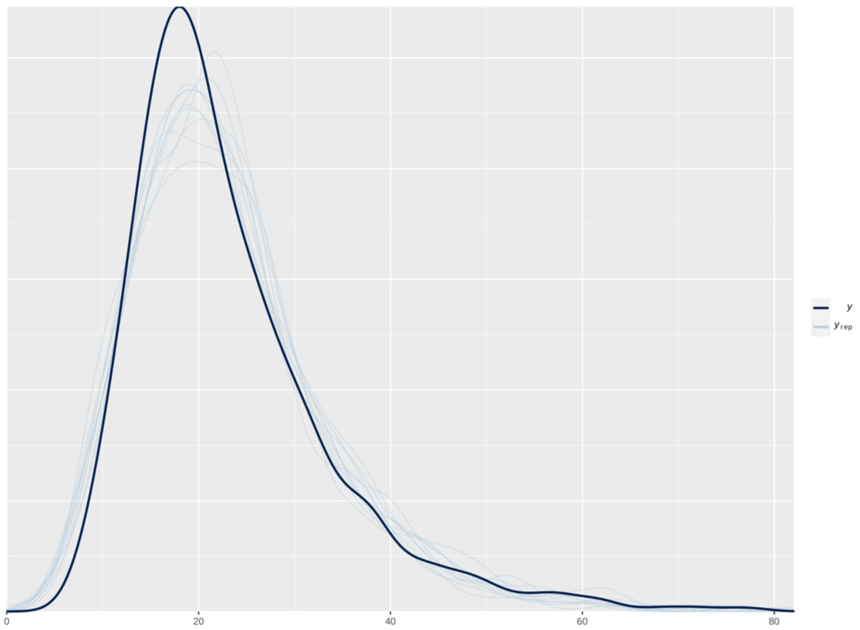


S9.1.2. Summary table of the Poisson Model for the frequency of grooming interactions

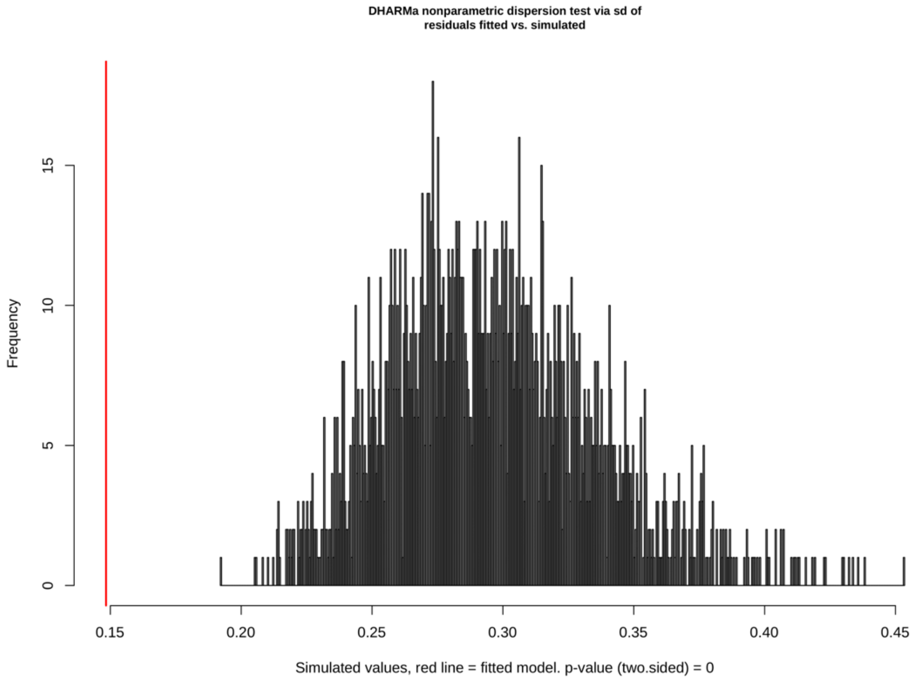
Summary statistics of a Bayesian hierarchical generalized additive mixed hurdle model (HGAM) for the frequency of interactions (strength) in spatial associations, using a Poisson distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline “wiggliness” (spline variance parameter).

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-2.86	0.27	-3.39	-2.28
	s(age)	-0.31	0.72	-1.74	1.14
	s(NDVI)	-0.03	0.43	-0.93	0.86
	s(troop.nb)	-0.09	0.53	-1.02	1.22
Smooth Terms	sds(age)	0.43	0.40	0.01	1.47
	sds(age ID1)	0.89	0.09	0.71	1.08
	sds(age ID2)	0.47	0.33	0.02	1.22
	sds(age cohort1)	0.62	0.21	0.28	1.07
	sds(age cohort2)	1.15	1.20	0.04	4.39
	sds(age troop1)	0.30	0.20	0.01	0.74
	sds(age troop2)	1.65	1.22	0.18	4.91
	sds(age mumID1)	0.21	0.16	0.01	0.59
	sds(age mumID2)	0.44	0.33	0.01	1.21
	sds(age sex1)	0.15	0.12	0.00	0.44
	sds(age sex2)	1.25	1.48	0.03	5.07
	sds(NDVI)	0.22	0.21	0.01	0.85
	sds(troop.nb)	0.31	0.33	0.01	1.21
	sds(rank ID1)	0.12	0.08	0.01	0.29
	sds(rank ID2)	0.42	0.31	0.01	1.16
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.79	0.01	0.76	0.81

S9.1.3. Comparing the observed outcome variable (strength) to datasets simulated from the posterior predictive distribution of the grooming interaction frequency model, using a Poisson distribution



S9.2.1. Under-dispersion in the Negative Binomial Model for the frequency of grooming interactions

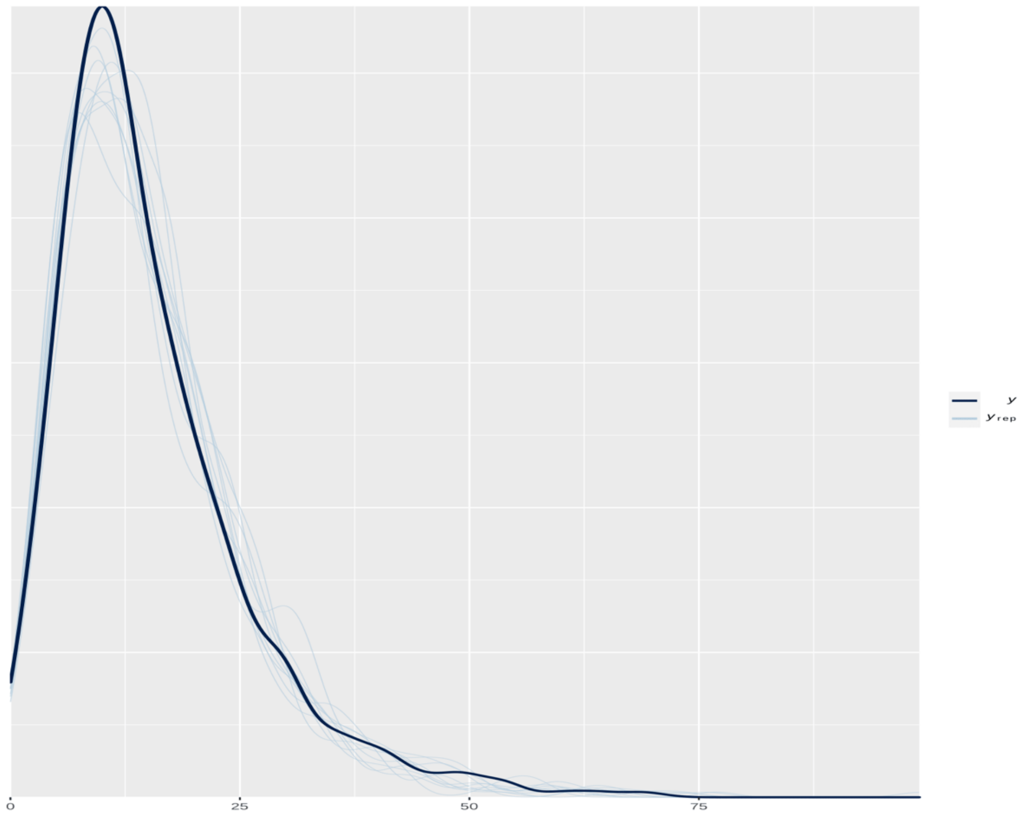


S9.2.2. Summary table of the Negative Binomial Model for the frequency of grooming interactions

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the frequency of interactions (strength) in grooming associations, using a negative binomial distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline “wiggliness” (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-3.49	0.35	-4.18	-2.77
	s(age)	-0.46	0.85	-2.04	1.19
	s(NDVI)	-0.36	0.58	-1.41	0.93
	s(troop.nb)	-0.10	0.56	-1.14	1.16
Smooth Terms	sds(age)	0.58	0.55	0.03	1.97
	sds(age ID1)	1.49	0.15	1.19	1.77
	sds(age ID2)	0.66	0.50	0.02	1.85
	sds(age cohort1)	0.90	0.32	0.31	1.61
	sds(age cohort2)	1.51	1.33	0.05	5.09
	sds(age troop1)	0.53	0.31	0.03	1.17
	sds(age troop2)	2.63	1.54	0.56	6.56
	sds(age mumID1)	0.33	0.25	0.02	0.95
	sds(age mumID2)	0.71	0.51	0.03	1.88
	sds(age sex1)	0.22	0.18	0.01	0.68
	sds(age sex2)	1.38	1.43	0.04	5.21
	sds(NDVI)	0.30	0.30	0.01	1.11
	sds(troop.nb)	0.29	0.30	0.01	1.03
	sds(rank ID1)	0.22	0.14	0.01	0.50
	sds(rank ID2)	0.62	0.47	0.02	1.73
Family-specific Parameters	Shape	45.66	19.26	23.59	93.18
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.78	0.02	0.73	0.82

S9.2.3. Comparing the observed outcome variable (strength) to datasets simulated from the posterior predictive distribution of the grooming interaction frequency model, using a Negative Binomial distribution



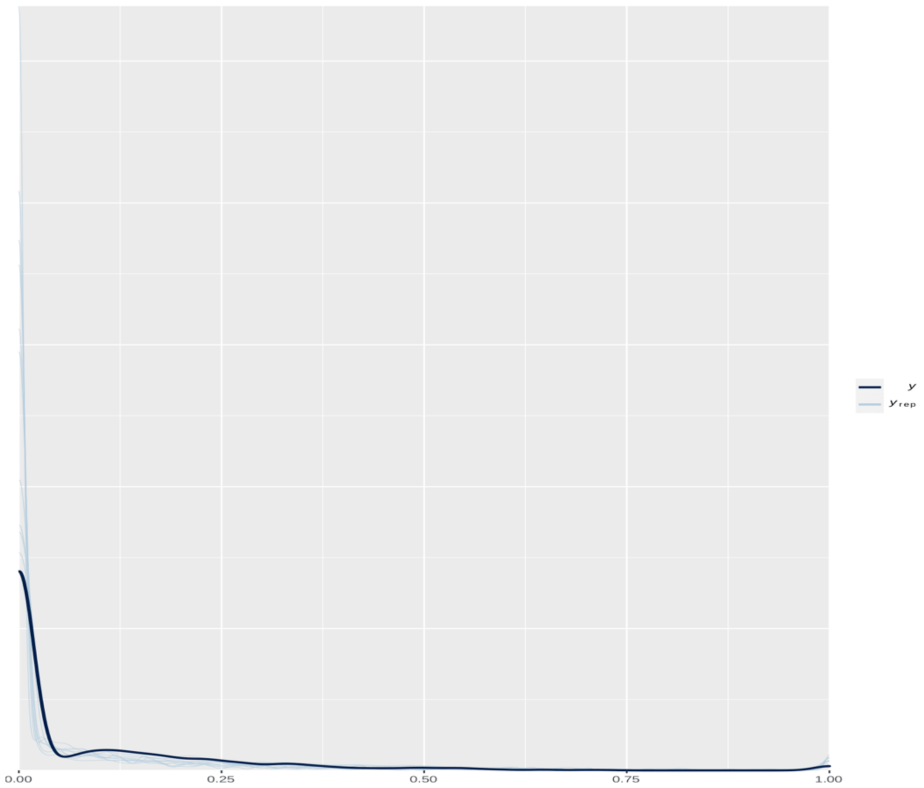
S10: Association rate with adults in spatial proximity associations

S10.1. Summary table of the zero one inflated Beta Model for the association rate with adults in spatial associations

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the spatial association rate with adults, using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-1.52	0.29	-2.05	-0.90
	s(age)	-0.35	0.96	-2.23	1.48
	s(scan.nb)	-0.82	0.69	-1.99	0.77
	s(NDVI)	-0.41	0.87	-2.14	1.29
	s(troop.nb)	0.09	0.59	-1.07	1.29
Smooth Terms	sds(age)	0.94	0.82	0.04	3.08
	sds(age ID1)	1.76	0.45	0.77	2.57
	sds(age ID2)	2.23	1.37	0.12	5.00
	sds(age cohort1)	2.71	0.63	1.65	4.18
	sds(age cohort2)	3.16	2.29	0.19	8.84
	sds(age troop1)	0.41	0.33	0.02	1.24
	sds(age troop2)	1.54	1.37	0.07	5.17
	sds(age mumID1)	1.17	0.61	0.08	2.32
	sds(age mumID2)	2.29	1.36	0.09	5.04
	sds(scan.nb)	0.38	0.44	0.01	1.59
	sds(age sex1)	0.85	0.62	0.04	2.26
	sds(age sex2)	1.72	1.64	0.07	6.23
	sds(NDVI)	2.04	1.14	0.41	4.69
	sds(troop.nb)	0.31	0.35	0.01	1.26
	sds(rank ID1)	0.49	0.29	0.02	1.08
	sds(rank ID2)	2.61	1.72	0.10	6.06
Family-specific Parameters	Phi	40.46	4.28	32.50	49.40
	Zoi	0.67	0.01	0.64	0.69
	Coi	0.02	0.00	0.01	0.03
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.12	0.04	0.06	0.22

S10.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the spatial association rate with adults model, using a zero one inflated Beta distribution



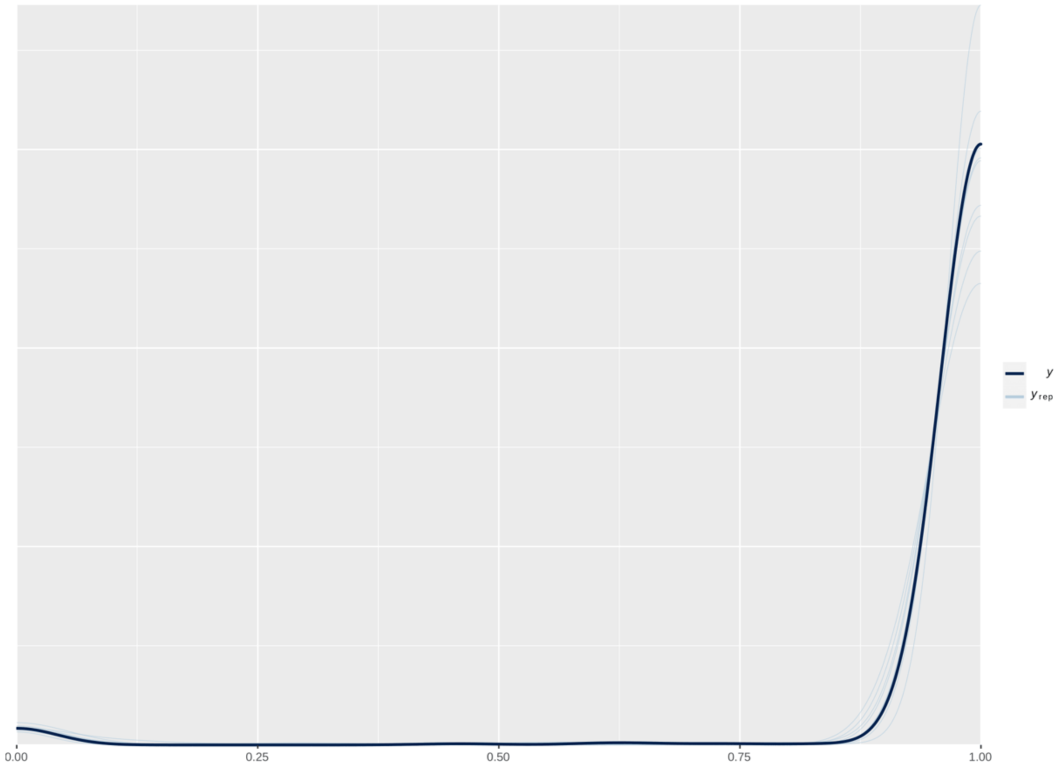
S11: Association rate with adults in grooming associations

S11.1. Summary table of the zero one inflated Beta Model for the association rate with adults in grooming associations

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the grooming association rate with adults, using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter).

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	0.81	1.54	-2.10	3.93
	s(age)	0.01	0.98	-1.93	1.90
	s(scan.nb)	0.13	0.96	-1.82	2.01
	s(NDVI)	-0.02	1.00	-2.01	1.99
	s(troop.nb)	0.08	1.01	-1.91	2.09
Smooth Terms	sds(age)	2.37	2.24	0.10	7.86
	sds(age ID1)	1.96	1.75	0.07	6.21
	sds(age ID2)	2.44	2.38	0.09	8.51
	sds(age cohort1)	2.02	1.83	0.08	6.81
	sds(age cohort2)	2.57	2.47	0.10	8.95
	sds(age troop1)	2.03	1.85	0.08	6.54
	sds(age troop2)	2.67	2.80	0.09	9.86
	sds(age mumID1)	1.94	1.68	0.10	6.21
	sds(age mumID2)	2.42	2.50	0.05	9.00
	sds(scan.nb)	1.87	1.82	0.06	6.38
	sds(age sex1)	2.03	1.91	0.03	7.16
	sds(age sex2)	2.59	2.57	0.07	9.00
	sds(NDVI)	2.09	1.82	0.09	6.72
	sds(troop.nb)	2.01	1.81	0.08	6.78
	sds(rank ID1)	1.90	1.61	0.09	5.97
	sds(rank ID2)	2.50	2.42	0.09	8.60
Family-specific Parameters	Phi	42.40	54.90	2.30	218.66
	Zoi	0.99	0.00	0.98	1.00
	Coi	0.97	0.01	0.95	0.98
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.00	0.00	0.00	0.00

S11.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the grooming association rate with adults model, using a zero one inflated Beta distribution



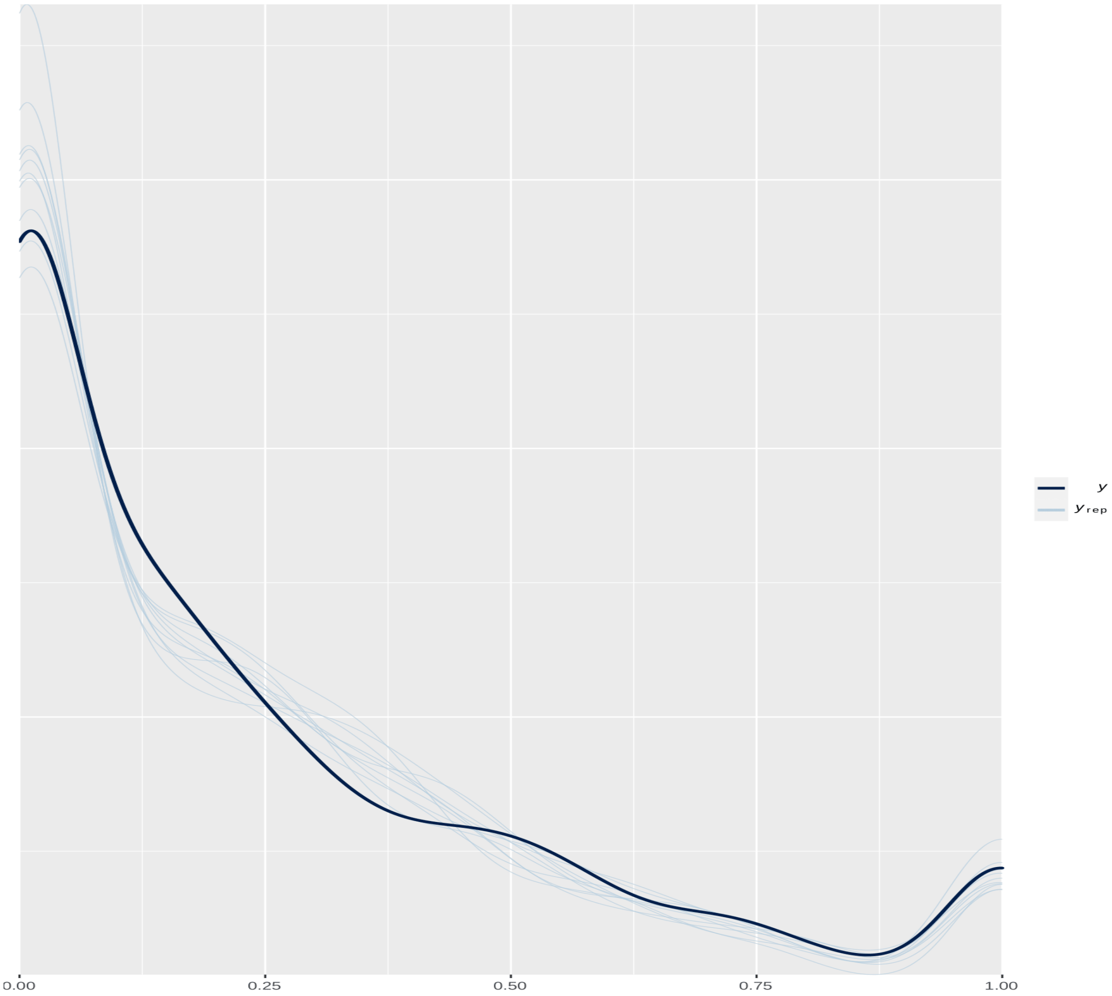
<u>S12</u>: Association rate with family members in spatial proximity associations

S12.1. Summary table of the zero one inflated Beta Model for the association rate with family members in spatial associations

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the spatial association rate with family members, using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-0.69	0.50	-1.60	0.37
	s(age)	-0.64	0.94	-2.47	1.18
	s(scan.nb)	-1.03	0.81	-2.40	0.85
	s(NDVI)	-0.61	1.00	-2.57	1.33
	s(troop.nb)	-0.18	0.85	-1.86	1.51
Smooth Terms	sds(age)	1.67	1.52	0.07	5.80
	sds(age ID1)	1.45	0.25	0.95	1.92
	sds(age ID2)	0.70	0.53	0.03	1.94
	sds(age cohort1)	2.62	0.66	1.52	4.15
	sds(age cohort2)	2.52	2.19	0.14	8.01
	sds(age troop1)	0.36	0.26	0.02	0.98
	sds(age troop2)	1.34	1.23	0.06	4.54
	sds(age mumID1)	0.70	0.37	0.04	1.37
	sds(age mumID2)	1.92	0.81	0.25	3.45
	sds(scan.nb)	0.56	0.47	0.03	1.73
	sds(age sex1)	0.67	0.46	0.03	1.74
	sds(age sex2)	1.81	1.82	0.05	6.38
	sds(NDVI)	3.01	1.27	0.91	5.86
	sds(troop.nb)	1.58	1.02	0.06	3.79
	sds(rank ID1)	0.25	0.17	0.01	0.61
	sds(rank ID2)	0.66	0.50	0.03	1.85
Family-specific Parameters	Phi	20.24	1.45	17.45	23.13
	Zoi	0.43	0.01	0.41	0.46
	Coi	0.15	0.01	0.12	0.18
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.16	0.01	0.13	0.18

S12.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the spatial association rate with family members model, using a zero one inflated Beta distribution



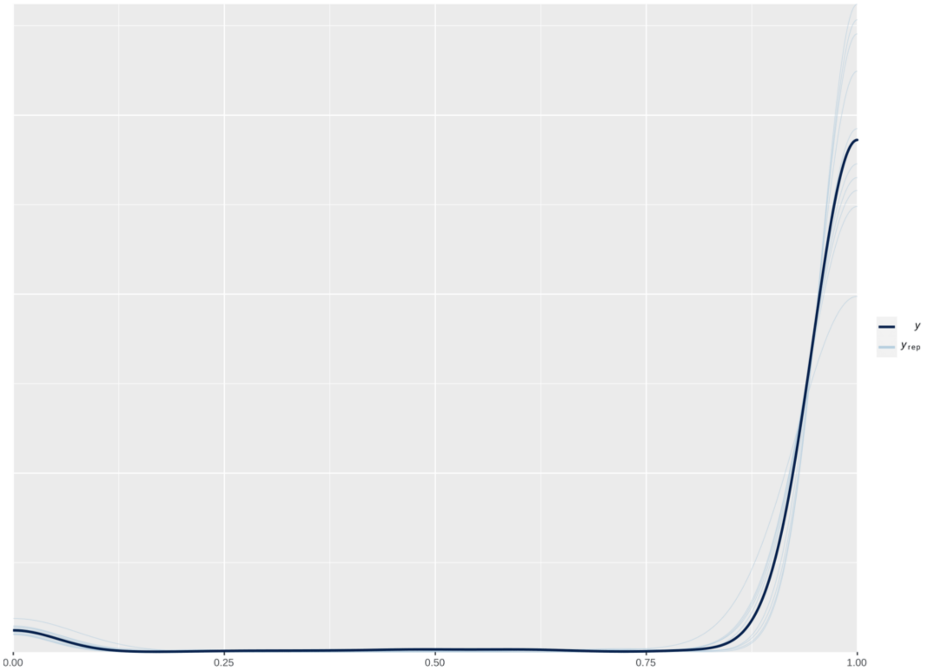
<u>S13</u>: Association rate with family members in grooming associations

S13.1. Summary table of the zero one inflated Beta Model for the association rate with family members in grooming associations

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the grooming association rate with family members, using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline “wiggliness” (spline variance parameter).

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	0.33	1.09	-1.81	2.53
	s(age)	-0.05	0.99	-1.99	1.91
	s(scan.nb)	-0.23	1.00	-2.12	1.71
	s(NDVI)	-0.02	1.02	-2.00	1.90
	s(troop.nb)	-0.05	0.96	-1.89	1.77
Smooth Terms	sds(age)	1.92	1.69	0.08	6.19
	sds(age ID1)	1.55	1.31	0.07	4.89
	sds(age ID2)	2.37	2.31	0.07	8.17
	sds(age cohort1)	1.80	1.51	0.08	5.60
	sds(age cohort2)	2.72	2.91	0.10	10.45
	sds(age troop1)	1.70	1.42	0.05	5.22
	sds(age troop2)	2.33	2.09	0.10	7.88
	sds(age mumID1)	1.60	1.32	0.05	4.99
	sds(age mumID2)	2.42	2.45	0.06	8.27
	sds(scan.nb)	1.49	1.29	0.08	4.69
	sds(age sex1)	1.57	1.37	0.07	5.01
	sds(age sex2)	2.36	2.36	0.06	8.25
	sds(NDVI)	1.50	1.35	0.07	4.97
	sds(troop.nb)	1.45	1.30	0.06	4.70
	sds(rank ID1)	1.13	0.99	0.05	3.68
	sds(rank ID2)	2.29	2.16	0.07	8.19
Family-specific Parameters	Phi	61.10	60.59	6.49	229.90
	Zoi	0.98	0.01	0.97	0.99
	Coi	0.96	0.01	0.94	0.97
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.00	0.00	0.00	0.00

S13.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the grooming association rate with family members model, using a zero one inflated Beta distribution



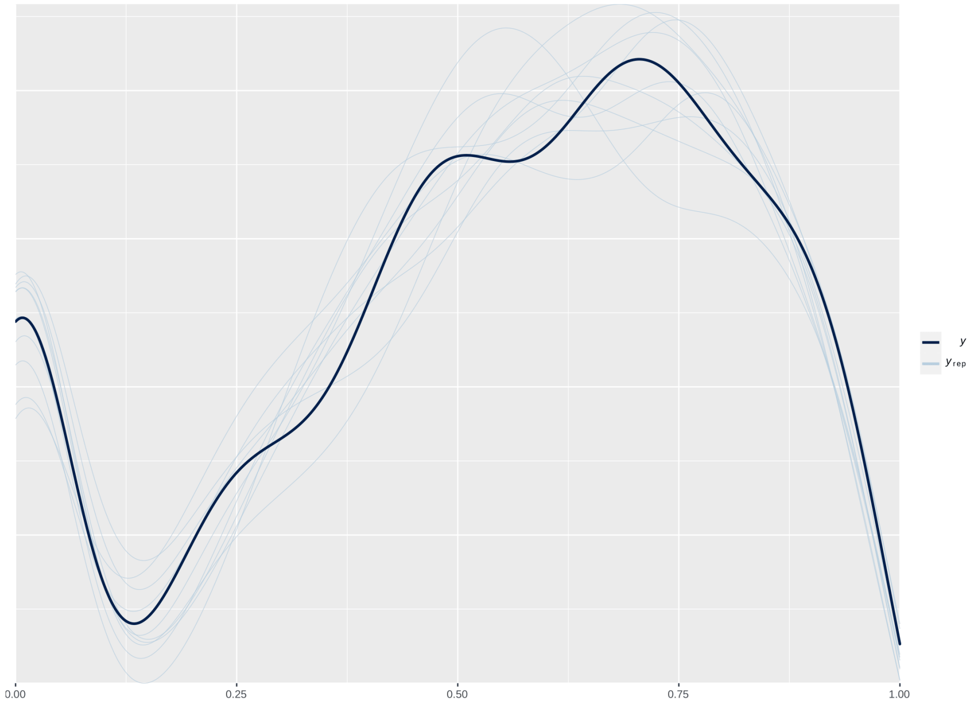
S14: Cosine similarity in spatial proximity associations

S14.1. Summary table of the zero one inflated Beta Model for the similarity in spatial partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity in spatial partners (cosine), using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline “wiggliness” (spline variance parameter)-1

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	0.30	0.48	-0.63	1.27
	s(age)	-0.03	0.93	-1.85	1.85
	s(scan.nb)	0.80	0.91	-0.92	2.60
	s(NDVI)	0.43	0.98	-1.48	2.40
	s(troop.nb)	-0.69	0.98	-2.44	1.23
Smooth Terms	sds(age)	0.67	0.62	0.02	2.26
	sds(age ID1)	0.73	0.17	0.38	1.06
	sds(age ID2)	0.92	0.60	0.05	2.25
	sds(age cohort1)	0.68	0.48	0.04	1.82
	sds(age cohort2)	3.91	2.46	0.42	10.20
	sds(age troop1)	1.58	0.46	0.72	2.55
	sds(age troop2)	1.91	1.61	0.09	6.01
	sds(age mumID1)	0.20	0.15	0.01	0.53
	sds(age mumID2)	1.16	0.63	0.08	2.38
	sds(scan.nb)	2.73	1.10	1.10	5.19
	sds(age sex1)	0.26	0.21	0.01	0.82
	sds(age sex2)	1.33	1.39	0.04	4.82
	sds(NDVI)	3.18	1.27	1.30	6.27
	sds(troop.nb)	3.91	2.37	0.09	8.88
	sds(rank ID1)	0.25	0.17	0.01	0.63
	sds(rank ID2)	0.84	0.57	0.04	2.09
Family-specific Parameters	Phi	4.53	0.23	4.10	4.98
	Zoi	0.14	0.01	0.12	0.16
	Coi	0.04	0.01	0.01	0.07
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.14	0.02	0.11	0.17

S14.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the similarity in spatial partners model, using a zero one inflated Beta distribution



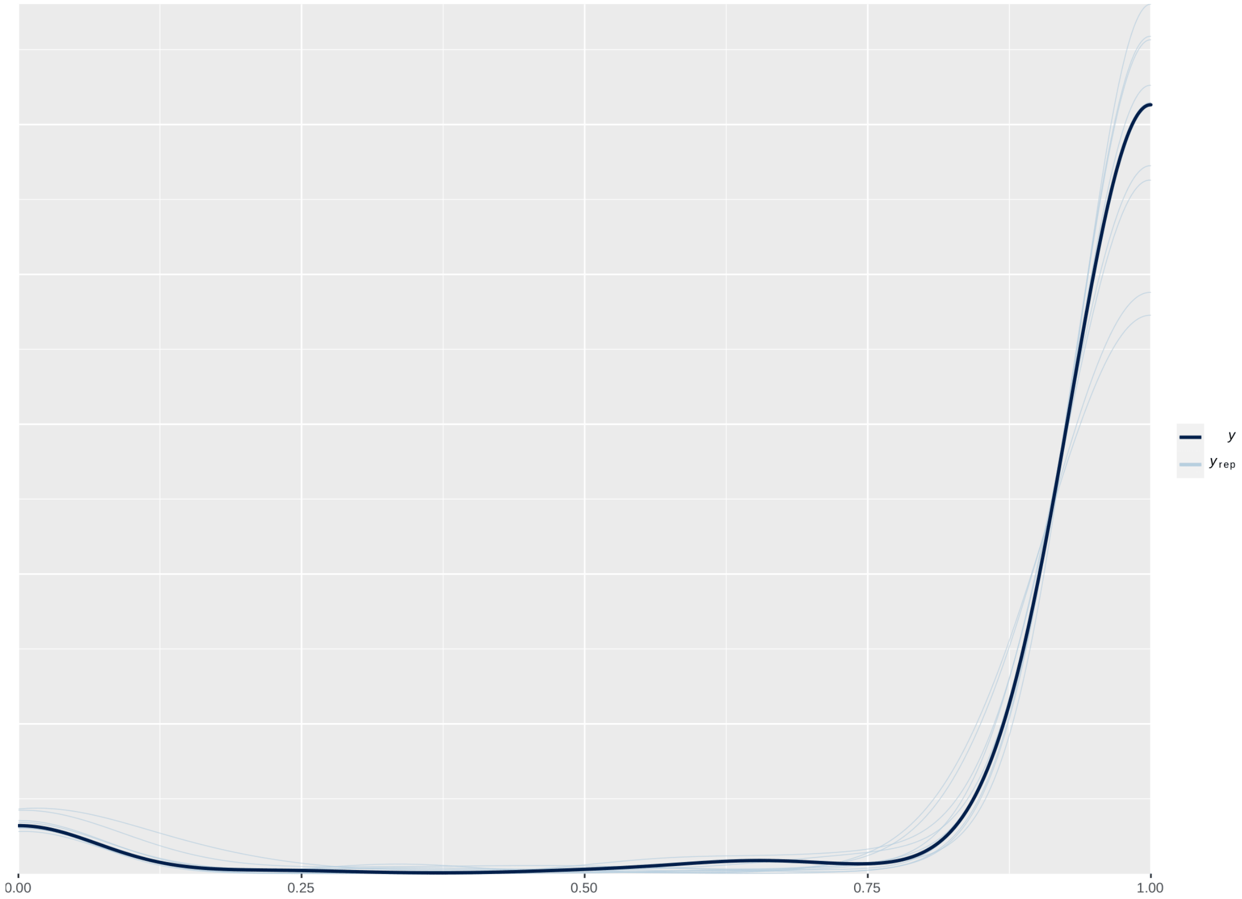
S15: Cosine similarity in grooming associations

S15.1. Summary table of the zero one inflated Beta Model for the similarity in grooming partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity in grooming partners (cosine), using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter).

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	1.48	1.17	-0.85	3.86
	s(age)	-0.02	0.99	-1.90	1.79
	s(scan.nb)	-0.12	0.98	-1.99	1.78
	s(NDVI)	0.03	0.90	-1.69	1.81
	s(troop.nb)	0.11	1.01	-1.90	2.04
Smooth Terms	sds(age)	1.90	1.77	0.04	6.08
	sds(age ID1)	2.24	1.97	0.06	7.97
	sds(age ID2)	2.84	2.69	0.08	9.98
	sds(age cohort1)	1.95	1.68	0.06	6.27
	sds(age cohort2)	2.64	3.03	0.09	9.00
	sds(age troop1)	2.06	1.70	0.07	6.21
	sds(age troop2)	2.67	2.68	0.11	9.50
	sds(age mumID1)	2.00	1.64	0.08	5.75
	sds(age mumID2)	2.83	2.77	0.14	10.35
	sds(scan.nb)	1.94	1.70	0.07	5.86
	sds(age sex1)	1.61	1.39	0.07	5.14
	sds(age sex2)	2.63	2.55	0.11	9.18
	sds(NDVI)	1.66	1.41	0.06	5.02
	sds(troop.nb)	1.49	1.43	0.04	5.21
	sds(rank ID1)	1.68	1.44	0.07	5.17
	sds(rank ID2)	2.82	2.95	0.08	10.42
Family-specific Parameters	Phi	61.88	68.03	6.75	352.81
	Zoi	0.95	0.01	0.92	0.97
	Coi	0.94	0.02	0.90	0.96
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.00	0.00	0.00	0.01

S15.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the similarity in grooming partners model, using a zero one inflated Beta distribution



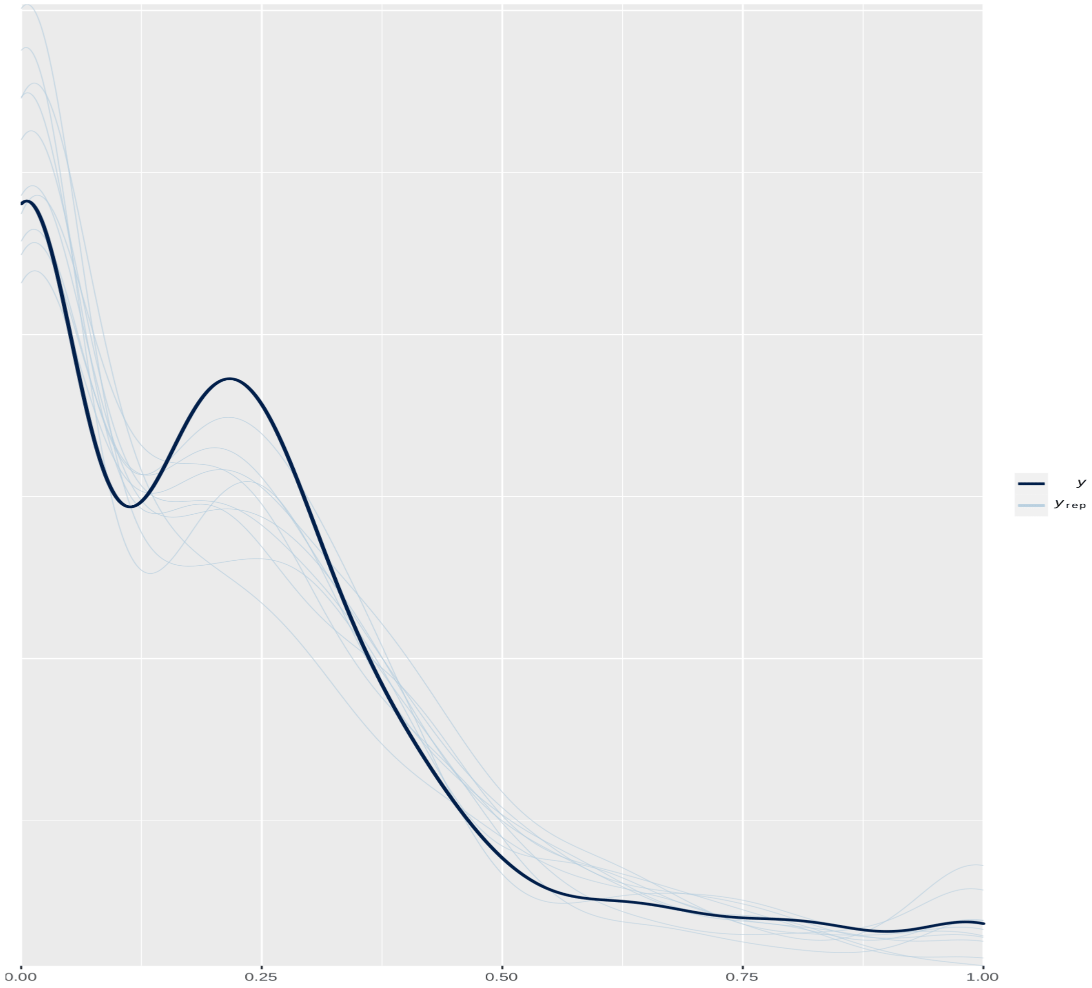
S16: Cosine similarity between spatial proximity and grooming partners

S16.1. Summary table of the zero one inflated Beta Model for the similarity between spatial and grooming partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity between spatial and grooming partners (cosine), using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter).

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-0.81	0.58	-1.96	0.40
	s(age)	-0.02	1.00	-1.95	2.01
	s(scan.nb)	-0.38	0.99	-2.23	1.56
	s(NDVI)	-0.22	0.81	-1.93	1.34
	s(troop.nb)	-0.90	0.72	-2.21	0.67
Smooth Terms	sds(age)	1.36	1.23	0.04	4.67
	sds(age ID1)	1.85	0.46	0.67	2.57
	sds(age ID2)	1.41	1.01	0.06	3.66
	sds(age cohort1)	2.76	0.67	1.62	4.24
	sds(age cohort2)	2.91	2.54	0.10	9.55
	sds(age troop1)	0.88	0.58	0.05	2.19
	sds(age troop2)	1.69	1.48	0.06	5.24
	sds(age mumID1)	1.01	0.58	0.06	2.16
	sds(age mumID2)	1.64	1.09	0.08	3.94
	sds(scan.nb)	1.45	0.90	0.30	3.71
	sds(age sex1)	0.52	0.44	0.02	1.62
	sds(age sex2)	1.66	1.71	0.06	6.29
	sds(NDVI)	0.77	0.77	0.02	2.46
	sds(troop.nb)	0.36	0.35	0.01	1.28
	sds(rank ID1)	0.24	0.18	0.01	0.67
	sds(rank ID2)	1.32	0.97	0.06	3.59
Family-specific Parameters	Phi	37.71	4.92	28.86	48.16
	Zoi	0.37	0.02	0.33	0.42
	Coi	0.07	0.02	0.04	0.11
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.27	0.02	0.23	0.32

S16.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the similarity between spatial and grooming partners model, using a zero one inflated Beta distribution



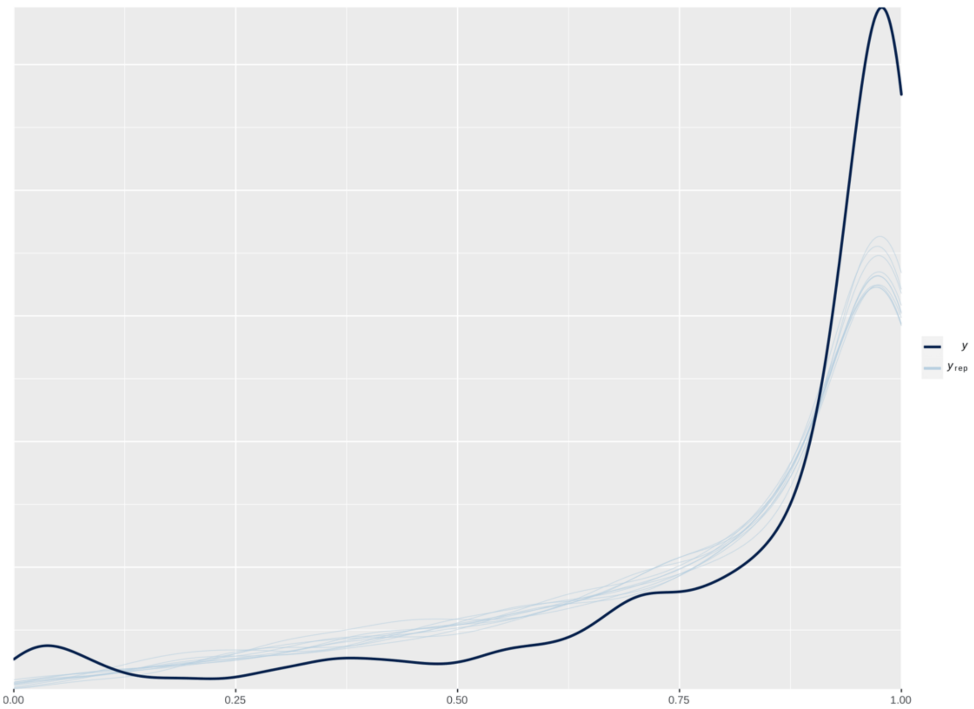
S17: Cosine similarity between the mother's and the offspring's weak grooming partners

S17.1. Summary table of the zero one inflated Beta Model for the similarity between the mother's and the offspring's weak partners

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity between mother's and offspring's grooming partners (cosine), using a zero-one-inflated beta distribution. CI = credible interval; SD = standard deviation; s() = spline. Smooth-term sds() = spline "wiggliness" (spline variance parameter).

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	1.25	0.32	0.57	1.86
	s(age)	0.42	0.89	-1.38	2.11
	s(scan.nb)	0.72	0.62	-0.58	2.00
	s(NDVI)	-0.52	0.66	-2.00	0.66
	s(troop.nb)	0.80	0.81	-0.77	2.37
Smooth Terms	sds(age)	1.19	0.87	0.08	3.34
	sds(age ID1)	0.34	0.23	0.01	0.83
	sds(age ID2)	0.71	0.51	0.02	1.86
	sds(age cohort1)	0.32	0.27	0.01	1.00
	sds(age cohort2)	1.03	1.04	0.03	3.96
	sds(age troop1)	0.72	0.34	0.08	1.43
	sds(age troop2)	1.71	1.43	0.09	5.27
	sds(age mumID1)	0.38	0.22	0.01	0.82
	sds(age mumID2)	1.42	0.62	0.13	2.56
	sds(scan.nb)	0.42	0.37	0.02	1.45
	sds(age sex1)	0.30	0.26	0.01	0.95
	sds(age sex2)	1.36	1.41	0.05	4.82
	sds(NDVI)	0.40	0.40	0.01	1.44
	sds(troop.nb)	0.83	0.46	0.24	2.04
	sds(rank ID1)	0.20	0.14	0.01	0.52
	sds(rank ID2)	0.64	0.48	0.02	1.71
Family-specific Parameters	Phi	2.25	0.10	2.07	2.45
	Zoi	0.00	0.00	0.00	0.01
	Coi	0.50	0.23	0.10	0.91
		Estimate	Estimate Error	Q2.5	Q97.5
	R^2 marginal	0.18	0.02	0.13	0.22

S17.2. Comparing the observed outcome variable to datasets simulated from the posterior predictive distribution of the similarity the mother's and the offspring's weak partners model, using a zero one inflated Beta distribution


0.00
0.25
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CHAPTER 7: DISCUSSION

This thesis had two aims: (1) to contribute to the development of analytical techniques to capture temporal variation within a variety of datasets and (2) to use this approach to offer insights into the formation and maintenance of social networks across juveniles ’social development. In what follows, I summarize the key findings of my thesis and situate them within the literature on primate juvenility and social dynamics. In addition, I reflect on my analyses ’ limitations while providing future research directions.

7.1 Methodological considerations

7.1.1 Longitudinal approach using social network analysis (SNA)

Throughout my work, I chose to consider the social integration of juveniles to be the result of a dynamic series of developmental processes during which relationships continuously change across time and contexts. I therefore adopted a longitudinal approach to capture the temporal dynamic structure of my data. The need to construct a dynamic time series of networks led me to first collaborate on the development of an R package. By doing so, my coauthor and I made use of a time-aggregated network approach that generated a time series of networks, using repeated snapshots of interactions within time windows. The extraction of continuous measures through time gave me the opportunity to detect shifts in the patterns of social interactions. The construction of these networks, however, gives rise to a large number of decisions to be made on the part of the researcher, depending on the question asked, the studied species and the method(s) of data collection. Consequently, flexible analytical steps to facilitate this process are needed. With this R package, I offered three steps for the implementation of this time-aggregated network approach: (1) bootstrapping to choose the appropriate window of time, (2) permutations to compare observed patterns to null models and (3) simulations to build and interpret statistical models. More concretely, with the use of simulated data, I showed that the bootstrap test could be used to identify the lower end of time window size choice, while permutations could be used successfully to interpret network measures (i.e., identify non-random network structure).

Although the offered framework is recent and helped me tackle my questions of interest, it already seems, in retrospect, to be outdated with respect to what it offers. For instance, a recent study has shown that permutation tests do not inherently account for the non-independence of data points, nor do they account for confounds when estimating effect sizes (Hart et al., 2021). My own work also showed limitations in the offered bootstrap test where sampling effort, within bootstrap tests, should be accounted for. As always, this calls for further methodological developments to improve the performance of permutation/bootstrap tests or, in the case of permutation-based methods, to move away from them altogether. It is apparent that analytical methods and tools improve rapidly, and such developments can quickly become overwhelming. During my PhD, I have come to realize that a constant effort is required to stay updated on findings related to one's own research and to new analytical advances.

Reading the literature, notably on social networks, it becomes obvious that comparisons across studies can be difficult due to the lack of consistency in terms of the tools, measures and/or modelling approach used. Although a myriad of available network measures and techniques for analysis offers great flexibility, the downside is that it reinforces a lack of consistency. For example, my analyses used a dynamic temporal approach. That is, rather than dividing data into seasonal blocks (Rondón et al., 2017; Teichroeb et al., 2009), I sought to capture the variation that is present within social relationships, and which is likely to be responsive to, for example, ecological and demographic change across seasons. Such variation is unlikely to be captured with a categorical variable. As such, this thesis benefited from using additive models, which meant I did not need to make any assumptions about the shape of the curve, so permitting the consideration of non-linear annual variation in a continuous manner. The use of hierarchical generalized additive models (Pedersen et al., 2019) in such cases is of great utility but not many have made the commitment to adapt to such approaches, as they require powerful computer software and are less straightforward to interpret than linear regression models. Furthermore, despite the necessary statistical software being more accessible, the use of long-term data requires computing power to which not everyone has access. Nevertheless, the development of new analytical methods and tools acknowledges the dynamic aspect of social systems, opening the door to theoretical and empirical questions of a temporal nature. Asking such questions led me to realize decisions made during data collection (e.g., sampling method, sampling effort etc.) may have downstream effects on later analyses, hence the importance of providing a detailed description of the study design (Ferreira et al., 2020). That is, time spent on (re)assessing ways of collecting data is essential in order to ensure that one's research questions can be properly addressed analytically. For instance, the qualitative categories used to characterize socio-ecological structures illustrate that the use of social descriptors (e.g., juveniles versus adults or a troop identity versus another one) may not be appropriate due to the inherent temporal component in their definition. That is, an individual identified as a juvenile may be sampled in a different manner to an adult, creating difficulties for later comparisons across the same individuals.

Finally, while a desire on the part of researchers to produce cutting-edge and striking studies may encourage a focus on the latest analytical tools, the use of such tools does not protect users from the methodological gaps already present in more basic approaches. For example, deciding what the network layers should represent and how to construct such layers remains a critical and underestimated step in the construction of any single or multilayer network. That is, different behaviours may each convey information when considered separately, and this may be lost when behaviours are pooled (Beisner et al., 2020; Beisner, 2015). van der Marel et al. (2021) have offered a data-driven approach to facilitate decisions about pooling data to help researchers in their decision-process. Another important step – and again one that needs further consideration – is the choice of the appropriate time scale over which to conduct analyses. The selection of an appropriate timeframe is important, as the failure to do so means that one does not adequately capture variation in a dataset and can thus result in inappropriate inferences. As such, we need to understand the impact of different time scales on the questions we ask, and how these relate to variation in behavioural patterns and to fitness outcomes. My stance is that we should remain attentive to where the need for improvement lies and not assume that an established technique is fit for purpose; improvements are ongoing, and what was usable today may not be tomorrow (as seen in Chapter 6 regarding the extraction of strong ties). Furthermore, when methods have been around and used for a while, there is the risk of falling into the habit of selecting methods without providing any justifications (as shown in Chapter 4 on social ranking methods). As such, this chapter joins with other voices in the discipline in calling for greater transparency, more detailed justification regarding the use of particular approaches/methods, and for making the data and R code publicly available.

7.1.2 Social ranking methods

The lack of justification in the choice of ranking methods is what led me to conduct the analyses presented in Chapter 4. I was surprised to see so many different methods being used, but without any justification for why a particular method had been chosen nor why the method was to be preferred over similar methods. The training-testing approach I advocate for is the kind of analysis that all researchers should be conducting. Looking back, I believe this kind of analysis represents the perfect example of the ‘extra’ steps researchers are not (consciously) willing to take. In fact, the lack of any decent information on reliability across methods is what led me to develop my own method, in the hope that others might find it useful; not least because social status plays an important part in the description of social structure in many animals (Snyder-Mackler et al., 2016). The aim of this analysis was thus to offer an approach that was data-driven and could be applied across a variety of datasets and species. In other words, my goal was not to determine in any absolute sense which method was most reliable, but to enable an assessment of the method that would produce the best results for a given dataset, based on the species, sampling effort and length of the data collection period. The training-testing approach meets these criteria as it is not tied to any specific requirements (like a minimum amount of data or study period length needed) or to any particular assumptions. Furthermore, this approach shifts the focus back to the raw data itself: that is, who interacts with whom and who wins?

While this analysis was conducted to address my own “selfish” needs, its broader purpose was to shed light on the way in which, when reading about an analysis, or even when conducting our own, we are sometimes not fully cognizant of the decisions that lie behind it and the consequences that follow. Ideally, researchers should try to stay away from arbitrary choices. Nevertheless, this is not an easy thing to do, and may be inevitable to some degree: many decisions made during my own analyses were done so arbitrarily. However, being conscious of them, rather than ignoring them, is the first step to encouraging change. The construction of my own method to extract strong ties is another good example of the need to question the use of particular methodological approaches, and not just adopt them unthinkingly simply because others have used them.

7.2 Juveniles ′social development

Having addressed certain methodological shortcomings, I shifted my focus to more theoretical questions, revolving around the development of juvenile social networks. Despite the juvenile period being recognized as a distinct developmental stage, there are still few long-term detailed studies of juvenile behaviour in wild primates. We also know relatively little about the processes behind the development and maintenance of social relationships (but see Kohn 2019). This is largely due to the fact that data must be collected over a long period of time, combined with immatures being harder to identify compared to adults. Therefore, projects of this nature require sustained and consistent long-term monitoring and are demanding of both time and resources. Such long-term data, however, are crucial to move the study of social dynamics to a deeper level of understanding with respect to early social experiences and how these influence the development of social relationships, as well as how social relationships, in turn, shape survival and reproductive success. Our studied population offered me the ideal opportunity to gain such an understanding of the process by which early life social engagement leads to the establishment of enduring social relationships and sex-specific social strategies.

7.2.1 Development of ego-networks: testing Kohn′s (2019) framework

In Chapter 5, I investigated a theoretical framework put forward by Kohn (2019) to account for the process by which juveniles build and maintain adaptive social networks. Contrary to the predictions of this framework, juveniles in our population did not display evidence of a clear process of exploration, pruning and consolidation. Social niche construction (SNC) did, however, appear to play a role in the establishment and maintenance of ego-networks composed of both weak and strong ties. This is of particular interest, from an evolutionary perspective, as social niches (i.e., ego-networks) shape the social conditions under which individuals live (Laland & Feldman, 2003), and so influence the likelihood of survival and reproduction. This is especially true with regard to the subset of strong ties composing juveniles' ego-networks, which reveals higher frequency of interactions with some partners. Being surrounded by more frequent partners may serve as social support, creating more predictability within social interactions and more stability in the juvenile's immediate social environment (Cohen & Wills, 1985; Lakey & Orehek, 2011).

Overall, this analysis revealed the constant presence of a subset of strong ties (a "social bubble") throughout juveniles' development. The notion of a social bubble is not new as female baboons have been shown to maintain a tight core of close associates with whom they form stable and equitable relationships, although it should be noted that, in many cases, the identification of such close associates has been assigned via an arbitrary cut-off (Schülke et al., 2010; Silk et al., 2003, 2006b, 2009, 2010a). In primates, individuals with more tightly knit social networks have lower baseline levels of cortisol metabolites in their feces (Brent et al., 2011b; Crockford et al., 2008). Given this, the presence of a social bubble suggests the existence of another level of structure within juveniles' ego-networks and raises the question of whether I focused initially on the wrong structural level and whether Kohn's phases occurred within these bubbles rather than across the ego-network as a whole.

7.2.2 Development of social bubbles

This possibility naturally led me to take a closer look at social bubbles. To do so, I investigated their formation and composition to get a better understanding of the influence of social bubbles on juveniles 'development and to investigate the mother's involvement in this process. Once again, spatial and grooming social bubbles did not develop following Kohn's (2019) framework. Instead, spatial bubbles tended to reduce both in size and level of social engagement across time and were composed of varying spatial partners. Grooming social bubbles were of constant size and composition through time, while social effort decreased. Even though spatial partner identities differed through time, spatial bubbles showed a consistent composition with respect to age-sex class, as juveniles were found to associate consistently with other immatures. In addition, they displayed seasonal variation in their association rates with family members, which increased during birth seasons. The grooming bubbles composition showed contrasting results as they were mostly composed of an adult and a family member (i.e., the mother). It was also apparent that spatial and grooming partners consistently differed through time, and did not converge in a manner suggestive of Kohn's processes of pruning and consolidation. Finally, juveniles displayed high similarity with their mother's weak grooming ties.

Although my analysis did not provide support for Kohn's (2019) framework in structural terms regardless of the level of focus, the possibility remains that I focused on the wrong time scale. Indeed, it seems possible that Kohn's (2019) phases may occur, to some degree, each time a change in size and composition occurs in the social group. That is, such changes may disrupt and relaunch the network formation process, reinforcing my original stance that social integration is a process of ongoing continual adjustments. Again, this can be achieved through SNC, which offers a mechanism by which individuals can form social bubble structures that best serve their needs given the ecological and social conditions they face.

7.3 Development of ego-networks and social bubbles – what do we know?

Taking the two social development chapters together, the marked seasonal variation seen in juveniles ’spatial social bubbles and their overall ego-networks contrasts with the lack of variation in grooming behaviour, regardless of the structural level of observation. Another clear contrast between spatial and grooming behaviours is the size of their social bubbles and their overall ego-networks, where the size in spatial associations was much bigger than in grooming. Lastly, in spatial social bubbles, both sexes displayed variation in their partner similarity while in grooming they sustained relationships with a constant and unique individual over time. Given these results, juveniles seem to display more flexibility in the structure of spatial associations, while their grooming structure appears to be more robust to large-scale changes. Such a clear contrast raises the question of whether these social bubbles result from an active process, where juveniles actively build their own network, or from a passive consequence of being associated with their mother, where juveniles let themselves go with the flow of their social group life.

One way to approach this question would be to first determine whether the structure of the juvenile grooming social niche emerges via spatial proximity first and foremost, or whether patterns of active social engagement (grooming) determine the structure of the spatial social niche. As of now and given my results, both views can be supported. That is, an active process would support Jarrett et al’s (2018) conclusion that juveniles not only develop the ability to cope with changes in the composition of their social world, but also play an active role in determining how and when they integrate socially. The flexibility displayed by juveniles in social associations also aligns with the proposals of Biological Market Theory (BMT) that individuals are predicted to behave differently depending on what they are trading and with whom (Barrett & Henzi, 2006). The observed seasonal fluctuations that align with the birth season help illustrate that individuals do indeed vary in value depending on the presence of other individuals. Juveniles ' ability to respond flexibly to changes in spatial social dynamics may help them to sustain a more robust grooming ego-network/bubble structure (i.e., social connections with their preferred grooming partner). Supporting this view is the finding that, despite the size of spatial bubbles offering immatures the opportunity to develop additional strong grooming ties, they apparently do not seize it, and grooming bubbles remain constrained. This suggests that a grooming bubble provides juveniles with a secure base from which to explore their spatial social world (i.e., a pattern in line with Bowlby's attachment theory: Bowlby et al. 1989) and they then invest their remaining social effort into weak grooming ties that offer different kinds of benefits (seen in Chapter 5). Alternatively, a passive process would entail that these juveniles are too young to impose their partner preferences on other group members. This would mean that it is the mother that controls the frequency of grooming interactions with offspring, and changes in effort therefore reflect the mother's shift in focus to other individuals, including younger siblings. This would also explain why juveniles have a restricted grooming bubble composed of their mother, while their spatial bubbles, which are much harder for their mothers to control, are mostly composed of other immatures (who are more likely to engage in other forms of social behaviour, e.g., social play).

With respect to the emergence of sex-specific social behaviours, grooming associations displayed continuous sex differences in juveniles 'overall ego-networks (also found Fairbanks, 1993; O'Brien, 1990; Jarrett et al., 2018), which disappeared when looking at their grooming bubbles. This suggests that sex differences, and potential variation in social strategies, may arise principally amongst a juveniles 'weak ties. These weak ties also showed high similarity with the mother’s grooming weak ties. The emphasis on weak ties in Chapter 6 confirms that the value of sociability may also lie in the formation of a more extended social network (McFarland et al., 2017), and not just in the formation of a small number of strong and consistent social relationships (Silk et al., 2003, 2009, 2010a, 2010b). In this case, weak grooming ties may provide the flexibility to use different social strategies whereas having focused grooming bubbles may not provide the possibility to make any adjustments. Regardless of such speculations, these results raise a number of questions regarding the influence of mothers on their offspring ’social development. While mothers ’network instability may not provide juveniles with the social conditions needed to prune and consolidate other grooming relationships beyond the mother herself, greater variation in the stability of maternal social networks within and between groups, and across different cohorts, may promote the development of higher levels of behavioural flexibility. This may explain why patterns of social behaviour in adulthood are variable across females, and why these differences link to fitness components (McFarland et al., 2017; Silk et al., 2003, 2009). Future studies should investigate individual variation to get an idea of whether, how and why juveniles differ in their behavioural flexibility as they age.

7.4 Limitations and future directions

Given my results, many questions remain to be addressed if we are to gain a clearer picture of juveniles’ social integration in this population. Investigating how a strong grooming tie is replaced after it is lost (e.g., following a death), and determining whether the replacement partner is drawn from the juvenile’s existing weak ties, may help us to understand further how strong and weak ties relate to one another. In addition, the identity of the replacement tie will also bring clarity to whether the juvenile’s new strong tie is likely to be kin or whether it will be one of the juvenile’s mother’s non-kin associates. Lastly, to deepen our understanding of strong ties, we could investigate how social effort is distributed within each dyad and whether some dyads stand out in terms of invested effort and stability. In other words, within social bubbles, can we find stronger ties than others (i.e., another additional level of structure)? This then would go back to my initial question concerning the differentiation of weak and strong ties: is the distribution of weights amongst strong ties skewed?

From a more global perspective, my thesis sought to identify how juveniles integrate into their social groups by studying spatial proximity and grooming social networks. This strong focus on socio-positive interactions represents a clear limitation in my thesis as socio-negative interactions may also influence social integration and, ultimately, fitness outcomes. For instance, in rhesus macaques, established social niches of particularly high or low aggression led to better survival outcomes (Brent et al., 2013b), while Barbary macaques that showed more aggression toward partners that themselves had nonaggressive relationships also experienced increased survival (Lehmann et al., 2015). The lack of such aggressive behaviours in this thesis reinforces the fact that they are rarely studied from a developmental perspective. However, their inclusion is sorely needed if one is to understand the complex interplay of aggressive and affiliative behaviours in the development of primate social relationships. The inclusion of aggressive interactions would also allow us to verify the hypothesis that social bubbles provide a more predictable environment. The same argument can be made with respect to play behaviour. One could look at whether social effort invested in play is converted into other social behaviours (grooming) as juveniles develop, and whether these play partners can be found within juveniles' grooming bubbles.

To tackle such questions, a multi-layered approach could be used to investigate the different dimensions of juveniles' social relationships (e.g., grooming, playing, aggression, spatial proximity). This would enable us to understand how these behaviours work in concert over the course of development, as well as determining whether the structure and composition of ego-networks/social bubbles in certain behavioural dimensions are more critical than others. By treating networks as dynamic, it also becomes possible to identify feedback loops – something we have yet to do for our population. For instance, dynamic networks can be used to better understand how individual behaviour generates social structures, and in turn how these social structures influence individual behaviour, ultimately leading to a better understanding of network development over time. More concretely, linking social structure and demography could provide a more complete understanding of how social structure changes as populations change (Shizuka & Johnson, 2020) and how different social systems evolve. For instance, the effect of demographic changes (e.g., troop size, as an index of social instability at the group level) on the development of social bubbles could be considered. The effect of social instability could also be studied in relation to the level of aggression displayed within these social bubbles. This would allow us to test the social niche specialization hypothesis, which posits that the presence of other group members causes individuals to behave differently from each other to reduce direct competition.

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