The role of age as a cause of social behaviour in male African savannah elephants (*Loxodonta africana*).

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Abstract

Social interactions can affect every aspect of an animal's life. Male savannah elephants (*Loxodonta africana*) spend most of their time with other bulls, so their companion choices are likely to have a significant effect on their long-term fitness. Compared to females, male elephants have received limited social behaviour research, despite being more involved in negative human-elephant interactions. Furthermore, studies of bull social structure do not display strong agreement in their results, which may be due to genuine inter-population differences or the use of statistical methods since proven unreliable.

In this thesis, I reevaluate the social structure of male elephants and question whether males form groups to obtain social information from more experienced bulls or to gain predator protection. To do this, I first develop an adaptation to social association estimation methods, then use a combination of social network analysis, threatening playback experiments, and causal modelling to investigate the effect of age on male social behaviour. Contrary to my hypotheses, I found no evidence of males grouping for the specific purpose of gaining social learning opportunities, with no effect of male age on social position, or for males protecting one another when the group is in danger.

With no previous studies investigating male group threat responses, my experiments provide new evidence against predator protection as a reason for male-male association. However, the formation of weak connections with many social partners may still facilitate rapid information spread, even if social learning is not the primary purpose of group formation, because each individual could pass the information to many others. In the future, we may be able to use this to promote elephant avoidance of human-dominated areas. Since I also show that male social structures are similar across populations, conservation practices based on social learning may be similarly effective in different places.

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Author’s Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged in the references section.

Chapter 2

Chapter 2 is available as a preprint at:
Mylne, H. K., Abell, J., Beale, C. M., Brent, L. J. N., Bro-Jørgensen, J., Evans, K. E., DA Hart, J., Sakala, D., Simpamba, T., Youldon, D., and Franks, D. W. (2024). Analysis of sparse animal social networks. *bioRxiv: The Preprint Server for Biology*.

The manuscript for this paper is under review at the journal PLOS One, and is reproduced in full in this thesis, with minor alterations. The text for this paper was written by myself, with input from all of my supervisors, and additional feedback from Dr Abell and Prof Brent. I performed all of the data processing and statistical modelling with support and guidance from Prof Franks. All authors approved the manuscript before journal submission.

Data and code

All code used in the production of this document can be found on my GitHub: https://github.com/HelenMylne. The code for Chapters 2 and 3 can be found within the repository labelled ”male_elephant_sna”, with Chapter 2 code in the folder ”methods_paper” and Chapter 3 making up the rest of the repository. The code for Chapter 4 can be found in the repository ”ele_playbacks”.

Most of the data for this thesis will be made accessible online following publication. The data from Mosi-Oa-Tunya National Park, Zambia, which I use in Chapters 2 and 3, are available in the Open Science Framework data repository, with permission for distribution provided by the African Lion and Environmental Research Trust and by the Department of National Parks & Wildlife of Zambia. The remaining data for Chapter 3 are the property of the Amboseli Trust for Elephants and are therefore will not be made publicly available. The data used in Chapter 4 will be added to an open access repository once the manuscript is submitted for publication.

Chapter 1

Introduction

1.1 How does social behaviour lead to social structure?

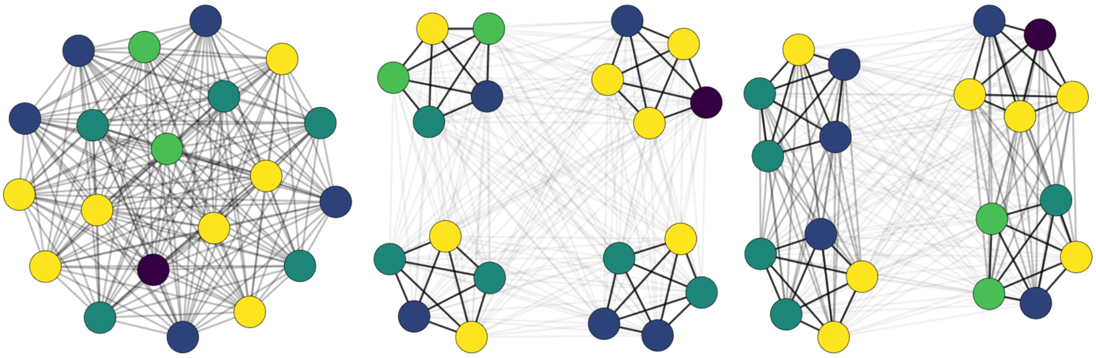
If asked to think of a starling (*Sturnus vulgaris*), the first thing I picture is not their iridescent feathers, but a huge murmuration of birds coming to roost for the night. When I think of a lion (*Panthera leo*), she is part of a pride of females and cubs, with at least one large-maned male, all interacting with one another and hunting cooperatively. Sociality is observed across the animal kingdom. The society — the set of individuals that interact with one another more regularly than with other individuals (Struhsaker, 1969 *in* Kappeler and van Schaik, 2002) — in which a gregarious animal lives can influence almost everything about that animal's life, from their movement and foraging decisions (King and Cowlishaw, 2007), to their gut microbiome (Sarkar *et al.*, 2020) and disease resistance (Pavez-Fox *et al.*, 2024).

The structure of a society emerges from the pattern of direct and indirect social interactions occurring between individuals (Nadel, 2013), and can be highly heterogeneous both within and between species. Understanding this social structure can allow us to answer questions about animal behaviour, such as the advantages of sociality for different species, the traits that may affect the social interactions of an individual, or why different populations of the same species may display variation in their social behaviour (Agnani *et al.*, 2018; Schradin *et al.*, 2018). Studying how and why individuals associate or interact with one another can be particularly important when making decisions about conservation and wildlife management (Buchholz, 2007; Blumstein, 2010), and understanding the causes of behavioural change (Fernald, 2015; Firth, 2020). Historically, conservation and animal behaviour were distinct fields, and findings from animal behaviour studies were not applied to conservation practices, with Sutherland (1998) finding almost a complete lack of crossover between subject-specific journals (only nine papers out of 326 across two journals included themes of both conservation and animal behaviour). Sutherland (1998) went on to identify 20 areas of conservation biology which would benefit from the inclusion of animal behaviour research, and discusses how actions such as behavioural manipulation, captive breeding and release schemes, and population monitoring could be improved by considering social behaviour. While he does not go into the details of how social behaviour may influence these fields, it is clear from his review and others that have followed (e.g., Buchholz, 2007) that we cannot ignore social behaviour and social structure when planning conservation.

Societies can vary in structure. An undifferentiated social structure is one in which individuals do not display specific assortment or preference for (dis)similar group mates so the social bonds between individuals are all of a similar strength (Fig 1i) (Whitehead, 2008). For example, in multi-species fish shoals, we see individuals displaying very limited group fidelity (Hoare *et al.*, 2000), which creates an undifferentiated social structure. Similarly, female bottlenose whales (*Hyperoodon ampullatus*) display an undifferentiated social structure (but males show long-term preferences for particular social partners; Gowans *et al.*, 2001). In undifferentiated social structures, all animals display similar levels of sociality, associating with a similar number of others and without assortment (though even here, many fish still preferred to associate with others of a similar size; Hoare *et al.*, 2000).

In contrast, in many animal societies, individuals display preferences for specific group partners, creating a community structure in which social partners fall into differentiated categories of interaction (Sutcliffe *et al.*, 2016). Community structure (also known as modularity) is observed when individuals form groups of preferred association or interaction partners (potentially, but not necessarily, assorted by particular trait values; Fig 1ii) and the bonds between groups are weaker than those within a group (Newman, 2006; Newman and Girvan, 2004). Sharing different levels of association or interaction with different partners allows an individual to exert greater influence on those within their group than on animals outside, through both direct (Sih *et al.*, 2009) and indirect (Brent, 2015) interactions.

In the most extreme cases, individual partner preferences within groups may create a community structure made of small subgroups nested within larger groups (also known as a multilevel society; Fig 1iii). For example, in vulturine guineafowl (*Acryllium vulturinum*), stable, closely-associated social groups containing both males and females will sometimes join with other social groups to roost and forage, with preferences for particular partner groups that are not based purely on home range overlap (Papageorgiou *et al.*, 2019). This creates a tiered community structure in which the closest bonds are within the social group, mid-strength bonds are held with members of preferred partner groups, and the weakest bonds are shared between birds in less preferred partner groups (Papageorgiou *et al.*, 2019). Many species lie somewhere in the middle of this spectrum of social complexity, and different populations may vary in their degree of community structure. For example, primate groups display heterogeneity in social network traits (Kasper and Voelkl, 2009). However, it is important to note here that direct comparison of social network metrics is strongly discouraged due to statistical differences created purely by sampling effort or network size (Faust, 2006; De Moor *et al.*, 2024).



(i) Undifferentiated **(ii)** Modular **(iii)** Multilevel

Figure 1: Different levels of social structure, ranging from i) undifferentiated, to displaying community structure which may be ii) modular, to iii) multilevel. Note these are based on simulated data, not observations. Node colours would demonstrate trait values of some kind, for example age of the individual. Social bond strength is shown by the colour intensity of the connecting line, so in iii) there are three different levels: very weak between groups, mid-weight within groups but between subgroups, and strongest within subgroups.

Understanding the emergence of social structure requires consideration of why animals form groups, the basis of their assortment preferences, and how those different grouping patterns can subsequently offer different advantages to the species that adopt them (e.g., van Boekholt *et al.*, 2021). For example, low selectivity in social partners can allow individuals to associate with many others in a short space of time, which may facilitate access to more mating opportunities by grouping with a wider pool of potential mates (Wells *et al.*, 1998; for reviews of the effects of gregariousness on mate availability, see Boulton *et al.*, 2015; Bowyer *et al.*, 2020). In contrast, small aggregations of individuals that are extremely familiar with one another and rarely associate beyond the group can provide a more cooperative environment through the formation of trust, reciprocity and forgiveness (simulation: Gianetto and Heydari, 2015), although the latter is generally portrayed as reconciliation in animal behaviour (De Waal and Aureli, 1997; Aureli *et al.*, 2002), likely because mutual post-conflict affiliation is easier to describe than true forgiveness. It is argued that community structure also reduces the risk of pathogen exposure (Cross *et al.*, 2009 *in* Silk *et al.*, 2017), though there is a growing body of evidence to suggest that socialising with many others can also protect against disease through effects such as microdosing of pathogens (Konrad *et al.*, 2012) or sharing of the microbiome to provide greater immunity (Archie and Tung, 2015; Sarkar *et al.*, 2020), and that only extreme differentiation between intra- and inter-group association may be sufficient to effectively inhibit pathogen spread in empirical networks (depending on the infection characteristics of the pathogen; Saha *et al.*, 2017). Here I discuss in turn the effect of two behaviours — social learning and group defence — on social structure, and how these social structures may then confer benefits to interacting group members. I have selected these particular behaviours because they can have important fitness and survival connotations for the individuals involved, and may have multiple different effects on emergent social structure depending on the mechanism of learning or defence in question.

1.1.1 Social learning

Social learning accelerates the process by which individuals learn novel behaviours through social interactions or associations (Gariépy *et al.*, 2014). Individuals with many associates (Bonacich, 1972a; Faust, 1997; Ruhnau, 2000), or those that bridge otherwise isolated sections of the community structure (Friedkin, 1991; Faust, 1997; Ruhnau, 2000), may act as conduits for information, facilitating transfer to new members of the population. Social learning is vital to the lives of many species (for some reviews of social learning, see the following: for primates, Box, 1984; for predator defence, Griffin, 2004; for behavioural mechanisms, Heyes, 1994; and for neurobiology, Gariépy *et al.*, 2014), and has the potential to rapidly improve the survival and reproductive output of a large proportion of the population (Henrich and McElreath, 2003; Griffin, 2004). Social learning is generally selected for in moderately heterogeneous environments to avoid the time and energy costs of constantly having to learn new behaviours individually through trial and error (Aoki *et al.*, 2005) but can also invade during stable periods if vertical transmission of a skill increases fitness (Feldman *et al.*, 1996; Wakano and Aoki, 2006).

Understanding the pathways through which social information spreads can be important for multiple reasons. For example, tool use in primates (Whiten and van de Waal, 2018; Pal and Sinha, 2022) and corvids (Striedter, 2013; Jacobs and Osvath, 2023) can help us understand cognitive development. For conservation, behaviours such as the cultural preference of different families of killer whales (*Orcinus orca*) can limit food availability to certain groups, even when other foods are still available (Whitehead, 2010), so protecting all of their potential food resources can be extremely important to species protection (Greggor *et al.*, 2017). Consumption of human food products — be that on small scale such as herring gulls (*Larus argentatus*) learning from watching humans (interspecific social learning) where anthropogenic food resources might be found (Goumas *et al.*, 2020), to large scale such as black bears (*Ursus americanus*) foraging on anthropogenic food waste (Hopkins, 2013) or crop-foraging[1] by elephants (both African savannah, *Loxodonta africana*, and Asian, *Elephas maximus*) and primates (Chiyo *et al.*, 2012; Wallace and Hill, 2012) — can have impacts ranging from a persistent nuisance through to potentially devastating for those living alongside the animals in question. Other negative human-wildlife interaction behaviours may also be learnt socially: killer whales around the Iberian Peninsula and in the Strait of Gibraltar have recently begun targeting boats, a behaviour which is thought likely to spread through the population and which is dangerous to both the whales and people (Esteban *et al.*, 2022). Studies of social learning can help to explain the evolution of social cognition (Wascher *et al.*, 2018), and improve wildlife management by incorporating the accelerated rate of changing behaviours into conservation decision-making. Understanding the spread through a population (Aplin, 2016) of those behaviours involved in negative human-wildlife interactions could have potentially life-changing impacts on local communities.

The pathway by which information spreads through a population may depend on the social learning mechanism (Gustafsson, 2013), whether that is imitation, emulation, or social facilitation (which comprises local enhancement and stimulus enhancement; Thorpe, 1956; Clayton, 1978) (for a review, see Heyes and Galef, 1996). However, to my knowledge there have been no studies explicitly investigating the effect of social learning mechanism on social structure (though several have studied social learning strategies adopted regarding which individuals to copy and when: e.g., Laland, 2004; van de Waal *et al.*, 2010; Farine *et al.*, 2015c; Beck *et al.*, 2023b), and it does not necessarily make sense that all mechanisms would have similar effects. Social facilitation occurs when the presence of conspecifics acts as motivation for an individual to learn (Thorpe, 1956; Dindo *et al.*, 2009) by drawing their attention to the relevant area or stimulus. Motivation should theoretically be maximised by forming many weak bonds,

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[1] I avoid use of the term ”crop-raiding”, because ”raid” implies an intentionally malicious act of theft (Peterson *et al.*, 2010), as opposed to individuals choosing to forage on the most palatable or nutritious plant matter available. Similarly, throughout this thesis I will be referring only to human-wildlife ”coexistence” or ”interactions”, not ”conflict”, because I do not see that framing humans as being against wildlife and nature in a conflict as either accurate nor helpful to perspectives of potential future scenarios.

because more partners may increase the probability of the relevant stimulus or area being brought to the individual's attention. Furthermore, because there is no actual behaviour copying required in social facilitation, the identity of the role model should not be important (see Laland, 2004 for a discussion of which individuals should be copied in social learning decisions). With this mechanism, I would therefore expect to observe a social structure with very limited social differentiation. In contrast, learning by imitation of exact behaviours (Laland, 2004) may be easiest when remaining with the same individual for a long time and observing them, especially if the behaviour is particularly complicated, so the need for imitation may create social structures in which individuals have preferred social partners from which they might learn. Furthermore, if conformity to group behaviour is used by immigrant individuals to increase social tolerance and their own integration into the group (as proposed by Harrison *et al.*, 2024), imitation may further affect social structure by promoting conforming individuals to be more preferable social partners. Finally, emulation, in which a naïve individual observes the positive outcome of another's action and then finds its own method of reaching said outcome (Tomasello *et al.*, 1987; Fugazza *et al.*, 2019), I would expect to be somewhere in the middle. On the one hand, emulation may be easier when associating or interacting with as many potential role models as possible (Montanari and Saberi, 2010), creating an undifferentiated social structure with maximum opportunities to observe positive outcomes. On the other, observing an individual for a long time may reinforce the benefits of the reward, such that emulation would promote community structure. Studies to explicitly model and test the links between community structure and social learning method are necessary to disentangle some of these possibilities.

1.1.2 Group defence

Social structures arising from group defence are similarly likely to vary depending on the mechanism by which predators are deterred. Simply being gregarious can reduce individual predation risk (Hamilton, 1971), regardless of the social structure, via effects such as dilution (Foster and Treherne, 1981; Lehtonen and Jaatinen, 2016) or enhanced predator detection when foraging, which also facilitates reduced individual vigilance (e.g., Powell, 1974; Berger, 1978; Sullivan, 1984; Boland, 2003; though studies of this effect can be confounded by increased foraging competition: Lima, 1995; Roberts, 1996; Hammer *et al.*, 2023). However, when groups actively work together to protect one another, this may have a greater influence on social structure. For example, predator mobbing, which is observed across taxa but has been predominantly researched in birds and mammals, occurs when a group of prey species band together to harass or attack a predator, even if the predator has not yet attempted a hunt (Altmann, 1956; for a recent review of predator mobbing, see Carlson and Griesser, 2022), with the result that the probability of successful predation is reduced. Alternatively, some species create defensive formations, putting the most vulnerable group members in the centre, with the largest and strongest defenders on the outside (e.g., musk oxen, *Ovibos moschatus*: Watson and Tener, 1967, and Wilkinson, 1971 *in* White *et al.*, 1985).

Differences in predator avoidance and defence tactics may lead to the emergence of different social structures. During group defence, individuals actively put themselves at risk to protect group members, which should only occur if it creates a long-term fitness (direct or indirect) benefit to the individual (Crofoot, 2013; Angulo *et al.*, 2018; van Schaik *et al.*, 2022), and avoid joining a mob if mobbing confers no fitness benefit (e.g., FitzGibbon, 1994). For example, barn swallows (*Hirundo rustica*) will usually only mob when they are protecting their offspring or mate, but not for other members of the population (Shields, 1984), so this would not promote the formation of close social bonds with other birds besides their partner. In contrast, defensive formations may require trust and familiarity with other group members, to be confident that they will cooperate in the face of danger, so promote the formation of more closely bonded groups (Gianetto and Heydari, 2015). In both cases, unrelated individuals may protect one another if they can then expect later reciprocity, in which the group will also protect them (Taborsky *et al.*, 2016). For example, pied flycatchers (*Ficedula hypoleuca*) are much more likely to join a mob at the nest of a neighbour, if that neighbour previously joined to defend the focal pair's nest (Krams *et al.*, 2008), creating a tit-for-tat rule of reciprocity (Axelrod and Hamilton, 1981). In the case of reciprocity, social structure is particularly important: an animal cannot expect reciprocation if they do not frequently interact, and it requires a level of familiarity with the partner to be confident that they will reciprocate in future (Trivers, 1971; Wilkinson, 1984).

1.1.3 Methods of studying social behaviour

Despite all this discussion of social structure, structure and social bonds are not directly observable (De Moor *et al.*, 2024): as researchers, we can use observations of group behaviour to assess potential social structure in animal groups, or experiments to observe changes in behaviour, to look for potential causes and consequences for animal society. For example, by observing behaviour during dangerous situations, we can look for signs of group defence and use this to identify the importance of strong social bonds to different species. Female guppies (*Poecilia reticulata*) will inspect a predator in cooperative pairs (Dugatkin and Godin, 1992; Godin and Davis, 1995), preferring partners with which they have a strong social bond (Croft *et al.*, 2006) but not those with which they are related (Brask *et al.*, 2019). This indicates that, in guppies, predation risk is more likely than kin selection to generate social structure. To fully understand the social bond between two individuals observed to mob a predator together or the social position of individuals most likely to participate in group defence (e.g., Crofoot *et al.*, 2011), it can be necessary to quantify and visualise their social relationships. One option is to use social network analysis to identify the likely social structure from observations of social associations or interactions between group members.

Animal behaviour presents questions pertinent to ecology, evolution, conservation, and animal welfare, for which we may choose to use social network models of the social bonds (edges) between individuals (nodes) in a population. For example, we may wish to identify whether the need for social learning and the mechanism that it takes are important causes of social structure in a population, which could have implications for species survival and therefore conservation (Franz and Nunn, 2009; Krause *et al.*, 2014; Farine *et al.*, 2015a). To answer these questions, we can use observations of associations or interactions to quantify the strengths of relationships between nodes (e.g., using association indices; Cairns and Schwager, 1987) to build a model of the underlying social structure, then track the spread of the behaviour through the population (e.g., Hobaiter *et al.*, 2014; Wild *et al.*, 2020; Beck *et al.*, 2023b; Reeves *et al.*, 2023; Coelho *et al.*, 2024). Alternatively, after modelling the network, we could build causal models or perform simulation experiments to assess the effect of individual traits on network edges (Hart *et al.*, 2023), which could then highlight specific partnerships that are important for social learning. For example, using social network analysis, Lilley *et al.* (2020) found that male beluga whales (*Delphinapterus leucas*) use socio-sexual behaviour to build social bonds and that sub-adults are more likely to perform these behaviours when a male juvenile or calf is present: this therefore implies that juvenile males are likely learning socio-sexual behaviour from sub-adult demonstrators, and the loss of these demonstrators may affect future breeding abilities. Social network analysis is therefore an important and versatile tool that we can apply to a wide range of animal behaviour questions, with potentially important insights for the future of conservation.

However, social network analysis does possess its disadvantages and complications: we are forced into certain assumptions regarding the underlying social network, and the appropriate method may not be readily obvious. Firstly, for the method to work perfectly, we would have to use observations that perfectly reflect the true unbiased distribution of interactions or associations, but in reality, we are forced to assume that the observed network is a good representation of the underlying latent network (De Moor *et al.*, 2024). Furthermore, even with perfect observations, social behaviours are only indirect measures of social preference (De Moor *et al.*, 2024), so again it is an assumption that the measure that we use — associations based on shared group membership and proximity, or interactions based on grooming, greetings or play behaviour — is closely correlated with true social bonds. Secondly, social network analysis commonly suffers from the use of inappropriate methods for the study question. When considering changing behaviour over time or the transmission of information or disease through a network, we need a dynamic network method that is capable of reflecting those changes (Farine, 2018). In contrast, a static network analysis may be more appropriate for questions relating to singular time points (Farine, 2018), or for which a single measure is required per node, such as average lifetime centrality (e.g., Barocas *et al.*, 2011). When performing hypothesis testing, many studies have reported a significant and directional effect of the explanatory variable after using permutation tests (Krackhardt, 1988). Because social network measures are, by definition, non-independent (Krackhardt, 1988; Croft *et al.*, 2011), permutations are used to break the interdependencies between social bonds shared between common individuals (Farine, 2013; Evans *et al.*, 2020; Puga-Gonzalez *et al.*, 2021). However, despite their apparent logic and common use, permutations do not in fact allow hypothesis testing (Weiss *et al.*, 2021), cannot control for non-independence (Hart *et al.*, 2022b), and are incapable of producing accurate effect sizes (Franks *et al.*, 2021). Permutations can only test whether a network structure differs from random (Weiss *et al.*, 2021). Simulation papers demonstrating the improper use of permutations are relatively recent in comparison to the majority of animal social network literature, so many of the studies we currently rely on for describing animal social networks have been based on improper methods, and should be reassessed.

1.2 Social behaviour among males

Sex differences in social preferences reflect differences in resource requirements or life-history traits (Magurran and Garcia, 2000; Nelson, 2005; Zilkha *et al.*, 2021), but in mammalian ecology, males have often been less well studied than females (particularly with regard to reproductive life-history; Nussey *et al.*, 2013; Moatt *et al.*, 2016; Archer *et al.*, 2022) so female sociality may be better characterised than males in the literature. There can be many good reasons for this, such as sex differences in landscape use (e.g., Albery *et al.*, 2021b), aggression toward researchers (e.g., McLennan and Hill, 2010; Ranaweerage *et al.*, 2015), or propensity to associate (e.g., Vance *et al.*, 2008; Best *et al.*, 2013; Tyrrell *et al.*, 2020) so making interactions more difficult to study. It may also come from female-biases in captive mammal populations (e.g., Bieber *et al.*, 2019; Ramos *et al.*, 2019; Tyrrell *et al.*, 2020), or that females are the population-limiting sex in the majority of species, due to greater reproductive investment, so gain greater interest due to their importance in population growth rates (Bessa-Gomes *et al.*, 2004). In contrast, bird and reptile research appear to be more balanced than mammal studies (e.g., Whitaker and Shine, 2003; Aplin *et al.*, 2012; Farine *et al.*, 2012; Arnberg *et al.*, 2015; Moyers *et al.*, 2018; Dragić *et al.*, 2021; McCully and Rose, 2023; Penndorf *et al.*, 2023). This may be due to differences in sex-biased dispersal between taxa, with mammals and reptiles showing predominantly female-biased dispersal, whereas birds show male-biased (Pusey, 1987; Trochet *et al.*, 2016). Alternatively, female-bias in mammalian studies could be because of the nature of their social and parental care systems: 91% of mammals show female-only care, whereas in reptiles and birds this is less than 10% (Reynolds *et al.*, 2002), reducing the extent to which females are the limit on population growth. There may therefore be two potential driving forces behind the female-bias in mammalian studies: i) males are harder to study (exacerbated among mammals where males are the dispersing sex), and ii) females are more strongly the population-limiting sex.

While there are good reasons for female-biases in the mammalian social network literature, there are also advantages of studying males. Understanding male social behaviour is extremely important with regard to conservation for a number of reasons. Firstly, males may be involved in more human-wildlife interactions: male African elephants and chacma baboons (*Papio ursinus*) crop-forage more than females (Jackson *et al.*, 2008; Chiyo *et al.*, 2012; Strum, 2012; Von Gerhardt *et al.*, 2014), and male lions are more vulnerable to negative human-wildlife interactions and retaliatory killing than are females, because subordinate males are more likely to be driven into proximity with humans by dominant males (Petracca *et al.*, 2019; Felix *et al.*, 2022). Secondly, there can be sex differences in territoriality and home range preferences. For example, male brown bears (*Ursus arctos*) have much larger home ranges than females, both as adults (Dahle and Swenson, 2003) and as philopatric subadults (Dahle *et al.*, 2006), so only studying females could underestimate the size of area required for their conservation (Goldingay, 2015; Jarnemo *et al.*, 2023). Similarly, male cichlid fish (*Neolamprologus multifasciatus*) are more reactive to increased risk of invasion and resource availability than are females (Suriyampola and Eason, 2015), so may be more affected by changing environmental conditions or population density. Finally, males also offer an overall contribution to the social environment and population structure by shaping the behaviour of females and other males. Male-male relationships may maintain cohesion in higher-order grouping structures, as seen in northern resident killer whales, in which males form a social link between otherwise-independent matrilines within a pod (Harms, 1997). Similarly, male territoriality can define female home ranges and home range overlap, highlighting how differences in resource availability shape social behaviour (Baird and Whitehead, 2000). Research into the causes of male behaviour, both individually but also within the context of the social environment and population social network, will help with the planning of new conservation management strategies that affect all members of the population, and it is critical that equal consideration be given to both sexes in animal behaviour research.

Having said this, individual male-male social relationships are reasonably well studied in certain contexts, namely those based on kin relationships and those which benefit mating. On the face of it, affiliative relationships between males are confusing (Díaz-Muñoz *et al.*, 2014), because they do not follow standard rules of selection: males, especially unrelated males, should always compete rather than cooperating with potential rivals (Qi *et al.*, 2017). Therefore, when male social structures do emerge, their form is dependent on the mechanism by which males gain evolutionary advantages.

Understanding the social relationships between individuals with varying levels of kinship helps to identify the evolutionary causes of male cooperative behaviour (Langergraber *et al.*, 2007; Widdig *et al.*, 2016). Kin-based relationships are the easiest to understand, because related males working together can enhance both their direct and inclusive fitness (Hamilton, 1963; Eberhard, 1975; Griffin and West, 2002). For example, in male lions and cheetahs (*Acinonyx jubatus*), brothers may form coalitions that work together to hold a territory, which can lower survivorship costs (Caro and Collins, 1987; Chakrabarti and Jhala, 2017), and improve their chances of successfully breeding, elevating individual fitness both directly and indirectly. In the case of lions, being part of a strong coalition capable of remaining in control of a pride for a long period can be especially important, as males not only need to obtain access to mates, but also to then defend them for at least two years until their offspring are no longer vulnerable to infanticide by incoming males (Bygott *et al.*, 1979). It is important to note here that, regardless of the relationships between males, infanticide by a new male can have significant subsequent effects on female behaviour as well (Chakrabarti and Jhala, 2019), so this is a prime example of how male social behaviour can severely impact female fitness. In both lions and cheetahs, males are the dispersing sex, and brothers will leave their natal group together and so form the coalition. Sex-biased dispersal is prevalent in many social species which can produce groups of males either remaining philopatric (Stacey and Koenig, 1990; Wrege and Emlen, 1994) or dispersing together (Widdig *et al.*, 2016), creating networks of related males (though evidence of related males aggregating as adults shows that philopatry and simultaneous dispersal are not the only mechanisms for the formation of male kin-based coalitions; Qi *et al.*, 2017). In many cooperatively-breeding birds, nest helpers are often philopatric males related to the breeding male (Greenwood, 1980; Greenwood and Harvey, 1982; Clarke *et al.*, 1997; Riehl, 2013), and dominant males with a large network of helpers may be more likely to successfully attract a mate than solitary males (Wrege and Emlen, 1994), so cooperation can increase both direct and indirect fitness. Understanding the importance of male-male kin relationships, both to the individuals involved and on a wider network level to females and rival males, and of how sex-biased dispersal affects social structure, will help to explain patterns of social bonds and helping behaviour in animal populations.

Kin relationships are not always necessary for the formation of male alliances, however: males can increase the probability of successful matings even by grouping with unrelated males. This may involve outcompeting other males that are alone or in smaller coalitions (Noë, 1994; Higham and Maestripieri, 2010; Díaz-Muñoz *et al.*, 2014), allowing ascension to more dominant positions (Schülke *et al.*, 2010) or more successful defence of territories (Lemoine *et al.*, 2022). These systems can be extremely complex, with multiple levels of community structure forming different types of alliance, which requires consideration of the complete social network to understand. For example, in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), males form multilevel alliances of unrelated males (Gerber *et al.*, 2020), in which each level represents different types of association and offers different advantages with regard to mating: the first order alliance of two or three males work together to mate guard a female; the second order alliance is the pool of favoured associates from which the first order alliance is drawn; and the third order alliance act as allies to back up the second order alliance in times of conflict (Connor and Krützen, 2015; Connor *et al.*, 2022). This complex multilevel male society contains social bonds of multiple different types and strengths, in which grouping with specific partners offers different advantages to each individual. Mating alliances can also form that do not involve fighting for access to females: males may use mating alliances with unrelated group-mates as an opportunity to practice courtship behaviours or increase the chances of inheriting a territory. For example, manakins (genus: *Chiroxiphia*) show cooperative courtship displays (DuVal, 2007; Díaz-Muñoz *et al.*, 2014; Lukianchuk and Doucet, 2014). Male manakins that engage in mating displays as a subordinate (DuVal, 2007) and that socialise a lot as a juvenile (McDonald, 2007) are more likely to gain dominant status and mating opportunities. Males can therefore improve their direct fitness by forming cooperative relationships with unrelated males, despite these males being potential rivals. Understanding the mechanisms by which this occurs and the social relationships formed between unrelated males could help to explain the evolutionary pathways by which male social structures emerge.

1.3 The importance of studying elephant behaviour

The African savannah elephant is a prime species for new studies of social behaviour, because they are highly social and have suffered population declines of approximately 30% between 2006 and 2016 (Chase *et al.*, 2016; Thouless *et al.*, 2016), making them endangered on the IUCN Red List (Gobush *et al.*, 2022). Illegal killing of elephants accounts for over half of recorded elephant deaths (CITES Secretariat, 2021), with an estimated 40 000 savannah elephants killed for their ivory in 2011 alone (Wittemyer *et al.*, 2014), while land conversion (Douglas-Hamilton, 1987; Nellemann *et al.*, 2013; Chase *et al.*, 2016; Mpakairi *et al.*, 2019; Ntukey *et al.*, 2022; Jeza and Bekele, 2023) and climate change (Nellemann *et al.*, 2013; Mpakairi *et al.*, 2020; Dejene *et al.*, 2021; Jeza and Bekele, 2023) further fragment their populations. Elephants also represent a species with which human-wildlife coexistence is extremely difficult. While there are no official collated numbers of people injured or killed by elephants per year, the numbers are known to be high: in 1989-1992, 22 people were killed by African elephants in just the Laikipia District of northern Kenya (Thouless, 1994), and in Sri Lanka in 1992-2001, Asian elephants killed 536 (Perera, 2009). Every human death is an individual tragedy that cannot be overlooked. Research into elephant behaviour is therefore critical to understanding the causes of negative human-elephant interactions, so that conservation actions may work to protect not only the elephants, but also the people who live alongside them.

Human-elephant coexistence is notoriously difficult, because of the impact elephants have on cultivated vegetation, which often has severe consequences for human safety, welfare and economics. When elephants opt to enter community lands and forage on crops, they destroy people's food and income supply, damage property, and endanger the lives of community members who try to chase them away (Hoare, 1995; Osborn and Parker, 2003; Sitati *et al.*, 2005; Dunham *et al.*, 2010; Stevens, 2018). Because elephant populations grow in some areas and shrink in others, the number and distribution of these events is likely to change, growing wherever elephants come to be in increasingly close contact with people. This is likely to be further exacerbated by climate change, which could cause an increase in human-elephant interactions if drought conditions cause the elephants to target water resources close to towns and villages (Thouless, 1994).

A wealth of studies has occurred investigating crop-foraging, from the environmental changes and farm characteristics that increase the probability of elephants entering a field, through to the possible mechanisms by which we can potentially mitigate crop-foraging through schemes such as offering farmers compensation. Elephants are most likely to forage on crops during the dry (Chiyo *et al.*, 2005) and late wet (Osborn, 2004) seasons, once the nutrient quality of wild grasses drops below that of crops (Osborn, 2004; Chiyo *et al.*, 2005). Fields are more likely to be foraged when planted with a diverse range of palatable crops (Stevens, 2018; Montero-Botey *et al.*, 2024), and when situated close to water bodies (Montero-Botey *et al.*, 2024) and/or protected areas (Tiller *et al.*, 2021), especially when the general landscape is highly fragmented (Hahn *et al.*, 2024; Montero-Botey *et al.*, 2024). Of the different potential mechanisms by which we might mitigate crop foraging, compensation schemes to pay farmers for damage have generally shown the least success (DeMotts and Hoon, 2012; Stevens, 2018). Physical barriers, including electric fences (O'Connell-Rodwell *et al.*, 2000; de Boer and Ntumi, 2001; Kioko *et al.*, 2008), ditches/trenches (Mackenzie and Ahabyona, 2012; Kyokuhaire *et al.*, 2023; Rogers *et al.*, 2023), and thorn scrub hedges (King *et al.*, 2011b; Von Hagen, 2018) are more effective, but elephants that learn to circumvent or break barriers can still cause severe and expensive damage (Kioko *et* *al.*, 2008). Finally, elephant deterrents can be quite effective but often require a lot of maintenance. Common deterrent methods include the use of honeybees (*Apis mellifera scutellata*; Vollrath and Douglas-Hamilton, 2002; King *et al.*, 2009; King *et al.*, 2011b; King *et al.*, 2017; Kiffner *et al.*, 2021), chilli/capsaicin (Parker and Osborn, 2006; Le Bel *et al.*, 2010; Kiffner *et al.*, 2021), flashing lights (Adams *et al.*, 2020), and farmers actively guarding their crops (often with fires, loud noise, and throwing projectiles; Osborn and Parker, 2002; Sitati *et al.*, 2005; Nyirenda *et al.*, 2012; Gross *et al.*, 2019). I do not have the space to cover crop-foraging and its mitigation in detail here, but see Denninger Snyder and Rentsch (2020) and Montgomery *et al.* (2022) for recent reviews of the crop-foraging literature.

From an ecological perspective, elephants are a keystone species, playing a vital role as ecosystem engineers in their local environment, so their declining population could also herald disaster for a wide array of other savannah species. Consuming 1-2% of their body weight in vegetation (Owen-Smith, 1988) and felling up to nine trees each per day in social displays and foraging for roots (Guy, 1976), male elephants increase low-level browsing available to mesoherbivores (Rutina *et al.*, 2005; Makhabu *et al.*, 2006) and facilitate the maintenance of important habitats for a wide variety of species. On a local scale, elephant tree damage provides refuges for small arboreal animals (Pringle, 2008) and understory-dwelling plants (Coverdale *et al.*, 2016); on a landscape scale they help to maintain the savannah grassland, preventing conversion to forest (Dublin, 1991; Jachmann and Croes, 1991; MacGregor and O'Connor, 2004), which provides space for many species that depend on open savannah habitats (Valeix *et al.*, 2011). Elephants are one of the primary causes of landscape scale changes to vegetation index in Africa (Hayward and Zawadzka, 2010): for example, in just nine years, elephants in Uganda's Murchison Falls Park thinned the trees down to just 20 per km^2 from 430-1060 per km^2 (Owen-Smith, 1988). While this is vitally important for many species, it can also lead to the extirpation of locally rare plant species that are particularly vulnerable to elephant damage (Lombard *et al.*, 2001), and in very high densities, elephants may rapidly convert areas from a stable wooded state to an open area (Spinage, 1990), potentially driving away woodland species (Cumming *et al.*, 1997). The more we understand about elephants, the easier it is to protect them and all the species that depend on the habitats they create, while also protecting those species more vulnerable to elephant damage.

1.4 Male elephant social behaviour

As previously discussed, many mammalian species have received far more attention regarding the behaviour of females than males, and elephants are no exception. The social system of male elephants is understudied relative to the females (O'Connell-Rodwell *et al.*, 2024a), such that the causes of social bond strength in male elephants are poorly understood. Male elephants are more challenging to study long-term than females, because they often travel large distances (Evans, 2006; Roux and Bernard, 2009), including crossing international borders, making it extremely difficult (if not impossible) to track their associations consistently. This, combined with their propensity to rapidly change social partners and alternate between spending time with others versus alone (Chiyo *et al.*, 2011; Lee *et al.*, 2011), means their social preferences are currently unclear, as are the advantages that each one gains from associating with others. However, males are also the more persecuted sex with regard to illegal anthropogenic killing. Because males usually have larger tusks than females, bulls are generally the preferred (though not exclusive) targets for poachers (Poole, 1989a; Poole and Thomsen, 1989; Barnes and Kapela, 1991; Mondol *et al.*, 2014; Chiyo *et al.*, 2015). On a more minor scale, but still with a significant impact, people will kill elephants that enter community lands in retaliation for elephants damaging their crops and endangering human lives (Douglas-Hamilton, 1987; Chase *et al.*, 2016; Thouless *et al.*, 2016). Since the majority of crop-foraging is performed by males (Chiyo and Cochrane, 2005; Jackson *et al.*, 2008; Von Gerhardt *et al.*, 2014; Songhurst, 2017) — potentially because the females are more risk-averse than males when they have young calves (Sukumar and Gadgil, 1988; Chiyo and Cochrane, 2005) — again it will often be males that bear the brunt of the threat. Reducing the difference in information available about males in comparison to females will help to focus wildlife management and protection efforts, leading to more efficient use of conservation time and funds.

Male elephants are known to alternate between social and asocial behaviour, spending approximately 63% of their time in all-male groups, and a further 18% in mixed-sex groups (Chiyo *et al.*, 2011). While joining groups that contain adult females makes sense for the sake of obtaining potential mating opportunities, it is currently unclear why male elephants spend so much time associating with one another, or if they display assortment when selecting male social partners. During their transition to independence from their natal family unit, young males will join bull groups and move away from the family with them, indicating that older males may potentially be important for offering safety to young males, or acting as role models from which they might learn the skills needed for life away from their family (Evans and Harris, 2008). For example, an important part of male development involves sparring to build strength and fighting skills, so they can later compete for mates (Laursen and Bekoff, 1978; Evans and Harris, 2008). Grouping with other bulls with similar strength and experience can provide them with sparring partners necessary for this development (Chiyo *et al.*, 2011). However, it remains unclear whether any benefits beyond finding sparring partners encourage male elephants to form groups.

1.4 Male elephant social behaviour

There are a number of significant knowledge gaps that require further investigation around male elephant social behaviour. First and foremost, we need to ask how much do male elephants repeatedly associate with the same individuals? Only a handful of articles exist to assess bull social structure and calculate network parameters, and they reach slightly different conclusions to one another. Male elephants have been found to generally display quite weak relationships with one another, with each pair of males spending less than 15% of their time together (Murphy *et al.*, 2020), and possibly as low as just 2.8% (Chiyo *et al.*, 2011). However, some estimates of male social association strength have suggested that males in the same sexual state (state identified based on their probability of associating with females) may spend as much as 31.0-33.4% of their time together (Goldenberg *et al.*, 2014). This is a very wide range of possible social bond strengths, and the source of these differences has not been investigated: it could be due to differences in sampling or the duration of observations used (De Moor *et al.*, 2024), or different thresholds for including particular individuals in the data (Farine and Whitehead, 2015), or it could be because of genuine differences between individuals or populations. If it is the latter, it is important to compare populations and see how they are similar and dissimilar, to avoid making assumptions that elephant conservation in one place will act similarly for a different population. For example, African honeybees are an effective deterrent of crop-foraging elephants in Kenya (King *et al.*, 2009) but not Zimbabwe (Karidozo and Osborn, 2005).

The applicability of conservation research across different populations indicates a second important knowledge gap: how much heterogeneity do we see in social behaviour between populations of male elephants? Population differences in social behaviour could arise in response to differences in abiotic or biotic environment (He *et al.*, 2019; Testard *et al.*, 2021). Differences in resource availability can influence social structure by reducing the time an individual can afford to allocate to social interactions (Foster *et al.*, 2012). Namibia's desert elephants would therefore be expected to display different social interactions than elephants in Botswana's Okavango Delta for example, because the difference in water availability and vegetation growth (Namib Desert: Henschel and Seely, 2008, Okavango Delta: McCarthy *et al.*, 1998) would mean the Okavango elephants could afford to spend more time strengthening their social bonds. However, social networks are extremely difficult to compare quantitatively (Faust, 2006; De Moor *et al.*, 2024), and these populations would be sufficiently different in terms of size and required sampling effort that simple measures of global network structure would be incomparable (Hart, 2023; De Moor *et al.*, 2024). Further studies are required to investigate the differences between populations of male elephants, and how we can reduce potential biases or methodological impacts on social network results. For example, there are currently no recommendations for how long researchers should observe a population of elephants before they can start to draw conclusions regarding the social structure, and not observing them for long enough could potentially bias the results.

A third gap in the literature surrounding male elephants is the purpose of their forming social groups. As previously discussed, there are numerous reasons for the formation of male-male social bonds across different species, including mating alliances, kin selection, increasing resource access, protection from predators, and accessing social learning opportunities. Bulls do not form mating alliances, showing a reduced likelihood of associating with other males when in a sexually active state than when sexually inactive (Poole, 1989b). In female elephants, it is about kin selection: families help care for their siblings, cousins and grand offspring, which includes protecting one another (Douglas-Hamilton, 1972), and acting as role models to pass along information to younger members of their family unit or clan group (Moss and Lee, 2011a; Mutinda *et al.*, 2011). Male elephants do not show the same strong kin ties as are present in female family units (Chiyo *et al.*, 2011; Santos, 2017), so they are not gaining kin selective benefits by grouping together, and it is unknown whether they will protect one another in times of danger. Similarly, while several studies have implied that social learning may be an important part of male elephant society (Lee and Moss, 1986, 1999; Lee *et al.*, 2011; Evans and Harris, 2008; Allen *et al.*, 2020), this has not been explicitly tested, nor has the impact of that on social structure been thoroughly examined. Potential social learning pathways of particular interest in male elephants are those that promote behaviours associated with negative human-elephant interactions, such as crop-foraging or fence-breaking. Males are more likely to be crop-foragers if their close associates are also crop-foragers (Chiyo *et al.*, 2012), and the youngest males that have only recently transitioned to independence are the least likely to enter fields (Chiyo and Cochrane, 2005). Considering the various possible mechanisms of social learning, crop-foraging is most likely spread via local enhancement when young males follow the paths laid by old bulls (Allen *et al.*, 2020), and fence-breaking by imitation or emulation, because they need to use their tusks or the fence posts to avoid being hurt by the electrical current (Kioko *et al.*, 2008; Mutinda *et al.*, 2014). Understanding the possible social learning pathways that promote behaviours leading to negative human-elephant interactions is likely to be critical with regard to conservation actions. We therefore must ask the question: what advantages do male elephants gain from forming social bonds with one another?

1.5 Thesis structure

This thesis is designed to investigate the social behaviour of male African savannah elephants, using a combination of both statistical and experimental methods. Specifically, I am looking to answer the following questions: i) To what extent do male elephants form social bonds with one another, and do they show evidence for community structure? ii) How does male age affect social structure, and what does this mean for theories of social learning as a cause of male-male social bonds? iii) How similar are independent populations of male elephants in their social structure, and how stable are their relationships over time? iv) By forming groups, do males gain advantages of protection or access to role models, and how might this affect social responses to novel and/or dangerous situations? Overall, I hypothesise that male gregariousness and social bond formation facilitate increased access to social information and protection from danger, working with the assumption that these would be advantageous for survival and long-term fitness.

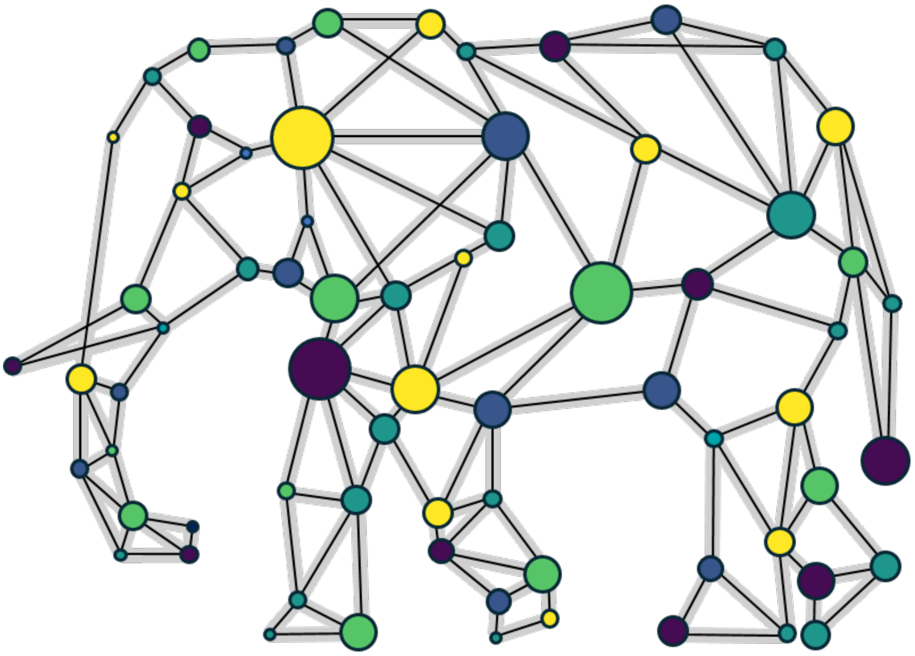
To answers questions i-iii, I began my study by attempting to build social networks for the assessment of male elephant social structure, but quickly began to find problems with the edge weights produced by the models. An edge weight is the strength of social bond between two individuals within a network. Many indices are available for this, including most commonly the simple ratio index (SRI; Cairns and Schwager, 1987), and more recently the Bayesian framework for Inference of Social Networks (BISoN; Hart *et al.*, 2022a; Hart *et al.*, 2023). Upon realising that the issue came down to the very low density of the male elephant social network, I found myself in need of a new model to estimate edge weights. In Chapter 2, I therefore start with an additional question: How can we improve measurements of edge weight to reduce bias and avoid the formation of spurious correlations in social network analysis, especially when networks are sparse? To answer this, I will compare the SRI and BISoN, both theoretically through discussion of their respective advantages and pitfalls, and empirically through the use of an example dataset that documents the social interactions between the male elephants of the Mosi-Oa-Tunya National Park (MOTNP), Zambia. I ask how frequentist and Bayesian methods differ in their performance when calculating edge weights in social networks, and how the differences in their outputs affect any subsequent analyses (in this case, network centrality). I identify the issues that surround each type of method, specifically with regard to sparse networks, which occur when many pairs of nodes do not associate with one another. Having identified these issues, I then present a solution for sparse network analysis, which involves the adaptation of the BISoN framework to better reflect the underlying social systems that generate the true edge weights within the elephant population.

Having identified that sparse networks require an alternative method of edge weight estimation, and developed a solution, I was then able to progress with my study of male social network structure (questions i-iii). In Chapter 3, I use the methods outlined in Chapter 2 to calculate the edge weights in two populations of male African savannah elephants, found in MOTNP, Zambia, and in Amboseli National Park (ANP), Kenya. I then go on to use these edge weights to question the factors influencing bull network position, and therefore how social learning may influence the social structure. I qualitatively compare the results between MOTNP and ANP to identify whether the role of age in defining male elephant social structure varies between populations. Within ANP, I also compare the results between models based on data collected at different temporal scales, to question the stability of male relationships and if social network analysis is dependent on the duration of the observation window used to collect association data, especially when dealing with highly intelligent and long-lived species.

Using these social network structures, I begin to question how social learning may affect the structure of male-male relationships, and the benefits that males obtain by forming groups. To answer question iv, in Chapter 4, I move away from social network analysis to instead use experimental methods to question how young males may use the presence of older males to gain protective or social learning benefits in the context of potentially dangerous situations to which they may be unfamiliar. Using a simulated threat scenario in Botswana's Makgadikgadi Pans National Park (MPNP), I compare how males of different ages respond to different stimuli, with regard to their social interactions with the rest of the group, questioning firstly if younger males respond by looking towards and following older males (evidence of social learning), and secondly if older males show any signs of protecting younger males. I do this by observing each focal individual's looking and movement direction relative to every other individual within the group, and identifying the age of their nearest neighbour throughout the playback. While I cannot test whether older males are truly improving the survival probabilities of younger males, these experiments can indicate their importance within the population by aiding young males in threatening situations, either passively by providing a role model that the younger bulls can copy, or actively by defending them from danger.

Chapter 2

Analysis of sparse animal social networks



Abstract

Low-density social networks can be common in animal societies, even among species generally considered highly social. Social network analysis is commonly used to analyse animal societal structure, but edge weight (strength of association between two individuals) estimation methods designed for dense networks can produce biased measures when applied to low-density networks. Frequentist methods suffer when data availability is low, because they contain an inherent flat prior that will accept any possible edge weight value, and contain no uncertainty in their output. Bayesian methods can accept alternative priors, so can provide more reliable edge weights that include a measure of uncertainty, but they can only reduce bias when sensible prior

values are selected. Currently, neither accounts for zero-inflation, so they produce edge weight estimates biased towards stronger associations than the true social network, which can be seen through diagnostic plots of data quality against output estimate. I address this by adding zero-inflation to the model, and demonstrate the process using group-based data from a population of male African savannah elephants. I show that the Bayesian approach performs better than the frequentist to reduce the bias caused by these problems, though the Bayesian requires careful consideration of the priors. I recommend the use of a Bayesian framework, but with a conditional prior that allows the modelling of zero-inflation. This reflects the fact that edge weight derivation is a two-step process: i) probability of ever interacting, and ii) frequency of interaction for those who do. Additional conditional priors could be added where the biology requires it, for example in a society with strong community structure, such as female elephants in which kin structure would create additional levels of network modularity. Although this approach was inspired by reducing bias observed in sparse networks, it could have value for networks of all densities.

2.1 Introduction

Social networks underlie all animal social behaviour, and analysing the factors that affect their structure can improve our understanding of how individuals interact. In this thesis, I am interested in the structure and functions of male African savannah elephant (*Loxodonta africana*) social relationships, including assessing the social network structure of multiple elephant populations. However, when I set out to build these social networks, I came across an unexpected problem: the data kept producing strange and spurious trends, which didn't make either biological, or in some cases even mathematical, sense. I realised that the elephant networks were sufficiently sparse that standard methods of social network analysis could not cope with the low density of social interactions.

Social network density forms an important part of social structure, defined by the proportion of dyads (all of the possible pairs of individuals) who could potentially associate within a population that do associate. Some animal social networks are dense, characterised by frequent interactions and connections among a high proportion of its members. Others are sparse, with a high proportion of dyads never associating with one another. This difference in network density can influence an individual's rate of social learning (Singh, 2005; Franz and Nunn, 2009; Hobaiter *et al.*, 2014) or their risk of pathogenic infection (Kretzschmar and Morris, 1996; Cross *et al.*, 2004; Naug, 2008; Silk *et al.*, 2017), which can cascade to population-level impacts. Differences in network density may be due to inherent differences in gregariousness between species, or inter-population variation in resource availability or predation risk imposing different limits on the propensity of populations to aggregate. Density may also influence our ability to assess social structure, if we do not successfully account for it during social network analysis, as I will show in this chapter. For this reason, it is necessary that I first identify a method by which to assess social structure in the elephants that is reliable despite their very sparse network. Previous studies of elephant social behaviour (Chiyo *et al.*, 2011; Goldenberg *et al.*, 2014; Murphy *et al.*, 2020) have implied potential differences in structure or association patterns between populations: in order to compare different populations to one another in the next chapter, I need to ensure that my methods can deal with potential differences in network density.

Studies of animal social networks tend to address gregarious species, typically characterised by dense social networks. However, being gregarious and living in groups is not the same as having strong social preferences: two species can be equally gregarious, but one has individuals associating randomly, while in the other they only associate with a few select partners. As of 2019, 78% of published studies focused on the social structure of either birds (e.g., Silk *et al.*, 2014; Farine *et al.*, 2015a; Beck *et al.*, 2023a) or group-living mammals (Webber and Vander Wal, 2019), such as cetaceans (e.g., Foster *et al.*, 2012; Weiss, 2021; Gerber *et al.*, 2022; Marfurt *et al.*, 2022), primates (e.g., Kasper and Voelkl, 2009; Brent *et al.*, 2011b; Sueur *et al.*, 2011) and social carnivores (e.g., Abell *et al.*, 2013; Dorning and Harris, 2019; Stratford *et al.*, 2020). Understandably, researchers generally focus on highly gregarious species because their associations are more frequent and they are more likely to be co-located so they are easier to sample for social network studies, and there can be clearer applications for the work concerning conservation (e.g., Abell *et al.*, 2013) or captive animal welfare (Kleinhappel *et al.*, 2016). However, this means that we know only relatively little about other taxonomic groups and species that may have sparser networks, such as solitary mammals (e.g., Connor *et al.*, 2023) or reptiles (e.g., Leu *et al.*, 2016). Less gregarious animals can still have strong friendships or specific preferences regarding who they should associate with, which might impact their behaviour and survival, including species such as mountain and western gorillas (*Gorilla beringei beringei* and *Gorilla gorilla gorilla*) that are generally considered highly social but can show relatively low average rates of social association (Rosenbaum *et al.*, 2016; Morrison *et al.*, 2020).

The two core components of a social network are the individuals within the population, called nodes, and the associations between them, known as the edges. In some networks, we only need to know if a connection exists between a dyad, but the strength of that association (henceforth ”edge weight”) is not important. In others, we need to know the probability of a dyad being observed together. For many studies, edge weights are the basis of further network structural analyses, making it critical to calculate them reliably.

Edge weight estimation methods are sensitive to the density of a network, so may be problematic when networks are sparse, as I will demonstrate in this chapter. Methods designed for dense networks may produce biased measures of edge weight, which can lead to further bias in downstream calculations of node centrality or network density, but this is not something that has previously been examined. Similarly, edges between unassociated dyads need to be modelled as zero-strength connections, but edge weight estimation methods may be either poor at detecting non-association or falsely identify zero-strength edges. In turn, errors regarding the presence or absence of zero-strength edges lead to over- and underestimation of average edge weight, which will affect all network studies, regardless of whether they are interested in edge presence or weight. The pitfalls of different methods, which I will identify in this chapter, should be considered to decide if zero-inflation is likely to influence edge weight estimation and if edges are more likely to be over- or underestimated.

Animal social network studies often struggle with limited data quality, exacerbating the difficulties of analysing sparse networks using common methods. Frequentist models — such as the commonly-used simple ratio index (SRI; Cairns and Schwager, 1987) — are biased towards extreme edge weights (0 and 1, respectively indicating that it is impossible for a pair to ever be together or apart), especially when sample size is low (Franks *et al.*, 2010; Hoppitt and Farine, 2018), and so accept zero edge weight values too readily. They are therefore liable to underestimating network density by overinflating the number of dyads showing non-association. Furthermore, they contain no measures of uncertainty so cannot highlight the dyads where edge weight is most likely to have suffered from low sample size. In contrast, as with any Bayesian analysis, Bayesian edge weight models can accept a non-flat prior that makes them more reliable than frequentist models when performed correctly. However, they introduce bias if the analyst chooses to use inappropriate priors designed for the analysis of dense networks. These edge weight priors can imply that non-association is highly implausible, producing posterior distributions biased towards stronger associations. This, in turn, can lead to errors in estimating network density. It is, therefore, inappropriate to use either the SRI or a Bayesian model with a prior designed for a dense network when analysing networks that are not fully connected, as I will later demonstrate. So far, this does not appear to have been an issue in publications, as Bayesian edge weight models are a relatively recent innovation and have only been used for populations with dense networks (e.g., Gettler *et al.*, 2023; Motes-Rodrigo *et al.*, 2023; Redhead *et al.*, 2023c, 2023a; Debetencourt *et al.*, 2024; Sadoughi *et al.*, 2024; Siracusa *et al.*, 2024; Testard *et al.*, 2024). However, as Bayesian models generally become more popular, it is likely that researchers will start to use them to calculate the edge weights of less gregarious species, for which a more robust analysis method needs to be established. We can overcome some of the issues with methods designed for dense networks by having very large quantities of data (Hoppitt and Farine, 2018; Hart *et al.*, 2023), but this is rarely a plausible solution in animal social network studies, and it does not solve all of the issues associated with edge weight estimation, as I will here discuss. In the next chapter of my thesis, I will be applying social network analysis to sparse networks: it is therefore important that first I identify a method that can cope with these data.

What is needed, is a model that reflects how the edge weights are generated in the natural system and incorporates the likelihood of obtaining a true zero, to avoid modelling a connection where one does not exist or biasing the model by supplying inappropriate information regarding the probability of extreme edge weights. All common methods — whether they are frequentist such as SRI (e.g. Croft *et al.*, 2009; de Silva *et al.*, 2011; Leu *et al.*, 2016; Stratford *et al.*, 2020; Beck *et al.*, 2023a), half-weight index (HWI) (e.g., Bejder *et al.*, 1998; Lusseau *et al.*, 2003; Napper and Hatchwell, 2016; Fang *et al.*, 2022; or HWIG when correcting for individual gregariousness; Godde *et al.*, 2013) or twice-weight index (TWI) (e.g., Turner *et al.*, 2017; van Leeuwen *et al.*, 2018), or Bayesian such as the Bayesian framework for Inference of Social Networks (BISoN; Hart *et al.*, 2022a; Hart *et al.*, 2023) (e.g., Motes-Rodrigo *et al.*, 2023; Sadoughi *et al.*, 2024; Siracusa *et al.*, 2024; Testard *et al.*, 2024) or STRAND (Ross *et al.*, 2022; Redhead *et al.*, 2023b) — model a network based on the assumption that the social processes that produce the edge weight contain only a single step: an individual deciding how much time to spend with another animal. This implicitly assumes a fully-connected network where every individual forms a connection with every other, and the only step in deriving the edge weight is determining how strong that connection will be. In such a model, edge weight may be correlated with dyad characteristics such as age (e.g., Turner *et al.*, 2017), kinship status (e.g., Chiyo *et al.*, 2011), phenotypic similarity (e.g., Zonana *et al.*, 2019), or anything else that has the potential to induce a preference (or not) for associating, but the decision over how much time to spend together is considered to be only a single step.

In contrast to these modelling assumptions, a network that is not fully connected has an additional data-generating step: before defining the weight of the connection, there is a precursory step that determines whether or not a dyad connects at all. This could be driven by a choice to avoid another individual (Farine *et al.*, 2015b; Leu *et al.*, 2016) or by spatial or temporal barriers that preclude individuals ever having the opportunity to associate (e.g., one member of the population dies before another is born, or no movement corridor exists between two subpopulations so their home ranges cannot overlap). This creates an additional step that defines the level of zero-inflation in the edge weights. Only once it has been defined that a dyad associates can the edge weight be determined. The sparser a network is, the more important it is to capture the first step of the underlying functional process. It is important to note that while this initial step of edge weight calculation has a Bernoulli outcome, the final network density is not a binary result of dense or sparse but a continuum composed of many dyadic edge weights that lie between zero and one. Models that assume a fully connected network become progressively worse as network density declines, but there is no intrinsic cost to always using a method that captures both steps of the underlying social process.

In this chapter I examine two different network modelling approaches for their applicability to sparse networks: the SRI (Cairns and Schwager, 1987), which is the approach that has historically been the most commonly used to estimate the association between individuals, and BISoN (Hart *et al.*, 2022a; Hart *et al.*, 2023), which is a newer method of using Bayesian models to estimate the association index with uncertainty and incorporate more appropriate prior information. I demonstrate the application of both of these methods on a sparse network of male savannah elephants. I show how Bayesian models overcome many of the limitations of the SRI but can suffer problems if supplied with priors that are not appropriate for the particular use case. Finally, I introduce a modification of the Bayesian framework that follows a two-step data-generating process, which can deal with the pitfalls of sparse network analysis. I propose that this modification be applied to networks of any density and would benefit future animal network studies. In Chapter 3 I will use this modification to also calculate the social networks for the elephants of Amboseli National Park, and then perform regression models to look for the causes of variation in male elephant social network position.

2.2 Challenges of sparse social networks for current common methods

2.2.1 Common network analysis methods

With gambit-of-the-group data (Franks *et al.*, 2010), both the SRI and Bayesian methods estimate the edge weight between individuals based on the total number of observations in which a dyad was together versus apart. However, despite using the same input data to estimate the same target measure, they suffer from different problems. As with any frequentist measure, SRI estimates are drawn based on the assumption that all possible edge weight values are equally likely — the equivalent of assuming a flat prior — so can produce any output edge weight, even when data are insufficient to support extreme values. To combat this, researchers often only include individuals with total sightings exceeding a threshold value, but taking a subset of the data creates its own issues, discussed below. As a Bayesian alternative, BISoN (Hart *et al.*, 2022a, 2023) and other Bayesian approaches such as STRAND (Ross *et al.*, 2022; Redhead *et al.*, 2023b) can use non-flat priors to inform the model of the prior probability of extreme values, so we can set up the model to be more uncertain about extreme edge values when the dyad observation count is low. Bayesian approaches, therefore, work better with lower sample sizes and uneven sampling than the SRI approach. However, as with the SRI, a single-step prior is appropriate only for fully connected, or close to fully connected, networks. For more sparse networks, we should appropriately modify the prior to reflect the biological processes: here, I consider the underlying two-step social process that first generates connections (or not) and then determines the weight of that connection.

The SRI is typically calculated as the number of times a pair of individuals were observed associating divided by the total number of sightings that either individual was observed:

$$\begin{aligned} SRI_{ij} &= together_{ij}/sightings_{ij} \qquad (2.1)\\ sightings_{ij} &= sightings_i + sightings_j + together_{ij} \end{aligned}$$

Where $together_{ij}$ is the number of observations in which individuals *i* and *j* were in the same group; $sightings_i$ and $sightings_j$ indicate the respective number of observations of individuals *i* and *j* in the absence of the other; and $sightings_{ij}$ is the total number of times they were seen as a whole. As a simple proportion, this measure expects extreme values such as 0 and 1 to be as likely as anything in between. It is a common misconception that frequentist models are less biased than Bayesian models because prior information is not incorporated. This has the opposite effect: a frequentist model still has a prior, but it is forced to be flat and uninformative, so it biases the results towards extreme values, making outliers just as plausible as the average value (van Zwet, 2019). The SRI also contains no measure of uncertainty: with this method, a value of SRI = 0 occurs when a dyad is never observed in the same group, with no greater uncertainty around edge weight estimates for poorly sampled dyads than those with many observations, but we should be more certain when more data are available.

These issues are the case regardless of network density, but their potential impact on analyses is exacerbated when dealing with extreme edge weight scores. In the real world, a lack of connection between individuals has important implications for social structure, information and disease transfer, and individual centrality. As the true network density declines, the likelihood of obtaining an edge weight of zero (spurious or correct) increases, and the SRI's lack of uncertainty and treatment of all possible edge weights as equally plausible become a greater issue. We must, therefore, be extremely careful about modelling zero-inflation, but the flat prior and lack of uncertainty seen in the SRI combine to make it very trusting of extreme edge weight values. It is important to note that while I am focussing on the SRI for this chapter, other frequentist edge weight measures, including the half-weight and twice-weight indexes, all suffer the same pitfalls.

Furthermore, to avoid confusion, it is also worth noting that pre-network permutation tests, which have known problems (Franks *et al.*, 2021; Weiss *et al.*, 2021; Hart *et al.*, 2022b), do nothing to deal with the issues faced by frequentist measures.

With Bayesian approaches, I still estimate the edge weight based on the proportion of total dyad sightings in which they were together, but now as a model parameter rather than a simple ratio calculation, for example:

$$\begin{aligned} together_{ij} &\sim binomial(sightings_{ij}, edgeweight_{ij}) \\ logit(edgeweight_{ij}) &\sim normal(\mu, \sigma) \end{aligned} \tag{2.2}$$

Where $together_{ij}$ and $sightings_{ij}$ are the respective number of observations of a dyad in the same group and in total, as above; and μ and σ are the prior mean and standard deviation for the logit-normal distribution of edge weight. Estimates of edge weight are now described by posterior distributions, which narrow as $sightings_{ij}$ increases, capturing uncertainty in the edge weight. Incorporating a user-defined prior can limit misleading outputs when the sample sizes are small, as the range of likely edge weight values is reduced. Through this use of sensible priors and quantification of uncertainty, Bayesian approaches are inherently more capable of dealing with the small sample sizes that are common in studies of animal social systems. While BISoN is not the only option available for the Bayesian estimation of edge weight (see also STRAND; Ross *et al.*, 2022; Redhead *et al.*, 2023b), I will focus on it in this chapter.

2.2.2 SRI requires deletion of data

With a flat prior and no implicit uncertainty measure, limited data availability about a dyad can produce unreliable SRI values. This is particularly common in animal social networks, so researchers will usually set an arbitrary minimum threshold number of observations per individual to include that node in the analysis (e.g., Bejder *et al.*, 1998; Croft *et al.*, 2009; Chiyo *et al.*, 2011; Napper and Hatchwell, 2016; Turner *et al.*, 2017; Murphy *et al.*, 2020). While this does prevent inaccurate edge weights created by the most poorly sampled dyads, it simultaneously introduces new issues (Kossinets, 2006; Huisman, 2009) that are often overlooked. Firstly, data are often hard-won and already limited, yet this practice requires the discarding of data, sometimes in large quantities. Secondly, data removal may not be completely-at-random (Rubin, 1976), which is known to introduce bias (Huisman, 2009; Krause *et al.*, 2018). For example, individuals that are less neophobic, more philopatric, or possess distinctive identifying features are more likely to be included in the analysis, because the probability of their having repeat observations is greater. If a study next performs a regression analysis on calculated network measures, this non-random data deletion can directly bias the results, especially if these factors are linked to the exposure or outcome variables in question. Thirdly, the specific value of these observation thresholds often varies between studies, as the actual choice of how many sightings is considered “enough” usually depends on the number of individuals that will remain after filtering out those poorly sampled. There is no definition for how many observations per node are required for network measures to be reliable. For example, Chiyo *et al.* (2011) included all male elephants with at least 15 observations in their three-year study period, while Murphy *et al.* (2020) used an inclusion threshold of just five observations per four-year sampling period. Therefore, comparing the results of different studies and identifying how many sightings are truly “enough” is difficult. Even with several sightings per individual, scores of 0 and 1 can be overinflated relative to their true underlying network, because there are only a certain number of possible edge weight values when sighting counts are low. We can increase the number of available observations through increased sampling effort, which means either increasing the number of hours per week spent in the field, or sampling over a longer period. However, this may often not be a plausible solution and, alongside the number of observations, it also remains unclear how analysts should go about deciding on the duration of their observation periods (Farine, 2018; Albery *et al.*, 2021a). This creates variation between studies in the duration of observations, which may in turn have substantial impacts on the results, though these effects are currently unknown. Studies would need to be carried out for each individual species to determine the duration of observation period that is biologically meaningful and representative of social relationships.

In contrast, employing a Bayesian framework prevents the requirement for data inclusion thresholds, which improves data quality and reduces biases caused by the possibility of data missing not-completely-at-random.

2.2.3 Bayesian models facilitate the use of more appropriate prior distributions

A model prior should always be carefully considered, which is not possible under the frequentist framework. Given how few papers have thus far used a Bayesian method for edge weight estimation, most social network analyses are based on flat frequentist priors, which are generally inappropriate (if nothing is known at all of the population in question, then a flat prior may still be a reasonable choice, though this would be extremely unusual). The *bisonR* (Hart *et al.*, 2022a) package for running BISoN models supplies very broad default priors, but the package authors strongly recommend tailoring them to each specific scenario. Most social networks contain at least some true zeros. Any model, frequentist or Bayesian, that uses a flat or very broad prior will struggle to model these zero values because they are modelling only the second step of what is inherently a two-step process.

Unlike the SRI, with BISoN I can change the model structure to incorporate two steps — first to determine if a dyad will associate at all, and second to define the strength of that connection — if I supply it with an appropriate prior, which package default priors are not. Here, I present a prior allowing BISoN to model both steps without changing the social network analysis workflow. While I could instead use a mixture model with zero-inflation to model a two-step process, using either a frequentist (see Appendix A1: Standard zero-inflated model) or Bayesian framework, I can keep the overall method relatively simple by changing only the prior structure. All network models should include some option to account for zero-inflation, and selecting the best method for measuring edge weights requires careful consideration: Bayesian techniques require integration of current understanding of the system and a prior predictive check, and can lead to biases if supplied with inappropriate priors, but their ability to estimate uncertainty and accept non-flat priors makes them more appropriate than frequentist methods.

2.2.4 Prior selection in a Bayesian edge weight model

Bayesian methods have been successfully applied to dense networks, using both simulated and empirical data (Hart, 2023; Motes-Rodrigo *et al.*, 2023; Pavez-Fox *et al.*, 2024), and their use in primate research has been discussed in subsequent publications (Bonnell *et al.*, 2023; Torfs *et al.*, 2023). However, the best way to use them for sparse networks has not yet been evaluated. Prior choices require careful consideration for any analysis, not just social networks. Fig 2a shows an improper uniform prior, in which all edge weights are considered equally likely before exposure to the data. By relaxing the assumption that all edge weights are equally probable, I can make the prior more informative. When I demonstrate the use of BISoN on an example dataset, I first show the outcome of this uniform prior ($edge\ weight_{ij} \sim Uniform(0,1)$), followed by the default prior supplied in the *bisonR* package (Hart *et al.*, 2022a): a wide symmetrical prior ($logit(edge\ weight_{ij}) \sim Normal(0, 2.5)$) that presumes very little about the average edge weight (Fig 2b). Third, I show the result of using a strong asymmetrical prior ($edge\ weight_{ij} \sim Beta(1,5)$) that indicates weaker edges are the most likely but still allows for some strong associations (Fig 2c). How the priors are defined depends on the researcher's knowledge and assumptions of the system: the sparser the network, the more right-skewed the prior distribution should be.

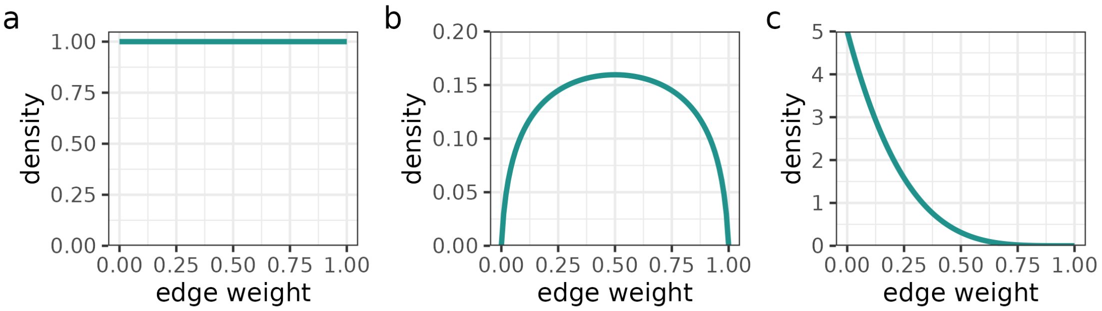


Figure 2: Prior assumptions for single-step BISoN models. Prior assumptions for a) SRI or a BISoN model with a uniform prior, $Uniform(0, 1)$; b) a BISoN model with a weak, symmetric prior, $LogitNormal(0, 2.5)$; and c) a BISoN model with a strong asymmetric prior, $Beta(1, 5)$.

Biases can appear in the edge posterior when the prior distribution does not reflect the underlying social process: knowing that the network is of a lower density can allow us to adapt the prior to a more suitable distribution, and the assumptions we can make based on that knowledge are critical to dealing with poorly sampled dyads. When the prior average is a long way from that of most dyads, it induces a systematic shift in the direction the data pushes the posterior from the prior. In a sparse network, many of the dyads will never associate, so a prior designed for a dense network will usually be shifted towards peaking at zero by the data. The data for poorly sampled dyads will, by definition, not be able to shift the posterior as far from the prior as the data from the well-sampled dyads, so if they all shift in the same direction, the level of sampling could potentially have a greater effect on the final edge weight than the actual raw data values. When this shift is consistently towards zero, poorly sampled dyads, on average, receive edge weight distributions with higher average values than well-sampled dyads. It is difficult to imagine a scenario in which the number of observations of a dyad would be strongly dependent on the strength of their social bond or vice versa, therefore this correlation highlights a problem with the edge weight data. I show this happening in the example analysis. Again, without well-sampled data, the choice of prior (including the SRI's uniform prior) becomes critical to the success of the edge weight estimation and all subsequent analyses.

2.3 Introducing a two-step prior for sparse networks

By varying the prior distribution, Bayesian methods can be tailored to a sparser or denser network. The modification that I propose simply extends this ability: to alter the BISoN prior structure to reflect a two-step social process producing the edge weights, in which step one defines the extent of zero-inflation and step two the weight of the non-zero social bonds. I structure the model to use two separate edge weight priors, selecting which to use depending on whether a dyad has ever been observed together (Fig 3), such as:

$$together_{ij} \sim Binomial(sightings_{ij}, edgeweight_{ij}) \tag{2.3}$$
$$edgeweight_{ij} \sim Beta(a, b)$$

If $together_{ij} = 0$: $a < 1$ and b = large

If $together_{ij} > 0$: $a = 1$ and b = small

Where again $together_{ij}$ refers to the number of times a pair was observed in the same group, and $sightings_{ij}$ is the number of times they were observed in total. This is not a major change to the method itself, as BISoN has always been capable of using a conditional prior. The change is that by capturing both parts of the underlying social process in a conditional prior, I only need to change one part of the overall method.

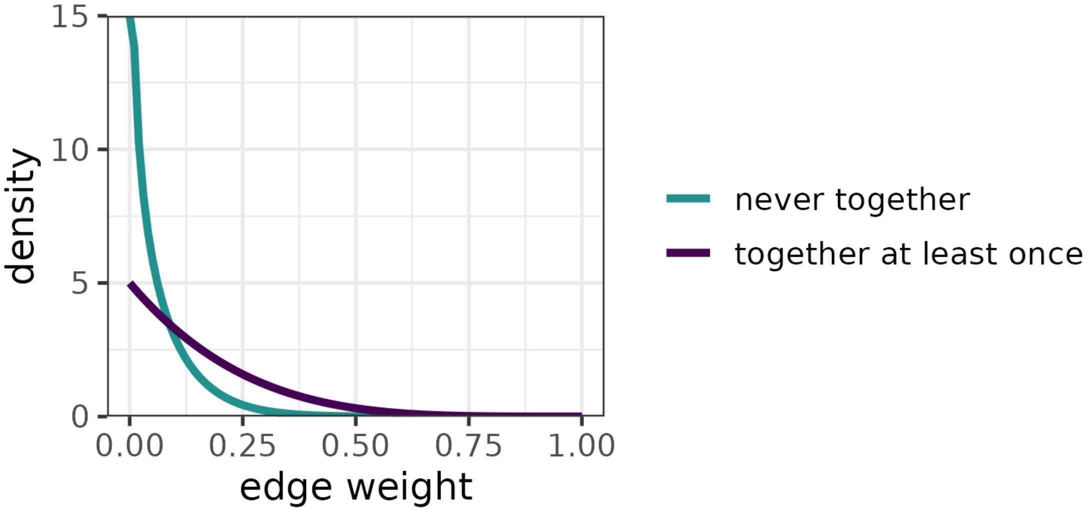


Figure 3: Conditional edge weight prior for a BISoN model of a sparse network. The blue line indicates the lower prior that will be selected when a dyad has never been observed in the same group (in this case $Beta(a = 0.7, b = 10)$). The purple line shows the upper prior choice for when a dyad has been observed grouping together on at least one occasion (in this case $Beta(a = 1, b = 5)$). While in this model I have chosen to still have this prior peak at zero, this reflects that I still expect very low edge weights amongst those that do associate, and the data immediately overwhelm the possibility of zero being an option. Note that the upper prior is the same as the strongly right-skewed prior shown above.

The new prior is simple to apply: if a dyad is never observed in the same social group, then the model will use a prior that increases the probability of an edge weight of zero; if a dyad has been observed interacting on at least one occasion, it will receive an edge weight calculated using a prior with less or no zero-inflation. This, therefore, allows the model to identify the most appropriate prior and incorporate the probability of non-association as an initial step before identifying the best edge weight distribution per dyad. As before, poorly sampled dyads will return an edge weight more similar to their respective prior, while well-sampled dyads will shift further. The model becomes less uncertain about a zero edge as the total sighting count increases: the uncertainty in these values indicates that zero is the most likely edge weight but still allows stronger relationships as a possibility when sampling is poor. In contrast, for a dyad observed together on at least one occasion, I use a wider prior that allows higher edge weights to be observed, again becoming more confident in the results as total sampling increases. The most logical step here may appear to be to make the single-step prior more right-skewed so it is closer to zero. However, if I were to use only one extremely right-skewed prior, such as the lower prior of this combination, to encapsulate the zero-inflation and the true associations, a prohibitively large amount of association data would be required for any truly strong edge weights to register.

The values a researcher might choose for the prior depend on their study species and expected edge weights. In the following example, I have opted to have the prior for associated dyads peaking at zero, but this is immediately overwhelmed by the data. This produces edge weight values that are still far more likely to be close to zero than to one, based on the evidence that male elephants do not appear to form strong relationships with one another (Chiyo *et al.*, 2011; Goldenberg *et al.*, 2014; Murphy *et al.*, 2020). If I were expecting to see a strongly bimodal distribution in the final edge weights, with some dyads never associating and others showing consistent association, I would shift my upper prior further from zero.

2.4 Example dataset

For this example, I used data on sparse networks based on associations between male elephants of the Mosi-Oa-Tunya National Park (MOTNP), Zambia, collected from May 2016 until December 2017 (permit number TJ/DNPW/101/13/18, supplied by the Department of National Parks and Wildlife, Zambia). This population is relatively small, totalling approximately 500 individuals, with similar numbers of males and females. The park is well connected to large areas of suitable habitat, and the elephants are free-ranging, so individuals may leave the area for long periods. Data were collected during daily drives through the park, marking down the identities of all individuals. From this, I created 504 days of gambit-of-the-group (Franks *et al.*, 2010) data comprising 213 males sighted in 481 groups. Finally, I converted this to a data frame containing every possible dyad with counts of the total number of times that dyad had been observed and how many of those occasions they were in the same group. Data analyses were run by calling Stan (version 2.26.1; Stan Development Team, 2023b) from R (version 4.2.1; R Core Team, 2022) using the *cmdstanr* (Gabry *et al.*, 2022) package.

2.5 Results from empirical data

2.5.1 Simple Ratio Index (SRI)

When I calculate the SRI values for this population (Fig 4a), I get an extremely high proportion of zeros (17385, equating to 77.00% of dyads). While a much lower number of dyads receive an SRI of one (12 dyads, equating to just 0.05% of the total population), the likelihood of these apparent permanent alliances would be exceedingly small given the population average.

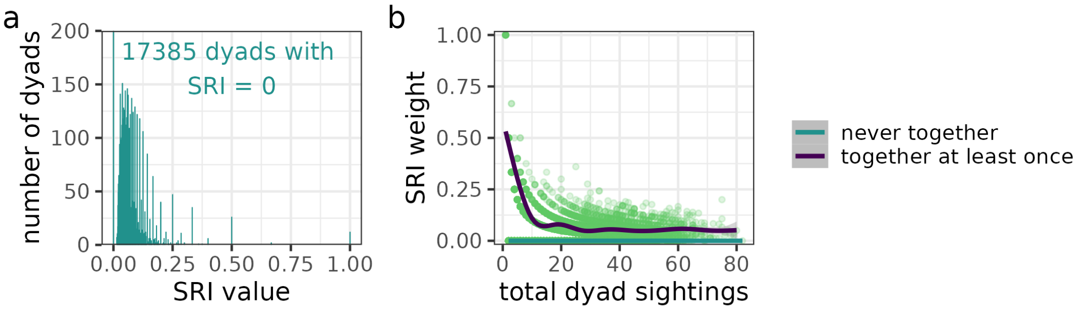


Figure 4: Edge weights for MOTNP elephants using the SRI. a) The vast majority of dyads have an SRI score of zero, indicating that the output is certain that these pairs never associate with one another, regardless of the number of sightings. b) This translates to a large split between the edge weights (green points) calculated for poorly sampled dyads that have (purple line) or have not (blue line) ever been observed grouping together. We see a very strong effect of dyad sighting count on the edge weight for dyads observed together on at least one occasion, until we reach around 12 sightings per dyad.

Given this, the standard next step with the SRI would be to set a threshold for the minimum number of sightings per node required to be included in the analysis. If I set this threshold to five sightings per node, the proportion of dyads with an SRI score of zero shifts down to 46.13%, and all dyads scoring a 100% association rate are removed. A threshold of 10 sightings per individual drops the 0% association rate down to 26.25%, showing high instability in the SRI outputs. This is highlighted by Fig 4b, which shows the association between the total number of observations per dyad, and the calculated edge weight for that dyad, stemming from the limited number of possible values that the SRI can take with low observation counts. The overall results would strongly depend on the threshold value I choose, which, as previously stated, is an arbitrary choice.

I could potentially use Fig 4b to determine a less arbitrary inclusion threshold by selecting the point at which the patterns in the edge weights weaken. However, this example shows that this is somewhere between 10 and 20 sightings per dyad. This would require removing at least all individuals with fewer than 10 observations. In this case, that would take the total sample size down from 213 to just 74 elephants. To remove 65% of the sample could severely bias the results if the remaining portion is not entirely representative of the total population. Therefore, I cannot rely on objective means to determine the threshold level.

2.5.2 Bayesian model with a single-step prior

When I use the BISoN framework with a single-step prior, there only appears to be a limited effect of prior shape on the posterior distribution, but the inclusion of zero as a possible edge value is very important. When using a fully flat or highly right-skewed prior, in which zero is a possible option, I obtain very similar posterior distributions (Fig 5a and 5c), whereas for a normal prior peaking at 0.5 for which extreme edge weights are unlikely (and actual values of 0 and 1 are impossible) the model produces an overall much broader and less skewed posterior (Fig 5b).

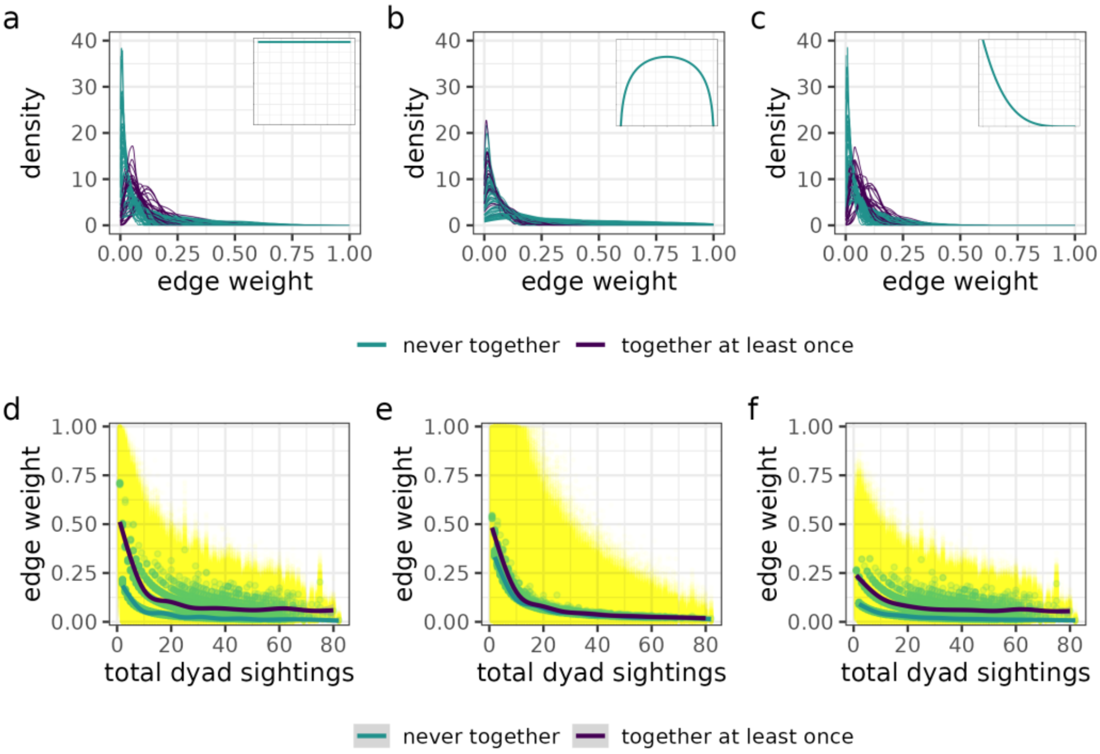


Figure 5: Edge weights for MOTNP elephants using BISoN models with single-step priors. Results using BISoN with uniform (left), default (middle) and right-skewed (right) priors (insets in top row show the respective prior for the column). a-c) The top row shows the posterior distribution for 100 randomly sampled dyads, with green curves indicating pairs that have never been observed in the same group and purple curves showing dyads that were observed in the same group on at least one occasion. The right-skewed and uniform priors produce posterior distributions that initially appear very similar because they still allow an edge weight of zero to be a plausible draw, whereas the default prior draws all values together. d-f) The bottom row shows the effect of total sighting count per dyad on their median (green points) and full (yellow points) posterior distribution. The blue line indicates dyads never observed together, while the purple line shows dyads observed together at least once. As the prior becomes increasingly right skewed, the effect of sighting counts on median edge weight declines.

I still have the situation in which there is a negative correlation between mean edge weight and total observations per dyad at low sighting counts, especially when using very broad priors, but now I have a calculated uncertainty around the mean. Looking at Figs 5d-f, we can see that poorly sampled dyads appear to show higher edge weights than well-sampled ones — an effect also observed in social network data for rhesus macaques (*Macaca mulatta*; Lauren Brent, personal communication) and white rhinoceros (*Ceratotherium simum*; Damaris Riedner and Josefine Bohr Brask, personal communication). Again, this is most severe for the logit normal prior, which draws all of the values towards the middle instead of creating variation between dyads. The effect is also stronger for the flat prior than for the right-skewed, for which the trend is substantially reduced because those dyads with the fewest sightings do not have sufficient data to discredit high edge weight model draws, so the posterior is very wide with high median values. Similar reasoning also explains the differences between BISoN with a flat prior and the SRI: with the SRI, low sighting counts largely score exactly zero, whereas with BISoN low sighting counts are given a very wide posterior (shown in yellow) so their median (green) is substantially above zero.

Based on these graphs, the best solution would appear to be to use BISoN with a strongly right-skewed prior, which can model the edge weights without creating strong patterns of social association based on data quality. However, this prior may not allow sufficient movement towards a higher edge value for dyads showing a strong social bond. Therefore, I need a prior that better reflects the underlying social process, such that it allows for some dyads to attain higher edge weights, but without increasing the prior average and causing poorly sampled dyads to consistently obtain a higher edge weight than well-sampled ones. Our modification to BISoN to use a prior that reflects the two-step underlying social process facilitates edge weight estimation in a manner robust to zero inflation and which allows stronger edges to be estimated.

2.5.3 Bayesian model with a two-step prior

When using the two-step prior, the posterior distributions of the edge weights (Fig 6a) initially appear very similar to those with single-step priors, though with greater confidence in some of the weakest edges, as I would expect. The median edge weight is associated much more weakly with the total number of sightings than with the uniform or symmetrical single-step priors (Fig 6b), even at low dyad sighting counts. While the shape of the curve for pairs seen grouping together is very similar to the single-step right-skewed prior, the overall effect of low sighting count has been removed by the model's increased ability to obtain median estimates very close to zero. I now have edge estimates that are more reliable than the previous BISoN models, as they use a prior that allows the modelling of zero-inflation.

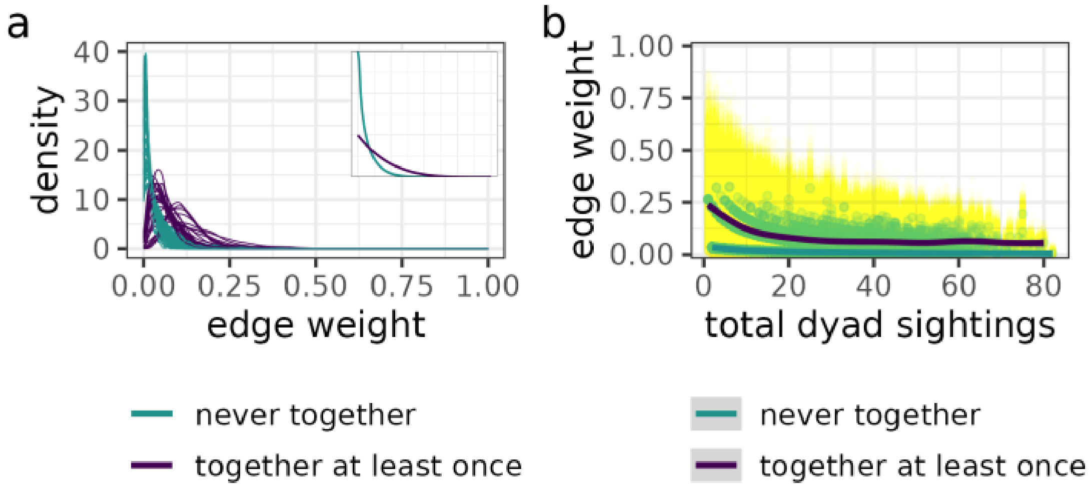


Figure 6: Edge weights for MOTNP elephants using a BISoN model with a conditional prior. a) posterior density lines for 100 randomly selected dyads (blue indicates density lines drawn for pairs never observed in the same group, purple for those seen together on at least one occasion); and b) edge weight as a response to number of sightings per dyad (full posterior distribution in yellow, median per dyad in green). While some effect of sighting count on the median edge weight for individual dyads remains, the impact is much reduced compared with the previous BISoN plots, and it lacks the values of 100% association observed with the SRI.

2.5.4 Using downstream network measures to assess edge weight quality

In general, we should be able to see directly in the edge weight values if there is a problem in the estimation method. Sometimes however, the impacts of the method are masked until subsequent analyses of the outputs. For example, in an analysis to identify the effects of individual trait values on network centrality, we may find that the centrality values contain spurious patterns, such as in the number of sightings or number of different partners that an individual is observed with compared to network centrality. Here, I will show that using an inappropriate single-step prior for edge weight can severely impact downstream analyses of network structure. I explore this using eigenvector centrality (Bonacich, 1972b), a measure of how connected an individual is to other well-connected individuals, because it is commonly used and is the centrality measure most robust to causal analysis (Dablander and Hinne, 2019). As with the edge weights, I can plot measures of centrality calculated per model against a) the number of other individuals in the population with which they were never observed associating, and b) their individual sighting count, and look for any unexpected trends that may indicate problems with the outputs.

When I plot the SRI-based eigenvector data against the number of non-associated elephants, there is a negative correlation (Fig 7a), exactly as expected. If, however, I compare the SRI-based centrality to the number of sightings per individual, we see a positive correlation for poorly sampled dyads (Fig 7b), which indicates that there is a problem with the estimation. This relationship is created by the extreme edge values caused by limited numbers of samples, especially for elephants observed fewer than 10 times. This could be used as an objective method of determining an inclusion threshold, but as before, this would require the discarding of more than half the data. I obtain similar trends when calculating the edge weight using a zero-inflated mixture model (Appendix A1: Fig A29).

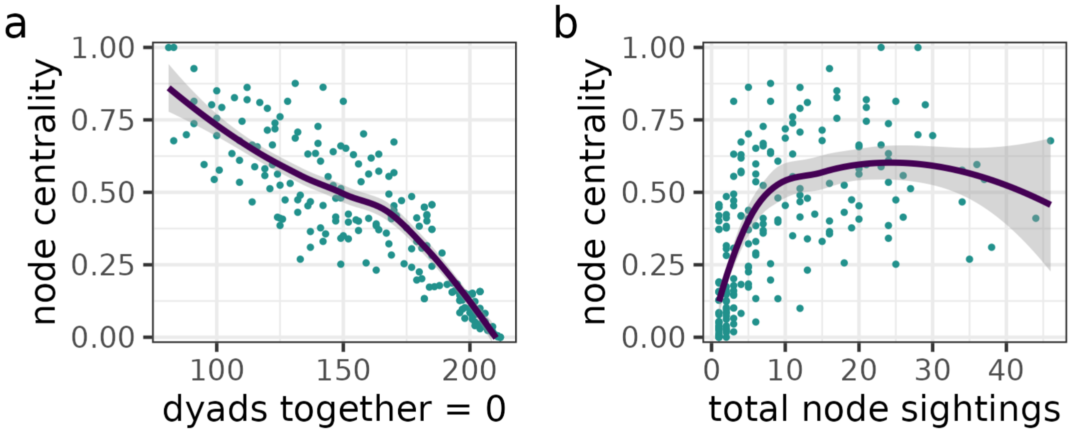


Figure 7: Eigenvector centrality estimates based on the SRI edge weight calculations. a) There is a negative relationship between SRI-based centrality and the total number of potential partners with whom a focal was never observed associating, which is as expected. However, b) indicates an issue with the SRI-based centrality in that there is a strongly positive effect of the number of observations per individual on their social position at low observation counts.

The eigenvector centrality plots based on the single-step BISoN models look very different to those from the SRI. Startlingly, there is an apparent reversal of the effect of the number of non-associated individuals in the population, such that elephants observed with the most partners receive the lowest centrality scores, while those observed with the fewest partners receive the highest (Fig 8a-c). This is, of course, nonsense. Eigenvector centrality as a measure combines the number of association partners an individual has with the number of association partners their partners have. The most central elephants therefore cannot be those with the fewest association partners. The edge weight estimation process must have an underlying error to create this trend.

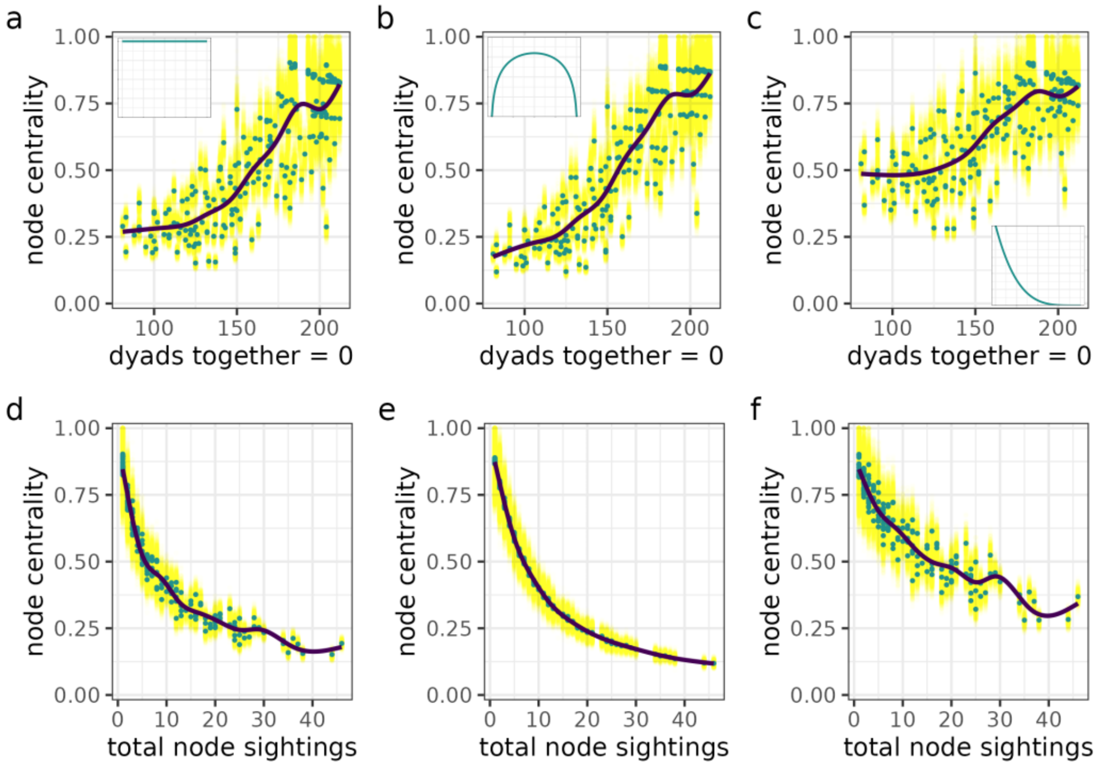


Figure 8: Eigenvector centrality estimates based on BISoN edge weight models with single-step priors. Priors per column are shown as insets on the top row: left to right uniform, default and right-skewed. In all graphs, yellow points indicate the uncertainty around the median, displayed in blue. a-c) The top row indicates the impact of number of dyad partners with whom an individual was never observed associating, where we see a spurious positive effect. The more right-skewed prior suffers more weakly from this than the uniform-based or default-based centrality, but still sufficiently to create serious cause for concern. There is no biologically or statistically meaningful explanation for this to be a correct trend. The pattern is explained by d-f) in which the elephants with the most observations occupy the social positions of lowest centrality.

This seemingly impossible pattern occurs because of an underlying trend in the number of observations per elephant (Fig 8d-f). Individuals with fewer overall observations contribute fewer sightings to dyad observations. When the edge weight prior is designed for dense networks, the posterior for most dyads is shifted closer to zero from the prior. Since the data for poorly sampled dyads are less influential on the distance the posterior can move, dyads with fewer observations consistently appear to have a stronger edge weight than well-sampled dyads. This effect is exaggerated when translated through to individual effects, and poorly sampled individuals end up in a higher proportion of poorly sampled dyads: individuals observed only rarely have the strongest average edge weights and, therefore, the highest eigenvector centrality.

Finally, we can now consider eigenvector centrality calculated from the edge weights produced using BISoN with a two-step prior and see that this model successfully avoids all downfalls from the other methods. Changing to a conditional prior has successfully reversed the spurious correlation between number of associates and node centrality (Fig 9a) by removing the effect of sighting count on eigenvector (Fig 9b). I have avoided creating estimates biased by the data quality, so any subsequent analyses using these data will be more reliable than those calculated using an improper prior, while also avoiding the need to remove poorly sampled dyads as I would have to do with the SRI.

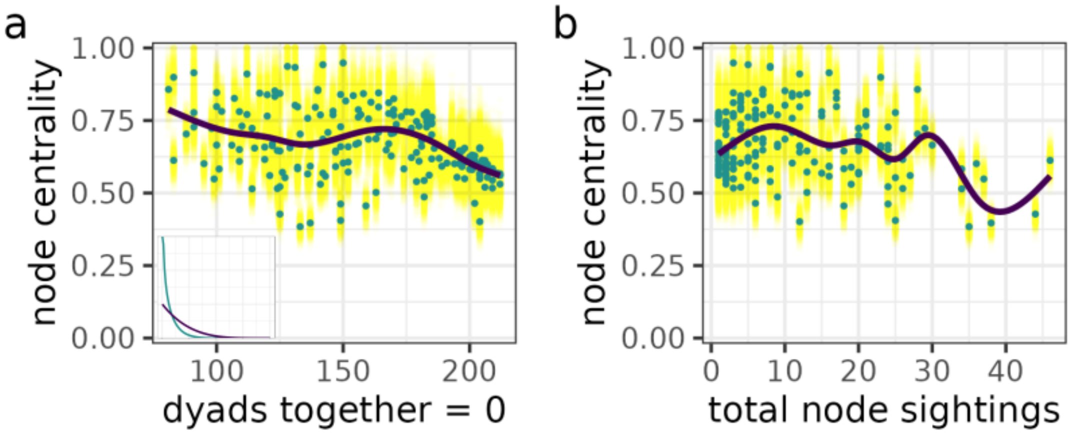


Figure 9: Eigenvector centrality estimates based on BISoN edge weight model with a two-step prior. a) Using the modified prior (inset), to reflect a two-step social process, I have successfully restored the negative trend in node centrality such that those seen with the most different dyad partners on average have the highest centrality, and those with the fewest have the lowest. b) Individual sighting count now has extremely limited effect on eigenvector centrality.

This quick sanity check of the eigenvector against the number of associates can instantly highlight if there is a problem with the edge weights, and show how sighting count could affect centrality. Our modification does not entirely eliminate this, and care should be taken to look for any anomalies. For example, in the MOTNP data, there is a single sighting where 89 elephants crossed the river and came up into the surrounding mopane forest together, of which 31 were males with known identities. For two males, this was their only observation. Therefore, these two individuals were "always" seen with one another and are in the "seen grouping together at least once" group for 30 dyad pairs. This means that, despite having very wide uncertainty margins for all dyads due to low total counts, they will still have an above-average median edge weight due to the nature of their single observation. When carried forward to a centrality analysis, these elephants will display a slightly elevated eigenvector centrality. Using the modified BISoN framework means this elevation is much lower than when using an unconditional prior or the SRI, and the number of individuals for which this could be an issue is reduced, limiting the impact on the regression. However, we still need to be aware of the potential for data artefacts that an occurrence such as this may leave. It is worth noting that while none of these methods is perfect, by using a method that incorporates current knowledge, quantifies uncertainty, and does not induce issues in downstream analytical data frames, we can rest assured that we are using the best possible option.

2.6 Discussion

I have shown that current animal social network analysis methods do not cope well with sparse network data. Frequentist measures such as the SRI suffer from an innate and unavoidable reliance on a flat prior, which overestimates the confidence that can be placed on extreme edge weight values. Combine this prior with an inability to incorporate uncertainty, and researchers must rely on setting arbitrary inclusion thresholds when analysing poorly sampled dyads, leading to data loss and potentially biased results. While Bayesian models can account for these problems in dense networks, they can still produce edge weights overly influenced by the frequency of sightings per dyad when inappropriate priors are applied to sparse networks. By modifying the BISoN framework to use a conditional prior, reflecting a two-step underlying social process, I can create a model where the edge weights are more reliable than those from the SRI, a zero-inflated mixture model, or an uninformed Bayesian model. As such, they are no longer overly dependent on data quality, which is commonly poor in animal social network studies.

When checking the models, I used several diagnostics to compare output quality and determine if the BISoN modification improved the current methods. The first question is whether a result fits with what is known of the population: the SRI produces far too many dyads with zero probability of ever associating, even when I set a high inclusion threshold. At just 66 km^2 (Youldon *et al.*, 2017), the MOTNP is not sufficiently large to preclude the interaction of elephants by simply never meeting, with a bull easily able to cross it in a single day. It is, therefore, extremely unlikely that this many dyads are truly never together, as there would not be enough space for them all to move without encountering other elephants. This allows us to make two informed assumptions: i) the proportion of zeros produced by the SRI is overinflated; and ii) that well-sampled dyads that are never recorded associating have elected not to do so, rather than happening to never encounter one another. When using BISoN, the conditional prior can help to alleviate the effect of sighting count on median edge weight by using the broader prior with a higher average only when I have evidence that the dyad has elected to sometimes associate. While this solution does not entirely remove the impact of limited sightings on edge weight, it does minimise it compared to a single-step prior.

At first glance at the edge weights alone, it seems that the conditional prior is not particularly advantageous over the right-skewed single-step prior: the basic outputs for the edge weight look fairly similar. However, I have now modelled the zero-inflation, which, while it appears to have only had a limited effect on the edge weights themselves, has a very noticeable and important impact on the subsequent analyses. The node centrality values produced can act as a suitable sanity check. While there appears to be little difference between the right-skewed BISoN outputs and the two-step BISoN outputs when I consider only the edge weights, the eigenvector centrality from a single-step prior in a sparse network creates an impossible situation in which individuals with more partners receive a lower centrality score. This trend is corrected by the use of a two-step prior. Such checks can be used to ensure the outputs make sense in downstream analyses.

Selecting the two distributions remains important for successful edge weight estimation when applying a two-step prior to a sparse network model. Making the zero-centred prior too strong will not allow enough variation when data are limited, but if too weak some of the possible edge weights may still present as too high and create trends in edge weight and centrality based on sighting counts. Similarly, if the probability mass for the non-zero prior is not shifted far enough from zero, any stronger relationships will be missed; shift it too much, and the same trends of increased edge weight with reduced sightings will be observed within the group who have been observed together. In this instance, I have opted for a large overlap between the priors such that dyads only seen once or twice will receive relatively similar posterior distributions regardless of which prior they are assigned to. By giving both priors a peak at zero, a dyad observed just once but who were together at that time will still have a low average edge weight (though the zero-peak is always immediately overcome by the data), matching the assumptions of a sparse network. This particular conditional prior is the one that works for this specific elephant population and is not a silver bullet prior that will work for all network analyses.

Every author should identify their own priors to create a set that works for their own population, which does not have to require that both priors peak at zero: unlike with the male elephants in this example, a network can be sparse but still contain some strong associations, in which case an upper prior that allows higher edge weights may be preferable. For example, if I were to repeat this analysis with the female elephants of MOTNP, I would expect a more bimodal distribution in the output because of the fission-fusion structure of female elephant society (Douglas-Hamilton, 1972; Moss and Poole, 1983; Wittemyer *et al.*, 2005). In this case, I could shift my non-zero prior to be more distinct from the lower, producing a bimodal distribution of edge weights, indicating strong social bonds within certain dyads. It could even be taken a step further to add more prior distributions as necessary. Again, using the example of the female elephants, I may, in this scenario, want the prior to reflect a three-step social process: a zero-centred prior for those never seen in the same social group, a right-skewed or more central prior for those who have been seen grouping together but who are unrelated; and a left-skewed prior for related females.

Multilevel community structures in which kinship groups fall within subgroups, which themselves join together to form larger association groups are common in animal societies. This method could be easily expanded to allow for the use of different priors depending on which level of association a dyad is expected to fall into.

It should be noted that the assessment of the edge weight is rarely the end of the analysis. Generally, we calculate the edge weights so that we can later assess trends in node-, dyad- or network-level characteristics. In Chapter 3, I will be using this method to calculate the edge weights for a second population of male elephants, before performing a regression model on node centrality. In such a study, the edge weight calculation only creates the data ready for a future regression model. There is no issue with checking the edge weights produced — just as we would check for errors in any other raw data — and running the model again using an improved prior if there is a problem. If edge weight outputs are dependent on the dyad sighting count, or there are issues with downstream calculations such as the centrality, there is no issue with adjusting the prior, so long as it still reflects our original understanding of the population.

2.7 Conclusion

The shape of the prior is, as with all analyses, the key to estimating edge weight, and using a prior structure that reflects the underlying social process is especially important for sparse networks, though the concept applies to dense networks too. With a frequentist model, this means considering the implications of a flat prior and including in the discussion any impacts this may have on the results. For a Bayesian model, it means tailoring the prior to the individual situation rather than using the broad default priors supplied by statistical packages, which will usually allow too much probability density over highly improbable edge weight values. In the case of sparse networks, whether the model is Bayesian or frequentist, we need to model the zero-inflation induced by the first step of the underlying social process. While a zero-inflated mixture model can do this better than the SRI, I still recommend that a Bayesian model with a conditional prior is a better option. This means allowing edge weights to sample down to zero using a lower prior and the possibility for stronger relationships with an upper prior. When investigating denser networks, the prior distributions may differ, but we can still consider the underlying social process as containing more than one step, even if the reduced proportion of zero relationships masks the effect. We can therefore use a conditional prior in a Bayesian framework to identify greater nuance in social network data, for networks of any density.

Chapter 3

The effect of age on male African savannah elephant social structure

Abstract

Animal social networks are shaped by associations and interactions arising from individual needs to access mates, resources, or social learning opportunities. Specific association partners may offer individuals competitive benefits, such as fighting abilities, learning opportunities, or pathogenic immunity. Male African savannah elephants (*Loxodonta africana*) have received limited study into their social relationships, and the few available studies have used data that differ in sampling effort. Here, I use the edge weight model from Chapter 2 to calculate male elephant social networks from observations from Zambia (213 males in 504 days) and Kenya (690 in 49 years), and assess how male age affects eigenvector centrality. I analysed the Zambian population as a single model, while the Kenyan data I split into two separate models, aggregating the data into 36 short (similar length to Zambian) or seven long time windows. I questioned: i) how male mortality changes with age; ii) the strength of male social bonds, iii) the degree of social differentiation among male bonds; iv) how male network centrality changes with age, and v) how these trends may differ between populations and observation periods.

Male mortality increased with age, but with a slightly elevated risk during transition to independence. Male relationships were extremely weak, with median edge weight ranging from 0.011-0.032 for short time windows and 0.008-0.022 for long time windows, similar to previous studies. I found no evidence for an effect of male age on eigenvector centrality, possibly due to shifting time and energy requirements surrounding musth. These results imply that social information could spread rapidly through the network, but that social learning is not a primary cause of bull social structure. Future interventions aimed at improving human-elephant coexistence should move towards deterrent strategies rather than elephant exclusion, using social learning to discourage approaching human settlements.

3.1 Introduction

Social interactions and associations can impact an individual's access to resources (Markham and Gesquiere, 2017, e.g., O'Connell-Rodwell *et al.*, 2011; Chakrabarti and Jhala, 2017), mating opportunities (Díaz-Muñoz *et al.*, 2014, e.g., Wrege and Emlen, 1994; Chakrabarti and Jhala, 2017; Connor *et al.*, 2022), and disease susceptibility (Hamede *et al.*, 2009; Archie and Tung, 2015; Ezenwa *et al.*, 2016; Silk *et al.*, 2017; Sarkar *et al.*, 2020). Individual choices can have subsequent impacts on population social network structure and social differentiation (in which certain social partners are preferred over others), for example by determining how closed a group may be to potential new members (Dunbar, 2018), the maximum size of the social group (Shizuka and Johnson, 2020), the likelihood of group fission or collective movement (Sueur *et al.*, 2010; King *et al.*, 2011a; Papageorgiou *et al.*, 2019), or the degree to which offspring follow their parents' social preferences (Ilany and Akçay, 2016). We can use observations of population social structure to assess the reasons why individuals aggregate, and the potential benefits they may receive from doing so.

Interactions can also offer social learning opportunities (Heyes, 1994; Laland *et al.*, 1996; Gariépy *et al.*, 2014; Aplin, 2016). By associating and interacting with individuals with different skills or knowledge than themselves, animals can obtain new information about the location of resources, for example, the honeybee waggle dance (von Frisch, 1946; Leadbeater and Chittka, 2007), or corvids following successful foragers from the roost (Sonerud *et al.*, 2001). Social learning also facilitates the development of novel behaviours via imitation (Thorndike, 1898; Galef, 1988; Laland, 2004; Gariépy *et al.*, 2014), emulation (Tomasello *et al.*, 1987) or social facilitation (Tolman, 1964; Clayton, 1978; Dindo *et al.*, 2009; Rørvang *et al.*, 2018). In some cases, young individuals may actively seek out older role models (e.g., orangutan peering behaviour: Schuppli *et al.*, 2016; Mörchen *et al.*, 2023). Through social learning, behavioural changes can spread rapidly (Whitehead, 2010), potentially leading to improved survival (Brown and Laland, 2001) but also causing potential problems. For example, barriers erected to reduce wildlife attacks on livestock or crops swiftly become obsolete when animals learn to circumvent them (Kioko *et al.*, 2008), which is accelerated by social learning. To recognise the pathways through which knowledge, behaviour and disease may spread, we must first consider population social structure and identify the interaction patterns facilitating social learning.

One species for which social learning is known to be important is the African savannah elephant (*Loxodonta africana*): a highly social species threatened with extinction due to a combination of habitat loss, ivory poaching, and negative interactions with local communities (Douglas-Hamilton, 1987; Nellemann *et al.*, 2013; Chase *et al.*, 2016; Gobush *et al.*, 2022; and see Chapter 1). Social learning is vital in elephant behavioural development, while living within in their natal family unit (Lee and Moss, 1999; Pinter-Wollman *et al.*, 2009; Moss and Lee, 2011a; Garai *et al.*, 2023).

Young elephants begin life living with their mothers, in stable matrilineal herds, so are surrounded by their female relatives (Lee, 1987; Lee and Moss, 1986; Moss and Lee, 2011a). Female calves usually remain in the same herd for their whole life (Archie *et al.*, 2011; Moss and Lee, 2011b), so have consistent social partners from whom they are able to learn. They display complex social relationships categorised into different strengths of social bond, with those more closely related also spending more time together and interacting more (Archie *et al.*, 2006). The family unit therefore provides the most opportunities for social learning (McComb *et al.*, 2001), with the wider clan group available as role models when families join together (Moss and Lee, 2011a, 2011b).

Male elephants on the other hand, disperse and separate from their family once they reach adolescence (Lee *et al.*, 2011), losing their primary role models. It is expected that social learning continues post-dispersal (Evans and Harris, 2008), with males now learning from other males: for example, $<$25% of crop-foraging events include females (Hoare, 1999; Jackson *et al.*, 2008; Chiyo *et al.*, 2011; Von Gerhardt *et al.*, 2014; Smit *et al.*, 2019) so most bulls are likely to learn to approach farms from other males (Chiyo *et al.*, 2012). Similarly, young male elephants isolated from older males when they enter musth for the first time become highly aggressive, and may attack and kill other animals, but this behaviour is unknown in the presence of older bulls (Slotow and Dyk, 2001; Slotow *et al.*, 2000, 2001). There is also some evidence for post-dispersal social facilitation of reproductive behaviours in male Asian elephants (*Elephas maximus*) (Rees, 2004), which may also occur in African elephants. However, this evidence is largely anecdotal, and cannot be generalised across populations, because we lack sufficient information about male associations. Social learning, and through it social structure, could therefore have important implications for elephant conservation and human-elephant coexistence.

A male elephant's transition to independence from their natal herd usually takes several months (Lee, 1987; Lee and Moss, 1986; Moss and Lee, 2011a), during which time they will increasingly associate with other bulls. Once separated, male elephants spend their lives associating with other males, with unrelated female herds when looking to mate, or alone (Lee *et al.*, 2011). Younger males are generally less likely to be observed alone than older bulls (Lee *et al.*, 2011; Allen *et al.*, 2020). Without the kin-relationships seen in female herds, male groups are far more unstable (Chiyo *et al.*, 2011), and group membership is highly dynamic (Goldenberg *et al.*, 2014; Murphy *et al.*, 2020).

Likely due to the difficulties of tracking an individual elephant over the full range that a male elephant may roam (Evans, 2006; Roux and Bernard, 2009), and the fact that females are often the focus of research in ecology as the population-limiting sex (Nussey *et al.*, 2013; Moatt *et al.*, 2016; Archer *et al.*, 2022), bulls have received limited study of their social structure. Their potential capacity to form long-term but weak (and therefore difficult to observe) social bonds by frequently moving between social groups, means that studies of elephants need to collect data for a long time before drawing conclusions. Furthermore, to investigate how social behaviour may change over the lifespan of an individual, it is helpful to know how long male elephants are likely to survive. Estimations of average life expectancy for wild bulls are generally quite low, ranging from 18.9 to 24 years (Moss, 2001; Wittemyer *et al.*, 2013), but individuals can live into their 60s (Moss, 2001). Average life expectancy may potentially be biased toward lower values because a male unobserved for a long time is often classed as dead when it could have instead moved to another area (Moss, 2001), but based on age structure we can be confident that they are shorter-lived than females. Understanding the risks of male mortality at different life stages could help explain age-based trends in social structure, including links between individual age and social status (with implications for social influence on others, or access to social resources including information or emotional support), and could potentially be used in future conservation work to predict the rate of population expansion or decline (Martin, 1995; Wittemyer *et al.*, 2021). The long-term nature of male relationships and the possibility of changing social patterns over time have therefore not been thoroughly investigated because of the practical difficulties of doing so, but investigating both lifespan and sociality simultaneously could help to display how mortality risk may affect behaviour.

3.1 Introduction

With few investigations into male behaviour, it was assumed that male elephants do not form strong social bonds with one another (Perry, 1953; Croze, 1974) and the social associations they do form are lost when in the presence of females (Moss and Poole, 1983). Over the past 15 years, evidence from social network analyses has appeared to generally, but not entirely, support this (Chiyo *et al.*, 2011; Goldenberg *et al.*, 2014; Murphy *et al.*, 2020). In one study, male pairs spent an average of just 2.8% of their time together (averaged across all 1 081 potential dyads included in the study; Chiyo *et al.*, 2011, and see Chapter 2), and in another average time together was 5.8-7.9% (Murphy *et al.*, 2020) when considering only males observed at least five times. However, when considering all dyads, this study estimated association rates of 9.9-14.2% association (Murphy *et al.*, 2020), and a third study estimated 11.7% of their time with the same associate (Goldenberg *et al.*, 2014). Furthermore, when considering only dyads in the same sexual state, estimates for dyadic association have even been reported as high as 33% of their time with the same associate (Goldenberg *et al.*, 2014). These differences in social bonds may arise due to genuine differences between populations: for example, variation in resource availability may mean that one population spends less time than another foraging or travelling, so can allocate more time to socialising (Foster *et al.*, 2012). Alternatively, the differences may arise from artifacts of data collection and analysis, such as differences in sampling effort per node (individual): for example, Murphy *et al.* (2020) uses only elephants with at least 5 observations, whereas Goldenberg *et al.* (2014) exclude all elephants with fewer than 20 observations in a sexually inactive state. Low rates of individual recapture can bias estimates of dyadic (pairwise) association (as shown in Chapter 2), suggesting more extreme values of relationship strength than truly exist and potentially creating disagreement in the literature over male elephant association strengths. Even in the same area and following the same data collection protocols, individual re-sighting rates may be higher in some time periods than others, for example due to variation in vegetation density or water availability. We also expect to see greater numbers of repeated sightings when a population is observed over a longer time window. However, there is no defined or recommended minimum time period over which to study elephant behaviour, nor have many studies compared multiple time windows to one another (but see Murphy *et al.*, 2020). We therefore need to re-assess the strength of social bonds among male elephants, to see how much time bulls spend with any one particular associate.

Studies also show some differences in their results regarding the effect of male age distribution on social behaviour. Eigenvector centrality is a measure of how much influence an individual has on the social network (Bonacich, 1972b). Most studies aggregate all data to a single time frame, creating a snapshot image of the social network in that period. Generally, these studies indicate that older males are potentially more important to the social structure than younger bulls

(Croze, 1974; Chiyo *et al.*, 2011; Allen *et al.*, 2020), but Lee *et al.* (2011) found only limited effects of age on male elephant association patterns. In contrast, two studies compared individual behaviour over time, analysing longitudinal changes in individual social position. When comparing across multi-year periods, no evidence was found to support a relationship between age and eigenvector centrality, but older bulls were found to be more stable in their network position than younger ones (using strength as a measure of centrality; Murphy *et al.*, 2020). This implies that more experienced males display more consistent behavioural strategies, and a more developed character-type (O'Connell-Rodwell *et al.*, 2024a). However, when comparing between sexual states, younger individuals have been found to be more central than older bulls when sexually active, but not when inactive (Goldenberg *et al.*, 2014) because older males are more likely to tolerate the presence of young bulls than rivals around potentially receptive females (Evans and Harris, 2008). The mechanism by which male social influence is related to age is extremely important for elephant conservation, as a means to determine how vital old males may be to the population (Allen *et al.*, 2020).

It is similarly important to understand why these studies have produced differences in their estimations of both social bond strength and the effect of age on network centrality, because this may influence how we implement elephant conservation. Firstly, the differences could be explained by the sexual state of the elephants, with bulls in a sexual state displaying different priorities regarding their social behaviour (Goldenberg *et al.*, 2014). Alternatively, the differences could be caused by real differences between populations, as I previously mentioned. These are both genuine differences in behaviour. However, a third option is that the differences between populations could be created artificially by slight differences in data collection or statistical methods, or by the use of permutation analysis, which has since been shown to be incapable of identifying causal relationships (Franks *et al.*, 2021; Weiss *et al.*, 2021; Hart *et al.*, 2022b), producing high rates of false positives (Weiss *et al.*, 2021; Hart *et al.*, 2022b) and incorrect effect sizes, which in the extreme can display the wrong sign compared to the true effect (Franks *et al.*, 2021). To further understanding of male elephant social networks and establish whether the differences in results between previous studies are caused by true inter-population variation, we must compare the social structure of multiple populations by applying identical research methods to all data sets. The availability of improved methods (Hart *et al.*, 2022a, 2023, and see Chapter 2) and more powerful computing software also facilitate more reliable analysis. It would therefore be valuable for research and conservation to revisit questions of male elephant social structure.

In this chapter, I analyse the association patterns of male elephants from two independent populations, and the structure of their social networks, to answer the following questions: i) How does age affect male elephant mortality risk? ii) How strong are male elephant social bonds? iii) Do males show evidence of social differentiation or community structure, by showing preference for certain individuals over others? iv) Do older males hold positions of higher network centrality than younger males? Finally, v) How can the population studied and the duration of the observation period affect the results of questions ii-iv?

For question i, I hypothesise that mortality risk will be highest for the youngest and oldest males in the population, with low mortality rates during middle age. Specifically, in early post-transition to independence, there will be a short period during which mortality is elevated because males are moving through unfamiliar environments (Lee and Moss, 1999), and in later life they will show increasingly high mortality rates as they become involved in more fights with other males (Poole, 1987, 1989b) and their tusks become more valuable to poachers (Barnes and Kapela, 1991; Mondol *et al.*, 2014; Chiyo *et al.*, 2015).

Regarding questions ii and iii, I hypothesise that males will share predominantly weak bonds, because male elephant groups are known to be transient and fluid (Chiyo *et al.*, 2011, and see Chapter 2). However, I expect to see evidence for social differentiation, with social bonds between pairs of similarly-aged individuals stronger than the population average, caused by preferences for size-matched wrestling partners (Chiyo *et al.*, 2011), young males dispersing from their family units together (Kate Evans, personal communication; Caro and Collins, 1987), or a more general preference for familiar individuals (McComb *et al.*, 2000).

Social differentiation based on age-related preferences could create an effect of age on social network position. For question iv, considering the potential benefits that young males may receive from social learning, I hypothesise that younger males will preferentially follow older males, forming longer associations with old bulls and short associations with other young males. In this scenario, young males would benefit from the social learning opportunities presented by watching the behaviour of older bulls, while also play-sparring with many other young males. Older bulls would therefore hold the positions of highest centrality, because they form stronger average associations than young males that have only brief associations with one another. An alternative possibility is young males will form more stable groups that move together between individual older bulls. In this second scenario, younger males should be the more central to the network, because older males would have the more transient associations. While I therefore expect to see a positive effect of age on centrality, with the oldest males being the most central, there is also the possibility that young male groups could create a negative effect.

Finally, for question v, I hypothesise that male elephants will all display similar preferences, and therefore that there will be no difference in edge weights or age effects between populations. Substantial differences between populations would suggest that environmental effects (such as water and food availability, climate, or operational sex ratio) are important in the social structure, making the application of research outputs across different locations impractical. Similarly, there may be temporal variation within populations: differences between time windows would indicate a plastic social structure, dependent on environmental conditions or population size, while differences between results for the same time period but analysed over breaks of different duration would highlight instability in male relationships. I hypothesise that average social bonds will be weaker in longer time windows because larger population sizes promote higher rates of zero-inflation in social bond strength (edge weight), but with no difference in effect of age on network centrality.

3.2 Methods

3.2.1 Study areas

The data for this study were collected from two independent locations. The populations differ in both size and duration of observations, which will indicate any global and local patterns in male behaviour. Crop-foraging is a significant issue for human-elephant coexistence in both areas.

The first dataset comes from the Mosi-Oa-Tunya National Park (MOTNP) in Zambia, an area of 66 km^2 (17° 48.897'–17° 58.300' S and 25° 45.040'–25° 53.490' E; Youldon *et al.*, 2017) where elephants were observed from May 2016 to December 2017. The park is bordered by Livingstone town, Dambwa forest, and the Zambezi River. MOTNP is a heterogeneous environment including areas of mopane woodland, open grassland, and marshland and riparian habitat. It supports a seasonal population of 450-500 elephants during the dry months (approximately April to December), when it is accessible across the river from the Zambezi National Park in Zimbabwe, which supports the elephants year-round. MOTNP contains no predators, which may serve to make it more attractive to females with young calves.

The second dataset is much longer, with observations from September 1972 to December 2021. The Amboseli National Park (ANP) in Kenya is 392 km^2 in size (2° 32.282'-2° 44.001' S and 37° 4.615'-37° 24.486' E), dominated by savannah grassland habitats, with some areas of woodland and marsh, and is embedded within the 3 500 km^2 Amboseli ecosystem (Moss, 2001). The elephant population is free ranging within and outside of the protected area, and contains around 1 400 individuals (Archie *et al.*, 2007), of which there is an even mixture of males and females. There is a lot of variation in individual movement patterns, with some males choosing to spend the vast majority of their lives in ANP, while others may migrate away for many years at a time.

3.2.2 Data collection

Data for both populations were collected using the following approach: researchers would drive through the national parks, collecting data opportunistically whenever a group was encountered. A group was defined as any number of spatially aggregated individuals (within a radius of 100 m; Chiyo *et al.*, 2011) whose behaviour and/or movement direction were cohesive. Data recorded were the date, time, location, group size, and a breakdown of the age, sex and identities of the individuals present. Individuals were recognised based on unique natural marks and injuries on the ears, tusks (Figure 10), body and tail. Because this study focuses on adult male social structure, only elephants over the age of 10 years are included, because this is approximately the youngest age that males start the transition to independence (Lee *et al.*, 2011). Data for MOTNP were supplied by the African Lion and Environmental Research Trust (ALERT, UK charity commission number 1120572, Zambia charity registration number ORS/102/35/3583), and for ANP by the Amboseli Trust for Elephants (ATE, USA not-for-profit number 501c3). Graphs showing the number of elephants observed in each age category are displayed in Appendix A2.1: Figure A32.

For the MOTNP dataset, which was just 504 days long, the entire dataset was incorporated into a single model. In contrast, the ANP data set was much larger, so I split it into 36 time windows of 500 days each to match the duration of MOTNP when answering questions ii-v. This facilitates comparisons of network trends across populations and within the ANP population over time. It also prevents estimation of the association rate between individuals not alive in the population at the same time: I removed from each data subset any individual not observed or that died within that time window. However, considering the longevity of elephants and the potential that they may continually associate with the same individuals year on year, 500 days is arguably quite short for a social network analysis study. To test if the duration of observation period affects the results of a study such as this, I performed a second analysis for the ANP data using seven time windows of 2 571 days to compare to the short windows.

A total of 215 bulls over 10 years old were recorded in and around MOTNP in 481 observations over the two year study. Of these sightings, 84 were of lone males, 165 were of male only groups, 198 were of groups that contained a mixture of adult males and females, 29 were of family units with whom a male of dispersing age still travelled, and five were in unknown group types. Observations per male were strongly right skewed, with up to 46 sightings per male but a median of only five observations each. Similarly, sizes of groups that contained males could be extremely large, with maxima of 118 elephants in a mixed group and 24 in a male only group, but with median group sizes of just six and three elephants respectively. 65% of MOTNP sightings

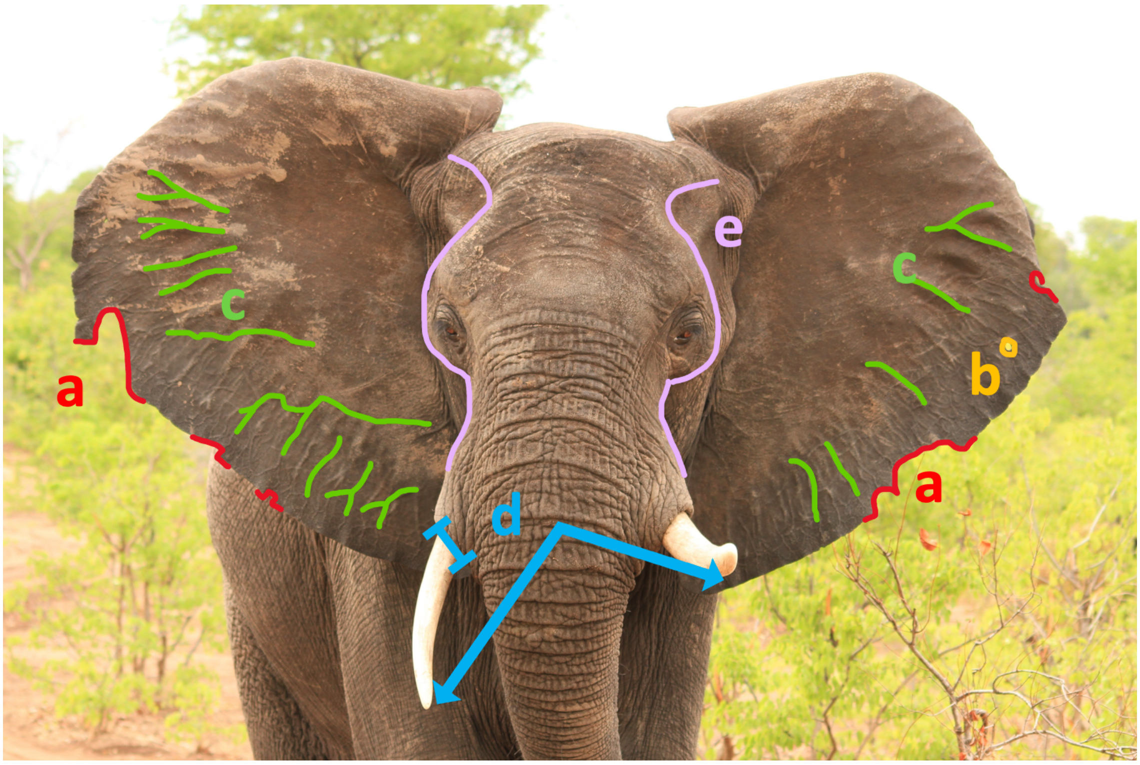


Figure 10: Identifying marks of a male elephant (ID number M40 from MOTNP). (a) notches and (b) holes in the ears develop when elephants tear their ears on trees, and can vary in shape, size, number and position. (c) Veins in the ears can sometimes be visible as well, acting like a fingerprint. (d) Tusk length, diameter, shape and configuration can also be used, along with the presence of any breaks, chips, cracks or grooves. The diameter of the tusks can also help to indicate age, with older males often having a thick tusk base. (e) Head shape is another indicator of male age: the oldest males develop a characterised "hourglass" shape, where it is very wide at the top of the head, the eyes, and the tusk base, but much narrower below the eyes and with large hollows in the forehead. At the timing of this photograph taken in 2016, M40 was classed as being 25-40 years old. This male was sighted 29 times throughout the study.

with males contained 10 elephants or fewer. Two elephants died during the observation period, reducing the total number included to 213, equating to a total of 22 578 potential dyads.

In ANP, 690 bulls were recorded independent of their family group in 24 386 sightings during the 49 years of observations. These sightings were relatively evenly split between male only and mixed groups, with 12 192 and 11 841 respectively (353 observations with unknown group composition). After removing individuals from each time frame that died within that window, and any elephants recorded associating with adult males but which were not yet 10 years old, the analysed dataset contained a total of 652 elephants in the short time windows, and 513 in the long windows. Elephants per window ranged from 29 to 215 (406 to 23 005 dyads), and from 86 to 243 (3 655 to 29 403 dyads), for short and long time windows respectively. In the short time windows, the distribution of sightings per elephant ranged from one to 70, with a median observation count varying from one to 27 between time windows. The longer observation period allowed for much higher numbers of repeat sightings, with a median of 11-82.5 per individual, and a maximum of 79-230 for a single elephant.

3.2.3 Age structure of male elephant populations

Age data from MOTNP are categorised based on estimating individual age from physical characteristics (Figure 10), such as body and tusk size, and head shape (Moss, 1996): $<$5 years old, 5-9 y, 10-14 y, 15-19 y, 20-25 y, 26-39 y, and $\geq$ 40 y). In contrast, ages for the ANP population are in years, with relatively high confidence in the birth dates, because the long-term nature of the ANP dataset means that the research team were able to track the family units and observe the arrival of all new offspring close to or after 1972.

To answer the first of my questions, I constructed a mortality curve using the ANP data to estimate the probability of survival to each year of life for a male elephant, assuming that ANP is a representative population. This analysis used all of the ANP data. To do this, I used the *BaSTA* package (Colchero *et al.*, 2012) in R to model the shape of the mortality and survival probability curves, using longitudinal mark and recapture observations of individual males throughout their lives (following the workflow described in Nielsen *et al.*, 2021). I expected that the probability of survival per year would decline through adult life, as larger tusks would make them more prominent poaching targets, and they become increasingly likely to engage in dangerous fights as they spend more time in musth (Poole, 1987, 1989b). I therefore used Weibull and Gompertz probability distributions, capable of modelling changing probabilities of mortality as an individual ages. I created models of ANP survival using both distributions to test which produced a better fit. I tested models with both a simple, unmodified shape, and a bathtub-shaped distribution. The bathtub shape allows for high death rate in early life but which drops rapidly at ages approaching maturity (Møltoft, 1983), so can model high rates of infant mortality. In this study, because I was only interested in adult social behaviour and therefore only included data for independent males, a bathtub curve instead indicates a high mortality rate during the period of transition to independence. I compared the four models (simple Weibull, simple Gompertz, bathtub Weibull, and bathtub Gompertz) using the deviance information criterion (DIC), and selected the one which best fit the data. The inclusion or not of a bathtub parameter in the best fitting model indicates if the transition period is a particularly dangerous time for young male elephants.

3.2.4 Dyad edge weight

To answer questions ii-v, I ran a social network analysis using the association data from ANP and MOTNP. Here I provide a brief overview only of the edge weight (strength of social connection, measured as the proportion of time a given pair of male elephants is seen together) estimation method (see previous chapter for full details). All edge weight estimation models were calculated following the Bayesian Inference of Social Networks (BISoN, as defined by Hart *et al.*, 2023) framework, using R (version 4.2.1) with RStudio (version 1.4.1717) as an interface for Stan (version 2.21.0), using a combination of *rstan* (version 2.21.2, Stan Development Team, 2023a), and *cmdstandr* (version 4.0.2, Gabry *et al.*, 2022).

I estimated dyadic edge weight using a BISoN model to fit a beta distribution that described the probability distribution for the proportion of time that each dyad (pair of elephants) spends together. I used input data of the number of times a dyad was observed in a group together and the total number of times that either node was observed. Because the output is a distribution of probable values, rather than a single point estimate, a wider distribution (and therefore a greater uncertainty) is produced for the pairs seen less frequently. These uncertainty values are then propagated downstream to the nodal regression model (see below) to quantify uncertainty in the nodal regression. Because the model is Bayesian, the edge weight prior can be tailored to a sparse network (see Chapter 2) since current studies of male social behaviour indicate low rates of male-male association (Chiyo *et al.*, 2011). I used a conditional prior in which the dyads that were never seen together received a more zero-inflated prior distribution than the dyads seen together on at least one occasion, as shown by Equation 3.1 (Chapter 2):

$$\begin{aligned} together_{ij} &\sim Binomial(sightings_{ij}, edgeweight_{ij}) \\ edgeweight_{ij} &\sim Beta(a, b) \end{aligned} \tag{3.1}$$

If $together_{ij} = 0$: $a = 0.7$ and $b = 10$

If $together_{ij} > 0$: $a = 1$ and $b = 5$

Where $together_{ij}$ is the number of times that dyad *ij* was observed in the same group, and $sightings_{ij}$ is the number of times they were observed in total, used to estimate $edge\ weight_{ij}$.

3.2.5 Nodal regression

I used Bayesian regression models to determine whether older males are more likely to hold positions of high network centrality than younger males, or vice versa. I used eigenvector centrality (Bonacich, 1972b) — calculated using the *igraph* package (Csárdi *et al.*, 2023) — as a response variable, because it is a measure of both direct and indirect social connectedness and has been shown to be the most robust for causal analysis (Dablander and Hinne, 2019). Eigenvector centrality indicates the level of influence that a node has on the network based on its connectivity to popular individuals: if older males act as sources of social information and young males do not display preferences for specific other youngsters, I expect to see old bulls as more influential within the network and therefore with a higher eigenvector centrality. A directed acyclic graph (DAG) showing the causal structure of the model is presented in Figure 11.

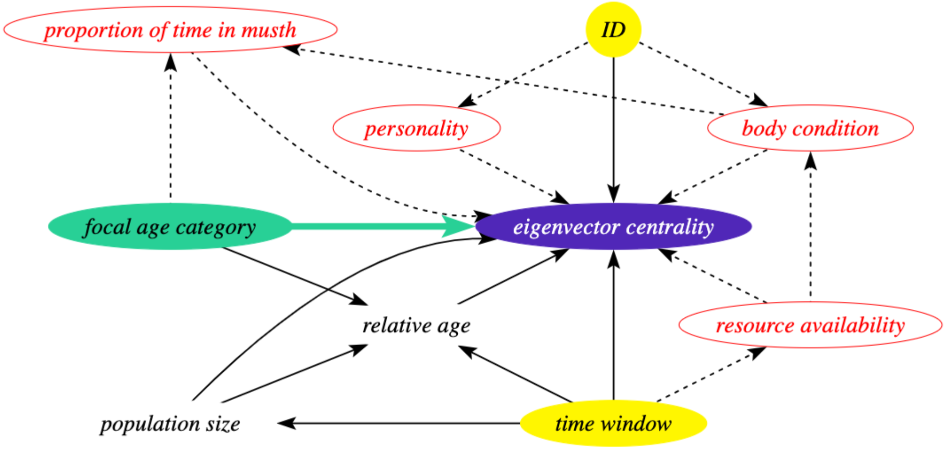


Figure 11: Directed acyclic graph showing the causal structure of the nodal regression. There are no open backdoor paths, and all causal variables are accounted for in the model structure. Focal age category, shown in green, is the explanatory variable, while eigenvector centrality in purple in the response. Random effects of time window and node ID are shown in yellow (ANP only). Red variables and dotted lines indicate unobserved variables and the paths through them.

For the explanatory variable, age, I used the recorded age category (category 1 = 10-14 yrs, 2 = 15-19 yrs, 3 = 20-25 yrs, 4 = 26-39 yrs, or 5 = over 40 yrs) for MOTNP, and the age in years at the start of each time window for ANP. Having two alternative data structures makes the results of the two populations impractical to compare quantitatively, but I will still describe any qualitative (dis)similarities that may arise. Despite testing the same hypothesis, the models for the different populations appear quite different in their codes, due to the structure of the data involved: MOTNP contains an ordered categorical predictor and is only a single time window, whereas ANP had a continuous predictor and required the inclusion of node-level and window-level random effects to account for the repeated measures throughout the observations. Model structure for MOTNP is shown in Equation 3.2 and ANP in Equation 3.3:

$$
\begin{aligned}
\mu_{EIGEN_i} &\sim MultivariateNormal(\theta_i, \eta_i) \\
\theta_i &= \alpha + \beta * \delta[1 : category_i] \\
\eta_i &= \Sigma_{EIGEN_i} + DiagonalMatrix(\sigma, N) \\
\alpha &\sim Normal(logit(0.05), 1) \\
\beta &\sim Normal(0, 2) \\
\delta &\sim Dirichlet(1, 1, 1, 1, 1) \\
\sigma &\sim Exponential(2)
\end{aligned}
\tag{3.2}
$$

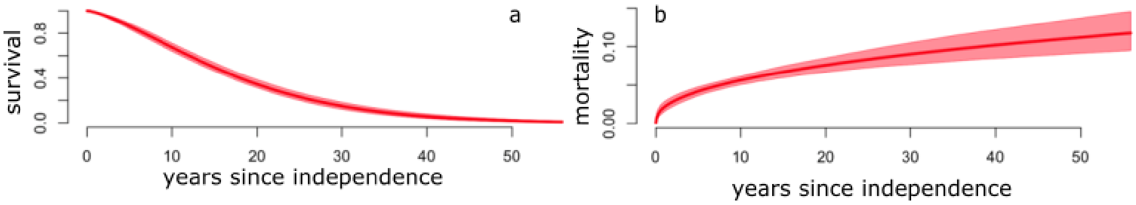
$$
\begin{aligned}
\mu_{EIGEN_i} &\sim MultivariateNormal(\theta_i, \eta_i) \\
\theta_i &= \alpha + \beta * years_i + W[window_i] + ID[node_i] \\
W &= w * \sigma_W \\
ID &= id * sigma_{ID} \\
\eta_i &= \sigma_{EIGEN_i} + DiagonalMatrix(\Sigma, N) \\
\alpha &\sim Normal(logit(0.05), 2) \\
\beta &\sim Normal(0, 0.8) \\
\sigma &\sim Exponential(2) \\
c(w, id) &\sim Normal(0, 1) \\
c(\sigma_W, \sigma_{ID}) &\sim Exponential(2)
\end{aligned}
\tag{3.3}
$$

Where μ_{EIGEN} and Σ_{EIGEN} are the mean and covariance of a multivariate normal approximation of the logit-transformed eigenvector centrality measures per elephant; θ is the linear model output indicating the impact of age on centrality, which is a categorical variable ($category$) for MOTNP and a continuous variable ($years$) for ANP; η is a covariance matrix; and N is the number of elephants present, either in the population for MOTNP, or in the time window for ANP. Parameters estimated within the MOTNP model were the intercept (α), slope of the effect of age on centrality (β), model standard deviation (σ), and a vector of effects per age category (δ). In ANP, $window$ and $node$ indicate the respective random effects, producing additional parameters for node (ID) and window (W) slopes. I used a separate likelihood per time window, but with global α, β and σ parameters. I confirmed that the priors were appropriate using a prior predictive check (Appendix A2.2).

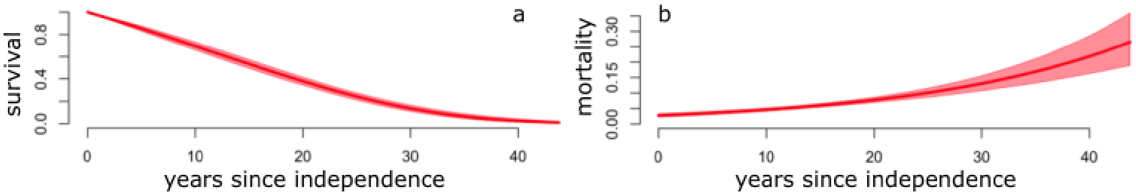
3.3 Results

3.3.1 Age structure of male elephant populations

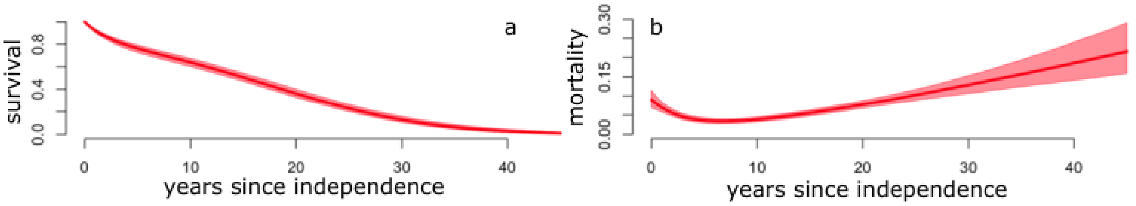
My first question asked how male age affects mortality risk throughout an individual's life, hypothesising that mortality risk would generally increase as males aged, except for during the youngest ages immediately post-transition to independence. All models of male elephant age structure looked reasonably similar, with the bathtub effect being very minimal (Figure 12). In all models, survival to 20 years post-independence (approximately 28-30 years old) is around 35-40%, and only ∼15% of individuals make it to 30 years post-independence. All mortality curves show an increasing probability of mortality with increasing age beyond the first five years post-independence, showing that older males are at greater risk of mortality. This can be expected in most populations due to common ageing effects such as reduced immunity or increased risk of injury during fights for mates, but could be especially severe in elephants because of their higher ivory value as they age.



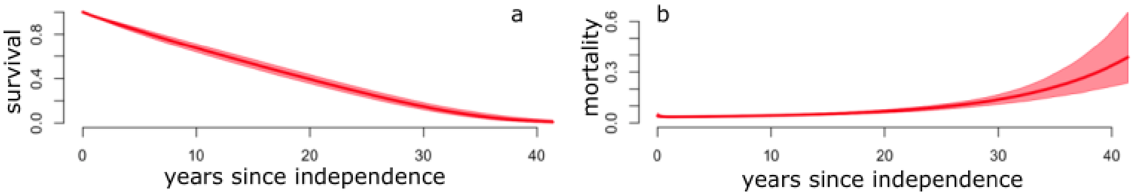
(i) simple Weibull: DIC = 9898.886



(ii) simple Gompertz: DIC = 9694.605



(iii) bathtub Weibull: DIC = 9721.131



(iv) bathtub Gompertz: DIC = 9601.075

Figure 12: Survival (a) and mortality (b) curves for ANP male elephants. Curves are based on the number of years since transitioning to independence, calculated using Weibull and Gompertz distributions, with a simple or bathtub shape. Survival curves indicate the probability that an elephant will survive to a particular age, given that they reached independence (age 0 on these graphs). In contrast, mortality curves document the probability of dying at a given age. DIC values are shown for each model, showing that the best fitting model is the Gompertz with bathtub shape (iv). Note that the axis scales vary between graphs.

Using DIC, I found the best fitting curve to be the Gompertz bathtub model (Figure 12iv), with the following parameters:

$$
\begin{aligned}
mortality &\sim GompertzBathtub(a_0, a_1, c, b_0, b_1) \\
a_0 &\sim Normal(-5.13, 0.720) \\
a_1 &\sim Normal(3.00, 0.105) \\
c &\sim Normal(0.0258, 0.00669) \\
b_0 &\sim Normal(-5.07, 0.567) \\
b_1 &\sim Normal(0.0948, 0.0178)
\end{aligned}
\tag{3.4}
$$

That the best fitting curve included a bathtub parameter indicates that the transition period is slightly more dangerous for young males than once they are older, but the effect is extremely small (Figure 12iv).

3.3.2 Dyad edge weight

My second and third questions asked about the strength of male elephant social bonds. I hypothesised that bonds would be predominantly weak but with some social differentiation, such that each elephant had one or two specific partners that they spent a lot of time with. Most relationships between males were indeed very weak, creating an overall right skew in the median estimates per dyad (Figure 13), but I found no evidence for social differentiation between potential partners, and no strong preferences among the elephants for having any one specific partner that they spent more time with. Note that to simplify reporting, the following summaries are computed from the median posterior estimates of each edge weight, ignoring the uncertainty estimated for each individual dyad, but I retain and propagate such through subsequent analysis. For MOTNP, median edge weight across all 22 578 dyads was 0.023 (mean ± standard deviation: 0.033 ± 0.033). Median edge weights for ANP in the short time windows ranged from 0.011 to 0.032 (0.026 ± 0.023), and from 0.008 to 0.022 (0.016 ± 0.014) for long time windows. For question v I hypothesised that the longer time windows would have weaker average social bonds compared to the shorter time windows. That the average ANP edges are weaker for the long time windows than the short, and with generally narrower probability distributions, indicates that I can be confident that the edges are genuinely weak in the short windows and not simply lacking data. Example network plots for each population and observation duration are shown in Figure 14, and a full set of all network plots can be found in Appendix A2.3.

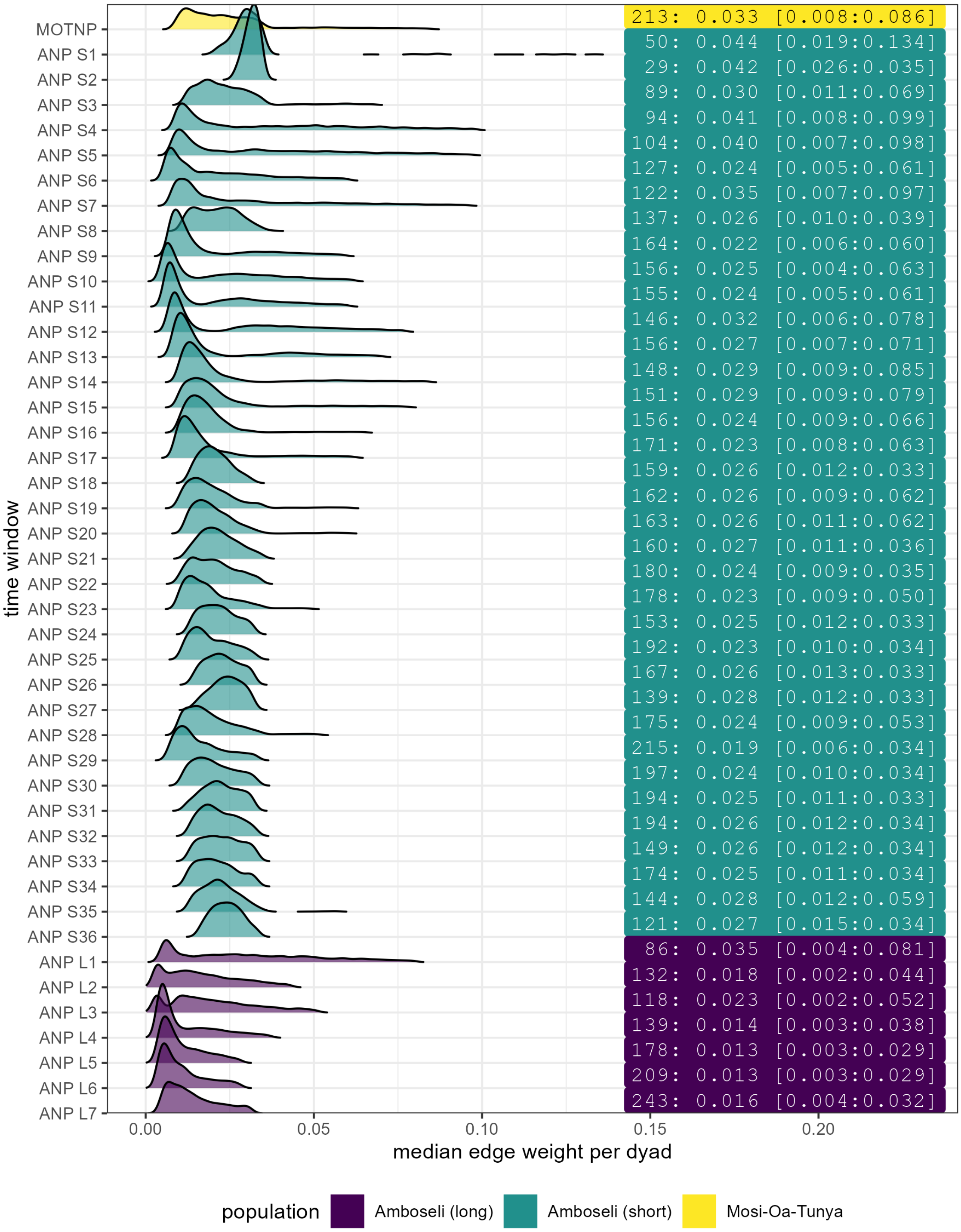
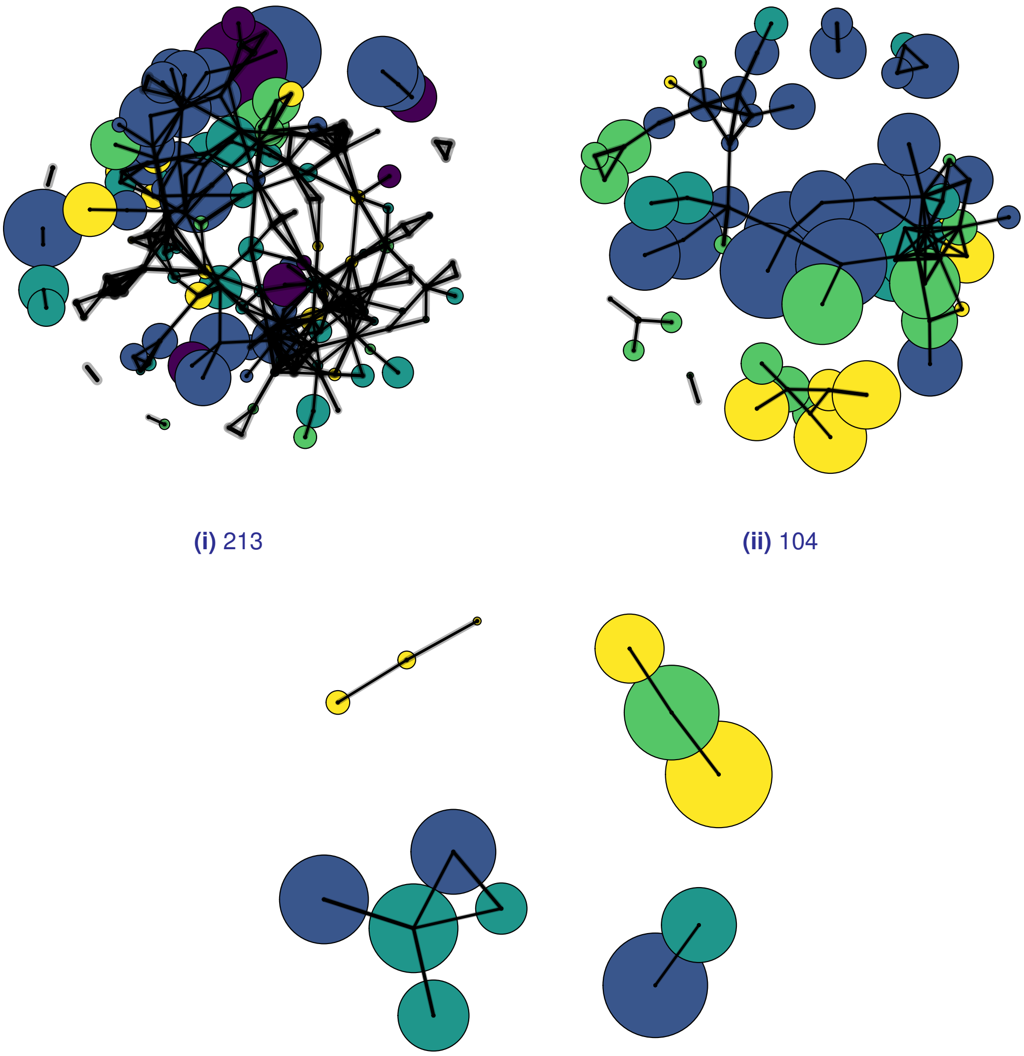


Figure 13: 95% distribution of dyad median edge weight estimates for each population time window. Colours differentiate network types: yellow is MOTNP, green is short time windows in ANP, and purple is long time windows in ANP. Values on the right show ”population size: mean [95% credible interval]”. Median edge weights per dyad are generally close to zero, with all curves peaking below 0.05.



(i) 213

(ii) 104

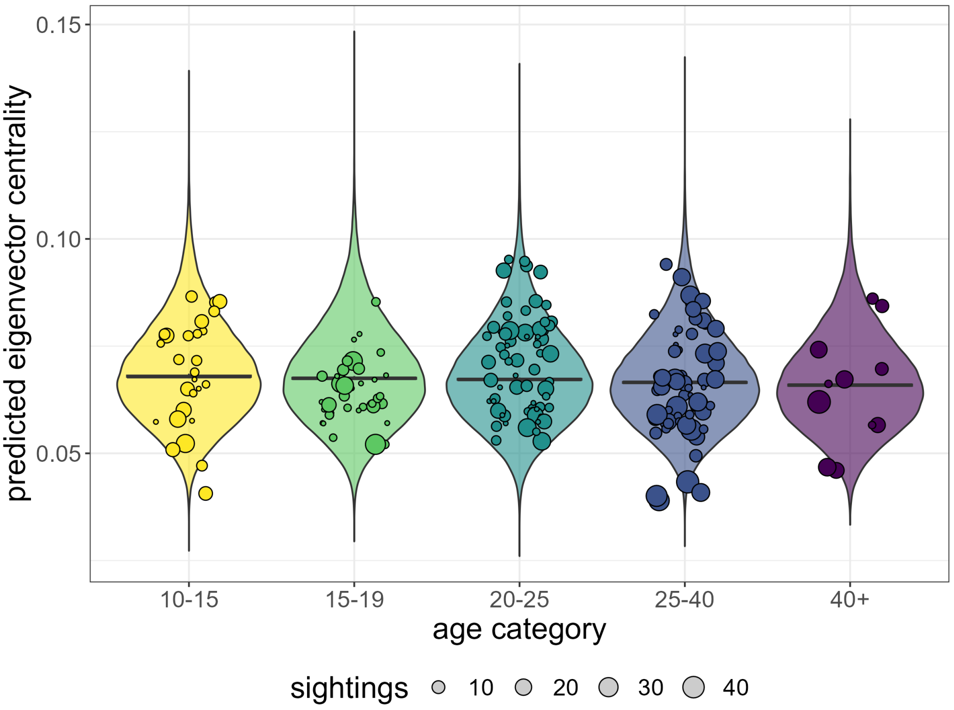
(iii) 86

Figure 14: Network plots based on edge weight estimations for a) MOTNP, b) the 5th 500-day time window for ANP, c) the 1st 2 571-day time window for ANP. Numbers beneath each plot indicate the total number of nodes in the time window. Circles indicate individual nodes within the network, with their size representing the number of times an individual was observed during the time window (not comparable between plots). Colours indicate the age category that an individual is estimated to be in: yellow nodes are 10-14 years old, green are 15-19, dark turquoise are 20-25, blue are 26-39, and purple nodes are $\geq$40 years old. Solid black lines between the nodes indicate median edge weights, while the wider grey lines indicate the uncertainty around these estimates. Note that the uncertainty is much wider when the nodes have only been observed rarely. Plot only shows social bonds $>$0.15, with no unconnected nodes, but all edges and nodes are included in downstream analyses.

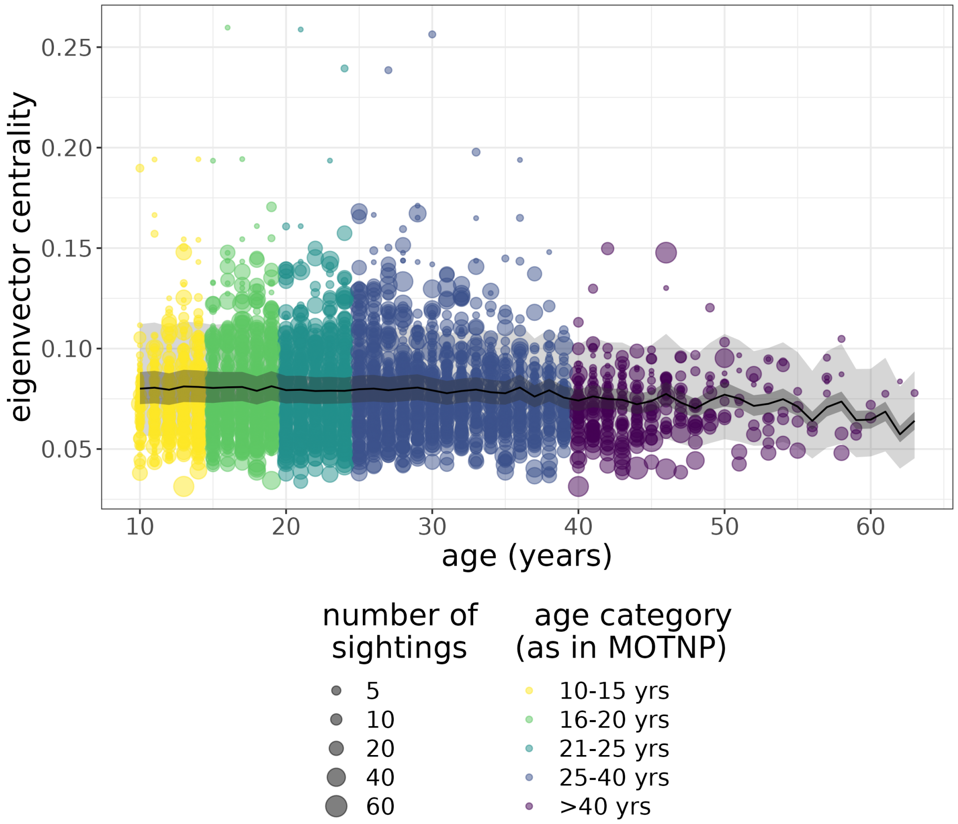
3.3.3 Nodal regression

My fourth question asked how age affected social network centrality based around the assumption that young males would follow older ones to obtain social learning opportunities. I had an overarching hypothesis that there would be an effect of age on centrality but alternative hypotheses about the direction of the effect depending on the movement of young males. However, the results of the nodal regression overall indicated that male age has little to no effect on eigenvector centrality. For the MOTNP population, the model showed no evidence for an effect of age on eigenvector centrality (Figure 15i), with very wide credible intervals of which approximately half the probability density was above or below zero: transitioning from 10-14 to 15-19 induced a difference of mean -0.0204, and 95% CI [-0.520:0.483], with 53% of the interval below zero; 15-19 to 20-25 = -0.00871 [-0.517:0.499], and 52% negative; 20-25 to 26-39 = -0.0114 [-0.513:0.493], and 52% negative; 26-39 to $\geq$40 = -0.000174 [-0.496:0.495], with 50% negative; and finally transitioning from the youngest to the oldest age category induced a difference of mean contrast of -0.00919 [-0.504:0.485] with 51% of the contrast distribution below zero.

Finally, question v asked about the effect of population and observation duration on the calculated social network. I hypothesised that the shorter and longer time windows would have a similar relationship between age and network centrality. For ANP, there is a qualitatively similar trend for both short (Figure 15ii) and long (Figure 15iii) time windows, with no overall effect of age on eigenvector centrality. For the short time windows, an increase of one year in age induced a -0.00263 ± 0.0271 [-0.0557:0.0504] change in eigenvector centrality, with 54% of the posterior distribution below zero; while for the long time windows, one year induced a 0.000515 ± 0.0671 [-0.131:0.132] change, with 50% of the posterior distribution below zero. Node ID had very little effect on eigenvector, with mean effects per node clustered around zero and large uncertainty spread to both positive and negative values for all individuals (Appendix A2.5: Figure A39). This was the case for both short and long time windows. Window ID did affect eigenvector centrality (Appendix A2.4: Figures A37 and A38), induced by the differences in network size among time windows (Appendix A2.5: Figure A40).

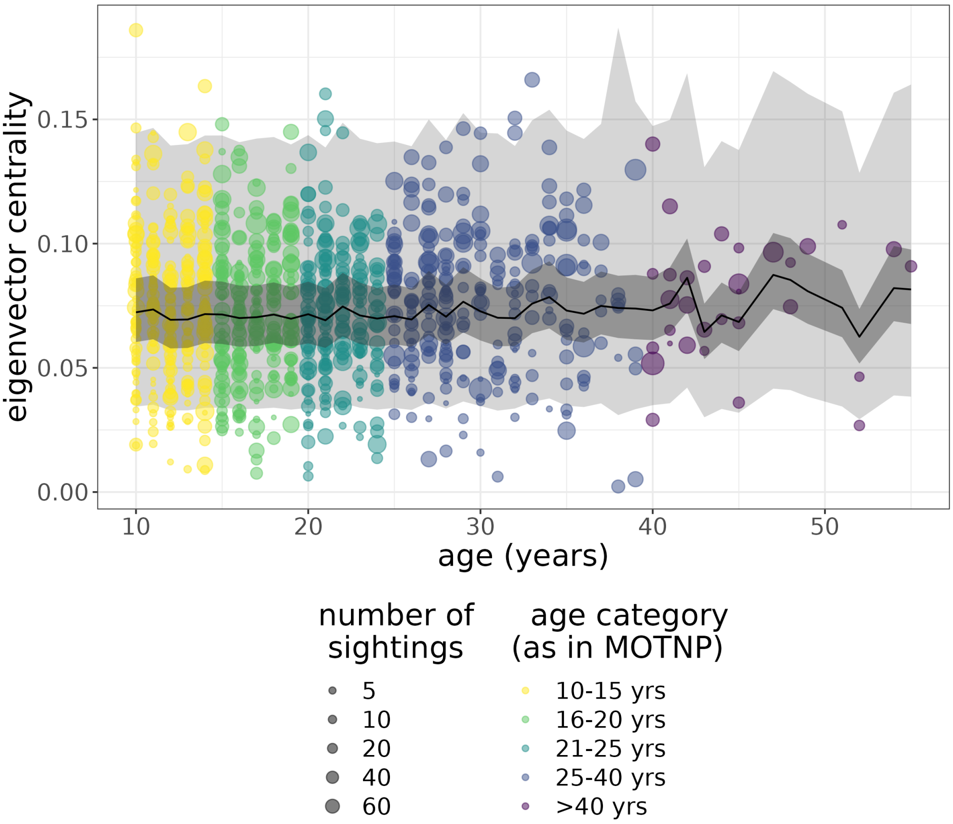


(i) MOTNP



(ii) ANP, short time windows

Figure 15



(iii) ANP, long time windows

Figure 15: Effect of age on eigenvector centrality for each population. (i) MOTNP, (ii) ANP with 500-day time windows, and (iii) ANP with 2 571-day time windows. Points show the median eigenvector centrality per node, with the size indicating the number of observations for that elephant (note that point sizes are not comparable between graphs). For MOTNP, which has categorical age values, the central box plot indicates the spread of median predictions, and the violin plot shows the spread of predicted values. For ANP, because the ages are continuous, the median prediction and spread of median predictions are shown by the line and inner shading, while the broader shading indicates the spread of predicted values. The colour of the points indicates the age category of the individual, such that ANP ages are comparable to MOTNP.

3.4 Discussion

I found mixed support for my hypotheses. I found that mortality risk did increase with age, and that the early-stage transition period was fractionally more dangerous than once they were settled into adult life, but that overall transition to independence is not an especially dangerous time for male elephants. With regard to social bond strength, I found that bull elephants form only very weak social bonds with one another as expected. However, I did not find evidence for social differentiation, or for certain dyads showing particularly strong relationships. Considering the potential effect of age on social network position, I hypothesised that there would be an effect, which would be positive or negative depending on the movement strategies adopted by young males. Contrary to this, I found no evidence that male social position is related to the age of the individual, with males of all ages showing similar network centrality and the posterior distributions for the effect of age being centred around zero for all models. Finally, my results did not differ between populations or time windows of the same length, but longer time windows did show lower average edge weight and similar centrality trends, as hypothesised. That the results were consistent between ANP and MOTNP suggests that these findings are not population-specific and indicate they may apply to male African savannah elephants as a whole. I can also conclude that male relationships are stable over these time periods, because there are similar trends in social structure between long and short time windows. Improved understanding of the social structure of male African savannah elephants could help to elucidate new methods of facilitating human-elephant coexistence, and explain the behaviour patterns of an important ecosystem engineer.

The edge weight distributions show that male elephants do not appear to form strong bonds with one another. I found similar bond strengths to those calculated by Chiyo *et al.* (2011) for all elephants, but weaker than Murphy *et al.* (2020) who obtained values ranging from 9.9-14.2% association when including all males in the analysis, or Goldenberg *et al.* (2014), who estimated association to be around 11% when including all males and over 30% when including only those in the same sexual state. This low rate of repeated interactions implies that there are unlikely to be strong fitness benefits to male elephants of forming close associations with specific social partners, else they would allocate more time and energy to strengthen these weak relationships (Foster *et al.*, 2012). Instead, bulls choose to constantly shift their group membership, so they interact with a large number of others but never for a long time with each. Forming many weak relationships instead of a few close ones could have social benefits such as an increased number of role models to imitate (Laland, 2004) or social partners to accelerate social facilitation (Laker *et al.*, 2021), but also disadvantages, including greater risks of pathogenic infection (Cross *et al.*, 2004; Silk *et al.*, 2017). However, my results also indicated that the networks were very sparse, so while they preferred weak relationships, many dyads were never seen to associate at all, or association was extremely rare, which may protect them from excessive pathogen exposure (Loehle, 1995; MacIntosh *et al.*, 2012).

These findings make elephants quite peculiar among other species with regard to male social behaviour. For many animals, especially those for which polygyny is the norm, amicable male-male associations are rare if they do not promote either improved mating opportunities (Díaz-Muñoz *et al.*, 2014) — for example, male alliances as seen in dolphins (Connor *et al.*, 2022), lions (Chakrabarti and Jhala, 2017), primates (Watts, 1998), bee-eaters (Wrege and Emlen, 1994) and fish (Díaz-Muñoz *et al.*, 2014) — or reduced predation risk — such as through the use of alarm calling to signal the presence of danger (Gyger, 1990; Chivers and Smith, 1998; McLachlan and

Magrath, 2020). Otherwise, solitary behaviour may be preferred because it reduces competition (Rubenstein, 1978) and the risk of infection (Archie and Tung, 2015; Silk *et al.*, 2017; Sarkar *et al.*, 2020, but see Ezenwa *et al.*, 2016). Fully grown male elephants have no natural predators (Joubert, 2006), and in musth when they are most likely to successfully mate (Hollister-Smith *et al.*, 2007) they become more solitary (Poole, 1989b) rather than strengthening male-male ties. It therefore makes sense that there is no evidence that males form strong social bonds with one another. That they do still form weak ties with a large number of social partners indicates that males must gain some kind of long-term fitness advantage from socialising. This may be general social learning opportunities, as previously mentioned, even if there is no preference for specific social partners who may have more experience. However, it could also be linked to improved immunity (through low dose protective exposure, a shared microbiome, and improved resource acquisition; Ezenwa *et al.*, 2016); reduced stress through access to peer support (Ray and Sapolsky, 1992; Sapolsky *et al.*, 1997; Shutt *et al.*, 2007; Brent *et al.*, 2011a) or faster recovery following a stressor (e.g., a poaching event) through improved social buffering (Thorsteinsson and James, 1999; Edgar *et al.*, 2015; Faustino *et al.*, 2017; Avellaneda and Kamenetzky, 2021; Gilmour and Bard, 2022); or the suppression of musth in young males (Evans and Harris, 2008). Further research is necessary to identify the advantages that males may gain by forming these weak social bonds.

My results from the nodal regression agreed with some of the previous studies of male elephant social networks (Murphy *et al.*, 2020; Goldenberg *et al.*, 2014 when considering sexually inactive males), but not others (Chiyo *et al.*, 2011; Goldenberg *et al.*, 2014 when considering sexually active males). The lack of effect of age on centrality contradicted both of my hypotheses regarding the movement behaviour of young male elephants. Neither the oldest nor the youngest elephants displayed higher centrality than any other age class. There are a number of possible explanations for why I found no effect. Firstly, both mechanisms may work in tandem, such that neither older nor younger bulls are more central than the other. If young males form transient groups that move between older males and old bulls are selective about who they associate with among each other — as found by Goldenberg *et al.* (2014), but Murphy *et al.* (2020) found no difference in relationship stability between old and young males — then young males will gain many weak associations with one another and mid-level with older males, while old bulls gain mid-level with young males and only a few but strong associations with one another. This would fit with the evidence from the nodal regression, but would suggest a hierarchy of relationship types, which I did not find in the edge weights.

A second explanation for why there is no effect of age on centrality is that it could be masked by changing body condition. Goldenberg *et al.* (2014) found that male elephants in a sexually inactive state did not show a relationship between age and centrality, which matches my results, but that young sexually active males showed higher centrality than old sexually active males. In this study, I aggregated all of the data for each dyad to two values per time window: sightings together, and total sightings (Franks *et al.*, 2010). I therefore could not include sexual state as a variable in the model, because over the course of a time window all males old enough to experience musth would do so for at least some of the time (Poole and Moss, 1981). Similarly, I did not account for body condition, which is linked to the musth cycle: musth is a time of high energetic cost, after which they require time to recover (Poole, 1989b), creating large fluctuations in body condition. In male Alpine ibex (*Capra ibex*), whose social network similarly involves frequent movement between different associates, centrality is caused by changes in body condition (Brambilla *et al.*, 2022). Older males have the longest musth periods, so may show the greatest fluctuation in body condition (Poole, 1989b), because they will use more energy by maintaining their musth for longer. If body condition similarly affects social behaviour in male elephants as it does in ibex, then older males will also show greater fluctuation in centrality with their shifting condition, such that on average elephants of all ages have similar median centrality. If I were to repeat this model without aggregating all of the dyad data within a time window, and instead treat every observation as a separate data point (Hart *et al.*, 2023), I could include body condition scores for each male, allowing testing of a) if condition affects centrality, and b) if age has an effect after controlling for body condition. However, to do so would require extremely powerful computing facilities, which were not available in this study.

A third possibility is that there are a combination of different mechanisms in play, so any preference to be nearer older males for social learning is masked. For example, if younger males associate with older males for social learning, but elephants of a similar age and size to gain sparring opportunities (Evans and Harris, 2008; Chiyo *et al.*, 2011; Poole *et al.*, 2011), this may balance out any preferences for older bulls. Similarly, older males may preferentially associate with one another for reasons such as companionship and social buffering (Kikusui *et al.*, 2006) or monitoring of mating rivals (e.g., grey kangaroos, MacFarlane and Coulson, 2009), but also stay close to young males as a means of suppressing their musth (Evans and Harris, 2008) or maintaining their own positive psychological state (O'Connell-Rodwell *et al.*, 2024a).

A fourth and final explanation is that older males are more likely to be found alone than younger males (Chiyo *et al.*, 2011; Lee *et al.*, 2011; Allen *et al.*, 2020). This could lead to no effect on centrality if older males consistently have stronger but fewer associations than younger males (Liao *et al.*, 2018). I chose to retain all observations in the analysis, including those in which the observed male was alone, to avoid biasing the data toward older males: removing sightings of lone individuals will raise the average edge weight because $sightings_{ij}$ will be lower for each dyad, but if older males are more often alone then this will systematically raise the centrality of older bulls. Combining this effect with another in which younger males are the most central could hide an effect of social learning on social structure.

Combining these results with the outcomes of previous studies suggests interesting implications for male elephant social structure and the possibilities for social learning. There is clearly no strong average effect of male age on social network position, and males are not spending long periods of time associating with specific individuals, in agreement with some of the literature (Chiyo *et al.*, 2011; Lee *et al.*, 2011). It therefore seems highly unlikely that young males are actively targeting more experienced individuals as social partners to obtain social learning opportunities, or that social learning by imitation or emulation is a major cause of male elephant grouping patterns (as is seen in primates, with individuals specifically selecting who to interact with to gain social learning opportunities; Whiten and van de Waal, 2018). However, this does not mean that social learning is irrelevant in these networks: by forming many weak associations that are not constrained to particular groups of males, closed off to association with other males outside of the group, there is little in the way of structure to impede rapid spread of novel behaviours or information through the social network (Silk *et al.*, 2017), and social learning by facilitation may be amplified. I therefore conclude that while male elephants do not necessarily cluster around the males that are likely to be the best role models, social learning is potentially still important to bull sociality.

My results have possible implications for wildlife management and conservation with regard to human-elephant coexistence. Social learning among male elephants accelerates the spread of behaviour through a population, so males that crop-forage or break fences may pass that behaviour on faster (Chiyo *et al.*, 2012) and so increase the frequency of negative human-elephant interactions (Greggor *et al.*, 2017). I would particularly expect crop-foraging to spread via social facilitation, as the older males draw the attention of young males to crop plants and therefore provide local and stimulus enhancement. While I did not find evidence for young males targeting older males for social learning opportunities, their simple social structure that lacks specific partner preferences does not impede the spread of social information in the same way that tight-knit groups would (Cross *et al.*, 2009 *in* Silk *et al.*, 2017): males can learn from any other individual, rather than being limited to individuals with whom they spend the most time, and many partners may increase motivation for social facilitation. Barrier methods to prevent crop-foraging may then have short-lived effectiveness (Kioko *et al.*, 2008), because once one individual learns to circumvent the barrier, the behaviour will be able to spread rapidly (Chiyo *et al.*, 2012) and make the new barrier obsolete. This knowledge can be used to recommend focusing on deterrent methods (Montgomery *et al.*, 2022), rather than barriers, because it explains why barrier methods are rarely successful long-term, and shows that avoidance behaviours may potentially be encouraged to spread through a population instead (Greggor *et al.*, 2017). For example, elephants have been shown to avoid the sounds of African honeybees (Vollrath and Douglas-Hamilton, 2002; King *et al.*, 2009, 2011b, 2017; Kiffner *et al.*, 2021), due to the potential severity of being stung in sensitive areas such as the trunk tip and around the eyes (Vollrath and Douglas-Hamilton, 2002). By simulating the presence of bees around males known to avoid the sound, it may be possible to discourage other males that have not experienced bee stings. However, since there appears to be no effect of age on social learning opportunities, the role models chosen for this would not need to be constrained to only older individuals.

The survival and mortality curves can also be used for planning of future conservation practices and wildlife management (Martin, 1995; Clutton-Brock and Sheldon, 2010). In all models, survival to 20 years post-independence was ∼35-40%, and to 30 years post-independence was ∼15-20%. This indicates that almost half of the male population that reach independence will reach breeding age (Lee *et al.*, 2011), and many will make it to their prime. In turn, this would suggest that the availability of breeding males should not be a limiting factor for elephant population growth (Archie and Chiyo, 2012; Wittemyer *et al.*, 2013). However, it should be noted that this is specific to ANP, and may not be representative of other areas with different rates of poaching or resource availability, and may be affected by changing climate altering the frequency of extreme weather events (Wittemyer *et al.*, 2021).

This study has shown that African elephants in two different populations behave similarly. However, further research would be necessary in populations with different demographics to see if the findings are truly universal. For example, bull areas occur where male elephants congregate in the absence of females (Stokke and du Toit, 2002; Lee *et al.*, 2011). These areas have extremely high male:female sex ratios (e.g., elephant sightings in Botswana's Makgadikgadi Pans National Park are approximately 98% male; Pitfield, 2017), leading to reduced numbers of musth bulls, because males leave the area to find females when they enter musth (Stokke and du Toit, 2002; Poole *et al.*, 2011). However, despite the very different social environment that they represent, bull areas have received very little attention with regard to social structure. I expect that males living in the absence of females or musth bulls may form different social structures to those living in areas with a more balanced sex ratio and higher reproductive competition, because musth bulls are much more aggressive than non-musth bulls (Poole and Moss, 1981) so are avoided by other males (Stokke and du Toit, 2002). Repeating this analysis in a bull area could yield interesting comparisons to see how males change their behaviour in the presence of potential mates. However, this can be more difficult as bull areas contain, by definition, migratory populations (Evans and Harris, 2008; Lee *et al.*, 2011), so each individual may have very few repeated sightings.

It would also be good to examine the edge weights in greater depth, to look for causes of social bond strength in node traits (Hart *et al.*, 2023). The network plots appear to show a slight preference for males grouping with others of a similar age (which was also observed by Chiyo *et al.*, 2011), but this is not a conclusive test of dyad preference. An analysis to assess how the ages of both males in a dyad and the difference in age between them affect dyadic edge weight would help to elucidate any potential remaining evidence for social learning: if males are likely to associate with age mates (Chiyo *et al.*, 2011), or if older males are more selective about preferring males of a similar age to themselves than younger males are (O'Connell-Rodwell *et al.*, 2024a), this would indicate that younger males could still be using older males as role models, though I would not expect this to be a strong effect given the nodal regression outputs.

3.5 Conclusion

In conclusion, bull elephants do not form strong social bonds and male elephant eigenvector centrality is not dependent on their age, so older males are not observed to be more influential over the social network than younger males. However, their propensity to associate only weakly but with many individuals potentially facilitates rapid social learning, because each elephant may interact with a high number of others in a short time. In future conservation efforts, practitioners should be aware that new behaviours (and pathogens) are likely to spread very rapidly through male populations.

Chapter 4

Group response of male elephants to threatening situations

Abstract

Animal threat responses reduce individual mortality, and in social species can improve group survival. Sometimes, the appropriate response to danger may vary depending on the threat encountered or the social context. Naïve individuals may copy others to learn the most appropriate response. Young male elephants (*Loxodonta africana*) learn how to respond to common natural threats within their family unit, but after transitioning to independence will face danger in a different social context. Where female elephants will work together to protect the group, it is unknown if males display a social response to danger. As the main crop-foragers, bulls play a critical role in human-elephant coexistence, so understanding how bulls learn to respond to anthropogenic threats is vital to supporting elephant conservation and local communities. In this study, I use playback experiments to groups of males in the Makgadikgadi Pans National Park, Botswana, to ask: i) if male elephants protect one another; and ii) if male elephants use social learning to identify the appropriate response to novel threats. I performed 48 experiments, evenly split between human (high threat, unfamiliar), lion (low threat, rare) and control (no threat, common) stimuli. I tested for evidence of males protecting and/or copying their group members by recording individual looking and movement direction relative other bulls, and choice of nearest neighbour. I then used Bayesian regression models to test the effect of age and stimulus on each behaviour. In contrast to previous studies of female elephants, I found no effect of the stimulus on any social responses, and therefore no evidence that males are actively protecting group members or learning how to respond to a novel stimulus from other bulls. I discuss the implications for human-elephant coexistence, and recommend future studies investigate the factors affecting the probability of elephants charging at farmers defending their crops.

4.1 Introduction

Social learning is widespread across taxa (Aplin, 2016; Mesoudi *et al.*, 2016; Allen, 2019), documented in insects (Coolen *et al.*, 2005; Worden and Papaj, 2005; Leadbeater and Chittka, 2007), fish (Brown and Laland, 2001; Brown and Laland, 2003; Brown, 2023), birds (Janik and Slater, 2000; Lachlan, 2008; Slagsvold and Wiebe, 2011; Aplin *et al.*, 2013; Wild *et al.*, 2022), cephalopods (Fiorito and Scotto, 1992; Sampaio *et al.*, 2021), and a wide array of mammals (Gariépy *et al.*, 2014), including, but not limited to, primates (Rapaport and Brown, 2008; Whiten and van de Waal, 2018; van Boekholt *et al.*, 2021; Carvajal and Schuppli, 2022), cetaceans (Cantor and Whitehead, 2013; Whitehead and Rendell, 2014), rodents (Galef, 2008) and carnivores (Thornton and Clutton-Brock, 2011). The most basic definition of social learning is that it is any form of learning that is facilitated by interaction or association with other individuals, which are typically, but not necessarily (Avarguès-Weber *et al.*, 2013), conspecifics (Box, 1984 *in* Heyes, 1994, Galef, 1988). Social learning can offer opportunities for learning new skills (e.g., tool use: Call and Tomasello, 1994; Krützen *et al.*, 2005), increasing foraging efficiency (e.g., being shown where a good food patch is located: von Frisch, 1946; Sonerud *et al.*, 2001), or aiding social integration into a new group (Harrison *et al.*, 2024). However, it can be especially advantageous when regarding high-risk or threatening situations: learning how to respond appropriately to potential danger is much less likely to be harmful if you do not have to experience the harm for yourself (Griffin, 2004).

Threat responses are key to animal survival (Bolles, 1970; Cooper and Blumstein, 2015; Tseng *et al.*, 2023). Some responses may be specific to the threat encountered. For example when facing some predators, the best prey strategy may be to flee, while for others it may be to face down or charge towards the predator until it backs down. In social species, the appropriate choice of threat response behaviour may not only improve an animal's own chance of survival, but also those of other group members, which may or may not be kin depending on the species. Being in a group reduces an individual's risk of attack through dilution (Foster and Treherne, 1981; Lehtonen and Jaatinen, 2016) and confusion (Olson *et al.*, 2013) effects, and additional social responses may further enhance the probability of individual survival. Social threat responses can include alarm calls to show that a threat is close by (Krams *et al.*, 2006; Griesser, 2013; McLachlan and Magrath, 2020), mobbing the predator until it leaves (e.g., Poiani and Yorke, 1989; Ono *et al.*, 1995; Stanford, 1995; Novaro *et al.*, 2009), or forming a defensive unit to protect the most vulnerable members (e.g., Watson and Tener, 1967; McComb *et al.*, 2014). Understanding how social species may alter their threat response behaviour depending on the composition of their social group can help to explain the evolutionary advantages of grouping behaviour. For example, producing alarm calls will increase the risk of an animal being noticed by a predator. Alarm calling can therefore act as a deterrent to the predator to indicate that they have lost the element of surprise (Bergstrom and Lachmann, 2001). However, it can also draw the predator's attention and help them to select a specific target (Maynard Smith, 1965), so prey individuals should only alarm call in the presence of group members that will benefit from the warning (Karakashian *et al.*, 1988; Gyger, 1990; le Roux *et al.*, 2008) and that the caller has a vested interest in protecting, usually kin (Zuberbühler, 2009). Similarly, predator mobbing behaviour should vary depending on the other members of the group: in Siberian jays (Griesser and Ekman, 2005) and barn swallows (Shields, 1984), adult breeders invest more in mobbing behaviour when their offspring are present and potentially in danger than when they are not, indicating that fitness advantage is dependent on social context.

Some of these social threat response behaviours are instinctual so do not need to be learnt (Misslin, 2003), but others must be added into an individual's behavioural repertoire over time. For example, juvenile vervet monkeys (*Cercopithecus aethiops*) must learn to respond in a specific manner to alarm calls signalling the presence of different predators, using cues from other individuals, particularly their mothers (Seyfarth and Cheney, 1980). While the innate fear response promotes a generalist response that is consistent across prey subjects to maximise survival probability against the majority of predators (Bolles, 1970), learning allows animals to apply different threat-specific responses dependent on the particular scenario (Fanselow, 2018).

4.1 Introduction

Unlike solitary species, in which individuals must learn from their own experience (though there is increasing evidence of social learning even in solitary species; e.g., Wilkinson *et al.*, 2010), social species have the added advantage that they may also learn from their families or older group members by imitating their responses (for reviews, see Griffin, 2004; Laland, 2004). In some cases, a young individual may disperse from their natal group before experiencing certain threats. In these situations, older members of their new social group may act as information sources from which a young individual may learn.

Young African savannah elephants (*Loxodonta africana*) learn many of their life skills such as the best foraging plants and the location of important resources within their family's home range by watching their older family members (Moss and Lee, 2011a). They will also learn how to respond to danger (Moss and Lee, 2011a; Shannon *et al.*, 2022). In a family group, adult females will form defensive rings around the youngest and most vulnerable group members, protecting them from danger (McComb *et al.*, 2001; Moss, 2001; Shannon *et al.*, 2022), so young elephants will learn first to bunch closer to the group then, once older, to protect the new most vulnerable members. They will also learn how to recognise danger and respond to an appropriate level: experiments have shown that older matriarchs, who have more experience with threats than young matriarchs, are better at judging the level of danger that a family may be in, such as assessing the number of lions present in an area (McComb *et al.*, 2011) and interacting with strangers versus familiar elephants (McComb *et al.*, 2001), and that females raised within disturbed herds without an experienced matriarch overreact to minor threats (Shannon *et al.*, 2022). Together, these indicate that young elephants learn to respond to potentially threatening situations both from their own experience, but also by watching and following their herd matriarchs. For young females, who remain in the same matrilineal unit for their whole lives, learning threat response behaviour from older family members facilitates rapid adoption of optimal group survival strategies with only limited risk to naïve youngsters. For male elephants, the responses they learn as a juvenile may not be appropriate once they leave their natal unit.

When male elephants leave their natal unit to join adult bull society at around 8-16 years old (Lee *et al.*, 2011), their social environment changes radically. Male elephant groups are much more transient than family groups (Chiyo *et al.*, 2011; Lee *et al.*, 2011; Goldenberg *et al.*, 2014; Murphy *et al.*, 2020, also see Chapter 3), and are not strongly driven by kin preferences (Santos, 2017, but see Chiyo *et al.*, 2011), removing much or all of the kin-selective advantages of protecting others. A young bull will therefore learn the most appropriate response to danger within the context of their natal herd, but will then face danger in a completely different social context. While elephant hunting by lions is rare, evidence suggests that their primary target is young males no longer so closely protected by their mothers (Joubert, 2006; Power and Compion, 2009), making newly-independent adolescent males far more vulnerable than their new adult bull group-mates. In the mortality analysis in Chapter 3 I found using DIC model comparison that the youngest elephants, still at the age of transitioning to independence from their natal herd, displayed a slightly elevated mortality risk compared to those already dispersed. I would therefore expect their threat response to reflect these changes. With little or no kin selection toward protecting other individuals, and a lower overall risk of harm to the group because few predators offer any severe danger to an adult bull elephant, it might be expected that there would be nothing to drive a group-level threat response. I am unaware of any studies that have investigated how bull groups respond to danger, but anecdotal evidence has suggested that male elephants will still sometimes form defensive groups to protect the youngest individuals (Kate Evans, personal communication).

It is currently unclear if bull elephants display group-level threat responses, such as protecting other group members or copying their reaction, or if an individual will vary their response depending on the level of threat experienced and the group composition. Understanding how individual, and potentially group-level, threat responses of bull elephants may change with group size, age distribution or the presence of specific group members could aid in their conservation. Male elephants play a critical role in human-elephant coexistence. Most crop-foraging events contain males (Hoare, 1999; Jackson *et al.*, 2008; Ahlering *et al.*, 2011; Chiyo *et al.*, 2012; Von Gerhardt *et al.*, 2014; Stevens, 2018), because males require more food to support their larger mass and are more willing to take risks than females with calves (Sitati *et al.*, 2003). If family units rarely enter crop fields, many young males will never have experienced the threat of humans before transitioning to independence, so farmers may present a potentially novel threat when chasing groups of bull elephants from their fields. Examining how groups of male elephants respond to a perceived human danger as a group could be valuable both to protecting the elephants and to minimising the risk of harm to people protecting their land, by understanding the probability of elephants responding aggressively. Furthermore, by contrasting the response of male elephants to humans against their response to a more familiar danger, we can look for evidence of young male elephants copying the reaction of older males, as a potential social learning strategy (Evans and Harris, 2008; Chiyo *et al.*, 2011; Allen *et al.*, 2020, 2021a).

In this study, I investigate how male savannah elephants respond to familiar natural and novel anthropogenic threats when in a group situation, testing two questions. i) Do male elephants exhibit protective behaviours toward group members, especially older bulls actively defending younger males? Protection might be something as extreme as forming a defensive ring around the youngest members, as seen in females; it could be a single older male stepping between a younger individual and the source of the threat; or it may just be a look or trunk touch to make sure that the youngster is safe. ii) Do male elephants use more experienced group members as information sources to learn how to respond to a novel threat? Adolescent males have been shown to follow older bulls, highlighting a possible role of old bulls as information resources for younger males (Chiyo *et al.*, 2011; Allen *et al.*, 2020, 2021a). These produce three overarching hypotheses: old male elephants protect young bulls in times of danger (henceforth, hypothesis 1); young male elephants use older males as social role models to learn how to respond to danger (hypothesis 2); or old and young bull elephants group together for both protective benefits and social learning opportunities (hypothesis 3). I test these hypotheses by using playback stimuli representing three different levels of threat and familiarity (unthreatening and experienced daily; low-level threat and experienced occasionally; and high-level threat that is experienced rarely or never) and studying their effect on three forms of male social behaviour: movement relative to other group members, visual attention toward the group, and nearest neighbour choice. In general I hypothesise that protective behaviours will be more dominant in response to low-level threats (because under high-level threats, males should defend themselves first), and social learning in response to novel threats (see Hypotheses section).

4.2 Methods

4.2.1 Study area and population

The Makgadikgadi Pans National Park (MPNP) is a large protected area of 1 524 km^2 (Department of Environmental Affairs and Centre for Applied Research, 2010), that lies to the east of the Boteti River in north-eastern Botswana. Botswana supports over 30% of the global population of African savannah elephants, but geographic biases in elephant research have resulted in less than 10% of studies being performed in the country (Gross and Heinsohn, 2023), so conservation management decisions about the largest remaining elephant population are being made based on evidence predominantly from elsewhere. The Boteti forms the border of the park, separating the protected area from local communities and provides the only permanent water source in the region. This water source drew elephants back into the area, having been pushed into the north of Botswana during the Colonial period, but so far it has been almost exclusively bulls that have returned to the region, creating a population that is approximately 98% male (Pitfield, 2017; Evans, 2019). The population is highly migratory, with males spending an estimated average of 47 days inside the park and 238 outside during each migration cycle (Pitfield, 2017). The population is also seasonal, with fewer present in the wet season. Due to the layout of the park roads relative to the areas where elephants like to congregate at different times of year, observations are even more seasonal, as the elephants prefer to remain in the thicker vegetation when it is windy (personal observation).

4.2.2 Playback experiments

Playback experiments were conducted opportunistically whenever we (HM and the field team) found a group of suitably-positioned bulls, using a series of auditory stimuli. I played the stimuli in a stratified random order, with every three experiments containing one of each stimulus type, but the order randomised within the block of three. I never played more than one stimulus to each group on the same day, to avoid causing undue stress or biasing the results by creating the appearance of multiple threats. In general, I aimed for groups that were resting under large trees, because these elephants were the most likely to remain close together and in one place for long enough to set up the experiments. Resting was, however, not a necessary requirement, and in some cases the group may have been feeding or walking at the time of playing the stimulus. I did not perform any playbacks to elephants drinking or on their way to the river, to avoid chasing them away from the water. I also avoided groups that contained females or individuals younger than 10 years old, to avoid youngsters being left behind or hurt if the group reacted severely. All field research for this project was carried out with permission from the Ministry of Environment, Natural Resource Conservation and Tourism (MENT) of Botswana (permit number: ENT 8/36/ 4 LII (44), supplementary permit number: WP/RES 15/2/2 XXXIV (98)). Ethics permission was supplied by the University of York Animal Welfare and Ethical Review Body (AWERB) and Biology Ethics Committee (memorandum of approval number DF202112).

In total I performed 61 playbacks to the elephants of the MPNP, using three different stimulus types to test male elephant group responses: the calls of a cape turtle dove (*Streptopelia capicola*), a common species that poses no threat to elephants, as a control stimulus (21 trials); lions (*Panthera leo*) roaring, a natural predator that bulls will experience inside the park regularly (20 trials); and humans imitating the noises they would make if chasing crop-foraging elephants away from their fields (20 trials). These three stimuli therefore represent increasing levels of potential threat, unfamiliarity and expectancy violation, with doves being harmless, familiar, and unsurprising to hear during the day in the national park, through to humans being dangerous, potentially unfamiliar to at least some members of the group, and very unexpected in the national park.

The lion and turtle dove sounds I obtained from the Global Biodiversity Information Facility (GBIF) database of wildlife sounds (Appendix A3.1: Table A9), and then edited or duplicated the recordings where necessary to obtain stimuli of 20-30 seconds in duration. For one lion stimulus that contained two males roaring together, I edited out the second male, and used both the unedited and edited versions at different points, because female elephants have been shown to be able to discriminate between different levels of lion threat purely from auditory stimuli (McComb *et al.*, 2011), and it is expected that two lions will be considered a greater threat than one. The human stimuli I recorded (using a Rode Videomic II microphone connected to a Huawei Nova 5T) directly from members of the local community. For each recording, I asked people to make whatever noise they would normally use to chase elephants away, with the aim of representing a wide range of potential deterrent sounds. These varied from whistling or singing, to shouting or screaming, usually while clapping, drumming, or hitting together two pieces of metal. These recordings were evenly split between men and women, because elephants have been shown to react more to male voices (McComb *et al.*, 2014), but 72% of farmers are women in this region (Stevens, 2018). All stimulus volumes were normalised and tested (using the Decibel X app on an iPhone 6s) to avoid systematic differences in response based on the volume of the stimulus.

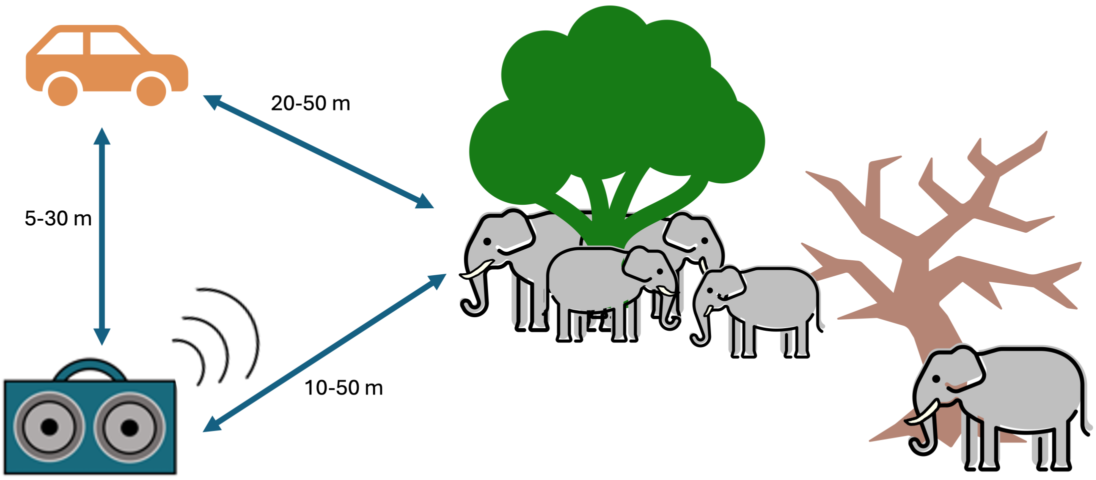


Figure 16: Playback setup. I set up the playbacks such that the speaker was laid on the ground close enough to the elephants that they would hear the sound, but far enough from the vehicle that the sound would not appear to be originating from the vehicle. I filmed each experiment from the vehicle using both long range and wide angle cameras. I took all distances from the approximate centre of the group. I generally aimed for groups of males resting under trees, because these were the most likely to remain in place while I positioned the speaker and vehicle.

I varied day-to-day which areas of the park we visited at different times, to minimise the risk of repeatedly testing the same individuals. When we located a group, I would lay the speaker (an Ultimate Ears MEGABOOM 2, set to maximum volume, capable to performing the full audible spectrum at a volume of 80 dB) on the ground 30-50 m from the group, before driving 10-30 m from the speaker to avoid the sound appearing to originate at the vehicle (Figure 16). I recorded the elephants' behaviour (Akaso II action camera and Canon 7D Mk I DSLR, equipped with a Sigma lens of 70 mm or 150 mm focal length), for three minutes before and after the stimulus. At each playback I recorded the date, GPS location, and the distances between the vehicle, speaker, and elephants. I also recorded the times of arrival, laying the speaker and playing the stimulus.

4.2.3 Video analysis

I extracted behavioural data from the video footage using the Behavioral Observation Research Interactive Software (BORIS; Friard and Gamba, 2016) program. This software allows accurate marking of the times within a video that each behaviour starts and ends, but requires manual assessment of each behaviour. For each video, I recorded the time of the stimulus in a separate file then performed all behaviour recordings with the videos muted so I was blind to both the type and timing of the stimulus, preventing any subconscious biases in the data caused by looking for a change when a stimulus began. Table 1 contains an ethogram of the behaviours of interest. I recorded looking direction and movement direction of every male relative to each other individual in the group, so for a group of N individuals there would be $N-1$ sets of data per focal: focal *A* looking direction relative to *B*, *C*...; *B* looking direction relative to *A*, *C*...; *C* looking relative to *A*, *B*... and so on. This procedure produces a total data frame per experiment of $N \times (N-1) \times duration(s)$ for each of looking direction, movement direction, and nearest neighbour choice. Probability of movement was irrespective of other group members, producing $N \times duration(s)$ only.

Table 1: Ethogram of behaviours considered in the study. Looking direction, movement direction and nearest neighbour I recorded separately relative to every other individual within the group, producing $N \times (N-1)$ data points per second per experiment. Numbers indicate the respective score for ordinal regression models (see methods sections for Looking direction and Movement direction). Note that just because individual *A* is nearest neighbour of individual *B*, this does not mean that individual *B* is necessarily the nearest neighbour of individual *A*.

Category	Behaviour	Definition
Movement	Moving	Takes at least one step in any direction
Movement direction	1) Away directly	Moving away along the shortest path
	2) Away at an angle	Moving away, but not along the shortest path
	3) Not towards or away	Move around or directly alongside
	4) Towards at an angle	Approaching, but not along the shortest path
	5) Towards directly	Approaching along the shortest path
Looking direction	1) Away	Head is angled such that neither eye is visible
	2) Side-on	Head is angled so that only one eye is visible
	3) Towards	Head is angled such that both eyes are visible
Nearest neighbour	Nearest neighbour	The individual closest to the focal. If two appear equally close, whichever is closest to the head.

For each video this produced a data frame containing the start and end times for every behaviour, beginning three minutes before the stimulus started and finishing three minutes after it ended (for two experiments, a full three minutes were not available before the stimulus started – for these, the stimulus started 82 seconds and 130 seconds into filming).

After extracting the start and end times for each behaviour from BORIS, I converted the data to a second-by-second format, indicating the behaviour per second per elephant recorded for each category, relative to each other male. Using the resultant data frame I fitted a total of six causal models (detailed below) to understand how the ages of the focal (individual being recorded) and target (individual toward which the focal's behaviour is being recorded) elephants, and the stimulus (type and time relative to the sound broadcast), may cause changes in the focal male's social behaviour relative to the target.

4.2.4 Statistical analysis

I analysed the data from the videos using a variety of Bayesian regression models, customised to each analysis. To identify the causes of male movement and of nearest neighbour choice, I used binomial regressions, and for the direction of looking or movement relative to the target, I used ordinal regressions. The explanatory variables of interest for all questions were the age of the focal male, the age of the target male (excluding the model of movement probability), the type of stimulus played (dove, lion or human) and the time relative to the stimulus (before, during or after). In all models for this chapter, I used random effects of focal ID (shown as $focal$ in equations), recording number ($recording$) and playback number ($trial$), because these were the units of repeated measurement where I expected variation between factor levels (see Figures 17–19 in the following sections for details). I performed all data analyses using R version 4.2.1, running Bayesian models with *brms* (Bürkner, 2017).

4.2.4.1 Hypotheses

My hypotheses for male behaviour differ depending on the answers to one or both questions. If male elephants group for reasons of protection but not social learning (hypothesis 1), then I hypothesise that all males will move more for threat scenarios than the non-threatening control, and that younger males will move more than older ones because they are more vulnerable. The direction of movement will depend upon the stimulus and age: for a low-level threat, all will approach one another (bunching; McComb *et al.*, 2014) so that the older males can protect the younger ones; for a high-level threat older males will hold their ground to give the younger males time to flee before following them, so younger males will move away from older males while older males approach younger ones. Furthermore, for protection without social learning, I hypothesise that older males will look at younger ones following a threat scenario, but younger males will not look at older bulls. Finally, in this scenario, there will be a change of nearest neighbour so older males will increase their likelihood of having a young male as their nearest neighbour following a threat stimulus.

If, however, the opposite is occurring, and males are grouping so that young males can learn from older ones, but older males do not offer protection to young males, my predictions change. Under the social learning scenario (hypothesis 2), I hypothesise that older males will ignore younger males, so will not approach or look towards young bulls, nor will they change their nearest neighbour. In contrast, young males will look at older males and approach them under both levels of threat scenario. As before, younger males will move more than older males, but with limited effect because young males copy older males. Older males will flee from a threat first so older males will move away from younger males and younger males will approach older males. Younger males will change their nearest neighbour, but older males will not.

Finally, if male elephants are grouping for both protection and social learning (hypothesis 3), their responses will be in the middle: I hypothesise that all will move a similar amount and bunch up in response to a low-level threat, but for a high-level threat older males will move away first and younger males will follow; all will look towards each other for a low-level threat and younger males will look towards older for a high-level threat; and nearest neighbours will change for all elephants.

A summary of these hypotheses is given in Table 2.

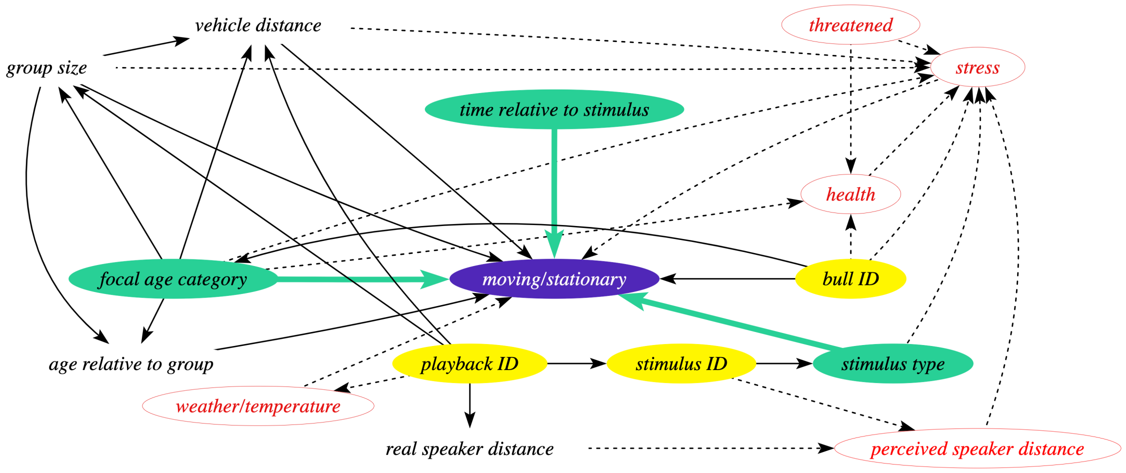
Table 2: Predictions for old and young male behaviour in response to a playback. Predictions are based on the hypotheses that male elephants group for reasons of protection only (hypothesis 1), social learning opportunities only (hypothesis 2), or both protection and social learning (hypothesis 3).

Behaviour	Stimulus	Protection (H1)		Social learning (H2)		Both (H3)	
		Young	Old	Young	Old	Young	Old
Movement probability	Dove (control)	No change	No change	No change	No change	No change	No change
	Lion	Yes	Some	Some	No change	Yes	Some
	Human	Yes	Yes	Yes	Yes	Yes	Yes
Movement direction	Dove (control)	No change	No change	No change	No change	No change	No change
	Lion	Approach	Approach	Approach	No change	Approach	Approach
	Human	Move away	Approach	Approach	Move away	Approach	Move away
Looking direction	Dove (control)	No change	No change	No change	No change	No change	No change
	Lion	No change	Prefer younger	Prefer older	No change	Prefer older	Prefer younger
	Human	No change	Prefer younger	Prefer older	No change	Prefer older	No change
Nearest neighbour	Dove (control)	No change	No change	No change	No change	No change	No change
	Lion	Prefer older	Prefer younger	Prefer older	No change	Prefer older	Prefer younger
	Human	Prefer older	Prefer younger	Prefer older	No change	Prefer older	Prefer younger

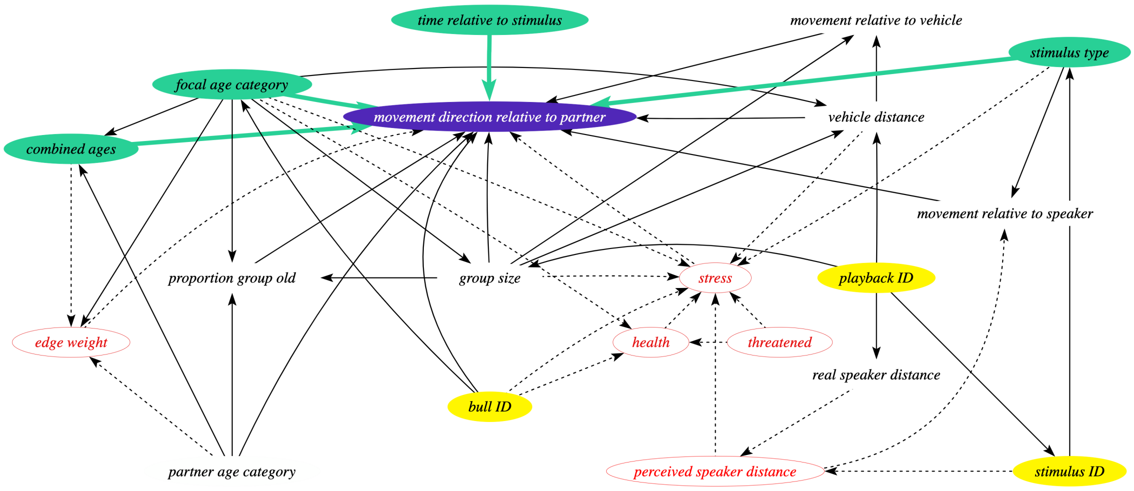
4.2.4.2 Movement behaviour

Movement behavioural analysis has two parts: first identifying the causes of individual movement in response to a stimulus and then, for the times that the focal male is moving, in which direction it moves relative to fellow group members. For the probability of movement I hypothesised that, regardless of whether grouping is for protection or social learning, younger elephants would be more likely to move than older males under low-level threat scenarios (lion) because younger males are more vulnerable, whereas all ages would move for high-level threat scenarios (human). In terms of movement direction, if protection is involved (hypothesis 1) then males will bunch in response to a lion, and older males will defend younger males in response to a human, by holding their ground to give younger group members time to move away. However, if social learning is involved (hypothesis 2), I hypothesised that young males will approach older males while old bulls will either ignore young males (lion) or lead them away (human).

To determine the causes of whether or not an elephant moved I used a binomial model (Movement Binomial Model, MBM), considering focal age and stimulus type as explanatory variables. Excluding all data points in which the focal individual was not moving, I then used an ordinal regression to test if the ages of the focal and target elephants, and the stimulus type played, caused differences in focal movement direction relative to the target (Movement Ordinal Model, MOM): directly away (category level 1), away at an angle (category level 2), neither towards nor away (category level 3), approaching at an angle (category level 4), or approaching directly (category level 5). Directed Acyclic Graphs (DAGs) are shown in Figure 17. In both models, I was interested in the total causal effect of age and stimulus type, so I did not condition on any mediators. While there are some complex relationships to be expected, there are no open backdoor pathways between exposure and outcome, so no additional variables should be conditioned on in order to observe the effects of those variables of interest.



(i) Probability that the focal will move



(ii) Probability that a moving elephant will be approaching a specific target

Figure 17: Directed acyclic graphs (DAGs) showing the causal structure for the movement models. These graphs show the assumed causal relationships contributing to (i) the probability of an elephant moving, and (ii) the probability that a moving elephant will be approaching a particular target elephant. Outcome variables are shown in purple. Exposure variables are shown in green, random effects in yellow, and unobserved variables are red-ringed. Thick green lines indicate direct effects of exposures on the response variable, while dotted lines show paths going though unobserved variables. The DAGs indicate that all paths are causal, leaving no open backdoor paths.

I created the following model to estimate the total causal effect of focal age and the stimulus on the probability of male movement (henceforth Movement Binomial Model, MBM), using the DAG in Figure 17i to understand which variables should (or should not) be conditioned on:

$$\begin{aligned}
move_{F_i} &\sim Bernoulli(\lambda) \\
\phi &= logit(\lambda) \\
\phi &= intercept + \beta_{age_F} * \delta_{age_F}[1 : age_{F_i}] + \\
&\beta_s * stimulus_i + \beta_t * time_i + \beta_{st} * stimulus_i * time_i + \\
&\sigma_F * \alpha_F[focal] + \sigma_R * \alpha_R[recording] + \sigma_T * \alpha_T[trial] \\
c(\beta_{age_F}, \beta_s, \beta_t, \beta_{st}) &\sim Normal(-1, 1) \\
\delta_{age_F} &\sim Dirichlet(2, 2, 2) \\
c(intercept, \alpha_F, \alpha_R, \alpha_P, \sigma_F, \sigma_R, \sigma_P) &\sim Studentt(3, 0, 2.5)
\end{aligned} \tag{4.1}$$

Where $move_F$ is a binomial indicator noting whether the focal elephant is currently moving, age_F is the age category of the focal, $stimulus$ is the type of stimulus played, and $time$ is the time through the experiment relative to the start of the stimulus. I coded time as a categorical variable for before the stimulus started, during the stimulus, and after it ended, because local farmers described that crop-foraging elephants would often return to their original behaviour as soon as the farmers stopped shouting. There are also three random effects of identity of the focal individual ($focal$), the recording number played ($recording$), and the experiment number ($trial$). For all models in this chapter, I used priors that gave a wide spread of variation around the central mean (Appendix A3.2). In this case, because of the low average probability of movement, I use a $Normal(-1, 1)$ prior for all slope parameters (Figure A41i). This low average time spent moving is due to the set up conditions of the experiment: to minimise the risk of elephants moving away during the setup I used groups that were resting under trees, which, by definition, meant they were very rarely moving for the first half of the observations. There was therefore a strong skew towards elephants not moving, which needs to be reflected in the prior structure. I used a fairly wide and flat prior for the random effects because I had no prior expectations for the extent to which individuals would vary in their behaviour, or if some of the sound files might contain additional confusing or fear-inducing sounds undetectable to the human ear.

To assess the causes of male movement direction, after excluding all observations in which the focal elephant was stationary, I used an ordinal regression (Movement Ordinal Model, MOM) with the following structure (see DAG in Figure 17ii to explain the choices of variables to be conditioned on):

$$
\begin{aligned}
MD_{FT_i} &\sim OrderedLogit(\phi_i, \kappa_k) \qquad (4.2)\\
\phi = intercept + \beta_{age_F} * \delta_{age_F}[1 : age_{F_i}] &+ \beta_{age_{FT}} * combinedage_{FT_i} +\\
\beta_s * stimulus_i + \beta_t * time_i &+ \beta_{st} * stimulus_i * time_i +\\
\sigma_F * \alpha_F[focal] + \sigma_R * \alpha_R[recording] &+ \sigma_T * \alpha_T[trial]\\
c(\beta_{age_F}, \beta_{age_{FT}}, \beta_s, \beta_t, \beta_{st}) &\sim Normal(0, 1)\\
\delta_{age_F} &\sim Dirichlet(2, 2, 2)\\
c(intercept, \alpha_F, \alpha_R, \alpha_P, \sigma_F, \sigma_R, \sigma_P) &\sim Studentt(3, 0, 2.5)\\
\kappa &\sim Studentt(3, 0, 2.5)
\end{aligned}
$$

Where MD_{FT} is the movement direction of the focal elephant (*F*) relative to the target (*T*); age_F is the age category of the focal individual (1 = 10-15 years old, 2 = 16-20 yrs, 3 = 21-25 yrs, 4 = 26-35 yrs); $combinedage_{FT}$ is an unordered categorical variable that is a combination of the focal and target elephants' ages (16 categories: Focal category 1 + Target category 1, Focal 1 + Target 2, Focal 2 + Target 1, etc.); and $stimulus$ and $time$ are the same as in the MBM. For this model I used priors of $Normal(0, 1)$ for the slope parameters because all of my hypotheses imply that there should be a combination of both positive and negative effects (Appendix A3.2: Figure A41ii).

4.2.4.3 Looking direction

The next model, the Looking Ordinal Model (LOM), tests if male elephants are more likely to look at group members following a threat stimulus than a control, to observe the behaviour of other individuals. I hypothesise that: under hypothesis 1 in which older males are protecting younger males, young males will not look at older males but older will look at younger; under hypothesis 2 in which younger males are gaining social information about threat responses, then younger males will look at older; and under hypothesis 3 in which both protection and social learning are important, younger will still look at older but older will only look at younger for a low-level stimulus in which older bulls are not at risk (Table 2). The LOM follows a similar structure to the MOM to look for a causal effect of the playback on whether an elephant is looking away from (category level 1), is side-on to (level 2), or is looking towards (level 3) the target.

The DAG for this model is shown in Figure 18, and as before, I need the total causal effect of male age and stimulus type to test my hypothesis, so there are no open backdoor paths between the explanatory and outcome variables. The resulting structure for the LOM is shown in Equation 4.3.

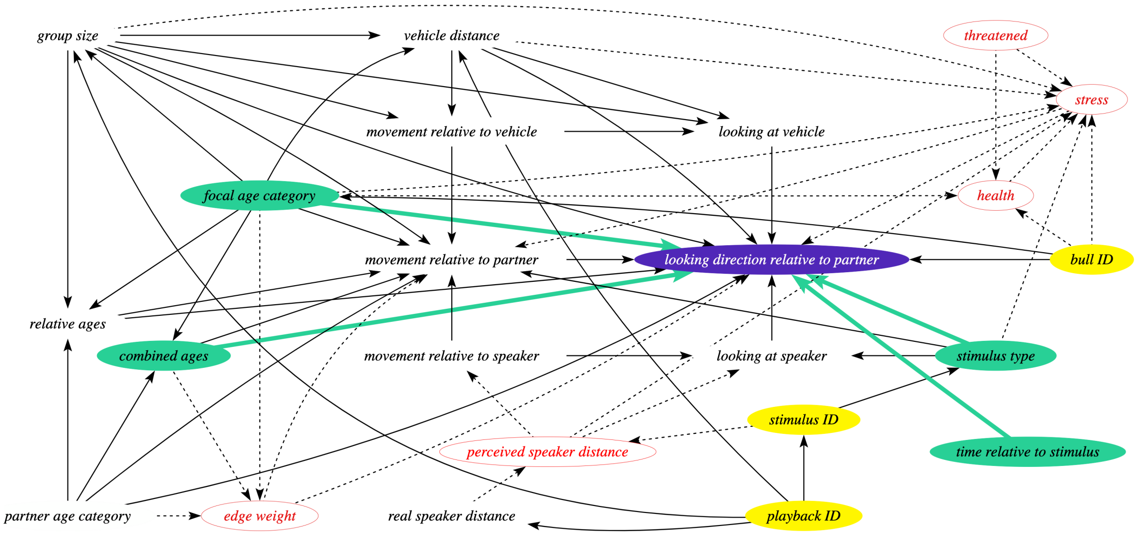


Figure 18: DAG for looking direction model. The graph is showing the causal relationships contributing to the probability of looking at, being side-on to, or looking away from another group member (displayed as a purple filled point). Exposure variables are shown in green, with their direct effects on the response in the thicker green arrows. Random effects are shown in yellow. Unobserved variables are contained in a red circle and their causal pathways are displayed as dotted lines. The DAG indicates that all paths are forwards between exposures and outcome, meaning there are no open backdoor paths to close.

$$\begin{aligned}
LD_{FT_i} &\sim OrderedLogit(\phi_i, \kappa) \qquad (4.3)\\
\phi = intercept + \beta_{age_F} * \delta_{age_F}[1:age_{F_i}] &+ \beta_{age_{FT}} * combinedage_{FT_i} + \\
\beta_s * stimulus_i + \beta_t * time_i &+ \beta_{st} * stimulus_i * time_i + \\
\sigma_F * \alpha_F[focal] + \sigma_R * \alpha_R[recording] &+ \sigma_T * \alpha_T[trial]\\
c(\beta_{age_F}, \beta_{age_{FT}}, \beta_s, \beta_t, \beta_{st}) &\sim Normal(-1, 1)\\
\delta_{age_F} &\sim Dirichlet(2, 2, 2)\\
c(intercept, \alpha_F, \alpha_R, \alpha_P, \sigma_F, \sigma_R, \sigma_P) &\sim Studentt(3, 0, 2.5)\\
\kappa &\sim Studentt(3, 0, 2.5)
\end{aligned}$$

Where LD_{FT} is the looking direction of the focal *F* relative to the target *T*. As before, age_F is focal age category, $combinedage_{FT}$ is a combination of both the focal and target age categories, $stimulus$ is the stimulus type, and $time$ is the time relative to the stimulus. For the priors, I again used a $Normal(-1, 1)$ prior, because resting elephants generally stood facing side-on or away from other group members (Appendix A3.2: Figure A41iii).

4.2.4.4 Nearest neighbour

Finally, to analyse which group member the focal chose to stand closest to, I used a binomial model (Neighbour Binomial Model, NBM), which took the data for all pairs of elephants at all time points to look for causal effects of focal age, target age, stimulus type and time relative to the stimulus on the probability of whether that specific target elephant would be the neighbour of the focal (DAG shown in Figure 19). Under all three hypotheses, a change in nearest neighbour following a stimulus would indicate a social response to the threat (Table 2).

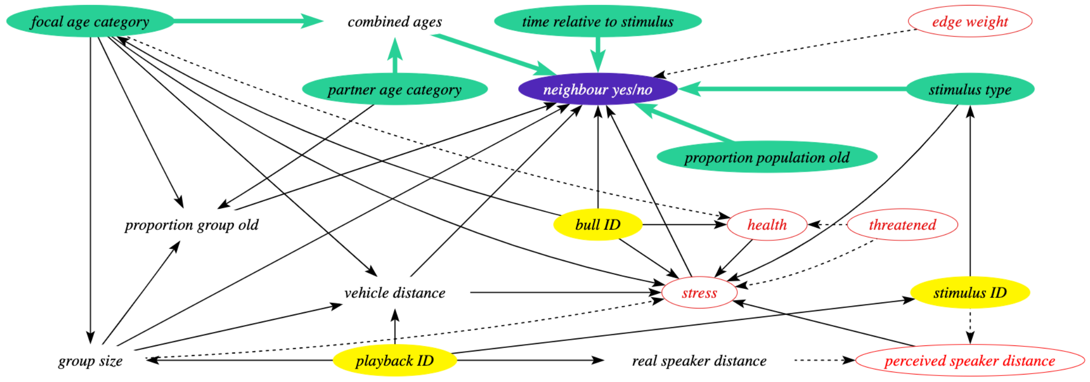


Figure 19: DAG for nearest neighbour model. This graph shows the causal relationships contributing to the probability of a specific group member being the nearest neighbour of the focal elephant in question. This model contains an extra variable: the proportion of the population that is old. In the case of males grouping for either protection or social learning, age is expected to affect neighbour choice, which will in turn affect the availability of old (or young) males to be the nearest neighbour. All paths are causal, leaving no open backdoor paths.

For this model I used the structure:

$$
\begin{aligned}
neighbour_{FT_i} &\sim Bernoulli(\lambda) \\
\phi &= logit(\lambda) \\
\phi = intercept + offset(logit(populationage)) &+ \\
\beta_{age_{FT}} * combinedage_{FT_i} &+ \\
\beta_s * stimulus_i + \beta_t * time_i + \beta_{st} * stimulus_i * time_i &+ \\
\sigma_F * \alpha_F[focal] + \sigma_R * \alpha_R[recording] + \sigma_T * \alpha_T[trial] & \\
c(\beta_{age_{FT}}, \beta_s, \beta_t, \beta_{st}) &\sim Normal(0,1) \\
c(\alpha_F, \alpha_R, \alpha_P, \sigma_F, \sigma_R, \sigma_P) &\sim Studentt(3,0,0.5) \\
intercept &\sim Studentt(3,0,1)
\end{aligned}
\tag{4.4}
$$

Where $neighbour_{FT_i}$ is a binomial measure for if the target T is the nearest elephant to the focal

F, and $stimulus$ and $time$ are as defined in the previous models. I have defined $combined\ age$ slightly differently in this model to avoid issues of overparameterisation. Here, I amalgamated the focal and target ages into just two categories, Young (10-15 yrs and 16-20 yrs) or Old (21-25 yrs and 26-35 yrs), so the age combination was limited to either both young, young focal and old target, old focal and young target, or both old. These categories are biologically relevant because they separate adolescence (10-20 years old) from adulthood ($>$ 20 years) (Evans and Harris, 2008). This model also contains an additional control variable: $population\ age$. This is a measure of the proportion of possible male elephant pairs in the population that are of each age combination (both old: 0.363; focal old and target young : 0.240; focal young and target old: 0.240; both young: 0.158). This offset accounts for the population availability of individuals of that particular $combined\ age$ variable, so that the final contrasts indicate bull preference for one neighbour or another over and above that which would be expected based on random chance. All other variables are as above. I used priors of $Normal(0, 1)$ for all slope parameters because I had no prior expectations for how neighbours may be selected. For this model, I reduced the breadth of the random effect priors to aid model fit (prior predictive check available in Appendix A3.2: Figure A41iv).

4.2.4.5 Calculation of average treatment effects

For all models, I calculated the total causal effect as the average marginal effect for each variable. To do this, I adapted the raw data to create an artificial dataset, then predicted from both and compared the predictions.

To calculate the effect of age in the movement and looking direction models, I created the artificial data by assigning each elephant to the next age category, and then changing the respective age combination to match. To retain the same set of categories, I assigned elephants in the oldest category to the youngest category in the artificial data. I calculated the average treatment effect for age category by subtracting the predictions taken from the raw data from the artificial predictions (note that overall treatment effects exclude elephants ”ageing” from the oldest to youngest age category).

For the effect of $stimulus{*}time$, I created artificial data by creating a complete dataset for each combination of stimulus and time, then compared the predictions from each artificial dataset. For ages in the nearest neighbour model I followed the same protocol using each of the four combination of focal and target age.

It should be noted here that none of the experimental groups to which I played a lion stimulus contained elephants in category 1 (10-15 years old), so there are no predictions or contrasts for this data combination.

4.2.4.6 Data exclusion

Due to a combination of technical faults with the speakers and cameras, and variation in the distances between the speaker and elephants, I excluded 13 experiments from the final analysis, leaving a total of 48 experiments, evenly split amongst the three stimulus types. This left data for 176 elephants (10 elephants under 15 years old, 60 in the 16-20 age category, 70 of 21-25 years old, and 36 were 26-35 years old) in groups ranging from two to eight individuals.

4.3 Results

4.3.1 Movement behaviour

4.3.1.1 Movement probability

Elephants spent a total of 16.23 ± 23.87% (mean ± SD) of their time moving before the stimulus began. This may not reflect typical activity levels for elephants because I generally targeted resting groups. During the stimulus they increased their movement to 35.42 ± 36.27% of observations spent moving, before declining to 28.44 ± 34.21% moving after the stimulus.

The MBM showed that elephants were more likely to move during a threat stimulus than the control (Figure 20), and less likely to move as they aged (Figure 21). Table 3 shows a breakdown of the effect of changing age category and changing stimulus type. I have not shown the differences between stimuli for the ”before” phase at any point throughout this study, because no measure showed any difference before the stimulus.

Table 3: Contrasts for MBM. Contrasts between age categories (top) and stimulus types (bottom) for probability of movement (MBM), shown as ”mean [95% credible interval] (percentage of contrast distribution below zero)”. Bold values indicate contrasts where over three quarters of the contrast values are either positive ($<$25% of contrast distribution is below zero) or negative ($>$75% of contrast distribution is below zero). A negative value indicates that changing from one age category to the next, or from one stimulus to another reduces the probability of movement.

Section	Contrast	Probability of Movement
Overall	10-15 → 16-20 (1 vs 2)	**-0.0511 [-0.235:-0.0000176] (98.8)**
	16-20 → 21-25 (2 vs 3)	**-0.0350 [-0.136:-0.0000344] (98.8)**
	21-25 → 26-35 (3 vs 4)	**-0.0423 [-0.175:-0.0000250] (98.8)**
	10-15 → 26-35 (1 vs 4)	**-0.150 [-0.482:-0.000138] (98.8)**
During	dove → lion	**0.152 [0.0000:0.461] (2.5)**
	dove → human	**0.231 [0.000320:0.566] (1.3)**
	lion → human	**0.0798 [-0.193:0.389] (24.0)**
After	dove → lion	0.0406 [-0.130:0.298] (33.4)
	dove → human	0.0322 [-0.223:0.364] (38.9)
	lion → human	-0.00838 [-0.312:0.270] (53.8)

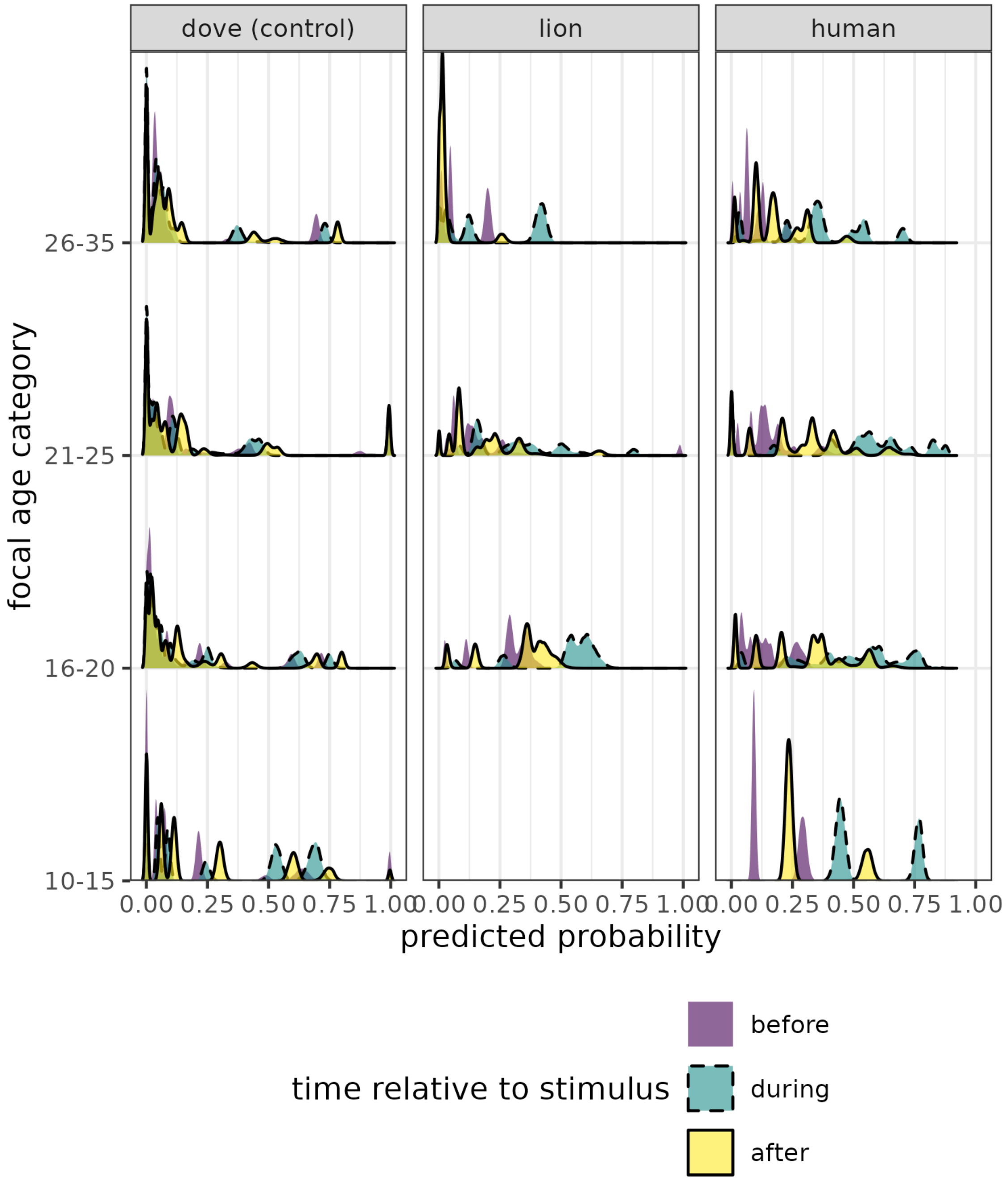


Figure 20: Predicted probabilities from MBM. Predictions are taken from the data. Columns show the stimulus played, while rows are the ages of the focal individuals. Note there is no probability distribution for a 10-15 year old in a lion playback, because none of these playbacks contained an elephant of this age. Colours and line types show the time of the observation relative to the stimulus. All distributions are very broad and multimodal, but lion and human stimuli predict a higher probability of moving than does the dove, and this effect is more pronounced during the stimulus than before or after.

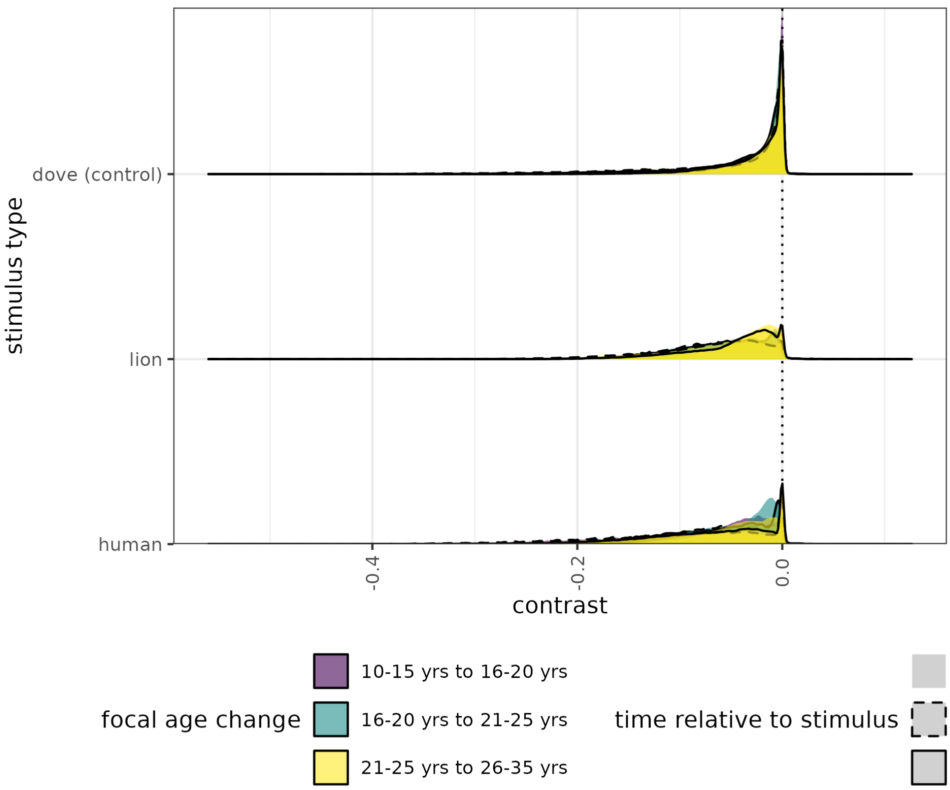


Figure 21: Differences between age categories in MBM. Contrasts between elephants in true versus altered age categories in their probability of moving in response to a stimulus (see section Calculation of average treatment effects). Colours indicate the age categories being compared, line types show the time relative to the stimulus. All effects are predominantly negative, regardless of stimulus type or time relative to the stimulus.

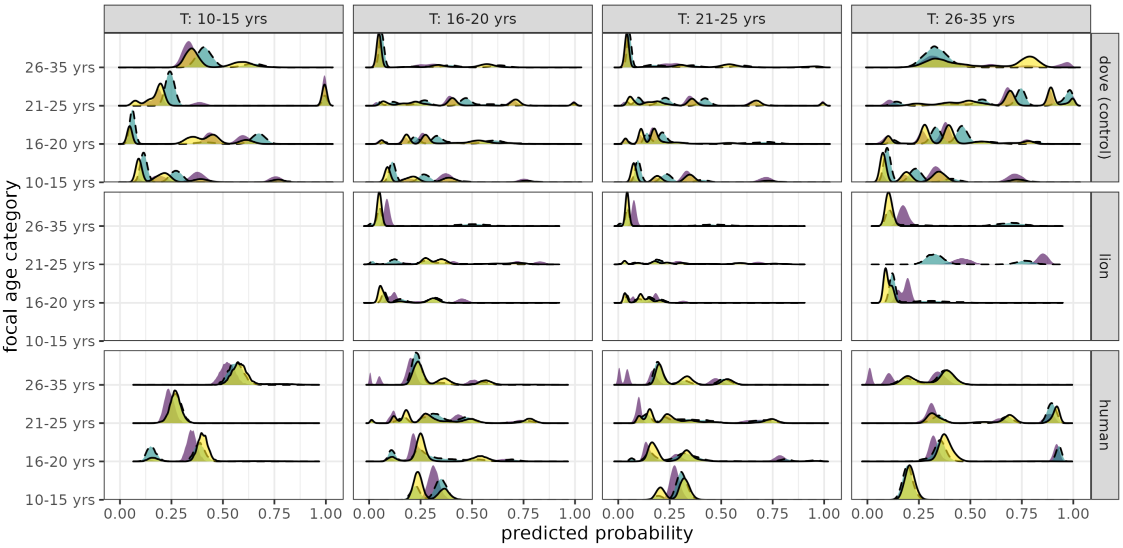
4.3.1.2 Movement direction

Table 4 shows the observations that an elephant spent moving in a particular direction as a percentage of the total time spent moving. Directly towards and away are the most common, while directly with is very rare. At first inspection, there does not appear to be an effect of experimental section. Table A10 (Appendix A3.3) shows the breakdown of these proportions split by the elephants' relative ages and the stimulus type.

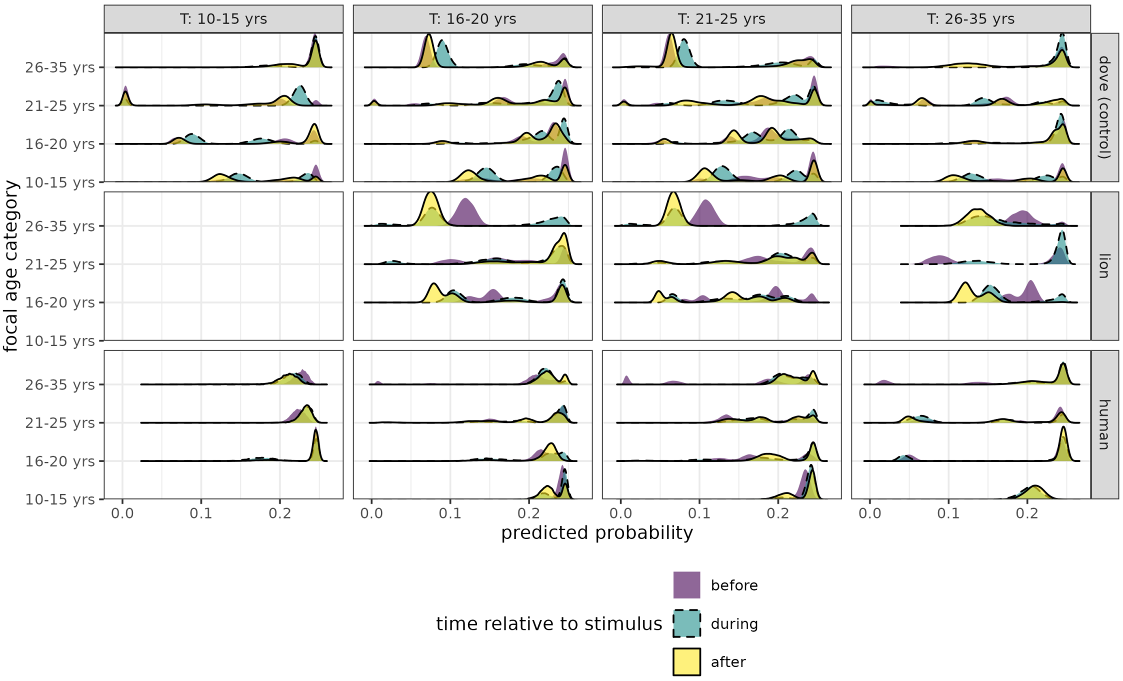
Table 4: Percentage of time the focal spent moving in different directions relative to the target. Values are separated into experimental phases, relative to the stimulus. Values are mean ± SD.

Direction	Before	During	After
Move away directly (1)	33.61 ± 38.28	36.17 ± 43.10	37.34 ± 40.64
Move away at an angle (2)	20.69 ± 29.14	22.08 ± 34.07	18.28 ± 26.51
Move directly with (3)	1.28 ± 7.74	4.22 ± 14.85	5.65 ± 16.63
Approach at an angle (4)	17.32 ± 28.43	14.96 ± 27.84	15.37 ± 26.17
Approach directly (5)	27.10 ± 36.01	22.56 ± 37.00	23.36 ± 34.67

The MOM indicates no evidence for an overall effect of focal age on male movement direction relative to the target (Figure 22). Increasing focal age by one age category led to an average change in probability of: -0.00302 [-0.185:0.195] (52.8% of contrast values negative) for moving directly away; 0.00110 [-0.0649:0.0688] (50.8% negative) for moving away at an angle; 0.0000445 [-0.0213:0.0202] (48.7% negative) for moving directly alongside another male; -0.000185 [-0.0697:0.0613] (48.1% negative) for approaching at an angle; and finally 0.00206 [-0.162:0.171] (47.2% negative) for a direct approach. However, when comparing individual age categories, it becomes slightly more complex: age category 3 may be slightly more likely to move away from the target than categories 2 or 4, suggesting that age category 3 may be most likely to lead the group. However, contrasts between other age categories showed no effect in either direction, and the difference between category 3 and categories 2 and 4 is not large, so care should be taken before drawing conclusions regarding potential age effects. Finally, all of the focal age contrasts are dependent on the age of the target individual, with larger effect sizes for older targets, indicating that decisions may be more consistently different between age categories when around older males than younger ones. Table 5 and Figure 23 show a full breakdown of focal age contrasts.

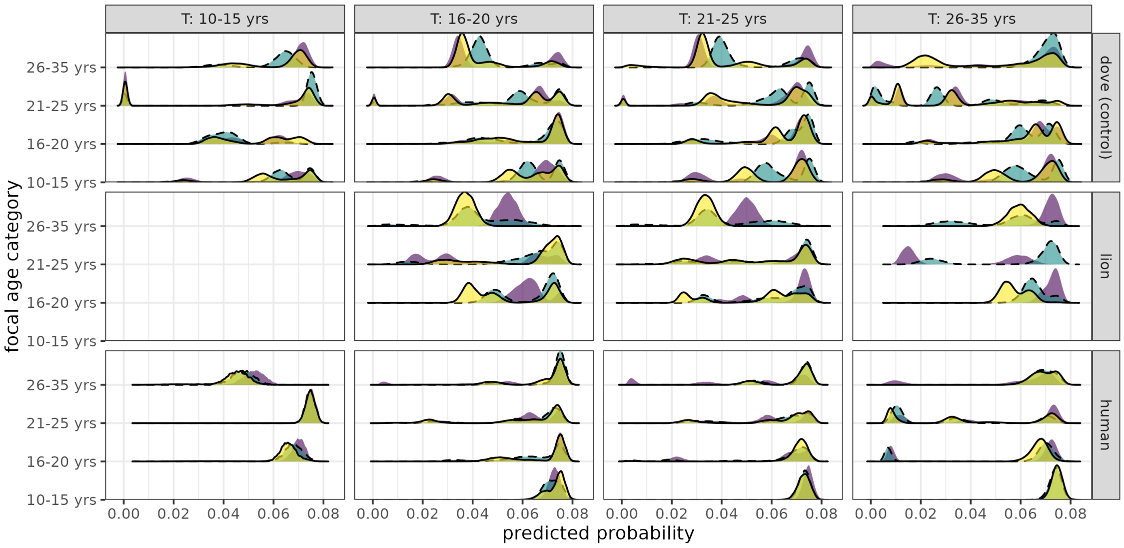


(i) Moving directly away from the target

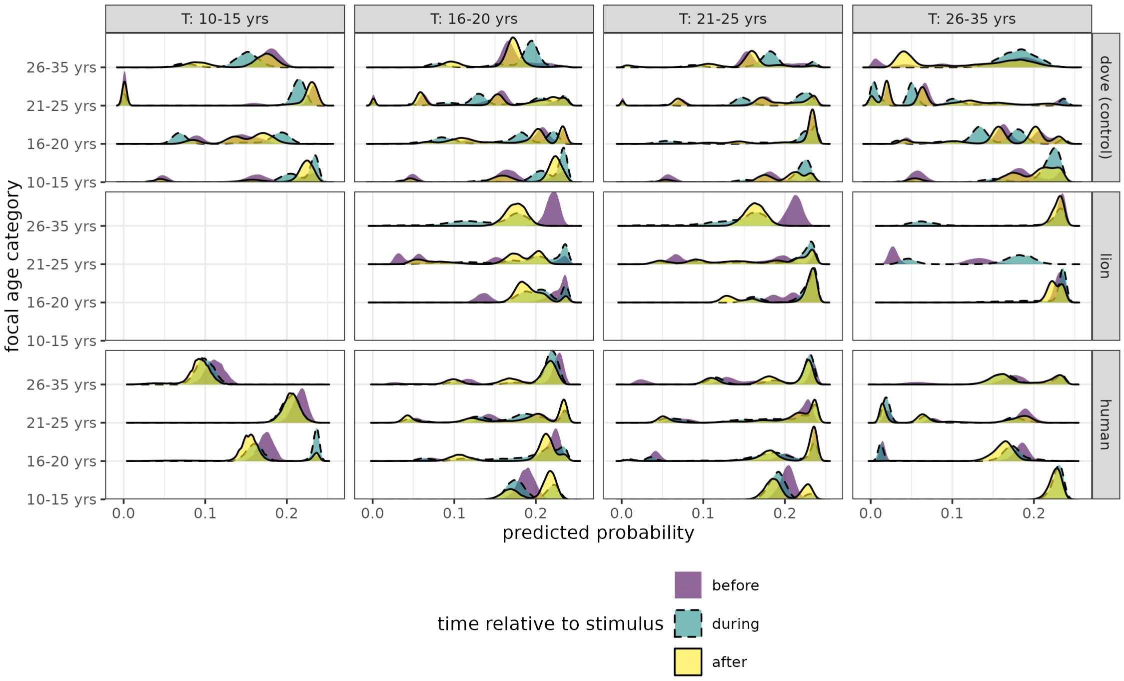


(ii) Moving away from the target at an angle

Figure 22

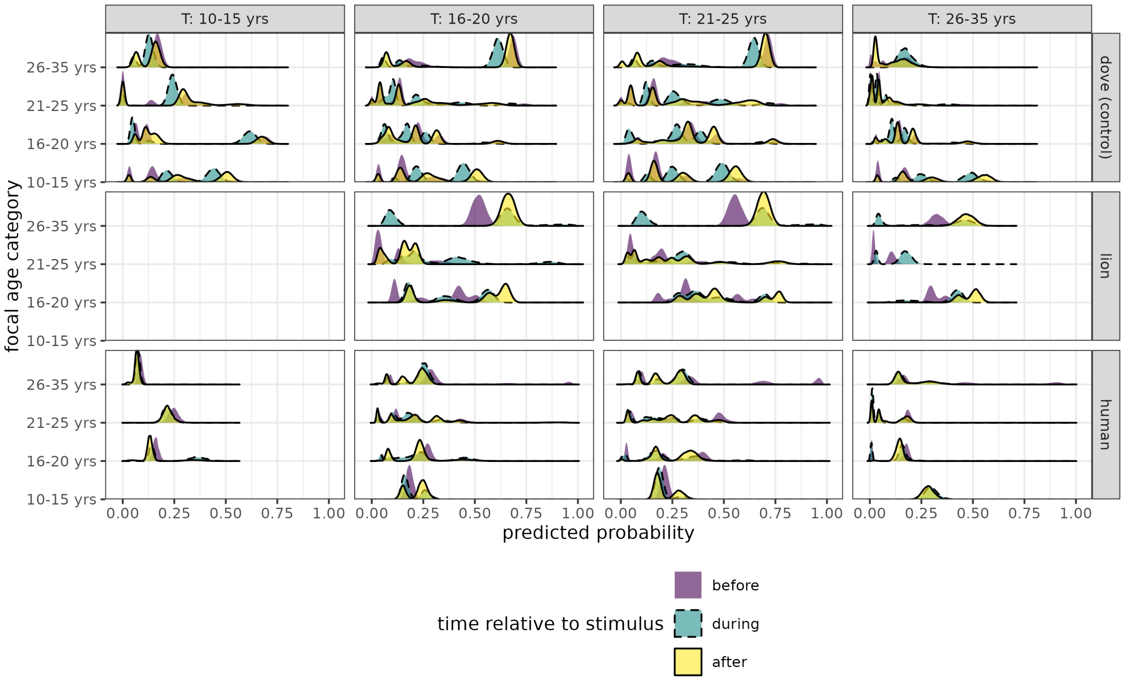


(iii) Moving side on to the target



(iv) Approaching the target at an angle

Figure 22



(v) Approaching the target directly

Figure 22: Predicted probabilities from MOM. Probability of moving i) directly away from, ii) away at an angle from, iii) neither towards nor away from, iv) towards at an angle, or v) directly towards, another elephant. Columns show the age of the target individual to which their movement is relative; rows show the stimulus played; fill colours and line types show the time relative to the stimulus. The predictions are taken from the data and indicate no consistent effect of focal age, target age or stimulus type on movement direction. Note that the scales are variable among panels and can display extremely narrow windows of probability, especially when predicting a transition from one extreme to the other.

Table 5: Contrasts for MOM. Effect of changing age category on predicted probability of moving in different directions relative to a target individual, reported as: mean [95% credible interval] (percentage of contrast values below zero). All 95% credible intervals span zero, with the majority being approximately centred on zero. Bold entries indicate those where over three quarters of the contrast distribution is either above or below zero. A negative result indicates that ageing from one category to the next decreases the probability of a movement direction relative to the target.

Contrast	Away directly (1)	Away at an angle (2)	Neither towards or away (3)	Approach at an angle (4)	Approach directly (5)
10-15 → 16-20 (1 vs 2)	0.0201 [-0.143 : 0.260] (46.0)	-0.00387 [-0.0713 : 0.0688] (58.4)	-0.00246 [-0.0253 : 0.0183] (59.1)	-0.00824 [-0.0919 : 0.0486] (55.4)	-0.00548 [-0.200 : 0.169] (54.0)
16-20 → 21-25 (2 vs 3)	**0.0556** **[-0.0668 : 0.223]** **(19.8)**	0.00796 [-0.0516 : 0.0669] (39.5)	-0.00124 [-0.0232 : 0.0167] (51.9)	-0.0137 [-0.0776 : 0.0400] (68.3)	**-0.0486** **[-0.183 : 0.0687]** **(80.2)**
21-25 → 26-35 (3 vs 4)	**-0.0615** **[-0.215 : 0.0504]** **(85.0)**	-0.00418 [-0.0707 : 0.0703] (58.1)	0.00173 [-0.0182 : 0.0233] (41.8)	0.0139 [-0.0422 : 0.0703] (28.4)	**0.0501** **[-0.0416 : 0.198]** **(15.0)**
10-15 → 26-35 (1 vs 4)	0.00934 [-0.194 : 0.243] (48.8)	0.00641 [-0.0673 : 0.0987] (45.0)	0.000780 [-0.0244 : 0.0260] (46.7)	-0.00244 [-0.0767 : 0.0739] (52.6)	-0.0141 [-0.279 : 0.180] (51.2)

Regarding the stimulus type, I found no overall difference in probability of moving in any particular direction either during (dove → lion: 0.00253 [-0.228:0.225], 47.2% of the contrast distribution below zero; dove → human: 0.00233 [-0.133:0.112], 44.2% below zero; lion → human: 0.000389 [-0.152:0.139], with 49.0% below zero) or after (dove → lion: -0.0000694 [-0.174:0.183], with 50.2% below zero; dove → human: 0.0000810 [-0.0781:0.0748], with 49.2% below zero; lion → human: 0.000157 [-0.173:0.160], with 49.6% below zero) the stimulus.

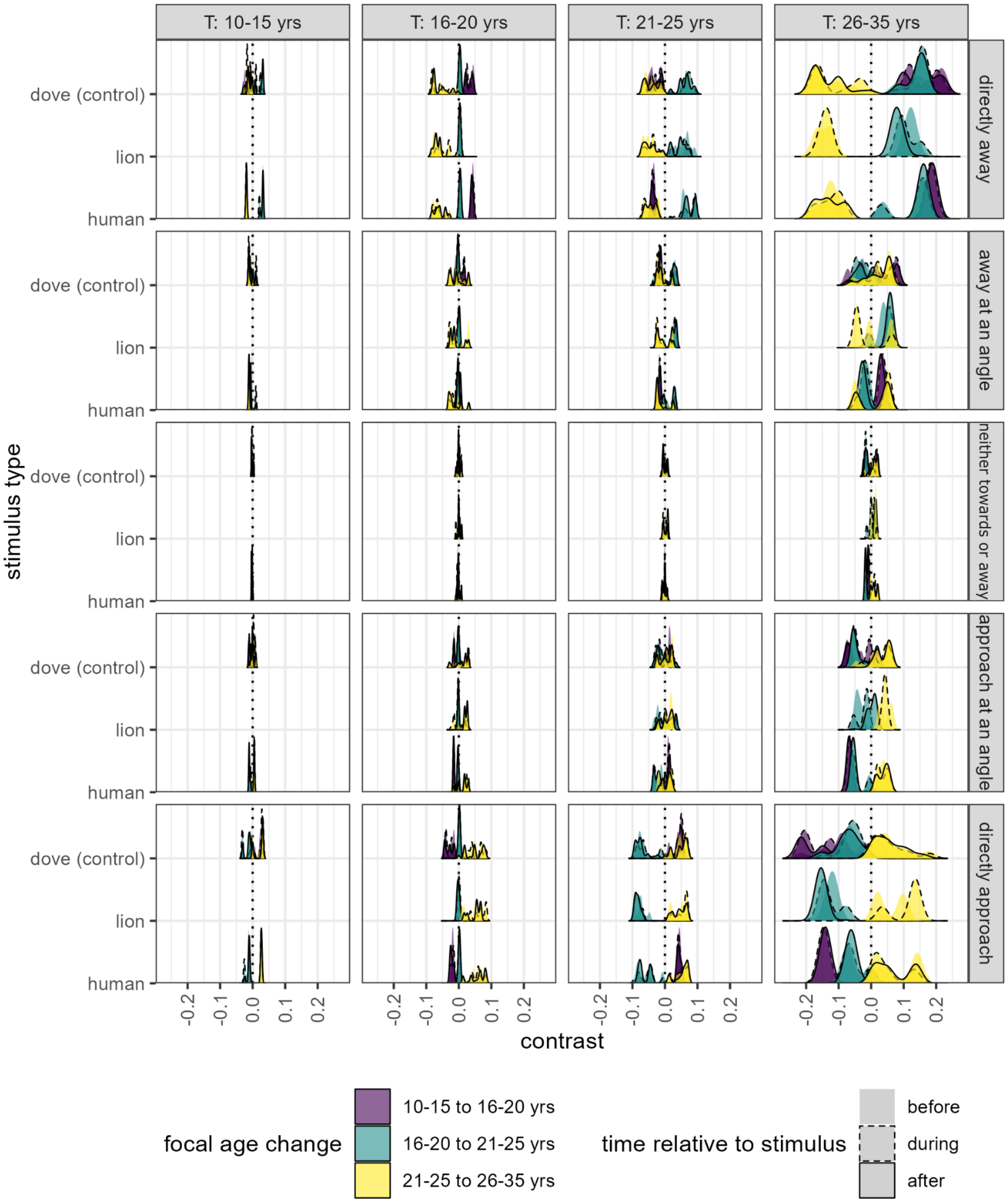


Figure 23: Differences between age categories in MOM. Contrasts between focal age categories show differences in the predictions depending on the age of the target individual. Columns show age of the target elephant, rows show the movement direction relative to said target, and colours show the age of the focal being observed. Stimulus type and the time relative to the stimulus are shown by the rows within each facet and the line type around the distribution. Males in the oldest and youngest age categories are more likely to approach others in the group than males in categories 2 and 3, with category 3 the least likely to approach. Contrasts increase in size with the age of the target individual, so movement direction is more consistent relative to older males than younger.

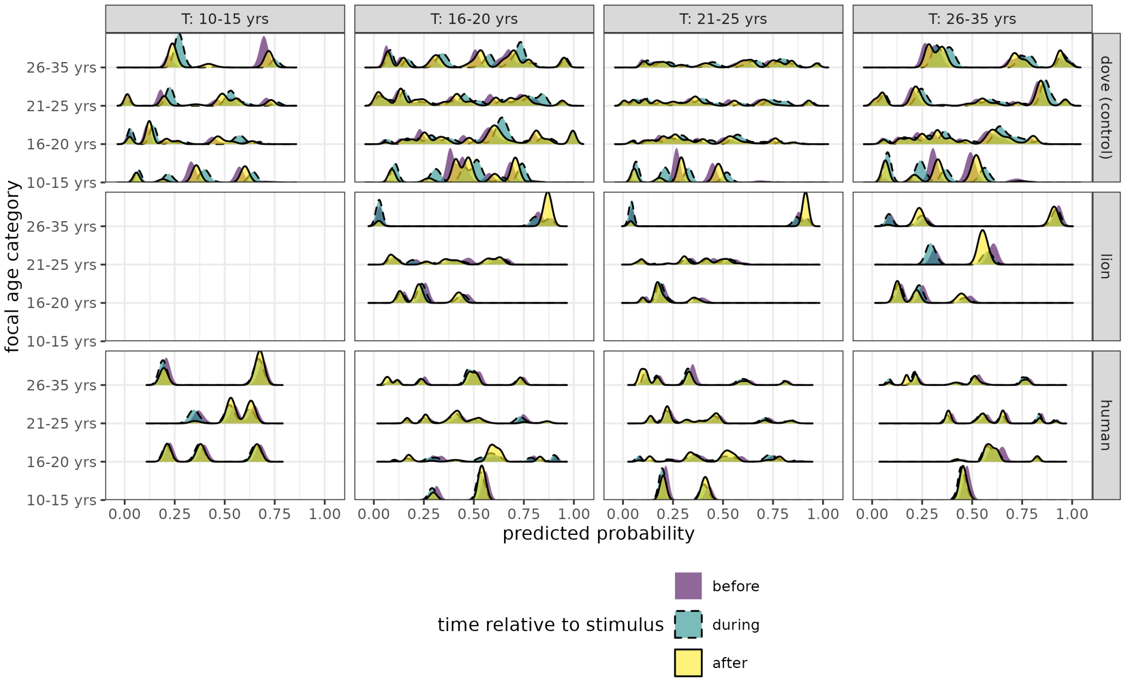
4.3.2 Looking direction

For looking direction, looking away was a slightly more common behaviour within all phases of the experiment than was being side-on to the target, whereas looking towards was substantially the least common. It is surprising that looking away was more common than being side-on, because side-on contains the widest angle, so under random decisions, elephants should be side-on the most. That side-on is less common than looking away suggests that it is an active choice to orient away from the group. A full breakdown of looking directions with regard to the age of the target male is available in Table A11 (Appendix A3.3). Note that if an elephant moved out of view, their looking direction could no longer be determined. Therefore the during and after values are likely to be affected by the proportion of the group that moved away from the experiment site in response to the stimulus and therefore were lost to view (see DAG in Figure 18).

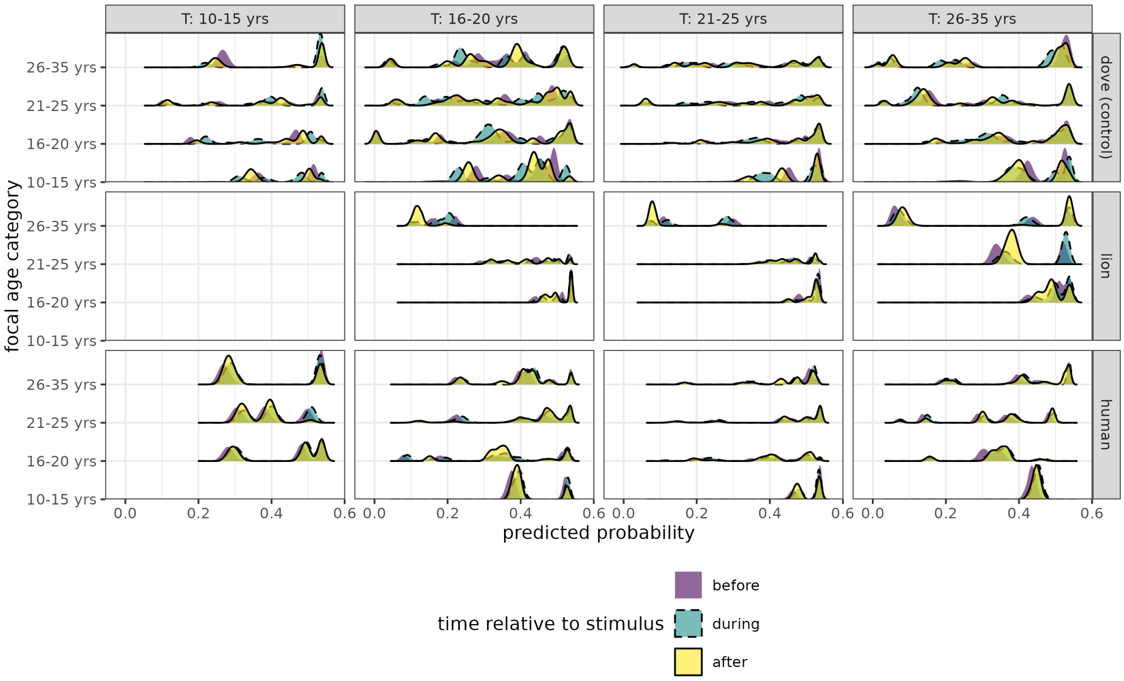
Table 6: Percentage of time spent looking in different directions by the focal relative to the target. Time periods are relative to the stimulus playing. Values are mean ± SD.

Direction	Before	During	After
Look directly away from (1)	44.41 ± 40.18	47.51 ± 43.56	41.83 ± 39.84
Side-on (2)	36.13 ± 33.23	35.88 ± 37.72	40.28 ± 34.38
Look directly towards (3)	19.46 ± 31.11	16.62 ± 31.15	17.88 ± 29.39

I found no average effect of focal age on looking direction: increasing focal age by one category led to an average change in probability of looking away from the target of 0.00237 [-0.182:0.225] with 53.8% of the posterior probability density below zero; being side on to the target of -0.00796 [-0.160:0.129], with 54.2% below zero; and looking towards the target of 0.00560 [-0.156:0.148], with 46.2% below zero. However, looking specifically at the contrasts between individual age categories, there is a tendency for the youngest elephants to be the most likely to look towards the target, and the least likely to look away (Figures 24 and 25). Table 7 shows a full breakdown of the changes between different categories.

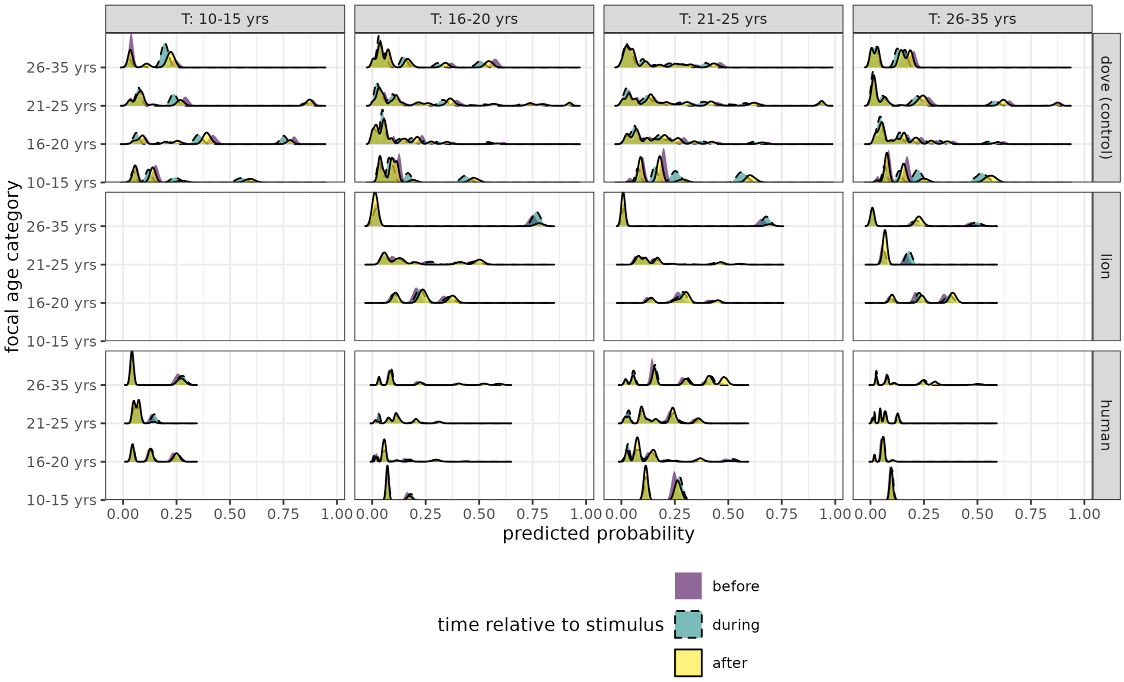


(i) Looking away from the target



(ii) Side-on to the target

Figure 24



(iii) Looking towards the target

Figure 24: Predicted probabilities from LOM. Probability of i) looking away from, ii) standing side on to, or iii) looking towards, another elephant. The predictions indicate generally lower probabilities of looking towards other elephants than side on to or away from them, particularly during threat stimuli. There is however, no difference between phases of the experiment. Younger individuals are slightly more likely to look towards and less likely to look away from others than are older individuals, but there is a lot of noise in the predictions as a whole. Note that the scales are variable among panels for ease of observation.

Table 7: Contrasts for LOM. Effect of changing age category on predicted probability of looking in different directions relative to a target individual, shown as ”mean [95% credible interval] (percentage of contrast distribution below zero)”. All 95% credible intervals contain zero, indicating no strong evidence for an effect of age on looking direction, but some do display a majority of the probability density as either positive (<25% below zero) or negative (>75% below zero). Values in bold highlight contrasts where over three quarters of the contrast values are either positive or negative. A negative value shows that ageing from one category to the next reduces the probability of looking in that direction relative to the target.

Contrast	Away (1)	Side on (2)	Towards (3)
10-15 → 16-20 (1 vs 2)	**0.104** **[-0.102 : 0.306]** **(16.6)**	**-0.0621** **[-0.221 : 0.114]** **(78.3)**	**-0.0424** **[-0.183 : 0.0608]** **(83.4)**
16-20 → 21-25 (2 vs 3)	-0.0286 [-0.170 : 0.229] (74.2)	0.00735 [-0.155 : 0.128] (43.0)	0.0213 [-0.192 : 0.151] (25.8)
21-25 → 26-35 (3 vs 4)	0.0144 [-0.217 : 0.191] (40.8)	-0.0132 [-0.143 : 0.132] (60.7)	-0.00109 [-0.124 : 0.152] (59.2)
10-15 → 26-35 (1 vs 4)	**0.0994** **[-0.163 : 0.382]** **(23.5)**	-0.00691 [-0.264 : 0.240] (50.8)	**-0.0925** **[-0.399 : 0.101]** **(76.5)**

Considering the stimulus type, it can be seen from Figures 24 and 25 that there is no difference between the stimuli in their effect on overall looking direction either during (dove → lion: 0.000 [-0.147:0.130], with 46.5% of the posterior contrast distribution below zero; dove → human: 0.000 [-0.129:0.115], with 46.4% below zero; and lion → human: 0.000 [-0.127:0.128], with 49.8% below zero) or after (dove → lion: 0.000 [-0.130:0.123], with 48.1% of the posterior contrast distribution below zero; dove → human: 0.000 [-0.106:0.108], with 50.7% below zero; and lion → human: 0.000 [-0.127:0.140], with 51.7% below zero) the stimulus.

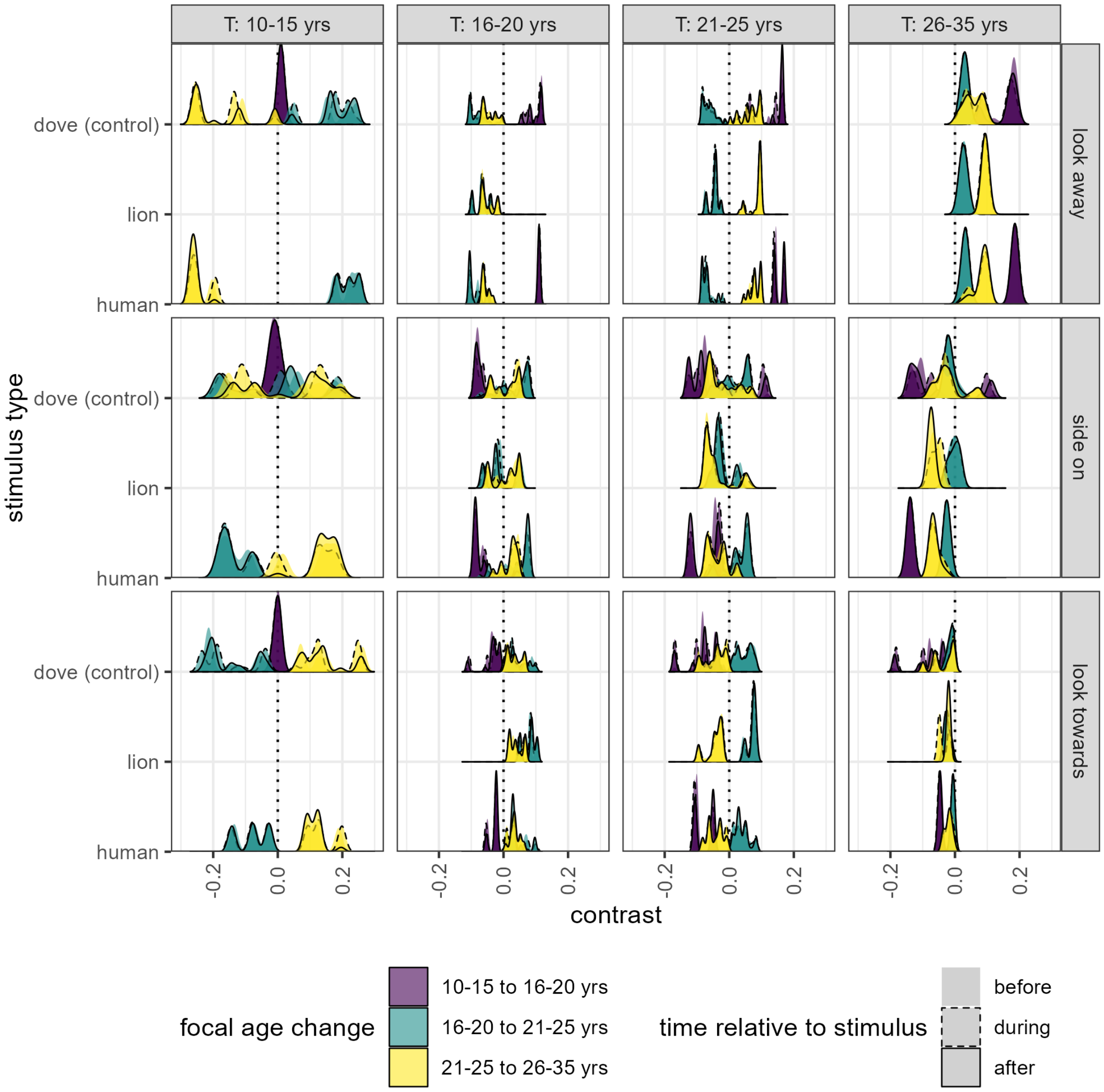


Figure 25: Differences between age categories in LOM. Contrasts between elephants in current versus future age categories (fill colour) in their probability of looking in a particular direction (facet rows) relative to the target (facet columns), in response to a stimulus (stimulus type shown on rows within panels, time relative to the stimulus shown by the line type around the density plot). I found that target males in the oldest category were increasingly likely to be looked away from and less likely to be looked at, as the age of the focal increased. Similar trends can be seen for age category 3, but not so pronounced. When the target is in category 2, there are generally no strong effects of age, though focals in category 2 are more likely to look away than focals in category 1. Finally, focal males in category 3 are the least likely to look towards males in category 1.

4.3.3 Nearest neighbour

Overall, old and young elephants spent a total of 57.60 ± 44.00% and 56.70 ± 42.00% of their time stood closest to an old male respectively. This equates to 31.38% of neighbour pairs comprising an old focal and old target, 31.74% of pairs as an old focal next to young target, 26.42% a young focal next to an old target, and 27.03% were both young. These proportions do not appear to vary substantially between different stages of the playback (Table A12).

For the NBM, I found very limited evidence for an effect of focal age on the probability of a pair being nearest neighbours, but a positive effect of an old target individual (Table 8, Figure 27), even after accounting for the higher number of old males than young ones in the population. Pairs comprising an old focal and a young target were the least likely to be neighbours, and pairs with an old target were the most likely (Table 8, Figure 27). Male elephants therefore always preferred to be closest to an old male, regardless of their own age. It is worth noting again here that nearest neighbour is not necessarily reciprocal, so just because the target is the nearest elephant to the focal does not necessarily mean that the focal would also be the nearest neighbour of the target.

In addition, when the target was young, young males were more likely to select them as a neighbour than were old males. This indicates some degree of age matching between elephants: either young males are next to one another because they are sparring partners (Chiyo *et al.*, 2011), or older males displace young males for prime positions in the shade or next to the oldest neighbours.

I found no effect of the stimulus type on probability of being nearest neighbours either during or after the stimulus played (Table 8, Figure 27), indicating that any preferences for older neighbours were consistent across both threatening and non-threatening scenarios, so were unlikely to do with young males looking for protection or role models.

Table 8: Contrasts for NBM. Contrasts in probabilities of being neighbours different between age category combinations and stimuli. For the age contrasts, F and T indicate Focal and Target, while Y and O show Young and Old respectively (so FY = Focal Young, TO = Target Old). Ages marked with an asterisk (*) indicate the age that has changed. Bold entries show contrasts where at least three quarters of the contrast distribution is either above or below zero. A negative value indicates that the change in age combination reduces the probability that the target is the nearest neighbour of the focal.

Section	Contrast	Mean [95% CI] (% below zero)
Overall	FY+TY → FY+TO*	**0.030 [0.0000:0.0523] (0.0)**
	FY+TY → FO*, TY	**-0.0312 [-0.0927:0.0147] (91.8)**
	FY+TY → FO*, TO*	**0.032 [-0.0103:0.0903] (8.0)**
	FY+TO → FO*, TY*	**-0.0616 [-0.132:0.0000] (99.8)**
	FY+TO → FO*, TO	0.00156 [-0.0441:0.0478] (48.5)
	FO+TY → FO, TO*	**0.063 [0.0000:0.0986] (0.0)**
During	dove → lion	0.0418 [-0.232:0.411] (44.3)
	dove → human	-0.0163 [-0.342:0.273] (55.8)
	lion → human	-0.0581 [-0.546:0.342] (58.0)
After	dove → lion	0.0486 [-0.220:0.420] (42.8)
	dove → human	-0.0230 [-0.341:0.259] (57.5)
	lion → human	-0.0716 [-0.551:0.319] (59.8)

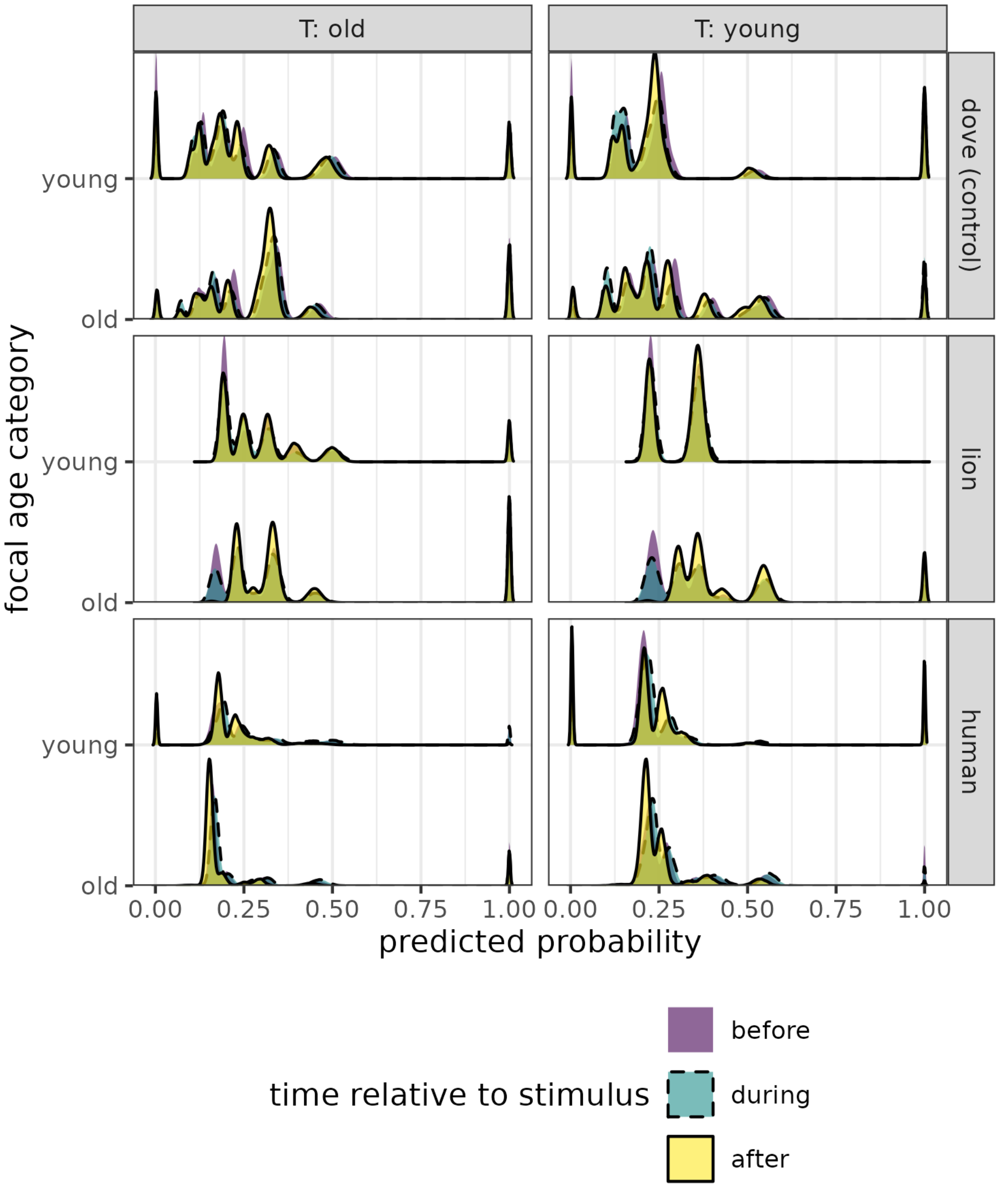


Figure 26: Predicted probabilities from NBM. Probability of being nearest neighbours given the ages of the focal (rows within facets) and target (facet column) individuals, the type of stimulus played (facet rows), and whether the measurement was taken before, during or after the stimulus (fill colours and outline types). There does not appear to be any noticeable difference between the stimuli or time relative to the stimulus, though the range of probabilities appears wider for the dove control than lion or human.

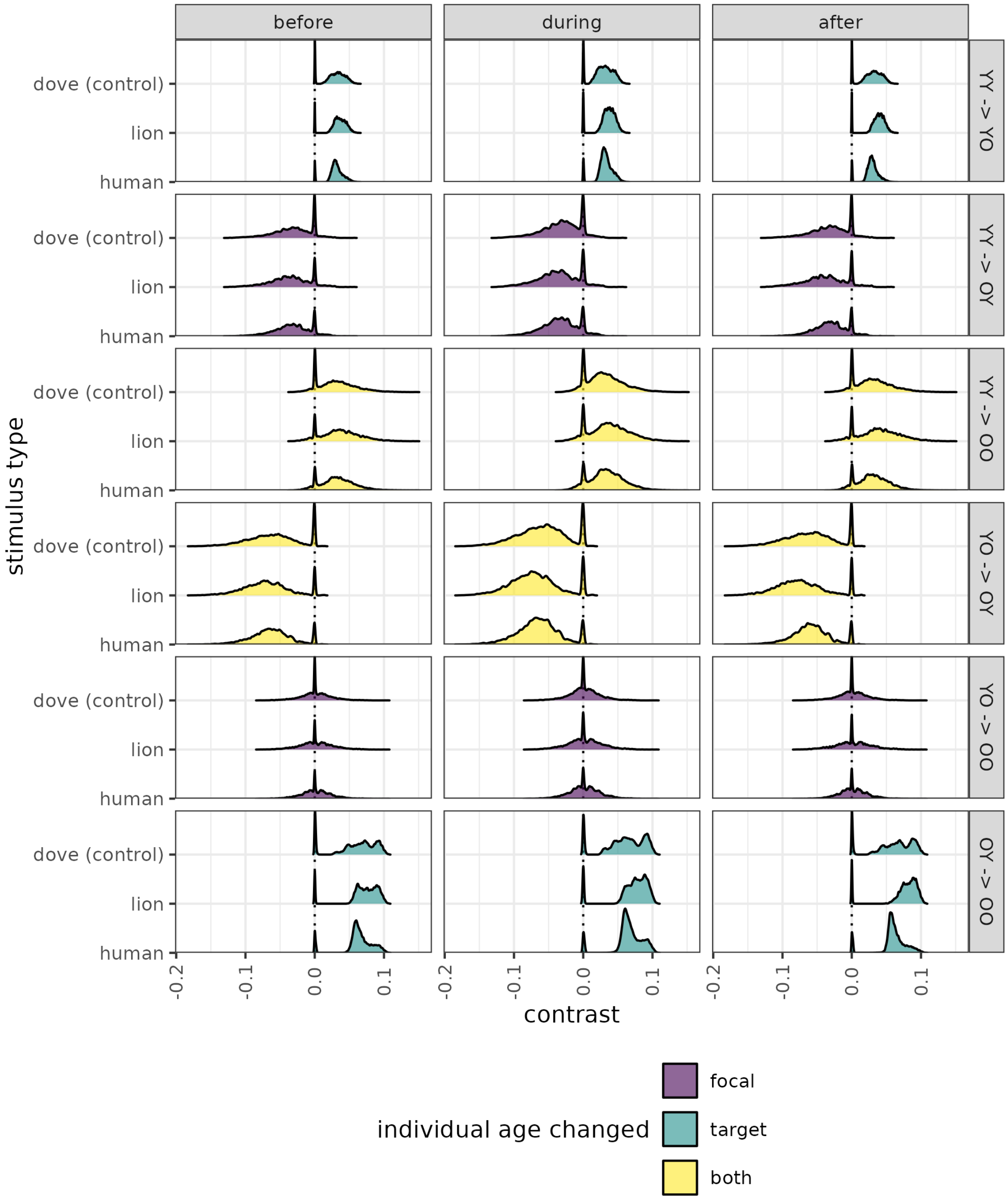


Figure 27: Differences between age categories in NBM. Contrasts between age category combinations show that older targets are preferred neighbours, with positive contrasts when the target age increases (green curves for target age changed, yellow curves for both change), and negative contrasts when the target age decreases (yellow curve). Changing only the focal age (purple curves) has no effect when the target is old, and leads to a reduced probability of being neighbours when the target is young. Male elephants therefore prefer to be closest to older males, regardless of their own age. There is no effect of stimulus type or time relative to the stimulus on nearest neighbour, so this preference for older male neighbours is likely a general pattern, not a threat response.

4.4 Discussion

Overall, I found some evidence for effects of age on male social behaviour, but that these effects were not related to the threat response. Elephants of all ages preferred to be closest to males in the older age categories (even after accounting for the fact that there were more adult males present during the experiments than there were adolescents), indicating that there were age-based social preferences within groups. This could be explained by the oldest males being able to displace others from the best resting spot, while the rest gather as close to it as possible. However, a preference for old neighbours supports similar findings from Evans and Harris (2008) in the Okavango Delta, who found using focal sampling of male groups that bulls of all ages preferred to be closest to males over 35 years old, which strongly suggests that this is a genuine preference. I also found that the youngest elephants were most likely to look towards other elephants and least likely to look away, and this effect was strongest relative to the oldest bulls. Newly-independent males are therefore more likely to be watching the oldest males, which could potentially indicate that the younger elephants are looking for learning opportunities, or find comfort in the presence of larger bulls. To my knowledge, gaze direction for social learning is not something that has ever been previously tested in male elephants. However, while these neighbour and looking direction preferences do show differences in social behaviour with male age, in both cases there was no effect of the playback stimuli on these behaviours, suggesting that these relate to more general social preferences rather than being specifically a part of the threat response. I found no effect of age or stimulus on male movement direction, so there is no evidence for male bunching or of a particular age category being faster to react. Despite a general lack of effect of the playback stimuli on movement direction, looking direction or nearest neighbour preference, the increased probability of movement during a threat response compared to the control shows that the elephants displayed a genuine lack of social response, rather than simply failing to recognise the potential danger. Overall therefore, contrary to my expectations, I found no evidence for a social response to threats in male savannah elephants.

There are several possible explanations for why there is so little difference in behaviour with age, with the only change being the overall likelihood of movement. The first is also the simplest: once male elephants reach maturity, they are no longer truly threatened by any non-human predators, but a human could then be a significant threat to all ages, so all respond equally to protect themselves. A second (and related) possibility is that threat response may encompass a fixed set of potential responses, which is not affected by age or personality, because the risks associated with behaving inappropriately to threatening situations are too high. The third is a little more complex. The majority of young male experience will be from within the family group, learning from their mother and older female relatives. Only after joining male groups will young bulls start to develop adult male behaviours. Initially then, after joining adult male groups, the behaviour of young bulls may all be fairly similar, while older males show greater personality variation than youngsters (O'Connell-Rodwell *et al.*, 2024a). Older males have therefore developed a wider variety of potential responses, so while each is more consistent in their own actions across situations, the average population response per situation may not have changed. Overall, however, my study has shown that male elephants do not display substantial differences in threat response behaviour as they age.

My results contrast with the strong prosocial behaviours displayed by female elephants when their group is in danger (McComb *et al.*, 2001; Moss, 2001; Shannon *et al.*, 2022). The difference is likely linked to the low levels of genetic relatedness between males in a group (Chiyo *et al.*, 2011; Santos, 2017), whereas female grouping patterns are strongly kin-driven (Archie *et al.*, 2006). In addition, the greater size of males means they are generally in less danger than a group with young calves. That males did not show either protective or observation behaviour toward other group members during a time of danger indicates that male group response is very different to females. However, one way in which males and females are similar in their response is that when males did move away from the area, they tended to do so together. A group that started fleeing in multiple directions would quickly re-aggregate. This is similar to females, displaying a safety-in-numbers strategy, preferring to be close together after a threat stimulus (Poole, 1996). However, females are led by a matriarch — usually the oldest female — and the whole group will generally follow her lead when threatened (McComb *et al.*, 2001), so the order of movement is age dependent. With the bulls, I found a slight indication that elephants in age category 3 may be more likely to move away from others, implying that males of this age may be the core individuals that the rest of the group follows, but this was not a strong effect.

It is difficult to compare the outcomes of this study with that from males of other species, because male elephant social groupings do not show the same patterns as other species: they do not display high genetic relatedness (Chiyo *et al.*, 2011; Santos *et al.*, 2019) so are not caused by kin selection, nor do they seem to benefit paternity through improved ability to monopolise females (Goldenberg *et al.*, 2014) and their membership is too transient to be considered an ”alliance” or ”coalition” (Smith *et al.*, 2023). In those scenarios, I would expect to see males defending alliance partners from danger or from incoming rivals (e.g., Feh, 1999; Connor and Krützen, 2015; Chakrabarti and Jhala, 2017), because the safety and survival of coalition partners can directly affect focal fitness. That I found no evidence for defence provides further indication that alliances do not benefit male elephants, else looking out for their association partners would be a selective advantage. That all males prefer to be closest to the oldest individuals, and that the youngest males are the most likely to look at others in the group, could potentially still suggest that younger males are looking for protection from older males, as in their natal unit they would have looked to older and larger family members, but the lack of response from older bulls shows that young males will not receive proactive protection.

It is important to note here, that while I did not identify any protective behavioural patterns of older males looking towards or approaching younger ones following a stimulus, I did occasionally observe behaviours that appeared protective. If a young male was closest to the speaker, sometimes, an older and larger bull would move in between the young one and the speaker, or just brush up against their side, in an apparently comforting gesture. Without further information, I cannot tell if these are genuine gestures of older males looking out for younger ones, or if they were random coincidences of timing. However, it should be kept in mind that these behaviours were not unheard of, so males may occasionally protect other bulls in dangerous circumstances, though my experiments indicate it is not the norm. Furthermore, these were only observed during lion playbacks, not human ones, suggesting that if male elephants do protect their group members, it is only when the risk to the protector is low.

Understanding how male elephants respond to danger as a group could help farmers to safely recognise when to chase or not to chase elephants from their fields. Generally, lone bulls deal with potentially threatening or stressful situations such as tourist vehicles (Szott *et al.*, 2019) or bees (Vollrath and Douglas-Hamilton, 2002) by moving away from the area, but sometimes they become aggressive. Human-elephant coexistence is extremely complex, and many farmers are injured or killed (Thouless, 1994; Perera, 2009) trying to protect their property and livelihoods. In my experiments, no elephants showed any indication of charging or mock-charging at either the vehicle or the speaker, preferring flight over fight. This tendency to flee is promising, because it suggests that most farmers who attempt to chase elephants from their fields should be at limited risk of being attacked. However, where the elephants may expect to be shouted at or chased when in the community lands, in my experiments, they would not be expecting it in the national park. If being startled makes elephants more likely to flee than charge, then experiments that include expectancy violation are not a fair test of the likelihood of displaying attack behaviours. Much more data are required to examine how group behaviour or composition may affect the probability that males will charge when they feel threatened. For example, evidence from an observational study of males at water access points showed that young males were more likely to show heterospecific aggression when older bulls were absent (Allen *et al.*, 2021b). This may imply that charging will be a more likely response when the group comprises only younger males, but further experiments would be required to confirm an effect of group age composition on charging behaviour. Stressed males are also more likely to become aggressive toward other bulls (Szott *et al.*, 2019), and crop-foragers have been shown to have elevated stress levels (Ahlering *et al.*, 2011), so elephants may be more likely to become aggressive and charge when being chased out of fields than when startled in the park by a simulated threat.

I noted during many of the playbacks that the elephants do not flee far when chased with human noises, supported by the fact that threat experiments only induced greater movement during the stimulus but not after it. Often, bulls would appear to panic and run away from the sound, but would slow to a walk or halt completely within only about 100 m from their original point. Furthermore, when explaining the purpose of the experiments to local farmers who agreed to be recorded for stimuli, I was told that the elephants do not flee as far as they used to. Elephants generally left the MPNP region for about 20 years when the Boteti River dried up (Stevens, 2018; Evans, 2019). When they returned, neither the elephants nor the people were used to living alongside one another. It seems that over time, the bulls are becoming less nervous around humans, if they flee less far when chased. It is currently unclear if there is also a reduction in the length of time for which chasing elephants away is effective: are they also returning to the fields sooner after being chased than they used to? Investigating how male groups respond to threats, not just in the period immediately after being chased, but in the subsequent few hours, could be highly beneficial to wildlife management attempting to improve human-elephant coexistence.

Repeating the experiments from this study would allow for some improvements to the experimental design, particularly with regard to movement speed. I did not include a measure of speed in the recordings of movement, because it would be impossible to accurately, and in a repeatable manner, judge from video footage alone if an elephant is moving slowly, at a medium speed or at a high speed, whereas the timing of movement is objective. However, excluding speed of movement as a measure does potentially create a scenario in which the less urgent movement appears to be a stronger response: a full minute of ambling slowly away will seem to be a reaction sixfold greater than 10 seconds of running away, because the measure is only the amount of overall time spent in motion. It was clear when performing the experiments that the elephants did indeed find the lion stimulus more disturbing than the dove control, and the human more disturbing than the lion: a general description of bull response would be that they ignored the dove, stood up to a lion, and fled from a human. This observation is not particularly obvious in the models, which I believe is because the overall time spent moving was similar between the lion and human (as shown by the MBM) but the elephants moved further and faster in response to a human than a lion. Any similar experiments performed in the future would benefit from recording the distance moved at specific time intervals as an indicator of the speed of movement, because I think it is likely that including the speed of movement would give a better indication of the intensity of response. However, I did not at the time identify any difference in probability of fleeing between older and younger males: repeating the study and recording the maximum distance travelled away from the speaker in different time increments could highlight potential differences between age classes, but given how limited the effect of age on movement probability was, I do not expect it would change drastically.

While this study did not show any impact of threat on social behaviour, increasing the number of trials could open several new potential questions for future investigation. For example, incorporating the behaviours of multiple elephants at once within the model could allow us to look for whether group behaviour is more coordinated within versus between groups. Alternatively, more explicit modelling of copying behaviour could test whether the behaviour of the rest of the group in the previous seconds alters the behaviour of the focal. In a longer-term study, in a population where individual elephants can be identified, it would be fascinating to conduct these experiments over the lifetime of an individual, and see whether particular individuals may be more likely to show social responses than others. However, given the lack of effect at all in this study, I believe that any impacts of behavioural coordination, the behaviour of other group members, or inter-individual differences, would likely be very small. This does not make them unimportant to understand, but would require a far greater number of trials than I was able to perform in my experiments.

4.5 Conclusion

This study is the first to test group response of male elephants to danger. While I did not find evidence for prosocial behaviour in the males to protect younger individuals, or for copying behaviour as a means of social learning, I did find some effects of age on social behaviour, and the experiments may act as a useful pilot study for future investigations of this kind. I recommend that future experiments should try to incorporate the behaviour of other individuals within statistical models, and look for differences between threat scenarios that trigger elephants to flee versus charge, which could be used to improve human-elephant coexistence: by knowing more about how the group is likely to respond to human presence, farmers might be able to improve their safety when defending their crop fields.

Chapter 5

Age as a cause of male elephant social behaviour

5.1 Summary of findings

In this thesis, I set out to investigate the social behaviour of male African savannah elephants, which have generally received less research attention than their female counterparts. Only limited studies have considered how male social networks are structured, and have reached different conclusions regarding the importance and strength of male-male associations (Chiyo *et al.*, 2011; Goldenberg *et al.*, 2014; Murphy *et al.*, 2020). In this concluding chapter I will first summarise my findings, before discussing how this new information may be used to improve elephant conservation, and compare the behaviour of bull elephants to males of other species. Finally, I will provide some recommendations for future research into male elephant social behaviour.

5.1.1 Analysis of sparse animal social networks

In the first data chapter, I compared the common methods used to estimate the strength of association between two individuals when calculating a social network, especially when the true social network is very sparse. I argued that the simple ratio index was liable to overestimate the association strength in sparse networks due to the use of flat priors. This will also be the case for other frequentist measures. Further, in such analyses data have to undergo a filtering process to remove individuals seen an insufficient number of times for their data to be considered reliable, due to a lack of an inherent uncertainty measure. In contrast, a Bayesian framework can use more informative priors and contains an inherent uncertainty in the shape of the posterior distribution, so should be more reliable.

In practice, I found that the wide priors designed for the analysis of dense networks were inappropriate and needed adjusting for application to sparse networks. This is because, in both the frequentist and Bayesian methods, current approaches assume a fully connected network, missing a step of the underlying social processes that creates zero-inflation in the true network edge weights. To achieve a model capable of dealing with this zero-inflation, I adapted the prior structure to reflect a two-step social process in the definition of the true edge weight: i) determining if two individuals will ever associate, and ii) if they do associate, defining the strength of that association. A similar effect could also be obtained by using a frequentist zero-inflated model, but this again ignores sampling biases because it depends on a flat prior and contains no inherent uncertainty. I recommend that future social network studies should avoid using frequentist measures of edge weight, but that Bayesian models should be based on conditional priors, with at least two alternative options, depending on prior knowledge of the complexity of the social network.

5.1.2 The effect of age on male African savannah elephant social structure

Using the two-step model developed in Chapter 3, I next assessed the role of age in structuring the social networks of male elephants. Confirming some earlier studies (Chiyo *et al.*, 2011; Murphy *et al.*, 2020) but not others (Goldenberg *et al.*, 2014), I found that bulls show very little evidence of forming strong social associations, instead choosing to form a larger number of weak associations. There was also no pattern of increasing eigenvector centrality as males aged, which again supports Murphy *et al.* (2020) and Goldenberg *et al.* (2014) when looking only at sexually inactive bulls. However, the nodal regression disagrees with the results from Goldenberg *et al.* (2014) for sexually active bulls and from Chiyo *et al.* (2011). This disagreement may be because of a difference in the inclusion criteria compared to Chiyo *et al.*, who were also studying the male elephants of ANP, and because of the separation of sexually active and inactive bulls by Goldenberg *et al.* which naturally reduced the network size for each. A lack of effect of age on centrality indicates that older males may not be the important sources of information that they were previously believed to be (Evans and Harris, 2008; Allen *et al.*, 2020). The combination of these two findings — that male elephants form many weak social bonds, but are not selective about which bulls they group with — indicates that while social learning may be an important feature within male social networks, it is not a major cause of their structure.

I also found no differences between the two populations, or between the time windows of different duration within the ANP data set. Murphy *et al.* (2020) worked in the Associated Private Nature Reserves in South Africa, providing association measures for a third population that were only slightly higher than in my study (around 5-8% associated for males observed at least five times). These results may, therefore, be representative of male savannah elephants as a whole, rather than being population-specific. I found that male relationships are stable between time periods of 500 and 2 500 days. Goldenberg *et al.* (2014) and Murphy *et al.* (2020) both used sampling periods of 4 years, which is about halfway between the two durations that I tested. That they also obtained similar association rates (when including both sexually active and inactive males) and found no consistent effect of age on eigenvector centrality further supports my finding that male relationships are stable over these time periods. This information will be important for future studies of male elephants, and indicates that conservation managers can share information across populations, rather than having to start from scratch in each location.

5.1.3 Group response of male elephants to threatening situations

In Chapter 4, I considered the role of social learning in male elephants' response to potentially dangerous situations. Social learning of threat response behaviours can be advantageous, because it avoids the need to personally experience a danger (Griffin, 2004). I hypothesised that younger males would look towards and follow more experienced males, allowing them to learn the appropriate response and react quickly. An alternative hypothesis was that older males would display protective behaviours towards the smaller and more vulnerable males. However, the playbacks showed no evidence for any form of full group response to potential danger: the stimuli induced no change in the probability of male elephants to look or move towards another male, be they older or younger (other than all heading in roughly the same direction if they fled), or to change their nearest neighbour. Male elephants are therefore following a threat response strategy of self-preservation only, responding in a manner to maximise their own probability of escape. More generally, I did find social effects of age outside of the threat response: the youngest males were most likely to look at other males, and both adolescent (young) and adult (old) elephants preferred to be nearest to adult males. Further research is needed to understand the reason for these effects of age on bull behaviour.

5.2 The advantages to male elephants of forming social groups

As I have eluded to a couple of times in previous chapters, my findings have indicated something quite peculiar about male elephant social behaviour: there does not appear to be any clear fitness benefit of male gregariousness. Given that grouping behaviour will increase competition for resources, why then do male elephants generally spend less than 20% of their time alone (Chiyo *et al.*, 2011)? In this section, I will discuss some of the possible reasons explaining why male elephants form groups.

First and foremost, is the question of social learning. Throughout this thesis, I have discussed the possibility of social learning among male elephants (Evans and Harris, 2008; Allen *et al.*, 2020), but I have generally found only very limited evidence to support the hypothesis that social structure may be caused by males seeking out social learning opportunities (Chapters 3 and 4). In my analyses, old bulls are not more popular within the social network and young males do not copy their reaction in response to danger, but old males are preferred neighbours and young bulls are more likely to be watching other group members than older males are. If I consider similar species that do display evidence for social learning in their social structure, my results do not match up. For example, in giraffes (*Giraffa camelopardalis*), males sometimes form small, transient, all-bull groups, just as the elephants do. However, male giraffes tend to group around a mature bull (Bercovitch and Berry, 2015), such that adult males have the highest closeness centrality (Lavista Ferres *et al.*, 2021). In giraffes, younger males are believed to actively choose to follow older males as a means of gaining information about the location of feeding resources and females (Bercovitch and Berry, 2015). The same is observed in male elephants (Allen *et al.*, 2020), but it is not sufficient to induce an effect on centrality (though I used eigenvector instead of closeness, to maximise the robustness of the metric to causal analysis; Dablander and Hinne, 2019). Couple this with a lack of evidence for a multilevel community structure in male elephant society (Chapter 3), and I do not believe that young males are clustering around old bulls in the same way as seen in giraffes. Similarly, guppies will preferentially group with shoals that have prior knowledge of resource availability over naïve shoals (Lachlan *et al.*, 1998), indicating social learning. However, guppies also prefer familiar over unfamiliar shoals (Lachlan *et al.*, 1998) which, if it were occurring in the elephants, would imply that males should have preferred grouping partners. Having found none of the social network patterns or threat responses that I expected to find, nor much similarity with other species, I do not believe that males are actively seeking social learning opportunities, and therefore that social learning is unlikely to be a cause of male social structure.

However, despite bulls not actively looking for social learning opportunities, male elephant social structure takes a form that can still facilitate rapid spread of social information (Chapter 3). Indeed, in a recent review by van Boekholt *et al.* (2021), they discuss the perfect social structure for promoting social learning in primates, which included being egalitarian with many social bonds, high levels of dispersal and population movement, and displaying fission-fusion dynamics. Elephants may not require exactly the same structural features as primate societies, but this sounds like a fairly good description of bull behaviour. For example, the musth cycle maintains an egalitarian social structure among bulls by creating constant fluctuations in social rank (Poole, 1987, 1989b), and by moving between bull areas and breeding grounds, males display high levels of population movement (Stokke and du Toit, 2002). Therefore, while social learning may not be a cause of social structure, it may be a consequence of it, if elephants pass information in a similar manner to primates (van Boekholt *et al.*, 2021). Furthermore, there is recent evidence of social learning from solitary species that prove social bonds are not a requirement for social learning (Allen, 2019): fruit flies (*Drosophila melanogaster*) show short term preference for food sources that have been previously chosen as oviposition sites (Durisko *et al.*, 2014). If strong social bonds are not always necessary for social learning, male elephants may therefore still be able to obtain important information from other group members, without investing time and resources into strengthening their social bonds. Overall then, while my results do not implicate social learning as a primary purpose of male elephant groupings, they do not prove that social learning is not occurring.

A second possible reason for male gregariousness that I have started to test in this thesis is improved survival during dangerous situations. Sociality enhancing survival has been documented across a wide variety of taxa, including social spiders (Bilde *et al.*, 2007), insects (Kohlmeier *et al.*, 2016), birds (Aydinonat *et al.*, 2014), carnivores (Almberg *et al.*, 2015), cetaceans (e.g., male orcas: Ellis *et al.*, 2017; bottlenose dolphins: Rankin *et al.*, 2022), and other mammals (e.g., giraffes: Bond *et al.*, 2021; yellow-bellied marmots: Montero *et al.*, 2020; Philson and Blumstein, 2023). Among primates, sociality can improve survival not just of the individual (humans: Holt-Lunstad *et al.*, 2010; macaques: Brent *et al.*, 2017; baboons: Alberts, 2019), but also of their offspring (Silk *et al.*, 2003, 2009). I could not test in this study the direct impact of social behaviour on male survival, but I found no evidence in the playbacks to indicate that male-male association offered protection from danger, either through actively working together to protect one another, or by observing one another to identify the most appropriate response to a potential threat.

As with social learning, I believe my study provides evidence that protection is the not main cause of males grouping together, but does not rule it out as a proximal advantage. There is some evidence that male elephants seek the protection of others: groups tend to be larger when further from protected areas (Chiyo *et al.*, 2014), indicating that they are more comfortable with more companions when in an area perceived to be dangerous. Gregariousness may therefore provide passive protective benefits even without active defence from other group members. Through dilution (Foster and Treherne, 1981; Delm, 1990; Wrona, 1991; Roberts, 1996), each individual is less likely to be targeted by hunters or predators when there are others around. For example, male zebras are more likely to form groups when the risk of predation is high for solitary individuals (Rubenstein and Hack, 2004). Similarly, having many individuals listening and smelling for danger increases the probability that one member of the group will detect a threat early and alert the rest (Elgar, 1989; Delm, 1990; Sorato *et al.*, 2012). During my experiments, I noticed that bulls rarely stood all facing in the same direction — other than when we first drove towards them and they looked at our vehicle — causing the data to show an unexpectedly high rate of looking away from the target (see Chapter 4, section Looking direction). This may simply be because this gives them more space to keep cool by flapping their ears, and allows them to cool one another, or because they can stand closer together so all fit in the shadiest patches. More likely however, I suspect it may enable them to monitor for danger in multiple directions simultaneously.

While social learning and protection are the two mechanisms that I have tested, this does not mean that they are the only plausible reasons for male elephant gregariousness. Increasing fitness through improved competitive ability or reduced costs of reproductive competition are common reasons for male-male association. Male elephants do not form mating alliances to outcompete solitary males: during musth, when they are most likely to successfully mate, they become more solitary rather than forming stable alliances (Poole, 1989b), and a musth bull even in poor condition will outcompete almost any non-musth bull (Poole, 1989b; Hollister-Smith *et al.*, 2007; Rasmussen *et al.*, 2008). However, forming groups can help to reduce dangerous reproductive competition through play sparring (Evans and Harris, 2008; Arnott and Elwood, 2009; Goldenberg *et al.*, 2014). Not only does sparring improve individual fighting abilities (Evans and Harris, 2008; Chiyo *et al.*, 2011), it also facilitates the development of a hierarchy that allows bulls to learn which individuals they should or should not risk challenging (Mesterton-Gibbons and Heap, 2014; Dubois, 2024). Mutual assessment of own and opponent's fighting ability helps males to avoid costly aggressive escalation (Poole, 1989b; Arnott and Elwood, 2009), and short term assessment — in the moment that rivals meet and prepare to fight — has been identified in a wide range of taxa, including fish (Enquist *et al.*, 1990), crabs (Dowds and Elwood, 1985; Jennions and Backwell, 1996) and insects (Hack, 1997). However, evidence is very limited for males associating as a means of gaining information about competitors. One possible example is male raccoons (*Procyon lotor*), in which affiliative groups form in the non-breeding season, but disband during the breeding season when males compete for females (Gehrt and Fritzell, 1998, 1999). It has been suggested that male non-breeding sociality may reduce breeding-season conflict and potential injury (Gehrt *et al.*, 2008). Bull elephants may be social as a way of gaining information about their potential future competitors (Evans and Harris, 2008), or incurring reduced aggression from familiar associates during times of reproductive competition (Fisher, 1954; Werba *et al.*, 2022). Given how sparse I found the male elephant networks to be, bull association is unlikely to be about actually forming a fixed hierarchy because there are too many potential competitors to assess (Bercovitch and Berry, 2015), but rather becoming more skilled at assessing competitive ability in others. While my results cannot deny this as a possibility, my observations of male social behaviour do not particularly support it either. If male-male association were purely about learning to fight and assess others' competitive ability, then play sparring should account for a substantial amount of daily activity. However, much of the time (especially in dry season) I found groups of males resting together under trees. I therefore do not believe that improved abilities to fight and to assess competitors can be the only advantages that they are gaining from socialising with one another.

An alternative but related possibility is that grouping helps to control mating behaviour by older males suppressing the musth of younger males (Poole, 1989b; Slotow *et al.*, 2000), as has been suggested by Evans and Harris (2008). This is an advantage to the older males who reduce their competition for mates, but may also benefit younger bulls that lack the control or body condition required for musth. Fewer musth bulls could lead to a reduction in social tension, creating a more stable and less stressful social environment, which could subsequently improve survival: in rock hyraxes (*Procavia capensis*), a species closely related to elephants (Stanhope *et al.*, 1998; Seiffert, 2007; Springer, 2022), survival is highest in groups where all individuals are equally central, because this reduces the stress of battling for better positions in the hierarchy (Barocas *et al.*, 2011; but note that unlike elephants, hyraxes form consistent groups). Musth suppression could reduce that tension and create a more egalitarian society, that promotes higher overall survival. I found that all bulls are equally influential in the network, which could be promoted by selection for reduced social tension through musth suppression. This hypothesis therefore is not undermined by my results, but further research into the effect of population variation in network centrality on survival rates would be required to provide positive support.

The final potential reason for male elephant gregariousness that I will discuss here is social buffering: the accelerated recovery after a severe incident that is observed in highly social animals when living in groups compared to when living in isolation (Davitz and Mason, 1955). Social buffering can improve both quality of life (Kikusui *et al.*, 2006) and individual survival. For example, Barbary macaques (*Macaca sylvanus*) have been shown to have higher survival under severe climate fluctuations when they occupy central positions in the social network (Lehmann *et al.*, 2016), and yellow-bellied marmots are more likely to survive the winter by having associates that are spread across many different social groups (Philson and Blumstein, 2023). Young male elephants have previously been shown to promote a positive psychological state in older bulls (O'Connell-Rodwell *et al.*, 2024a), which suggests that social buffering may be important to bull society. I here present two reasons why I believe that social buffering could explain male elephant gregariousness: climate instability and ivory poaching. Firstly, Africa's climate is highly variable throughout the year, with significant differences in both temperature and rainfall between the seasons that are becoming increasingly severe with climate change (Nicholson, 2017). Socialising with other males may therefore facilitate easier transition between seasons, especially in years with particularly intense heatwaves or droughts (variability selection; Potts, 1998). More connected individuals may also survive better after sudden and severe changes to the social environment (Nunez *et al.*, 2015), which could be highly relevant to a species so long persecuted for their ivory (Beachey, 1967; Douglas-Hamilton, 1987; CITES Secretariat and TRAFFIC, 2020). Ivory poaching has created strong selection on physiological changes (Campbell-Staton *et al.*, 2021) and can have long-term social impacts on individual behaviour (Garai *et al.*, 2023), indicating it will have been sufficient to induce behavioural evolution. Overall, while social buffering is not an effect I was able to test for in this thesis, I believe it is something that should be considered in future bull research.

5.3 Implications for elephant conservation

As an iconic flagship species and ecosystem engineer, African savannah elephants are of prime conservation importance. Despite this, their overall population is in severe decline, and they were upgraded to endangered on the IUCN Red List in March 2021 (Gobush *et al.*, 2022), after they were identified as a distinct species from the African forest elephant (*Loxodonta cyclotis*) (Hart *et al.*, 2021). Conservation practice must use all available information about elephants in order to maximise the probability of successful action to protect this keystone species.

One of the greatest challenges in elephant conservation is managing negative interactions with the people whose land they use and share. Crop-foraging is a serious issue across the range of savannah elephants (Perera, 2009; Montgomery *et al.*, 2022), and can lead to severe or fatal injuries to people attempting to chase the elephants away from their land (Osborn and Parker, 2002; Nelson *et al.*, 2003; Perera, 2009; Dunham *et al.*, 2010; Davies *et al.*, 2011). Furthermore, crop-foraging elephants may also cause expensive damage to fences (Kioko *et al.*, 2008), and dig up water pipes used for crop irrigation or settlement water supplies (Niskanen, 2006; Long *et al.*, 2020), creating further problems for local communities. This is only likely to be exacerbated by shrinking areas of natural land and by climate change reducing availability of water and forage in protected areas (Ngcobo *et al.*, 2018). Any information about elephant behaviour that can be used to reduce these interactions, should be used to its maximum potential, especially under the added pressures of human population growth and climate change. It is important to note here however, that while elephants do contribute substantially to crop losses, their direct impact is often overestimated (Lee and Graham, 2006; Mackenzie and Ahabyona, 2012; Kiffner *et al.*, 2021; Kyokuhaire *et al.*, 2023), so additional information about the nature of crop damage caused by other species is also important to include when planning conservation actions.

In this thesis, I have focused on the potential role of social learning in male elephant society. Because female elephants are rarely involved in crop-foraging and similar negative human-elephant interactions (Jackson *et al.*, 2008; Chiyo *et al.*, 2012; Strum, 2012), understanding how male elephants are behaving and how they learn to act in a certain way could be key to solving some of these issues. My findings' implication that male social structure may facilitate social learning means that we could still potentially use social learning as a tool in elephant conservation, even if social structure is unlikely to be caused by males looking for learning opportunities. While conservation may not necessarily be able to target males of a specific age or network position, the overall probability that social information will be passed through the population is reasonably high. By using classic barrier methods such as electric fences or thorny bushes, we perpetuate the problem, as bulls simply learn to break these and then pass that knowledge on to other elephants (Chiyo *et al.*, 2012). However, by focusing our attention on more effective deterrent strategies, we may be able to teach individual males to avoid certain areas, with the subsequent effect that others are then similarly discouraged from entering human settlements.

This is not a new idea: traditional deterrent strategies such as crop guarding and setting fires (Osborn and Parker, 2002; Sitati *et al.*, 2005; Nyirenda *et al.*, 2012; Gross *et al.*, 2019) have been used for decades, with the more recent addition of chilli and beehives (Osborn and Parker, 2002; Vollrath and Douglas-Hamilton, 2002; Nelson *et al.*, 2003). However, none of these are universally effective, nor is there much coordination of strategies between different areas. For example, in Kenya, the use of beehive fences has proven relatively successful, with elephants avoiding the sounds of bees and the smell of honey (Vollrath and Douglas-Hamilton, 2002; King *et al.*, 2007, 2009), but in Botswana, beehives do not survive well so the elephants do not know to avoid them and they prove ineffective (Adams, 2016). My recommendation here is to increase the focus on deterrents, and to promote the use of a variety of deterrent options. For the playback stimuli, I simply asked people to ”act as you would if you were chasing elephants from your property or fields”. All of the sounds were effective, but some caused the elephants to run faster, further, or for longer than others. This is similar to what was reported by a farmer in Xhumaga: the elephants do not run as far as they used to, and they stop running as soon as the farmers stop shouting. Considering my results from the social network analysis and playbacks, I believe that multiple deterrent strategies representing different levels of threat will be more effective at protecting crops than a singular deterrent. By increasing the range of deterrents, the elephants will be less likely to learn that one or another is not dangerous, and through social learning, they may learn to avoid large areas despite individually only experiencing a small number of deterrents.

While negative human-elephant interactions are highly dangerous to elephants, this is not the primary cause of their declining population: ivory poaching continues to decimate elephant populations (Hauenstein *et al.*, 2019; Schlossberg *et al.*, 2019; Gobush *et al.*, 2022), with the preferred targets being those with the largest tusks. This is almost always the oldest males (Poole, 1989a; Poole and Thomsen, 1989; Barnes and Kapela, 1991; Mondol *et al.*, 2014; Chiyo *et al.*, 2015). Selective harvest of old bulls could potentially have devastating impacts for the remaining population. For example, the loss of older males is likely to lead to social issues in younger males that enter musth earlier than they naturally should, as happened in Pilanesberg National Park, South Africa (Slotow *et al.*, 2000, 2001; Slotow and Dyk, 2001). However, some potentially less extreme effects are also possible. It has been shown that selective harvest of females could severely harm the social structure of family groups (Wiśniewska *et al.*, 2022) and their ability to assess danger (Shannon *et al.*, 2022). Using data from long-term social observations, we could similarly test for changes in bull social structure in the years following severe poaching events, with the expectation that loss of the most central individuals would have greater impact on network connectivity and efficiency of social diffusion than loss of the same number of individuals selected at random (Wiśniewska *et al.*, 2022). However, without evidence for older males being particularly influential in the social network, this selectivity may be less damaging than previously feared (Evans and Harris, 2008; Allen *et al.*, 2020). This is not to say that poaching should no longer be considered a severe issue for elephant conservation — the extreme losses created by the ivory trade are still driving the population downwards — but rather that some of the social impacts of specifically targeting old males may be reduced. It has been suggested that the selective removal of old bulls could reduce social cohesion (Chiyo *et al.*, 2011) or limit the pool of knowledge within a population, thus curtailing social learning opportunities for young males (Evans and Harris, 2008; Allen *et al.*, 2021a, 2021b). However, with a population in which all individuals are similarly central, each individual does not need a specific role model to access resources. There will therefore be social effects, but likely not as strong as in females. Furthermore, by following elephant highways, remaining individuals can further reduce the impact of lost older males, as the paths used by older males will remain detectable for a long time (Allen *et al.*, 2021a), and will be strengthened every time another elephant follows them. I would like to note here that while I do not expect that the selective removal of older males will exacerbate the problem of rapid population decline, I believe it would be extremely useful to model the potential effects of node-removal (Amoruso *et al.*, 2020) to assess how populations may respond to perturbation of the social network (e.g., Testard *et al.*, 2021).

The final threat to elephants that I will discuss here is habitat fragmentation and degradation (Gobush *et al.*, 2022). As well as potentially causing an increase in human-elephant interactions (Graham *et al.*, 2009; Gara *et al.*, 2021; Moeng, 2022), human populations and anthropogenic climate change reduce the availability of well-connected elephant-suitable habitat, which in turn reduces their access to resources (Gara *et al.*, 2017, 2021; Buchholtz *et al.*, 2021) and limits population mixing (Lohay *et al.*, 2020). While I have not been able to investigate the effect of the external environment on elephant social behaviour in this thesis, Chapter 3 does give some insight into the potential effects. As male elephants do not appear to be selective about their choices of social partner, a reduced range of potential associates may have a fairly negligible effect on social structure: they will not struggle to find individuals that match their specific preferences. However, small habitat fragments could limit food availability and create competition within groups. In orcas, it has been shown that low food availability reduces the amount of time that individuals spend socialising (Foster *et al.*, 2012). In this case, we may expect to see males spending more time solitary and less time socialising, so making an already sparse network even sparser. This will then limit their access to any advantages to reproduction, survival or health that they do gain from being gregarious, potentially making them more vulnerable to a rapidly changing environment.

5.4 Ideas for future research

This thesis adds to the small amount of research currently available on male elephant social behaviour, but there are many avenues of enquiry that we are yet to investigate.

Firstly, it would be good to see a closer examination of the factors that affect the strength of a dyadic edge weight. My analysis shows no average effect of age on social structure. However, in this model it is impossible to see if there is an effect of age difference on individual social preference. In the case of young males opting to follow older males to use them as role models or as protectors, I would expect to see a preference for large age gaps between social partners.

In contrast, if greater advantages are presented by grouping with individuals of a suitable size for sparring, I would expect that males of a similar age would share stronger social bonds. Unfortunately, I was not able to produce a model of this type for this thesis, because doing so requires extremely powerful computing facilities to cope with the high number of nodes and edges, the interaction between nodal age categories, and the non-independence within and between time windows. However, analysing the effects of the ages of both members of a dyad together could help to provide further indication of if age may yet be a cause of social structure in male elephants.

A second area for research is into the role of bull areas, and whether male social structure differs with a changing sex ratio. Bull areas are regions rarely frequented by female family groups but where male elephants can often be found (Stokke and du Toit, 2002; Lee *et al.*, 2011; Pitfield, 2017). A range of theories have been proposed for the purpose of these areas (e.g., sex differences in foraging requirements, Shannon *et al.*, 2006; or greater risk-aversion among females than males, Harris *et al.*, 2008), but their social benefits have not, to my knowledge, been considered. One hypothesis is that they are refuges for post-musth recovery: musth bulls will harass other males, so the less aggressive non-musth bulls will remove themselves from areas inhabited by females (Stokke and du Toit, 2002; Poole *et al.*, 2011), in order to regain their strength. Despite this creating two very distinct social environments, so far no studies have compared the social network structure of male elephants occupying bull areas versus areas where females are present (but see Goldenberg *et al.*, 2014 for a study of the difference between males in a sexual versus non-sexual state). In a bull area, males have very limited reasons to be antagonistic toward one another, and since fighting is costly, this should promote more connected, affiliative social networks. Observing any differences in social structure between bull and non-bull areas could help to highlight the importance of bull areas to male elephants, and again highlight potential reasons for male gregariousness. This would not be an easy study, because by definition bull areas are migratory populations, so observations per individual are usually limited: in the MPNP, males are only present for an average of 47 days before they leave again (Pitfield, 2017), creating a database of sightings in which the vast majority are only observed once (Kate Evans and Thatayaone Motsentwa, personal communication). However, without understanding precisely why these areas constitute an important resource to bulls, it becomes difficult to ensure that conservationists adequately incorporate them into strategic planning.

Thirdly, as I previously discussed, I could not test some of the alternative possible reasons for male social behaviour, including direct survival improvements and social buffering. While examination of survival would be an extremely difficult thing to study in elephants, I do believe it could produce some invaluable insights for their conservation. Population comparisons have shown how variation in conditions can change behaviour: social disruption has been shown to have long-term impacts on elephants by using comparisons between disturbed and undisturbed populations (Shannon *et al.*, 2022; Garai *et al.*, 2023). Similar studies could therefore be used to consider the effect of sociality on survival and health. For example, the social behaviour of males in populations with varying climate extremes could be compared to determine if social buffering plays an important role in male survival through severe weather, with implications for conservation in the face of climate change. Alternatively, studies of the effect of individual network centrality on lifespan, or population variation in centrality on life expectancy, could highlight how male social structure may improve survival (although my results from Chapter 3 indicate that there is likely to be only limited variation in centrality between individuals and populations).

Fourthly, there has been very limited research into elephant personality — the set of consistent behaviours that are performed by an individual across a variety of contexts (Stevenson-Hinde *et al.*, 1980; Gosling, 2001; Dall *et al.*, 2004; Caspi *et al.*, 2005; Réale *et al.*, 2007) — and its role in conservation. I have observed first-hand that male elephants each have their own personality, but currently an empirical study of it is missing from the literature. Personality studies of wild elephants are extremely challenging, because they require reassessment of the same individuals over and over again for many years. However, sufficient data now exist that some forms of personality could be analysed, opening up a plethora of new questions. Do some males prefer larger groups or display consistently high network centrality, while others are aggressive toward unknown individuals so remain on the periphery of the social network? Understanding these patterns could aid with predicting the outcomes of various conservation actions, by indicating the range of potential responses that might occur on an individual scale, rather than considering the overall population. Personality is most classically illustrated by the boldness-shyness axis (propensity to investigate a threat) and the exploratory index (propensity to explore the surroundings) (Stevenson-Hinde *et al.*, 1980; Gosling and John, 1999). Boldness and explorative behaviour will partially shape an individual's social interactions, and the social environment of those around them: bolder animals should be more willing to integrate with new individuals (Wilson, 1981). However, bold personalities are also linked to a greater risk of mortality (Smith and Blumstein, 2008). In elephants, bolder or more explorative bulls should be more likely to crop-forage, because they are more likely to move away from their known home range and be willing to enter a human settlement. Bull social behaviour contains a wealth of potential for personality research, including the specialisation of individual roles within society (Réale and Dingemanse, 2010), differences between groups or individuals with varying physical characteristics (Koski, 2011), and the integration of social networks and collective behaviour (Aplin *et al.*, 2014; King *et al.*, 2018; Gartland *et al.*, 2022). For example, are there differences in male willingness to move to new areas versus staying in the same protected areas for extended periods, and does this depend on the social bonds shared with others in the population?

Finally, more research is required into male elephant vocal communication. As with many other fields, vocalisations have generally focused on female elephants, except for the very specific musth rumbles given by musth bulls (Morris-Drake and Mumby, 2018). Recent research has shown that female elephants use names for one another, which may be assigned by the mother from a young age (Pardo *et al.*, 2024). It is unknown currently whether male elephants also use these names, and if the name assigned by the mother is used throughout life or if it changes with time or social partner. Similarly, recent advances have indicated that males produce similar ”let’s go” rumbles to females when initiating a movement away from an area (O’Connell-Rodwell *et al.*, 2024b). This would suggest that some males are showing active leadership of the group, where previously male leadership was thought to be passive (Allen *et al.*, 2020). Further research into male group movement initiation based on social network structure (King *et al.*, 2011a) and into male-male acoustic communication may improve understanding of bull leadership, and could highlight new vocalisations which may not have been identified in females. Investigations into male elephant vocal behaviour would elucidate far more detail about their social association and leadership behaviour than is currently known.

5.5 Concluding remarks

To conclude, in this study I have found no evidence to suggest that male elephants display strong social preferences for specific individuals, nor for patterns of male social influence or importance based on the age of the individual. This has involved adapting previous methods to be more reliable for use in social network analysis, so I am confident in this result, despite its disagreement with some previous studies that have indicated older males are more central to the network. I have not found evidence for any single large advantage conferred to male elephants by forming groups, indicating that gregariousness in male elephants is instead likely caused by many small benefits, which may include access to many social partners from whom one might obtain information and who may passively reduce predation risk, but not actively protect one another. These results can be used in future conservation efforts to improve the effectiveness of deterrent strategies for reducing elephant entry into crop fields, and minimise the risk to farmers attempting to chase elephants from their fields.

Chapter 6

Appendix

A1 Analysis of sparse animal social networks

A1.1 Standard zero-inflated model

To model a two step process does not necessitate that we use a Bayesian framework. The choice to still use BISoN over a frequentist model comes down to the multitude of reasons outlined in this paper regarding the problems with flat priors and the ability to incorporate uncertainty into edge weight estimates. However, if we were to choose a frequentist framework for this model, we could still model a two step social process with the same data by using a mixture model instead of the SRI.

Mixture models allow the use of a zero-inflation term to model the first step of the edge weight derivation process. Here I used the package glmmTMB (Brooks *et al.*, 2017) to create a binomial model with zero-inflation of the form:

$$cbind(together_{ij}, apart_{ij}) \sim (1|dyadID_{ij}) \tag{A6.1}$$

$$apart_{ij} = sightings_i + sightings_j$$

Where $together_{ij}$ is the number of observations in which individuals *i* and *j* were in the same group, and $sightings_i$ and $sightings_j$ indicate the respective number of observations of individuals *i* and *j* in the absence of the other.

This model produces an output that has similarities to both the SRI and the conditional BISoN model. As in the SRI, the outputs are frequentist. They are therefore single-point estimates, so have no inherent uncertainty calculated within them, and are based on a prior assumption that all possible values are equally likely. However, the inclusion of the zero-inflation term has now produced an overall bimodal distribution (Fig A28a) that more accurately reflects the assumptions of the conditional BISoN.

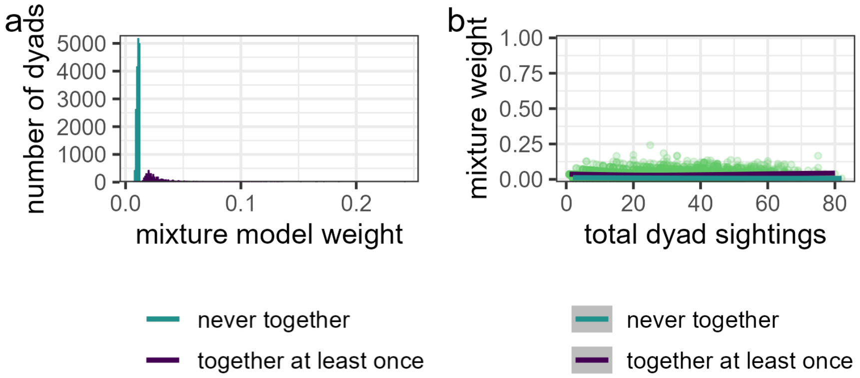


Figure A28: Edge weights calculated using a frequentist zero-inflated mixture model. a) The distribution of estimates for the whole population is bimodal, indicating the zero-inflation and two-step underlying process. The edge weights are much closer to zero than produced using the other methods, creating a situation in which b) the total sightings have very little influence at all on the edge weight calculated, for either dyads that have (purple) or have not (blue) been observed in the same group.

The model tells us that the global logit edge weight is very low at -4.378 ± 0.0228, but with a large variance among dyads of 1.094. When we plot the edge weight against the number of sightings per dyad, we see no effect at all of sighting count on the edge weight, but the edges are all measured as extremely weak. On the face of it, this looks like it could be the best of all the models, but when we check the eigenvector values for it, we see the same issues as in the SRI: there is a strong positive correlation between number of sightings per node and the eigenvector centrality, and unlike the SRI this extends as high as nearly 30 sightings before reaching a plateau (Fig A29). If we were to remove all elephants with fewer than 30 observations from the analysis dataset, we would be left with only nine individuals from our original 213, dropping 96% of our network. Given this, we still recommend using a conditional prior in a Bayesian framework over a frequentist mixture model.

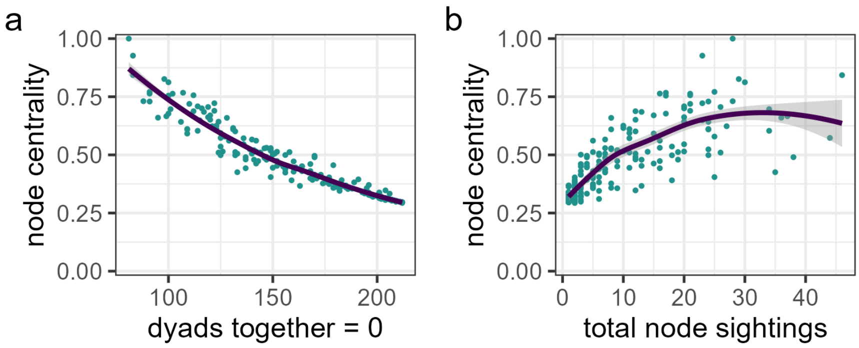


Figure A29: Centrality estimates from a zero-inflated mixture model. a) There is a negative correlation between the number of potential dyad partners that an elephant never associates with and their eigenvector centrality calculated from a binomial zero-inflated mixture model, which is as we would expect. However, as with the SRI, we also see b) a positive effect of total number of sightings of an individual and their node centrality score, which is not a trend that we should observe.

A2 The effect of age on male African savannah elephant social structure

A2.1 Elephant age distributions

Age distributions and total counts of elephants for each population (and time window in the case of ANP). Bars are coloured based on MOTNP age categories, to show the respective portions of the ANP data that lie in each category. Numbers show the total count and population percentage per age category.

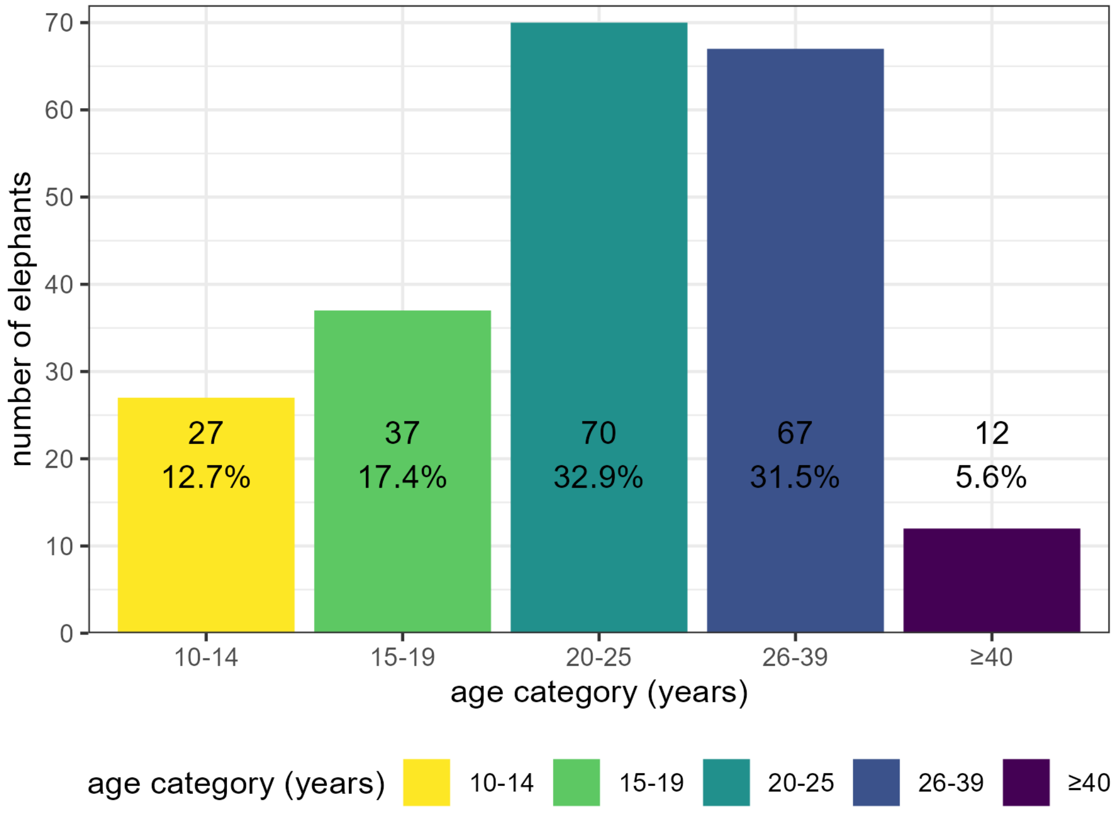
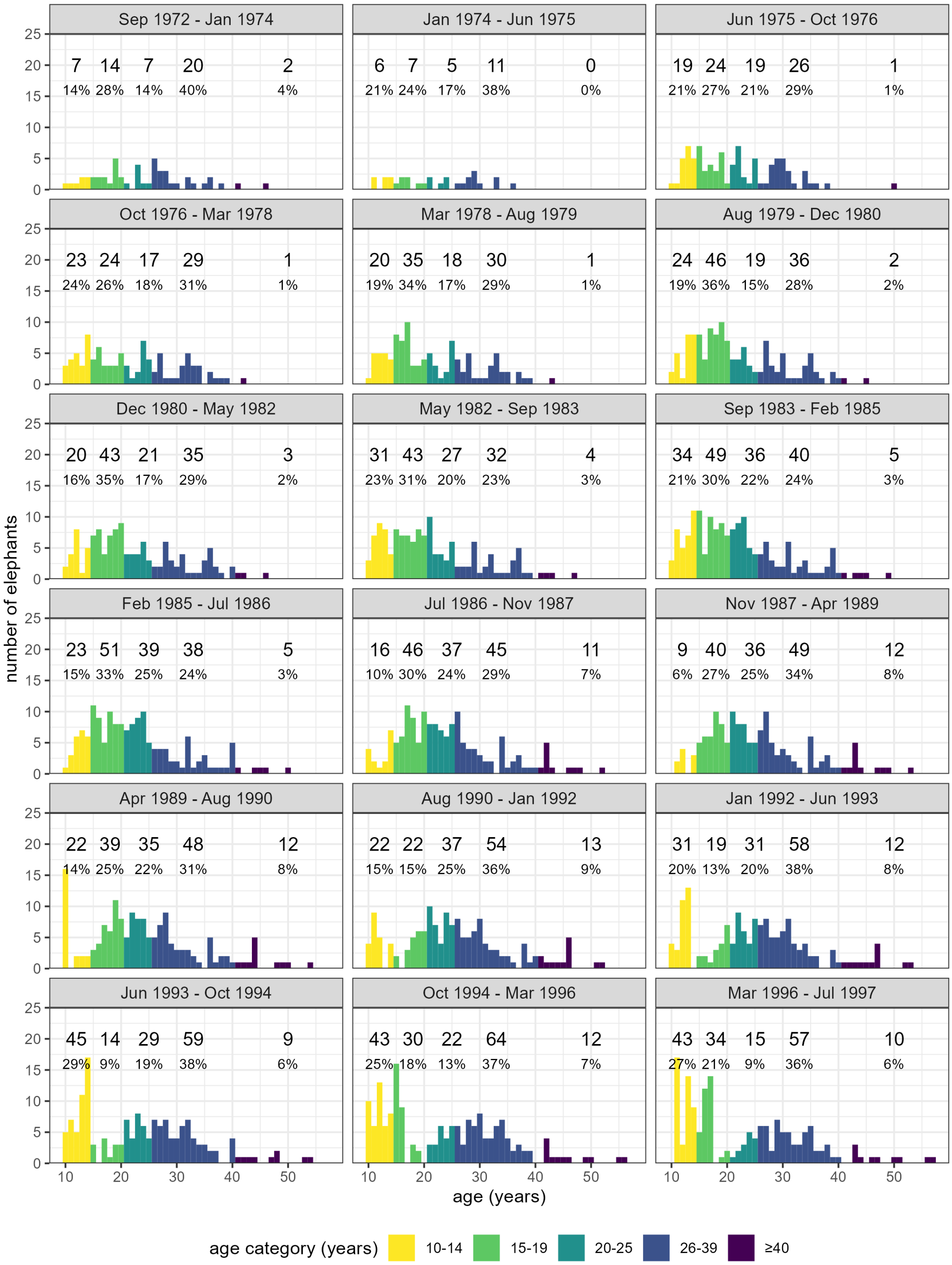


Figure A30: Relative number of elephants in each age category for MOTNP. Yellow indicates the youngest elephants, while dark purple shows the oldest category. The numbers indicate the total count, and the percentage of the population, found in each age category.



(i) Short ANP windows 1-18

Figure A31

(ii) Short ANP windows 19-36

Figure A31: Age distributions for all short ANP time windows. Yellow indicates the youngest elephants, through to dark purple showing the oldest, based on MOTNP categories. The numbers indicate the total count, and the percentage of the population, found in each age category.

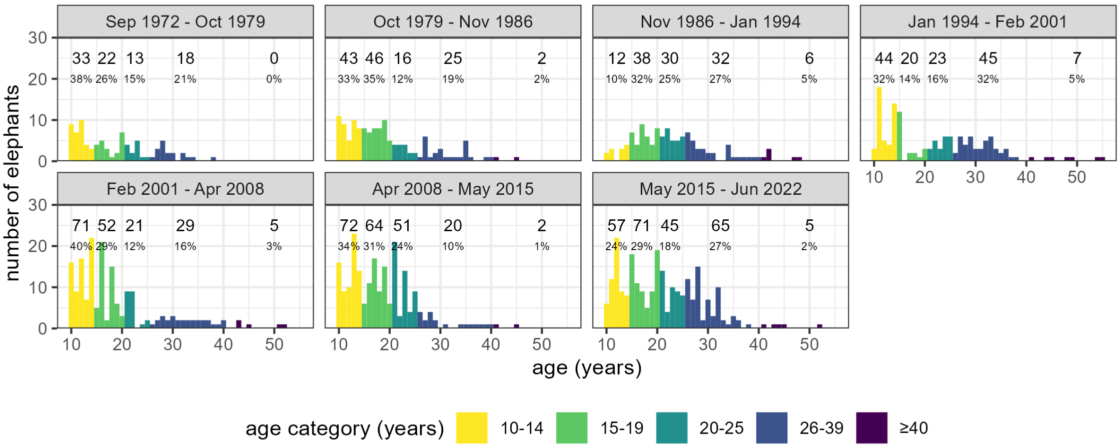
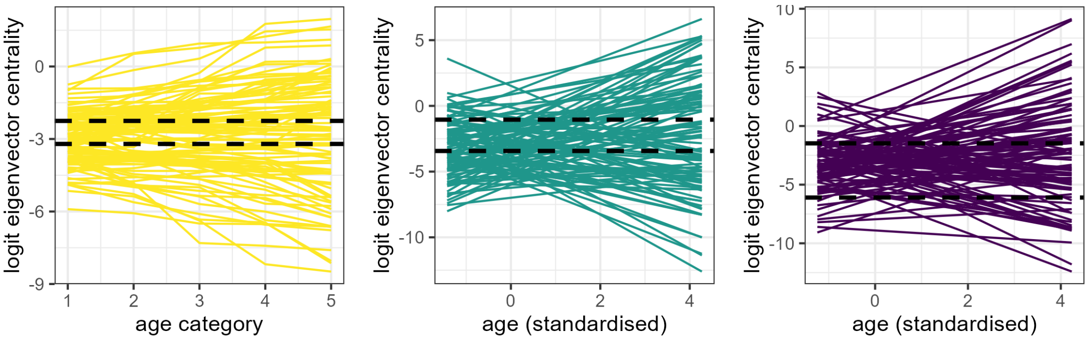


Figure A32: Age distributions for all long ANP time windows. As for short windows, colours relate to the MOTNP age categories for comparison between populations. The numbers indicate the total count, and the percentage of the population, found in each age category.

A2.2 Prior predictive checks



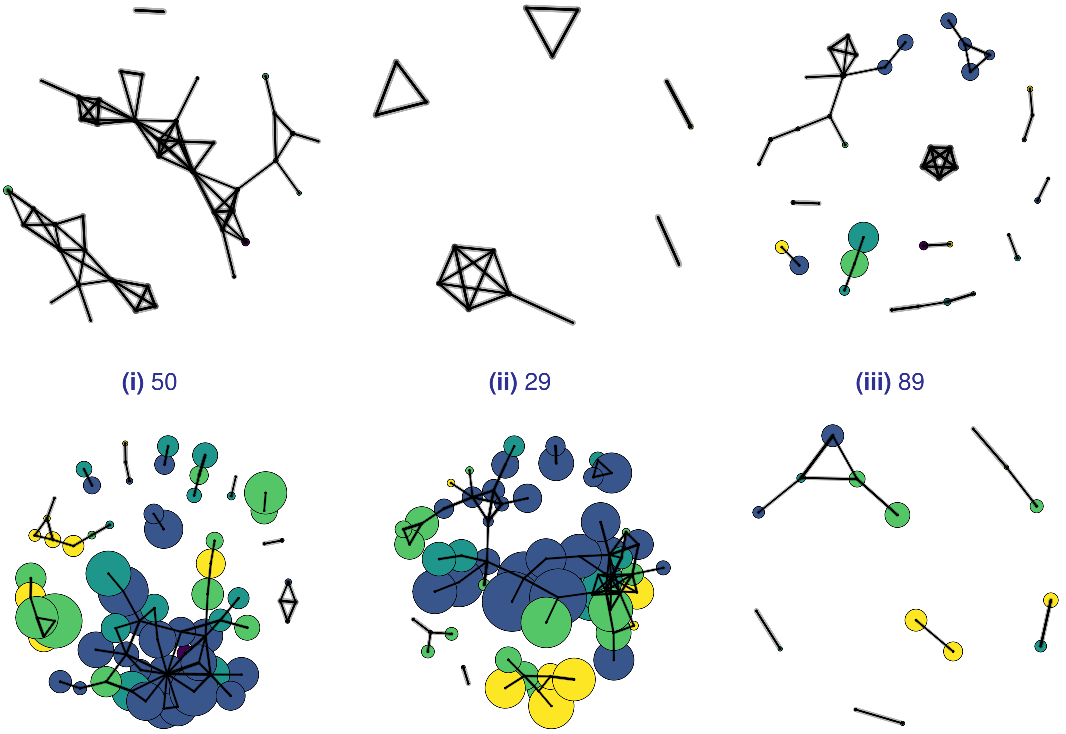
(i) MOTNP **(ii)** ANP short **(iii)** ANP long

Figure A33: Prior predictive checks for nodal regressions for a) MOTNP, b) short ANP windows and c) long ANP windows. All models share the same slope prior (though MOTNP looks different due to a different way of using the prior). ANP models share the same intercept and random effects priors. MOTNP and ANP (b-c) share the same mean intercept, but differ in the standard deviation of the intercept, due to substantial differences between MOTNP and the long ANP range of centralities. The intercept mean $logit(0.05)$ was selected from Chiyo *et al.*, 2011.

A2.3 Network plots

A2.3.1 ANP short time windows

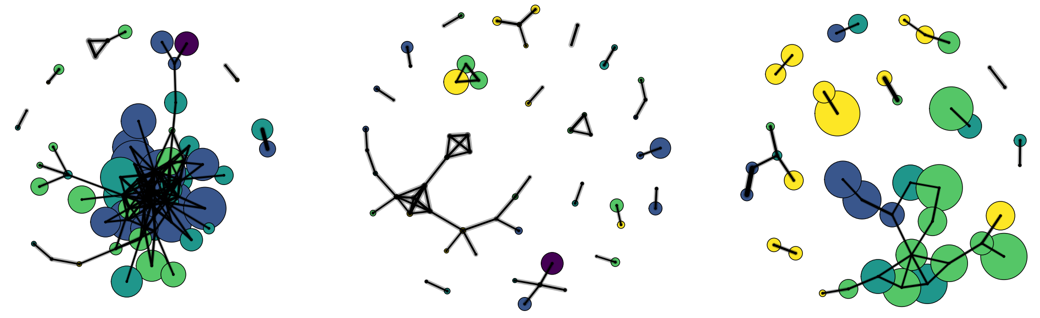
Network plots based on edge weight estimations for ANP windows of 500 days showing all connections with median strength ≥ 0.15 and all individuals with at least connection of this strength. For all plots, node size represents the log-transformed number of sightings, and node colour shows the age of the individual with yellow as the youngest and dark purple the oldest. There appears to be a lot of variation between windows in the length of branching chains of connected individuals, with some forming complex webs, where others form small modules. However, examining the cause of these differences was beyond the scope of this chapter.



(i) 50 **(ii)** 29 **(iii)** 89

(iv) 94 **(v)** 104 **(vi)** 127

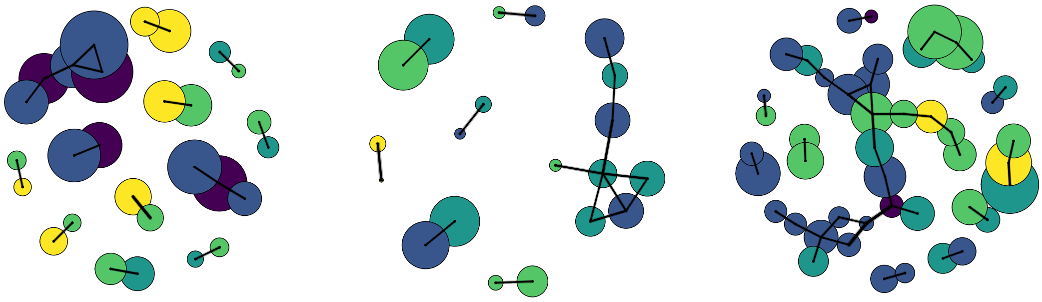
Figure A34



(vii) 122

(viii) 137

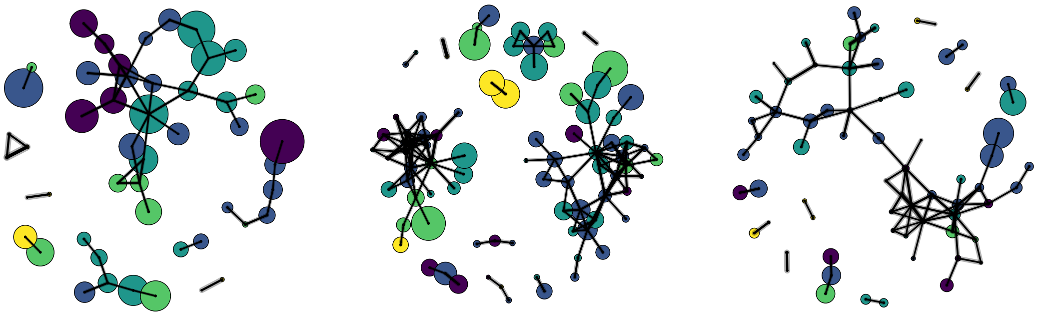
(ix) 164



(x) 156

(xi) 155

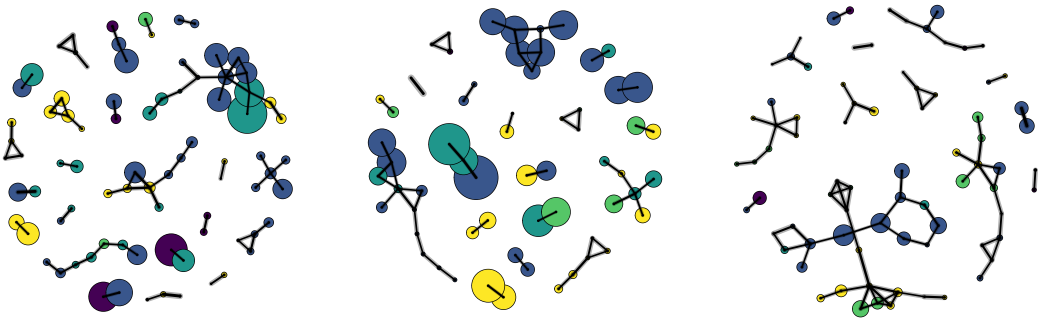
(xii) 146



(xiii) 156

(xiv) 148

(xv) 151

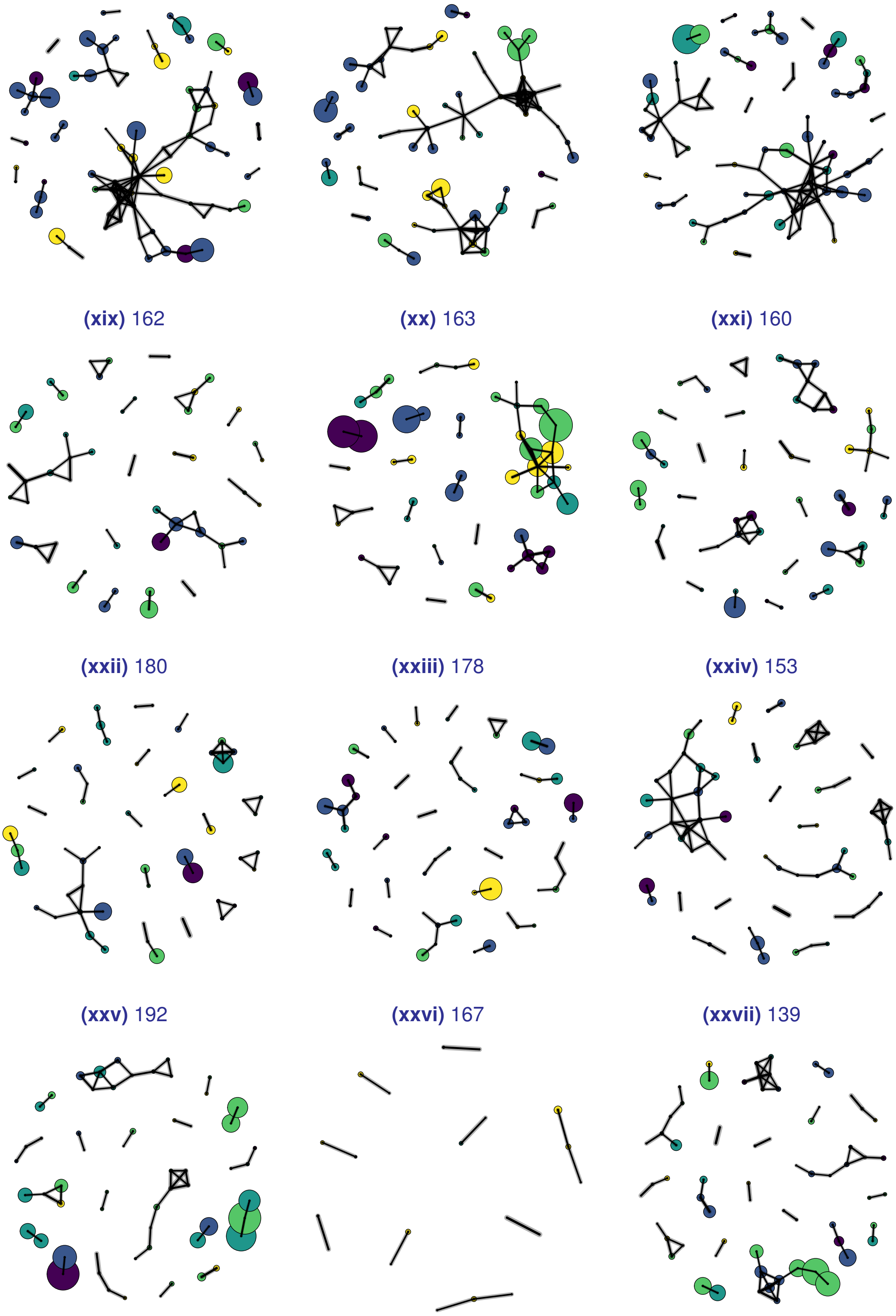


(xvi) 156

(xvii) 171

(xviii) 159

Figure A34



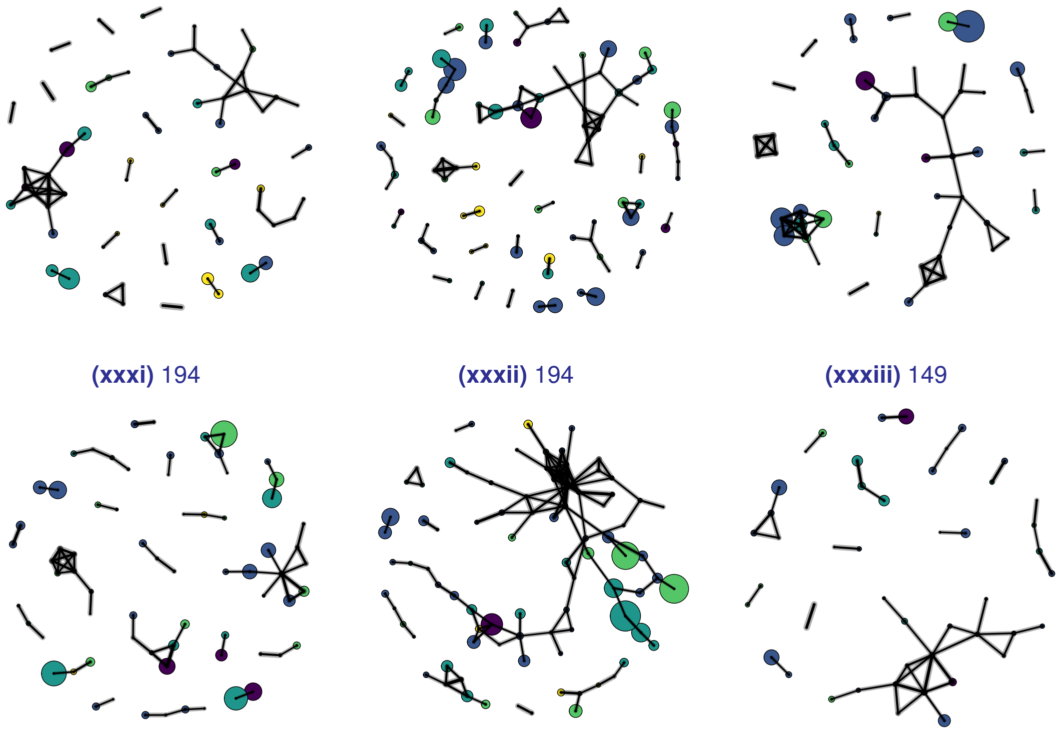
(xix) 162 **(xx)** 163 **(xxi)** 160

(xxii) 180 **(xxiii)** 178 **(xxiv)** 153

(xxv) 192 **(xxvi)** 167 **(xxvii)** 139

(xxviii) 175 **(xxix)** 215 **(xxx)** 197

Figure A34



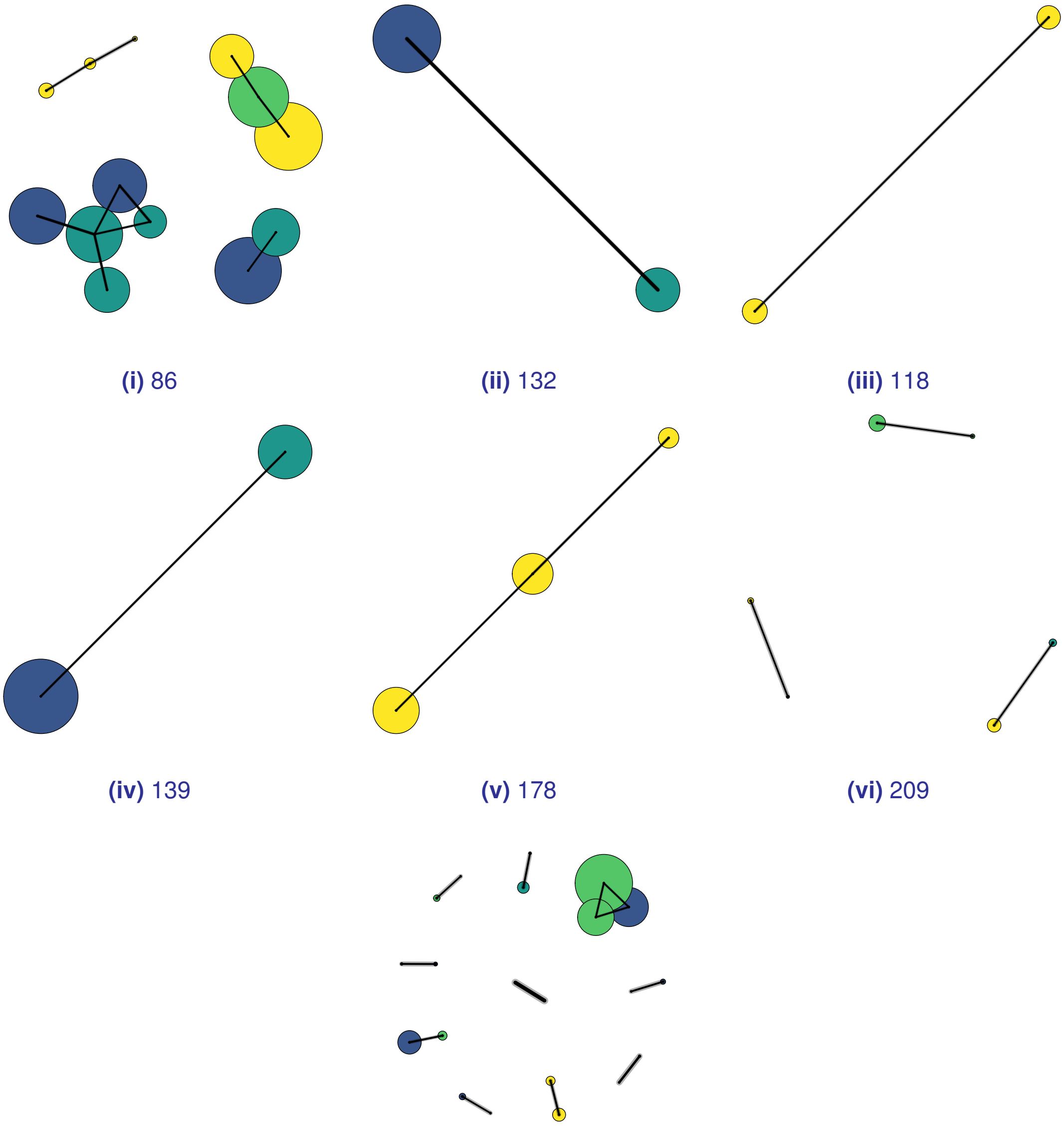
(xxxi) 194 **(xxxii)** 194 **(xxxiii)** 149

(xxxiv) 174 **(xxxv)** 144 **(xxxvi)** 121

Figure A34: Network plots based on edge weight estimations for ANP short time windows. Numbers underneath each plot indicate the total number of elephants in each time window.

A2.3.2 ANP long time windows

Network plots based on edge weight estimations for ANP windows of 2 571 days. In the first set of graphs, I have shown all connections with median strength ≥ 0.15 and all individuals with at least connection of this strength, to illustrate a comparison to the shorter time windows. However, the long windows displayed lower average edge weights, causing these graphs to appear extremely small, despite the size of population analysed. For this reason, I have included a second set of graphs for the long ANP time windows, at a threshold of 0.10 for a comparison of network size and complexity. Note that due to the nature of the differences in total sighting count, node sizes can be compared between time windows of the same duration and population, but not between window durations or against those of MOTNP.



(i) 86

(ii) 132

(iii) 118

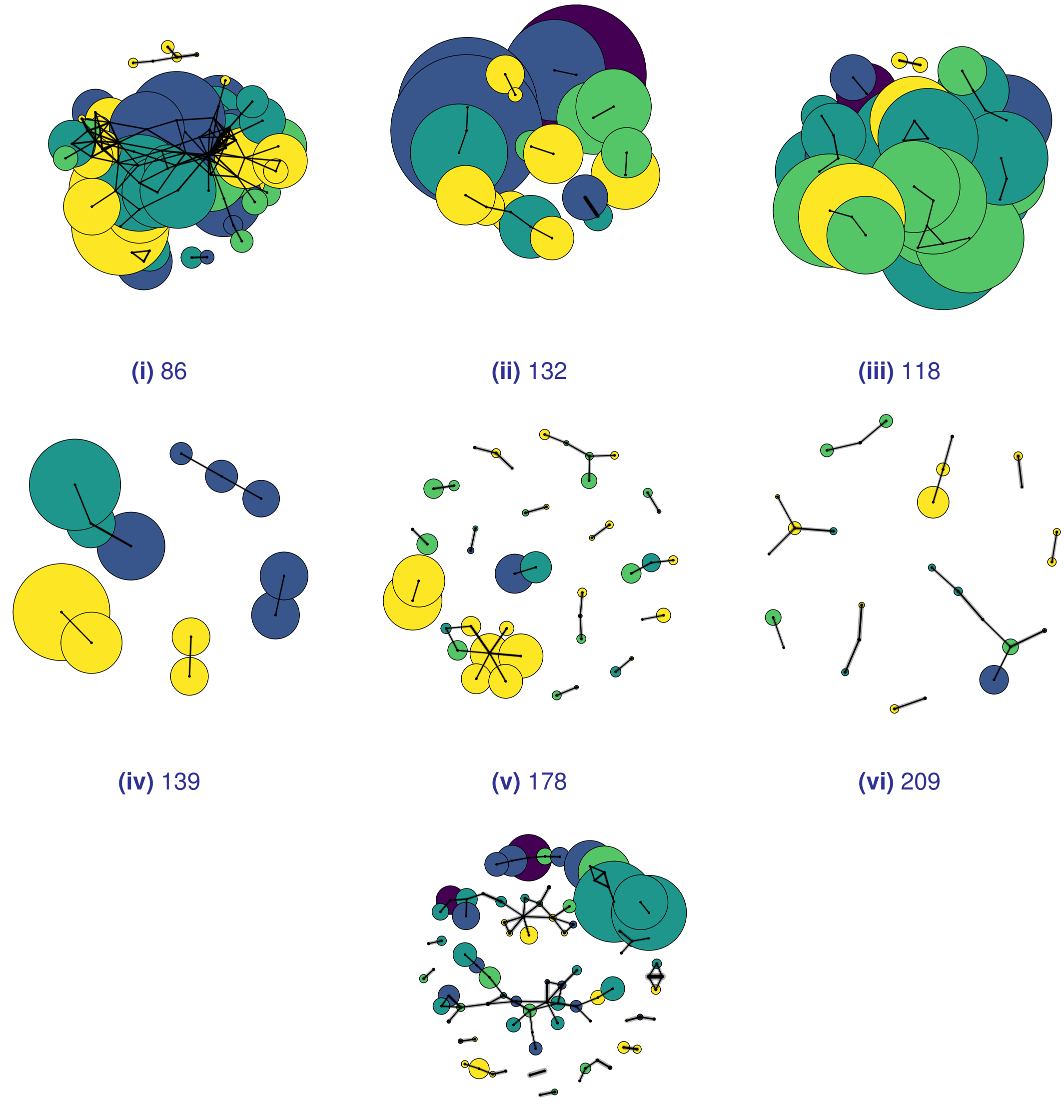
(iv) 139

(v) 178

(vi) 209

(vii) 243

Figure A35: Network plots based on edge weight estimations for ANP long time windows. Numbers underneath each plot indicate the total number of elephants in each time window. Plots show all edges with a median weight ≥0.15.



(i) 86

(ii) 132

(iii) 118

(iv) 139

(v) 178

(vi) 209

(vii) 243

Figure A36: Network plots based on edge weight estimations for ANP long time windows. Numbers underneath each plot indicate the total number of elephants in each time window. Plots show all edges with a median weight $\geq$0.10.

A2.4 ANP nodal regression plots, split by time window

Nodal regression results showing variation by time window for ANP windows of 500 days. For all plots, colours represent the age categories that each elephant would be assigned to in the MOTNP ageing system.

A2.4.1 ANP short time windows

For the short time windows, all appear to have very similar average eigenvector centrality except for the first two time windows, which are higher and with greater variation than the later windows. This is likely due to having a smaller network size than later time windows. These differences may reflect a genuine change in the population at around this time, or it could be due to other external influences. For example, at this time, Amboseli Trust for Elephants was only just starting out, and may still have been identifying the best methods for individual identification and group observation, so creating the appearance of more variation in the population, when in fact it was variation in sampling method.

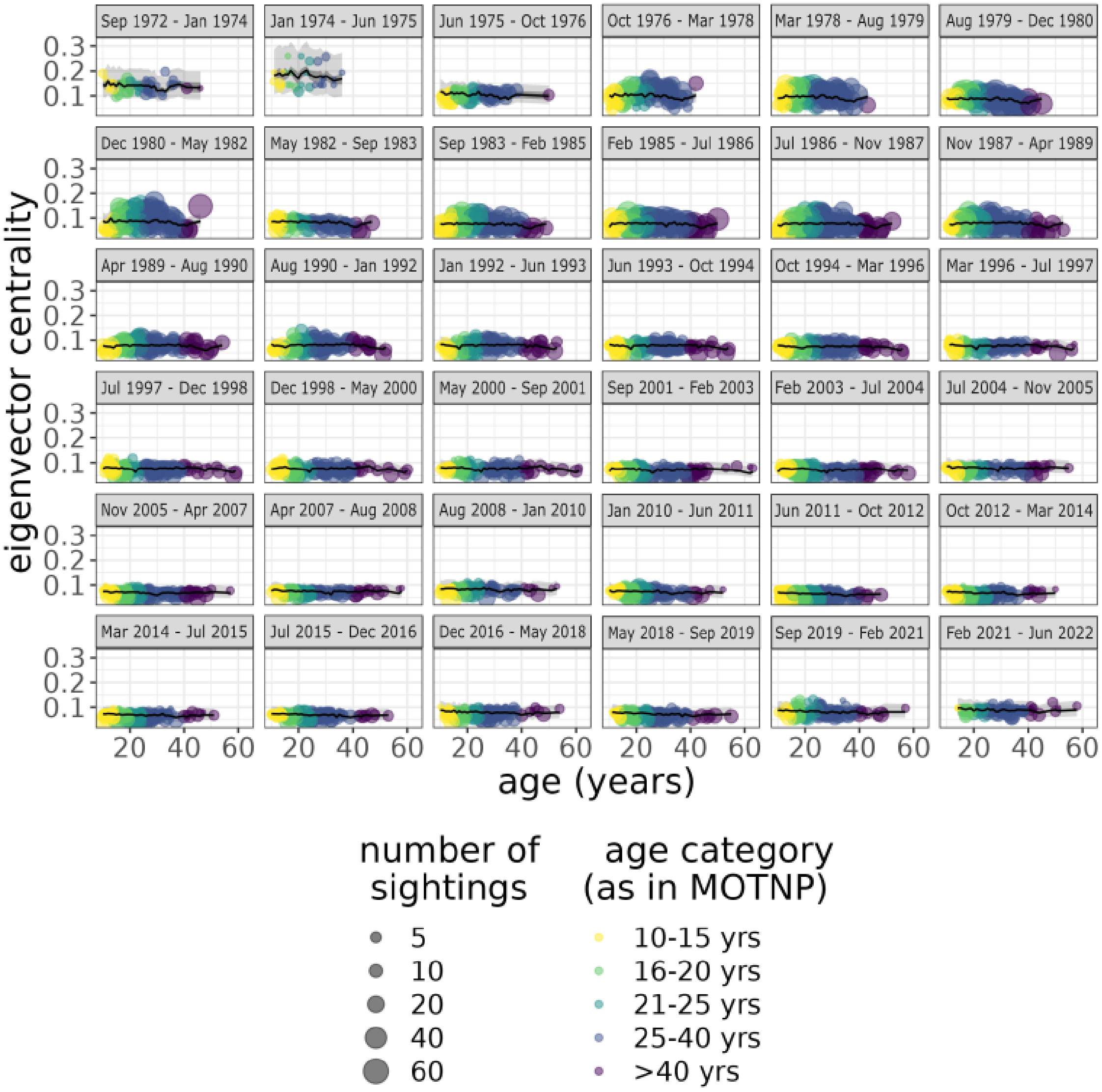


Figure A37: Nodal regression plots for short ANP time windows. Plots are faceted by time window to show the variation (or lack thereof) in effect of age on eigenvector at different time points.

A2.4.2 ANP long time windows

For the long time windows, I no longer see the first time period as having more variation in eigenvector centrality than later windows, but there does appear to be a slight decline over time such that window seven has lower average centrality than window one. However, despite the change in intercept, there does not appear to be any difference in the fit of the model slope with increasing time window.

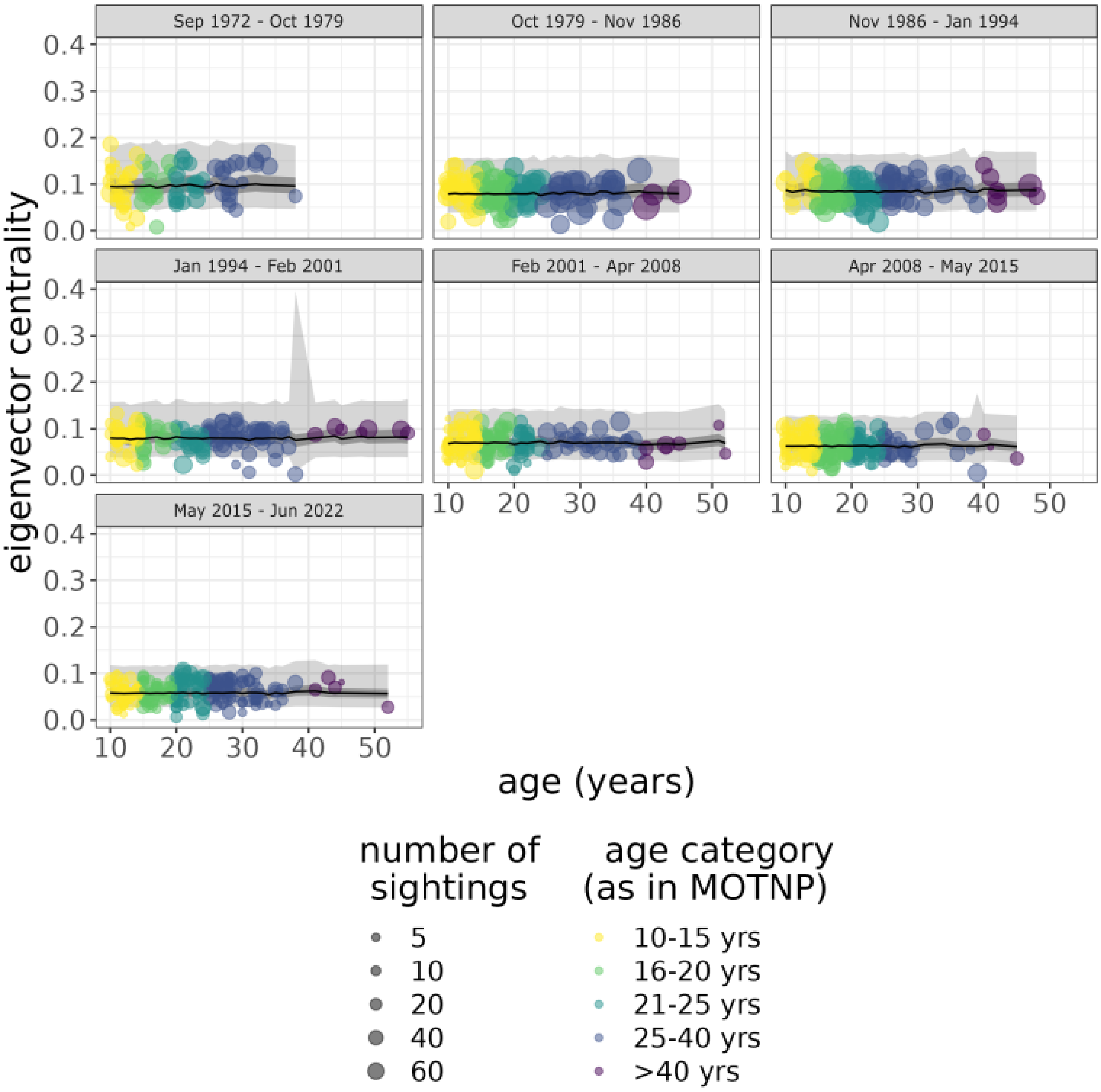


Figure A38: Nodal regression plots for long ANP time windows. Plots are again faceted by time windows to show the lack of variation in effect of age on eigenvector at different time points.

A2.5 ANP nodal regression random effects

A2.5.1 Node random effects

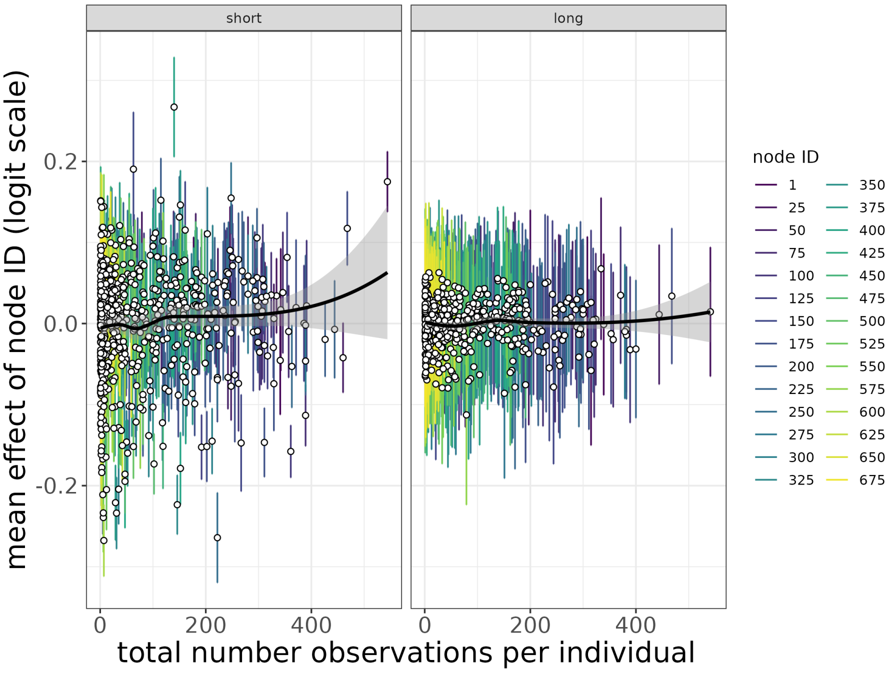


Figure A39: Random effects of node ID for ANP nodal regression. There is no strong effect of node ID for either short of long time windows, with very wide uncertainty in all estimates, and mean estimates clustered around zero. This is largely unaffected by the number of times in which an individual was observed, and also by the number of windows in which an individual was observed. Long windows show much greater uncertainty in their estimates of the effect of node ID on eigenvector, as there are fewer time windows and therefore fewer repeated measures per individual.

A2.5.2 Window random effects

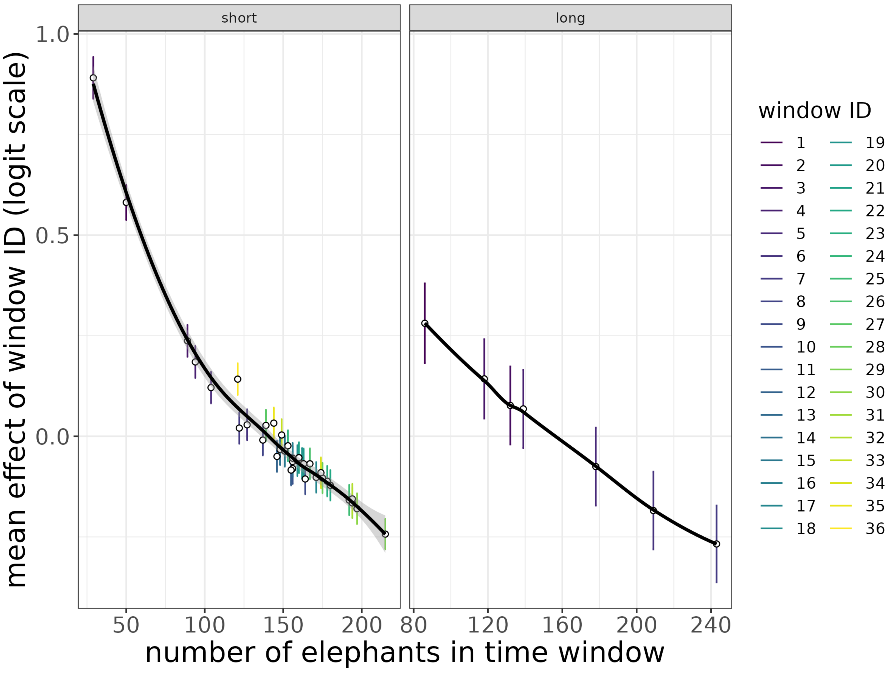


Figure A40: Random effects of window ID for ANP nodal regression. Random intercept of window varies quite substantially (note this is on the logit scale), and is strongly influenced by the size of the network (scales differ between graphs). This makes sense, as more elephants recorded by ATE means more elephants with whom an individual must be sighted in order to obtain a high eigenvector centrality.

A3 Group response of male elephants to threatening situations

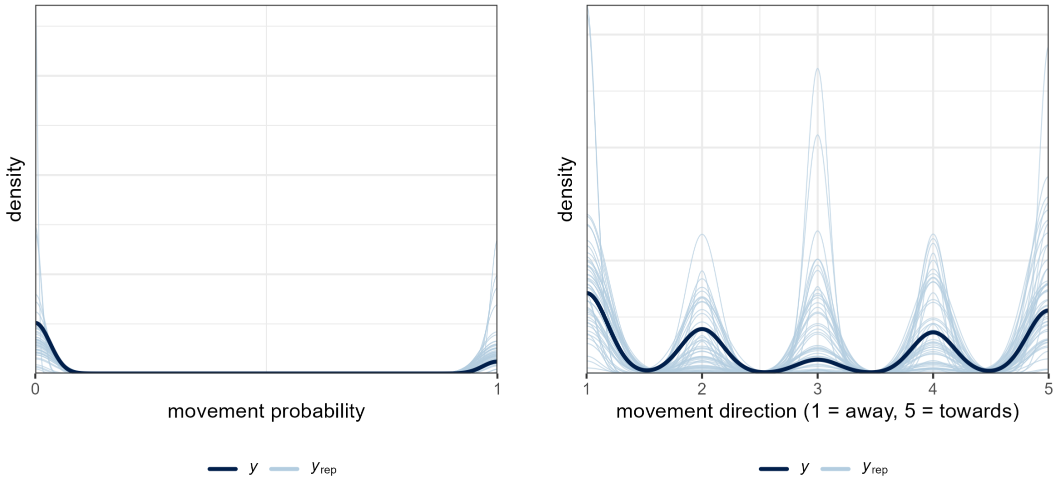
A3.1 Recordings used to create playback stimuli

I created the sound files for the cape turtle dove and lion playbacks using GBIF recordings, selecting those with the clearest sound and least background noise.

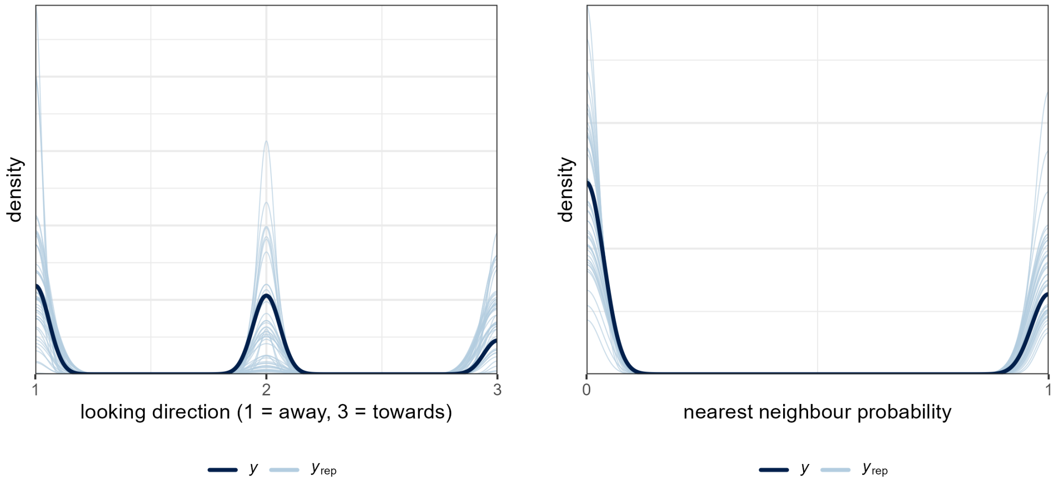
Table A9: Details of original recordings for stimulus generation. All dove calls were accessed on 25th July 2022, and lion roars on 27th June 2022. ID numbers noting a/b/c indicate where I used multiple segments of a recording to create different stimulus tracks.

Type	ID	Recordist	Location	Recorded
Cape Turtle Dove	1	Derek Solomon	South Africa	2006
	2a	Lynette Rudman	South Africa	2021
	2b	Lynette Rudman	South Africa	2021
	2c	Lynette Rudman	South Africa	2021
	3	Peter Boesman	South Africa	2016
	4	Peter Boesman	South Africa	2016
	5	Peter Boesman	South Africa	2016
	6	Peter Boesman	South Africa	2017
	7	Tony Archer	South Africa	2019
	8	Tony Archer	South Africa	2021
	9	Tony Archer	South Africa	2021
	10	Tony Archer	South Africa	2021
Lion	11	Dewald du Plessis	Botswana	2019
	12	Dewald du Plessis	Botswana	2019
	13	Museum für Naturkunde	Berlin (captive)	1959
	14	Museum für Naturkunde	Berlin (captive)	1968
	15a	Museum für Naturkunde	Berlin (captive)	1998
	15b	Museum für Naturkunde	Berlin (captive)	1998
	16	Museum für Naturkunde	Berlin (captive)	1999
	17	Museum für Naturkunde	Berlin (captive)	2003
	18	Museum für Naturkunde	Berlin (captive)	unspecified
	19	Museum für Naturkunde	Berlin (captive)	1959
	20	Museum für Naturkunde	Berlin (captive)	1959

A3.2 Prior predictive checks



(i) MBM **(ii)** MOM



(iii) LOM **(iv)** NBM

Figure A41: Prior predictive checks for the i) movement binomial model, ii) movement ordinal model, iii) looking ordinal model, and iv) neighbour binomial model. Pale blue lines indicate draws from the prior, while the dark blue line shows that the raw data fit with the prior distribution. For MBM and LOM, the slope priors are set to be $Normal(-1, 1)$ to reflect low probabilities of movement or looking towards one another. For MOM and NBM, where I have no prior expectations one way or the other, I have used a symmetrical $Normal(0, 1)$ prior for the slopes.

A3.3 Proportions of time per activity throughout playback

Table A10: Proportion (mean ± SD) of time spent moving towards, alongside, or away from other elephants during each stimulus type and time period.

Section	Partner age relative to focal	Approach directly (5)	Approach at an angle (4)	Move directly with (3)	Move away at an angle (2)	Move away directly (1)
Before (dove)	Younger	28.95 ± 37.67	8.86 ± 24.06	3.28 ± 11.03	21.13 ± 34.15	37.77 ± 43.52
	Matched	27.18 ± 40.19	14.35 ± 29.13	0.74 ± 5.57	19.34 ± 33.73	38.38 ± 44.28
	Older	36.44 ± 42.53	17.02 ± 31.27	3.09 ± 13.52	14.81 ± 28.66	28.63 ± 39.52
During (dove)	Younger	24.09 ± 40.89	10.17 ± 26.68	6.79 ± 18.99	15.10 ± 33.22	43.84 ± 46.78
	Matched	26.02 ± 39.59	12.27 ± 26.44	5.67 ± 15.67	13.38 ± 29.73	42.67 ± 49.26
	Older	26.60 ± 41.14	8.96 ± 23.70	5.18 ± 19.06	15.70 ± 35.09	43.55 ± 48.79
After (dove)	Younger	24.20 ± 36.05	9.61 ± 23.84	7.07 ± 18.71	20.43 ± 26.75	38.69 ± 38.85
	Matched	20.23 ± 35.81	13.60 ± 30.60	12.33 ± 28.92	16.74 ± 28.30	37.09 ± 44.01
	Older	25.30 ± 38.74	15.51 ± 31.39	5.45 ± 12.61	15.93 ± 28.93	37.82 ± 42.64
Before (lion)	Younger	26.31 ± 42.78	20.10 ± 35.43	0.96 ± 4.08	19.10 ± 29.17	33.52 ± 38.80
	Matched	21.91 ± 30.23	23.79 ± 32.78	0.00 ± 0.00	19.44 ± 22.71	34.85 ± 33.87
	Older	18.28 ± 26.88	34.80 ± 31.48	0.00 ± 0.00	27.52 ± 20.66	19.40 ± 22.76
During (lion)	Younger	43.85 ± 47.93	11.54 ± 28.24	0.00 ± 0.00	7.87 ± 23.96	36.74 ± 48.24
	Matched	26.96 ± 38.26	21.23 ± 31.11	3.33 ± 18.26	33.02 ± 41.98	15.45 ± 28.17
	Older	38.63 ± 39.15	28.01 ± 27.37	0.00 ± 0.00	7.06 ± 24.19	26.30 ± 40.32

Section	Partner age relative to focal	Approach directly (5)	Approach at an angle (4)	Move directly with (3)	Move away at an angle (2)	Move away directly (1)
After (lion)	Younger	12.48 ± 19.71	16.40 ± 24.16	12.55 ± 19.34	17.64 ± 24.13	40.94 ± 31.75
	Matched	19.12 ± 30.83	11.71 ± 19.84	5.27 ± 12.86	25.39 ± 35.85	38.52 ± 42.25
	Older	50.38 ± 39.94	24.80 ± 27.13	3.52 ± 11.39	7.27 ± 13.22	14.03 ± 30.47
Before (human)	Younger	36.90 ± 33.90	26.82 ± 29.57	0.50 ± 3.46	14.81 ± 23.55	20.97 ± 29.53
	Matched	24.74 ± 30.20	16.62 ± 23.12	0.00 ± 0.00	23.67 ± 27.33	34.97 ± 33.79
	Older	13.47 ± 24.23	11.63 ± 18.03	0.00 ± 0.00	29.68 ± 28.92	45.22 ± 38.60
During (human)	Younger	16.38 ± 33.44	19.07 ± 30.44	3.90 ± 10.30	29.67 ± 36.10	30.98 ± 40.71
	Matched	17.31 ± 32.47	16.93 ± 27.79	7.03 ± 18.09	28.00 ± 31.33	30.73 ± 37.57
	Older	14.99 ± 28.06	15.23 ± 28.76	1.64 ± 7.20	27.96 ± 32.51	40.19 ± 40.79
After (human)	Younger	19.33 ± 30.97	17.14 ± 23.19	2.09 ± 7.88	22.00 ± 26.83	39.44 ± 39.86
	Matched	19.45 ± 28.15	24.38 ± 25.73	1.77 ± 11.36	19.56 ± 24.24	34.83 ± 39.54
	Older	17.75 ± 25.05	15.76 ± 19.98	5.50 ± 16.19	20.54 ± 22.97	40.45 ± 40.08

Table A11: Proportion (mean ± SD) of time spent looking towards, side on, or away from other elephants during a control (top), lion (middle) and human (bottom) stimulus.

Section	Partner age relative to focal	Look towards (3)	Side-on (2)	Look away (1)
Before (dove)	Younger	22.34 ± 34.17	31.11 ± 33.20	46.55 ± 42.43
	Matched	24.29 ± 34.77	28.28 ± 30.64	47.43 ± 42.56
	Older	23.25 ± 35.96	35.72 ± 35.90	41.02 ± 41.42
During (dove)	Younger	15.49 ± 29.88	34.20 ± 38.30	50.31 ± 46.01
	Matched	16.86 ± 34.03	27.72 ± 40.07	55.43 ± 48.16
	Older	18.14 ± 34.48	39.19 ± 42.81	42.67 ± 46.70
After (dove)	Younger	16.68 ± 27.48	39.20 ± 34.26	44.12 ± 39.64
	Matched	13.06 ± 26.37	41.23 ± 39.51	45.70 ± 43.08
	Older	20.87 ± 34.58	39.12 ± 37.36	40.01 ± 40.73
Before (lion)	Younger	17.53 ± 31.30	36.44 ± 31.64	46.03 ± 40.43
	Matched	17.44 ± 26.05	43.78 ± 32.44	38.77 ± 36.28
	Older	26.83 ± 27.81	38.75 ± 31.13	34.43 ± 30.56
During (lion)	Younger	29.00 ± 43.25	21.26 ± 36.99	49.74 ± 47.14
	Matched	15.29 ± 28.10	47.20 ± 36.52	37.51 ± 39.50
	Older	30.50 ± 35.30	28.74 ± 32.36	40.76 ± 41.99
After (lion)	Younger	27.86 ± 30.71	40.85 ± 22.50	31.29 ± 32.25
	Matched	17.05 ± 30.10	39.07 ± 31.23	43.88 ± 38.33
	Older	34.55 ± 25.55	46.13 ± 20.32	19.31 ± 31.48
Before (human)	Younger	22.21 ± 32.01	36.99 ± 33.40	40.81 ± 41.58
	Matched	11.54 ± 22.07	42.88 ± 32.17	45.58 ± 37.35
	Older	6.63 ± 18.07	37.89 ± 33.73	55.48 ± 37.75
During (human)	Younger	17.69 ± 31.19	44.75 ± 33.90	37.56 ± 38.03
	Matched	13.28 ± 24.07	40.12 ± 33.65	46.61 ± 37.41
	Older	9.07 ± 21.70	32.59 ± 31.40	58.34 ± 37.55
After (human)	Younger	19.01 ± 27.50	43.28 ± 31.13	37.71 ± 38.60
	Matched	14.92 ± 27.36	42.05 ± 33.84	43.03 ± 38.62
	Older	8.16 ± 17.26	42.03 ± 33.42	49.81 ± 37.58

Table A12: Proportion (mean ± SD) of time spent with nearest neighbour in each of the four categories.

Section	Stimulus	FO + TO	FO + TY	FY + TO	FY + TY
Before	Dove	0.29 ± 0.44	0.28 ± 0.43	0.23 ± 0.40	0.21 ± 0.39
	Lion	0.55 ± 0.47	0.20 ± 0.37	0.19 ± 0.37	0.05 ± 0.19
	Human	0.32 ± 0.43	0.25 ± 0.40	0.26 ± 0.42	0.18 ± 0.35
During	Dove	0.31 ± 0.46	0.28 ± 0.45	0.25 ± 0.43	0.16 ± 0.36
	Lion	0.55 ± 0.50	0.20 ± 0.40	0.20 ± 0.40	0.05 ± 0.20
	Human	0.26 ± 0.41	0.30 ± 0.44	0.29 ± 0.45	0.15 ± 0.35
After	Dove	0.33 ± 0.45	0.25 ± 0.41	0.21 ± 0.39	0.22 ± 0.40
	Lion	0.46 ± 0.50	0.25 ± 0.43	0.20 ± 0.39	0.09 ± 0.26
	Human	0.34 ± 0.44	0.29 ± 0.42	0.25 ± 0.42	0.11 ± 0.28

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