Importance of older males: influence of age structure on social dynamics between males in an elephant bull area.

Submitted by Connie Allen to the University of Exeter

as a thesis for the degree of Doctor of Philosophy in Psychology

In October 2021

Declaration: I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

This thesis explores male sociality in African savannah elephants (*Loxodonta africana*), focusing on the influence of age structure on social dynamics between males in a male dominated area. There is much to learn regarding the nature of relationships in non-reproductive all-male groupings and the benefits afforded to males in associating with each other. Moreover, in long-lived species, all-male groupings provide an opportunity for individuals of vastly different age and experience to interact, and there may be different benefits afforded to males of different age in associating with one another.

I conducted focal animal sampling of male elephants aggregating at hotspots of social activity, and a camera trap survey of elephant movements and behaviours on elephant pathways in Makgadikgadi Pans National Park, Botswana.

I found differences in grouping and performance of several behaviours with male age. Adolescents were more likely to travel in all-male groups, and mature bulls were more likely to travel alone, suggesting association with other males is more beneficial for younger males. Adolescents performed greeting behaviours at greater rates than adults, and such behaviours may facilitate further beneficial interactions between males. Adolescents also directed more aggressive and fear-related behaviours to non-elephant targets when alone, compared to when with other males. Adolescents may therefore perceive themselves to be at greater risk when socially isolated, and grouping with other males may reduce predation risks, and improve adolescents' ability to safely navigate unknown, risky environments. Males' olfactory responses to pathways and experimentally placed

urine deposits, however, did not vary with age, suggesting remote monitoring of same-sex conspecifics is equally important across the life course. Urine from adult males was more likely to evoke heightened responses than urine of adolescent males, suggesting males may be able to discern the age of same-sex conspecifics from their remote deposits. Such remote assessment of potential affiliates, threats or competitors sharing the environment is likely beneficial for males living in highly fission-fusion societies.

I also found evidence for important social roles of older males in all-male groupings. Older males were more likely to lead their group movements, suggesting they may guide younger, less experienced males in locating critical resources. Male elephants were less likely to direct aggression to non-elephant targets when more males from the oldest age cohort were present. Older males may be particularly effective assessors of environmental risk, and elephants may perform less aggressive behaviours to non-elephant targets when more older males are present due to reductions in anxiety. Alternatively, older males may police other males' aggression behaviours.

The African elephant is of conservation concern and a species involved in several unresolved human-wildlife conflicts. Throughout this thesis I therefore also relate findings to potential management and conservation implications.

Dedication

This thesis is dedicated to my wonderful Mum, Deniece Allen, who was unable to see the work through to completion. Mum, I wish I could have shared the marvellous things I saw in Botswana, and amazing discoveries we have made with you. It has been a tough journey getting here without you, but completing this PhD was always for you.

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During my years in Botswana, I was based at the Elephants for Africa research camp in Makgadikgadi Pans National Park. The staff, volunteers and fellow students at Elephants for Africa provided me with crucial research insights and planning, introduced me to the study system, and helped integrate me into the study area. I would like to thank Kate Evans, Stephen Harris, Jess Isden, Rebecca Dannock, Thatayaone Motsentwa, Walona Sehularo, Hayley Blackwell, James Stevens, Aaron Kerr, Helen Shaw, Rebaabetswe Radinaane and Masego Mokobela. Most of whom also assisted with data collection for various aspects of this thesis, with hundreds of hours enjoyed together observing elephants along the Boteti River.

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Definitions & Abbreviations

The following definitions and abbreviations can be found throughout this thesis:

MPNP: Makgadikgadi Pans National Park

aOR: Adjusted odds ratio

CI: Confidence intervals

GLMM: Generalized logistic mixed-effects model

Ref: Reference class

IQR: Interquartile range

IUCN: International Union for Conservation of Nature.

N: Number

SD: Standard deviation

SEO: Scent emitting organ

African elephant: African savannah elephant (*Loxodonta africana*). From 2021, the IUCN red list lists the African savannah elephant as a species separate from the African forest elephant (*Loxodonta cyclotis*) (IUCN, 2020). For ease of reading, I refer to the African savannah elephant, the subject species, as “African elephant” throughout this thesis. Where referring to other elephant species in the thesis, such a distinction is clearly stated.

Chapter 1: Introduction

1.1 General introduction

1.1.1 Non-reproductive all-male aggregations and all-male groups: formation and function

With male fitness primarily limited by access to mating opportunities with females, sexual selection theory predicts that relationships between males of a species will be primarily competitive (Trivers, 1972; Andersson & Iwasa, 1996; Lindenfors & Tullberg, 2011). This competition is predicted to be particularly intense in slow breeding, large mammal species, where males have far higher optimal mating rates, and invest drastically fewer resources per offspring compared to females, which have a lengthy gestation and lactation period (Clutton-Brock, 1985; Wedell et al., 2006; Hollister-Smith et al., 2007; Chelliah & Sukumar, 2013). Operational sex ratios in large mammals tend to be heavily male skewed as a result (i.e. at any given time there are more males available to mate compared to females) (Clutton-Brock & Parker, 1992), and research on male-male interactions has consequently tended to be heavily focused on agonistic encounters and competition, such as territorial defence (Grinnell & McComb, 2001; Mitani et al., 2010), mate guarding (Schubert et al., 2009), or establishment of dominance hierarchies in order to gain access to females and mating events (Clutton-Brock et al., 1979; Poole, 1989a; Robinson et al., 2006; le Roux & Bergman, 2012; Jennings & Gammell, 2013).

However, alongside this inherent male intrasexual conflict is the seemingly contradictory observation that many large mammals segregate into male and female groups to some degree in their social organisation. Bachelor herds are observed in most group living polygamous ungulate species (Clutton-Brock et al., 1982; Vilá, 1995; Ruckstuhl & Neuhaus, 2002; Szemán et al., 2021), and all-male groups form in many primate societies (Qi et al., 2014; Snyder-Mackler et al., 2012). Behavioural ecologists attribute social segregation of the sexes to both ecological and social drivers (Conradt, 2005; Bonenfant et al., 2004). Examples of ecological drivers include divergent forage, prey, mineral or water requirements of the sexes (owing for example to different metabolic requirements due to body dimorphisms between the sexes, or increased pressure of gestation and lactation on females) that leads to a consequent occupation of different habitats (Jarman, 1974; Barboza & Bowyer, 2000; Pérez-Barbería et al., 2008). Secondly, differences in predation risk (for example body size differences, or the additional pressure for females of increased predator risks on vulnerable dependent offspring), may also push males and females to occupy different habitats (Main et al., 1996; Bowyer, 2004; Corti & Shakleton, 2002; Croft et al., 2006). Social factors can also play a role in sexual segregation, firstly differences in activity budgets can lead to an inability of the sexes to remain in proximity with one another (to remain as a group, members must synchronise activities to some degree, such as foraging, resting and walking) (Ruckstuhl & Neuhaus, 2002; Ruckstuhl, 1999). Furthermore, both attraction to the same sex and avoidance of the opposite sex are proposed to influence social segregation of males and females (Conradt, 2005). Females may avoid males due to unwanted sexual harassment (Wielgus & Bunnell, 1994; Darden & Croft, 2008), while non-breeding, subordinate males may avoid, or be excluded from areas with females due to harassment and aggression from dominant, sexually active males (Feer & Dubost, 1981; Stokke & du Toit, 2002). Alternatively, animals of the same sex may be attracted to one another to reduce conspicuousness to predators (in sexually dimorphic species), or to facilitate social learning or the development of sex specific behaviours, such as to access sparring partners (Bon & Campan, 1996; MacFarlane & Coulson, 2009; Pérez-Barbería & Yearsley, 2010). Overall, however, it is likely that several factors contribute to the segregation of males from females within a species (Bonenfant et al., 2004).

Once sexually segregated, males can either live alone, be grouped together with other males, or be flexible in transitioning between these two states (Waser et al., 1994; Goldenberg et al., 2014). Membership in all-male groups is very often fluid and transitory with high levels of fission-fusion dynamics (Aureli et al., 2008). Males are often facultatively social (O'Brien et al., 2020), flexibly transitioning between solitary living and a varied group size and composition depending on their internal state, and the costs and benefits to grouping in their current social and ecological environment (Rajpurohit et al., 1995; Aureli et al., 2008; Couzin & Laidre, 2009; Barocas et al., 2016; Goldenberg et al., 2014). At one extreme, associations in all-male groups may be random, reflecting males temporarily associating in a particular ecological space for the fitness benefits described below (Parish et al., 1997; Lettevall et al., 2002; Ramos-Fernández et al., 2006). Alternatively, despite a frequent turnover of group membership and often high degree of fission-fusion dynamics, all-male groups may represent complex social systems, with stable associations of repeated partner preference or social bonds influenced by kinship (Chiyo et al., 2011a; Dal Pesco et al., 2021; Connor & Krützen, 2015), age similarity (Bon et al., 1993; Ruckstuhl & Festa-Bianchet, 2001; VanderWaal et al., 2013; Gerber et al., 2019), strong long-term bonds or alliances independent of kinship (Randić et al., 2012; De Moor et al., 2020), or high-value traits such as greater age and experience (Chiyo et al., 2011a; Bercovitch & Berry, 2014; Gerber et al., 2021), and high rank (Noë, 1992; Kajokaite et al., 2019). Yet as the dispersing sex in most social mammal species (Stephen Dobson, 1982; Li & Kokko, 2019), male sociality and its benefits to an individual's fitness have typically been more difficult to study both in terms of theory and practicality. That is compared to female sociality in philopatric groups, where female social bonds can be more directly attributed to inclusive fitness (i.e. the indirect benefits attained from supporting kin), and individuals' reproductive performance can be more easily measured (e.g. maternity is easier to assign than paternity) (Silk, 2007). Moreover, the highly fluid and loose relationships that often characterise all-male societies present challenges for data sampling in wild populations (Chapman et al., 1993; Murphy et al., 2021). As a result of these challenges, more research is still needed to better understand the complexity and organisation of male associations in all-male societies.

With competition for resources (females) as an obvious "push" factor driving males apart from one another, several factors can act as "pulls" to promote male sociality in all-male groups. Males can associate in all-male groups to gain direct reproductive benefits. That is, males may cooperate with other males to attempt to jointly monopolise females (e.g. male alliances in African lion, *Panthera leo*, and primate species ousting dominant and resident males at group takeover events (Packer & Pusey, 1982; Noë & Sluijter 1990; Bissonnette et al., 2009; 2014); or male alliances in bottlenose dolphins, *Tursiops truncates*, cooperatively herding receptive females for mating (Connor et al., 1992; Connor & Krützen, 2015)). Alternatively, all-male groups can also occur in species that are not attempting to cooperatively take over female groups or access receptive females, hence these males do not appear to gain direct reproductive benefits from their association (Ruckstuhl & Neuhaus, 2000). Males in non-reproductive all-male groups may be temporarily sexually inactive due to breeding seasonality (Turner et al., 2005; Prins, 1996), they may be building reserves between attempts to access females whilst avoiding harassment from dominant, sexually active males (Stokke & du Toit, 2002; Lee et al., 2011), or they may be sexually immature or post-prime condition, unable to contend with more dominant individuals in mixed-sex, or one-male lead groups (Robbins, 1996; Asa, 1999).

Temporarily sexually inactive males that associate in all-male groups, rather than live alone, may experience fitness benefits related to more immediate survival, or to an improved potential for mating opportunities in the future (Ruckstuhl & Neuhaus, 2000; Clutton-Brock, 2009). Non-reproductive males may associate with other males for improved predator protection and the opportunity to cooperatively divide time spent being vigilant (Roberts, 1996; Waterman, 1997; Averbeck et al., 2010), thermoregulation benefits (Gilbert et al., 2009), cooperative hunting benefits (Blundell, 2002; Lührs et al., 2012), opportunities to assess or develop competitive abilities (Latour, 1981; Pérez-Barbería & Yearsley, 2010; Chiyo et al., 2011a) and opportunities to acquire ecological and social information from informed and experienced individuals, including social learning of sex specific behaviours for recently dispersed immatures (Rajpurohit, 1995; Evans & Harris, 2008). Comparatively less is known concerning the reasons why males group together in sexually segregated species during times that they are non-reproductive, or regarding the social interactions between males in these non-reproductive all-male groups. Improving our understanding on these topics is a key aim of this thesis.

A brief mention should be made to the fact that males observed occupying the same ecological space in time may not, however, be best described as socially coordinated all-male groups. Across studies of social species, defining solitary animals from groups, aggregations, higher tiers of grouping such as “colonies” and “clans” and ultimately the society, can be problematic and differ between study species (Wittemyer et al., 2005; Kerth, 2008; Ioannou et al., 2011; Ward & Webster, 2016; DuVal et al., 2018). Overall, individuals that are in a group are argued to interact with one another more than with members outside their groups (Kerth, 2010). Whereas at aggregations, individuals’ spatial proximity to one another may simply reflect a social tolerance at a commonly desired ecological resource, with little to no interactions between individuals (Parish et al., 1997; Christal & Whitehead, 1997; Fishlock, 2010). This can be explained by the resource dispersion hypothesis (reviewed in Johnson et al., 2002), whereby patchy yet abundant resources can support multiple individuals owing to the low to no cost to individuals in sharing resources, leading to a conspecific tolerance. For non-reproductive males for example, in the absence of mating opportunities, at valuable but localised, non-monopolisable ecological resources (such as larger water resources, patches of high mineral content soil, clustered food patches), the high risk of injury and high energy expenditure of being unnecessarily aggressive to other males may lead to a mutual tolerance of close proximity males (Jarman, 1974; Derocher & Stirling, 1990; Robbins, 1996; Christal & Whitehead, 1997). However, whilst the proximity of individuals to one another at aggregations is argued to be linked solely to the commonly desired resource and not any internal social organisation between individuals, even within such non-socially coordinated aggregations, there is still the potential for important social interactions between individuals. Shareable, localised ecological resources may even provide key opportunities for primarily solitary males to eavesdrop on or meet one another, or to test dominance and exchange information with otherwise non-socially associated males (Derocher & Stirling, 1990; Fishlock, 2010). Whilst distinction of groups from aggregations in all-male societies can be nebulous, these distinctions are not a prime focus of this thesis. We did not aim to establish whether males live in socially coordinated all-male groups or whether all-male groups are better described as aggregations, but were interested in the social interactions of males within such social groupings. For the purpose of this thesis, when referring to all-male groups and all-male aggregations collectively, I use the term "all-male groupings".

1.1.2 Interactions between males in non-reproductive all-male groupings and the influence of age

The social interactions that occur between males in non-reproductive all-male groupings is less often the focus of research. In long-lived species, all-male groupings can provide males with an opportunity of exposure to individuals of vastly different age, level of development and experience (Gibson & Guinness, 1980; Estes, 2004; Grueter, 2009; Chiyo et al., 2011a). Moreover, there may be different benefits to males of different age in associating or interacting with similarly or divergently aged males (Bercovitch & Berry, 2014). Not only can expression of behaviours vary with male age (Evans & Harris, 2008; Granweiler et al., 2021), but the behaviours of, and social processes between males (e.g., aggression, risk taking behaviour, leader-follower dynamics) may be influenced by the age structure of other individuals present (Slotow et al., 2000; Jennings et al., 2011).

Research on the interactions between males in non-reproductive all-male groupings has typically focused on agonistic behaviours and sparring or playfighting behaviour, with a key benefit to male-male sociality argued to be competitor assessment, and how an improved access to male partners can help males develop competitive skills (Clutton-Brock et al., 1979; Miller & Byers, 1998; Goldenberg et al., 2014). Concerning agonism, males in all-male groupings may still need to assess potential competitors, and establish dominance hierarchies, both to secure future mating opportunities (Jarman & Jarman, 1974; Feist and McCullough 1976; Blank et al., 2015) and to have priority access to critical ecological resources, even in the absence of current mating opportunities (Appleby, 1980; O'Connell-Rowell et al., 2011; Wingfield et al., 2005). However, in general, agonistic interactions tend to be mild between males in all-male groupings compared to between males in groups associated with females, or in the non-breeding compared to the breeding season (Bützler, 1974; Murray, 1982; Robbins, 1996; Grueter, 2009). Similarly, any aggression between males in all-male groupings may be highly ritualised, hence is less energetically costly and carries a lower risk of escalation. For example, in guanaco (*Lama guanicoe)* all-male groups, energetically costly and physically dangerous fighting decreases after the breeding season, but the duration of ritualised, low energy "ear threats" increases between males (Wilson & Franklin, 1985). Agonistic behaviours are an example of a behaviour that can be influenced by a males' age, as well as the age structure of his social environment. Whilst theoretical models predict male aggression will generally increase with an individual's age (Kemp, 2006), the relationship between aggression rate and male age varies between species. All-male groupings are often observed in polygynous, sexually dimorphic species (Mysterud, 2000), where dominance is often strongly associated with increased body size, assumably indicating a greater fighting ability and body condition (Owen-Smith, 1993; McElligott et al., 2001; Pelletier & Festa-Bianchet, 2006). Greater body size is often also associated with greater age in these species, since these males often take several years to reach full size maturity (Hollister-Smith et al., 2007; Lee & Moss, 1995; Pelletier & Festa-Bianchet, 2006; Hass & Jenni, 1991). Consequently, in many all-male groupings, older males are the most dominant, hence tend to express more aggression and dominance assertion behaviours to same sex conspecifics compared to subadult, or subordinate males, and in these species there are clear linear dominance hierarchies with age (Wilson & Franklin, 1985; Roden et al., 2005; Bergeron et al., 2010). However, in many polygynous species, prime reproductive condition can peak before a male's full life span, and often old, post-prime males also reside in non-reproductive all-male groupings (Estes, 2004), who are no longer able to compete with prime condition males for mating opportunities. Often rates of aggression, and general involvement in negative interactions are particularly low in post-prime males (Charles & Carstensan, 2010), and these individuals may avoid close, intimate interaction with other males altogether (Bergeron et al., 2010). Furthermore, the ages of other animals present may also have an influence on the agonistic behaviours of an individual. For example, in primate mixed sex-groups, conflicts between subordinate members of a group that may be disruptive to group cohesion are policed by powerful (often older) individuals (Flack et al., 2005a), and lower adult-young ratios in horse groups leads to greater aggression in young horses due to adult regulation of young horse's aggressive behaviours (Bourjade et al., 2009). Similar effects in all-male groups, with male aggression potentially being influenced by the presence of individuals of greater age in all-male groupings, would be a particularly interesting direction of research to follow, for improving our understanding of the potential influence that same-sex conspecifics have on male aggressive behaviours.

Concerning play fighting and sparring behaviour, males across species exhibit a preference for similar aged partners (Pellis & Pellis, 1996; Granweiler et al., 2021), and younger males (e.g., adolescents or subadults) play fight and spar at greater frequency than older males (Wilson & Franklin, 1985; Miller & Byers, 1998; Le Pendu et al., 2000; Evans & Harris, 2008; Chiyo et al., 2011a; Granweiler et al., 2021). Age-matched males, who tend to be of similar size and strength to one another, are hypothesised to be optimal partners for developing and maintaining competitive skills through sparring and playfighting (Sigmund, 1993). Sparring and play fighting may simultaneously aid in settling dominance disputes between similar ranked individuals, particularly those new to the all-male society owing to recent dispersal (Miller & Byers, 1998; Le Pendu et al., 2000; Evans & Harris, 2008; Chiyo et al., 2011a; Granweiler et al., 2021). When play fighting and sparring do occur between males unmatched in size or age in all-male groupings, these interactions tend to be less boisterous, lower in intensity, and gentler in nature compared to between age-matched males, and may function to build or maintain social bonds, or be used as measures of an individual's relative strength to particular partners (Barrette & Vandal, 1990; Lee & Moss, 2014; Granweiler et al., 2021). Finally, there is also evidence that the age structure of the social environment can influence sparring behaviour, for example in giraffes, *Giraffa camelopardalis giraffa*, mature males intervene to terminate sparring bouts between younger males (Granweiler et al., 2021).

Beyond providing opportunities to develop competitive skills and establish dominance hierarchies through agonistic interactions and sparring/playfighting activity, associations between males in all-male groupings can also provide an opportunity for a diverse array of other behavioural interactions. These include grooming (Pappano, 2013), homosexual behaviours (Robbins, 1996; Leca et al., 2014), cooperative hunting (or other collectively achieved tasks) (Lührs et al., 2012), reconciliation of conflicts (Silk, 2002), and information transfer between individuals, such as learning of sex specific behaviours, about risks and threats, or how to locate key ecological resources in the landscape (Rajpurohit, 1995; Box & Gibson, 1999; Evans & Harris, 2008; McComb et al., 2011a; Coelho et al., 2015). More research in these areas would be highly beneficial, for furthering our understanding of the benefits that males may acquire through association with other males of similar or divergent age in non-reproductive all-male groupings, especially considering that males in some species spend most of their life in such social contexts (Owen-Smith, 1984; Chiyo et al., 2011a; Estes, 2004).

This thesis will explore changes in male grouping and aspects of male behaviour with age, as an indicator of potential benefits afforded to males by associating with one another. I also explore the interactions between, and influences of similar or divergently aged males on one another in all-male groupings, with a particular focus paid to the social role that older individuals potentially play in these groupings. Older individuals often have more central roles in social networks and may therefore exert a greater influence over others for whom they may be perceived as particularly high value social partners (Mutinda et al., 2011; Chiyo et al., 2011a; Tokuyama & Furuichi, 2017). For example, in Campbell's monkeys *Cercopithecus campbelli*, the vocalisations of older individuals elicit more attention and responses from conspecifics compared to younger individuals, despite being performed less frequently (Lemasson et al., 2010). Older, experienced individuals facilitate development of skills and behaviours in a range of mammals (Thornton & Clutton-Brock, 2011). Older males (who may have many years more experience) may be preferentially targeted as associates for close proximity, or investigated by younger, more naïve, recently dispersed males for social learning of behaviours (Pereira, 1988; Rajpurohit et al., 1995; Evans & Harris, 2008; Thornton & Clutton-Brock, 2011; Coelho et al., 2015). Similarly, older males may be followed in space owing to their enhanced knowledge of location of critical resources in the environment, as older individuals in many species are often observed to lead their group movements (Maransky & Bildstein, 2001; Mueller et al., 2013; Berry & Bercovitch, 2014; Brent et al., 2015; Tokuyama & Furuichi, 2017). Experienced individuals (often older) may also transmit information regarding safety to less informed (often younger) individuals nearby. For example, in African savannah elephants, *Loxodonta africana*, older matriarchs are better at responding appropriately to cues indicating predation risk, which they communicate to their group mates (McComb et al., 2011a). In horses, unrelated but informed (habituated) adult demonstrators reduce the fear reactions of young, naive horses (Rørvang & Christensen, 2018), and foals weaned in the company of unrelated adults have reduced aggressiveness and exhibited less stress related behaviours compared to foals weaned with peers only (Henry et al., 2012). Similarly, the presence of older, more experienced males in all-male groupings may act as an indicator to other males of the safety and risk level of the current environment. Older males may thus be particularly effective social buffers against risk related stress owing to this role (Kikusui et al., 2006).

The potential social roles of older males in all-male groups are even more crucial to understand considering in many species these individuals are considered reproductively redundant and socially replaceable, with selective harvesting of older males being common practice in many trophy hunting management plans (Ginsberg & Milner-Gulland, 1994; Baker, 1997; Stalling et al., 2002; Sæther et al., 2004). Such removal of key figures from all-male societies may have detrimental effects on the behavioural ecology of males; for example, it may disturb group cohesion, social dynamics, social development and dominance hierarchies, as well as reduce males' access to a pool of social knowledge on location of ecological resources, sex specific behaviours, and effective risk assessment (Slotow et al., 2000; Bradshaw & Schore, 2007; Milner et al., 2007; Fenberg & Roy, 2008; Muposhi et al., 2017).

1.2 Thesis rationale

When not pursuing mating opportunities, male African savannah elephants (hereby referred to as African elephants) spend a large proportion of their time in association with other males in all-male groups and all-male aggregations in bull areas. Such male dominated environments provide ideal study sites for exploring the function and benefits to male elephants of male-male sociality. Male African elephants are long-lived and undergo extensive learning and social maturity across their life spans, and some researchers suggest older males may act as repositories of ecological and social information to younger males. In this thesis I explore the interactions and influences between different ages of males in this species with dynamic and diverse social relationships. I focus on the following social phenomena: leader-follower dynamics, risk assessment, repression of aggression, establishment of new contacts, and remote social monitoring of same-sex conspecifics over time and space. My thesis aims to highlight the need to investigate the social role of mature males beyond their mating contribution, and to expand our understanding of the importance of older individuals in long-lived species.

Whilst African elephants are of conservation concern, males in particular come into conflict with communities living alongside the species, and can pose a threat to rural people's lives and livelihoods. I therefore also aim to improve our knowledge of a male elephant's natural social behaviour and social needs, including the roles of particular aged individuals in maintaining a healthy male society, in the hope that this information can be used to better guide conservation and management of African elephants without exacerbating conflicts.

1.3 Sociality of male African elephants *Loxodonta africana*

All-male groupings with individuals of mixed age are observed in the African elephant (Chiyo et al., 2011a; Lee et al., 2011). At extremes, entire geographical regions can be occupied by only males, referred to as "bull areas" (Lee et al., 2011; Evans, 2019; Croze & Moss, 2011), which provide ideal study sites for exploring male-male sociality. The species is also an ideal study system for understanding the influence of age on male social interactions and dynamics, because males have the potential for a long lifespan post dispersal (natal dispersal is between the ages of 10-20, but males can live to be over 60 years old (Lee et al., 2011; Lee & Moss, 2011)), providing an opportunity for vastly different ages to associate in all-male groupings. In the sections that follow I discuss what is currently known regarding the formation and function of all-male groupings in male African elephants, the nature of social interactions that occur between males, and the benefits afforded to different aged males in associating in all-male groupings. I also highlight gaps in our knowledge regarding the drivers for males to be social across different life history stages, and introduce how the chapters of this thesis will use the African elephant as a model species for understanding the interactions between different aged males in a long-lived mammal, and the potential important social roles of older males in all-male groupings.

1.3.1 Musth and the formation of bull areas

Arguably the most influential factor on an individual male's social behaviour, the phenomena of musth must first be addressed when attempting to understand the shapers and influences on male elephant sociality (Poole, 1987; Poole et al., 2011; Goldenberg et al., 2014). As the world's largest land mammal, the African elephant unsurprisingly has a lengthy gestation and lactation period (Moss, 1983, 2001). As such, sexually receptive females are an extremely rare resource, with females only coming into oestrus for 3-6 days every 3-9 years (Moss, 1983; Poole & Moss, 1989; Moss & Lee, 2011). No benefit therefore can be gained by males to attempt to monopolise females, and instead males adopt a "roving male" mating strategy (Whitehead, 1990), whereby males move between groups of females seeking mating opportunities. This roving behaviour is particularly concentrated into musth periods each year, with distinct periods of heightened sexual activity in individual males characterised by changes to physiology and behaviour, notably increased aggression to other males, increased association with females (Poole, 1987; 1989a; 1989b) and a rise in androgens such as testosterone (Ganswindt et al., 2005; Hollister-Smith et al., 2008). Unlike the annual rut (the mating season of many ruminants whereby males also increase aggressive behaviours to other males and pursue matings with females (Clutton-Brock et al., 1979)), musth phases are experienced asynchronously between males (Rasmussen, 2005; Poole et al., 2011). Onset of first stable musth is not experienced by males until the age of around 30 years (Poole et al., 2011), and duration and regularity of each years' musth phase increases as a male ages (Poole et al., 2011). Musth males are socially dominant to non-musth males, regardless of age differences (Poole, 1989a). Together with the fact that musth males are preferred by oestrous females (Poole, 1989b), this dominance leads to musth males dominating paternity success, fathering some 74% of calves (Hollister-Smith et al., 2007). However, non-musth bulls do also succeed in fathering calves, with success increasing with age (Hollister-Smith et al., 2007). Males begin occasionally achieving paternity success around 26 years, but peak in success between 45 and 53 years (Hollister-Smith et al., 2007). As musth duration also increases with age, the increasing contributions that musth and age make to a male's reproductive success overlap to a great extent (Poole et al., 2011).

Prior to around 26 years of age males are therefore not considered a competitive age for mating (Hollister-Smith et al., 2007; Poole et al., 2011). Furthermore, as non-musth males are subordinate to musth males, even older non-musth males may not benefit from actively pursuing mating opportunities. Musth is extremely metabolically costly, and males drastically drop in body condition during this phase (Poole, 1989a). To enter musth state again and sustain a longer musth in future, non-musth males are thought to dedicate time and energy to growth and building body condition in bull areas, away from harassment from aggressive musth bulls (Poole et al., 2011; Stokke & du Toit, 2002). When not in musth, adult male elephants spend most of their time segregated from females, with most time spent in association with other males rather than alone (Lee et al., 2011; Chiyo et al., 2011a; Goldenberg et al., 2014). Furthermore, when not in a musth state, the social networks of male African elephants are substantially larger and denser compared to when in musth (Goldenberg et al., 2014). Internal sexual state therefore seems to have a strong influence on the social behaviour of male African elephants.

Male avoidance of conflict with musth bulls is proposed to be a key social driver for geographical segregation of the sexes and the formation of “bull areas” in African elephant ecology (Stokke & du Toit, 2002). An individual’s behaviour and selection of habitat is expected to be linked to its reproductive strategy to optimise fitness, with the needs of male and female elephants likely diverging significantly (Main & du Toit, 2005). As reproductive strategy is heavily linked to energy intake, ecological drivers are proposed to influence spatial segregation of the sexes in African elephants (Stokke and du Toit 2002; Shannon et al. 2006; Lindsay, 2011). In general, females invest energy directly to reproduction and calf rearing (e.g. costly gestation and lactation) from as early as 8.5-14 years of age (the average age of first calf conception (Lee & Moss, 2011)), whilst males invest energy in growth as well as building reserves for energetically costly musth periods (Lee & Moss, 1995; Shannon et al., 2006; Poole et al., 2011). Additionally, African elephants are a sexually dimorphic species (by around 20 years of age females reach maximum height, whilst males continue to grow into their 40's, with males measuring on average 60-70cm taller than females (Lee & Moss, 1995)). The sexes therefore likely have different nutritional and water requirements, which may push males and females to utilise forage and their environment in different ways. Whilst it is suggested that the activity budgets of males and females are broadly the same, and a lack of coordination between individuals concerning time spent feeding, drinking, walking and resting is not enough to drive the observed segregation of males from females (Shannon et al., 2008), past research suggests differences in how males and females utilise forage is enough to drive the segregation of sexes seen in African elephants (Shannon et al., 2006). For example, smaller females (with their additional gestation and/or lactation pressures) are more selective of the forage they consume and focus on maximal quality nutritional intake (Stokke & du Toit, 2000; Shannon et al., 2006). Whereas larger males perform longer feeding bouts of abundant, lower quality forage (Shannon et al., 2006), which may be an effective energy intake owing to their lower metabolic rate and longer retention time of food in larger digestive tracts compared to females (Gross et al., 1996; Pérez-Barbería et al., 2008; Lindsay, 2011). Furthermore, for females, beyond the nutritional demands of lactation and gestation, reproductive success also extends to calf protection (Main & du Toit, 2005). For example, whilst males spend more time at drinking points per visit than females (Shannon et al., 2006), such open habitats may be prime areas for lions to predate on calves associated with females, who may avoid spending prolonged time in such vulnerable habitats (Joubert, 2006; Loveridge et al., 2006). Males in general appear less sensitive to predators and anthropogenic risks and occupy more risky habitats that are closer to human settlements and outside protected areas (Chiyo et al., 2014; Kioko et al., 2013). Such differences in risk aversion may also influence tendency for males to be found in certain areas, where females are absent (Croze & Moss, 2011). Finally, social affinity to the same sex may also play a role in the segregation of male and female African elephants, for example females may associate with one another for allomothering benefits (Moss & Lee, 2011; Lee & Moss, 2011). For males, association with other males may provide opportunities for developing and maintaining competitive sex specific skills such as sparring (Evans & Harris, 2008; Chiyo et al., 2011a). Indeed, as early as juvenescence, males engage in more play and sparring behaviour than females (Lee & Moss, 2011), and after 24 months males develop preferences for same sex, same age, novel (not members of their natal family) sparring partners (Lee & Moss, 2011). This demonstrates how even from a young age, same sex unrelated individuals appear to be of high value to male elephants (Lee & Moss, 2014).

1.3.2 Benefits of all-male groupings for male African elephants and the influence of age

Bull areas, with mating opportunities absent for males, provide a model example of the conditions that allow for potentially beneficial groupings and interactions to occur between males as described above in **1.1.2.** Within bull areas, male African elephants travel and forage alone or with other males (Lee et al., 2011). Several benefits are thought to be provided to male African elephants by associating with other males. The tendency for males to be alone increases with male age (Lee et al., 2011), and younger males are found in larger groups than older males (Evans & Harris, 2008), suggesting the costs and benefits of male sociality change across the life course of males.

A key benefit for male elephants to associate with one another is to access sparring partners, for the maintenance and development of fighting skills (Chiyo et al., 2011a; Evans & Harris, 2008). Sparring also aids males in making contact with new associates (Lee & Moss, 2011). Furthermore, through sparring, males can simultaneously establish dominance hierarchies in a non-aggressive, less dangerous manor, and competitor assessment also suggested as a key benefit for male-male associations in African elephants (Goldenberg et al., 2014). Males of all age engage in play behaviour and sparring activity (Lee & Moss, 2014); however, this behaviour is more frequent among adolescents (the African elephant adolescent life history stage is generally agreed to be between the ages of 10-20 years (Evans & Harris, 2008; Lee & Moss, 2011)) (Evans & Harris, 2008). Adolescents likely engage in more sparring behaviour because they have a greater need to develop strength and motor skills, as well as to establish associations and their place within the bull social hierarchy, being younger and more recently dispersed from their natal herds (Lee et al., 2011). Furthermore, sparring in African elephants most often occurs between age matched individuals (Chiyo et al., 2011a), perhaps because development of these competitive fighting behaviours and skills (albeit in a safe context) is predicted to be most effective when partners (or “rivals”) are matched in physical strength and ability (Sigmund, 1993).

Secondly, a key benefit to male sociality in African elephants is proposed to be access to a greater pool of social and ecological knowledge. This may be particularly important for more naïve, recently dispersed adolescents, who until recently have depended on adult females in family groups for key decisions concerning where to travel and when, what to eat, and when they are at risk (Mutinda et al., 2011; Lee & Moss, 2011; McComb et al., 2011a). African elephants appear to place particular value on the decisions of certain conspecifics in their environment. For example, matriarchs that initiate group movements are more likely to recruit other elephants to follow them compared to non-matriarchs (Muntinda et al., 2011). Greater age appears to be a key trait that elephants associate with superior knowledge (Mutinda et al., 2011; McComb et al., 2011a). It is also suggested that older males occupy a similar role as matriarchs do in the male society, with younger males potentially targeting them as repositories of ecological and social knowledge (Chiyo et al., 2011a; Evans & Harris, 2008; Murphy et al., 2019), but this idea remains largely untested. In this thesis I investigate the hypothesis that older males are targeted as associates for their superior knowledge, and investigate whether older males are more likely to lead collective movements of all-male groups along elephant pathways, which are routes that connect critical resources in the environment such as food patches and water sources (Mutinda et al., 2011; Von Gerhardt et al., 2014; **Chapter 2**). Older males occupying the front of groups, and younger males occupying following positions may suggest younger males target older males for their heightened experience, and older males may have important roles (albeit perhaps unintentionally) in sharing and passing on ecological knowledge to younger generations (Reebs, 2000; Maransky & Bildstein, 2001; Biro et al., 2006; Lee & Teichroeb, 2016). Furthermore, in **Chapter 4** I investigate whether older males are preferentially targeted with trunk-mediated “greeting” behaviours (the trunk is directed to organs on the target that emit olfactory information; the mouth, temporal glands and genitals) by younger males at all-male aggregations of African elephants, which may indicate attempts to initiate further social contact with, or discern information from high-value, experienced individuals (Smith et al., 2011; Lee & Moss, 2011).

Thirdly, male African elephants may associate in all-male groupings to buffer against predator and anthropogenic risks, both to increase chances of immediate survival (i.e. cooperative vigilance, or dilution effects (Delm, 1990)), as well as to minimise the detrimental and costly stress such risks may place on an individual’s physiology (Lima, 1998; Romero, 2004; Gobush et al., 2008; Vijayakrishnan et al., 2018; Zanette & Clinchy, 2020). Predation pressure as a “pull” factor to male elephant association likely varies with age and is likely stronger for adolescents. Whilst a healthy mature bull has no natural predators, lions in Botswana successfully hunt young males aged 10-15 years (Joubert, 2006). Anthropogenic risk however represents a threat to all elephants regardless of age, with human induced mortality being a significant, if not leading cause of adult male death in many populations (Moss, 2001; Wittemyer et al., 2013). Male elephants form larger groups when there is a greater anthropogenic risk (Chiyo et al., 2014), and in **Chapter 3** I explore how social isolation in an area with moderate human presence influences the performance of “fight or flight” type behaviours of male elephants, as a proxy for their perception of and responses to their current risk level (Stankowich & Blumstein, 2005; Bates et al., 2007). Following again from the hypothesis that older males hold parallel roles in the male society as matriarchs do in female groups (McComb et al., 2011a), I explore whether older male African elephants act as communicators or indicators of current risk level, and whether they are particularly effective social buffers against risks for other males, by exploring if older male presence influences the performance of “flight or fight” type behaviours in other males at all-male aggregations (**Chapter 3**).

The benefits to all-male grouping outlined so far better explain why younger males would associate in all-male groups. The benefits offered to older male African elephants in associating with other males rather than traveling alone, may be less intuitive to understand. Older males are the preferred nearest neighbours of males of all ages (Evans & Harris, 2008) and have more central roles in the male social networks, with higher eigenvector centrality and greater number of associates (Chiyo et al., 2011a). Older males therefore appear to be highly desirable contacts to other males, but it may be that older males are largely passive in these associations and simply tolerate the diversity of contacts they attract. Older male giraffes are similarly targeted by younger males for ecological information. Bercovitch & Berry (2014) suggest this interest is tolerated by older males as the energetic cost of persistently driving away “followers” would be too great. Such dynamics may also be at play with older male, non-musth male elephants tolerating younger males.

Theoretically, however, older males can also benefit from association with age-mates. As with younger males, this could also be to maintain competitive skills and resolve and reaffirm dominance hierarchies (Goldenberg et al., 2014), and perhaps to acquire information from equally experienced males equipped with divergent but beneficial knowledge. Indeed, research in Kenya found only older males associate with their own age class more than expected by chance, whilst younger males (>30 years in this study) associated with similar aged males as expected by chance (Chiyo et al., 2011a). In other words, whilst adolescents may be interested in males of all ages to gain social benefits (e.g., age mates for sparring, but older males for knowledge acquisition), for older males, only fellow older males may provide benefits as sparring partners and sources of advantageous knowledge. Older males may also associate in all-male groups to buffer against anthropogenic threats, as older males may be more at risk of mortality by illegal poaching and legal trophy hunting activity compared to smaller adolescents because they have larger, heavier tusks and bodies (Poole, 1989c; Moss, 1990; Wittemyer et al., 2013; Selier et al., 2014). Finally, outside of musth, the dominance hierarchy of male elephants is linear with age (O’Connell-Rodwell et al., 2011), meaning older males are the most dominant. There is evidence to suggest older, dominant male presence may repress younger elephants from entering into, or sustaining musth (Slotow et al., 2000). Sexual inhibition of competitors may also therefore potentially be one benefit provided to older males in associating with other males in all-male groupings. In a similar way, when linear dominance hierarchies are disrupted in African elephants, lower ranking individuals engage in more agonistic behaviours (O’Connell-Rodwell et al, 2011). I expand on this finding in **Chapter 3** and explore whether reduced older male presence at all-male aggregations is associated with increased aggression (both to other elephants and non-elephant targets) in other males. In doing so, I explore if older bulls potentially function as policers or regulators of aggression in all-male societies (Flack et al., 2005a; Bourjade et al., 2009)

1.3.3 Fission-fusion nature of all-male groups in African elephants

Like all-male groups in many species (see **1.1.1**), African elephant all-male groups have a high degree of fission fusion dynamics, with great variation in group size, tenure of group membership and composition of individual males within groups (Aureli et al., 2008; Lee et al., 2011; Chiyo et al., 2011a; Morris-Drake & Mumby, 2018; Murphy et al., 2019). Female African elephants also demonstrate fission-fusion dynamics, but within a multi-level society, with the smallest unit of fissure tending to be a core family group of related females (which is held together by strong kinship ties (Archie et al., 2005)). Family groups fuse together to form "bond groups", and multiple bond groups fuse to form "clans" according to factors such as resource availability (Western & Lindsay, 1984; Wittemyer et al., 2005; Archie et al., 2005). In contrast, the individual male represents the smallest unit of fissure within the male society, and each male can flexibly fissure and fuse into varied group sizes as the benefits and costs to sociality vary with his external environment and internal state (Chiyo et al., 2014; Goldenberg et al., 2014). Some studies suggest males may also weakly preferentially associate with kin in all-male groups (Chiyo et al., 2011a), while others have found no such preference (Ahlering et al., 2012). There is frequent turnover of membership in all-male groups of African elephants, although there is evidence that older males are more stable in their social networks (Murphy et al., 2019). Furthermore, there is also evidence for preferred associates or "friends", who tend to be males close in age (Lee et al., 2011), although it is rare for a male to spend more than 10% of his time with any one particular individual male (Archie & Chiyo, 2011). In bull areas, males are presented with a variety of potential social partners with whom they can choose to associate with, or break off from and travel on their own. Localised but shareable resources in the environment that are utilised routinely by males (for example drinking sites) may act as key sites for information exchange or for establishing contact with new associates (Fishlock et al., 2016; Fishlock & Lee, 2013). In **Chapter 4** I explore if males aggregating at a social hotspot river resource preferentially target novel individuals with trunk-mediated “greeting” behaviours, compared to those they arrived with at the resource. These behaviours may indicate a male’s interest in obtaining information on new potential associates, and/or they may act as signals to facilitate further interaction with other males in a highly fission-fusion society (Aureli & Schaffner, 2007).

1.4 Applying knowledge about animal behaviour to wildlife management and conservation issues

One would be remiss to study African elephants without considering their conservation status and the contributions that a greater understanding of the social behaviour of male elephants might provide to conservation efforts (Mumby & Plotnik, 2018). Wildlife managers, governments and landowners increasingly use scientific knowledge about animal behaviour to better guide policy and conservation strategies regarding wild animal populations (Martin, 1998; Buchholz, 2007; Angeloni et al., 2008). By understanding the natural needs and behaviours of animals, we can step towards solution-based research (Lindenmayer et al., 2013) and strive for an improved coexistence in shared habitats, as well as relieve and negate negative interactions between humans and wildlife. Pushes to implement knowledge of animal behaviour to conservation issues has largely focused on foraging behaviour and dispersal (central to population dynamics) (Berger-Tal et al., 2016). In contrast, applications drawn from a greater understanding of animal social behaviour, learning, anti-predator behaviour, animal personality and communication have remained comparatively untapped (Berger-Tal et al., 2016). In each chapter of this thesis, I therefore relate my behavioural findings to potential elephant management and conservation implications.

Across Sub-Saharan Africa, African elephants and humans share habitats and interact in many domains (Lee & Graham, 2006; Thouless et al., 2016), with both species capable of acting in ways that inflict severe negative consequences on the other (Osborn & Parker, 2003a). Whilst global demand for ivory has fuelled the killing of hundreds of thousands of elephants across Africa in the past century (Wittemyer et al., 2014), African elephant numbers are also in decline owing to habitat loss (Hoare & du Toit, 1999; Chase & Griffin, 2009; Mpakairi et al., 2019) and retaliation killing (Hoare, 2000; Songhurst, 2017), to the extent that the species is of conservation concern and listed as endangered by the IUCN (Thouless et al., 2016; IUCN, 2020). Conversely, people living alongside elephants unacceptably suffer livelihood losses to elephant crop foraging and other property damage (Hoare, 1999; Mackenzie & Ahabyona, 2012), mortality from elephant attacks (Songhurst, 2017), and live with fear, stress and restricted movements owing to close elephant presence (Mayberry, 2015; Mayberry et al., 2017). In many regions, elephants are responsible for the majority of wildlife conflicts reported by rural people (O’Connell-Rodwell et al., 2000), and dissatisfaction with how elephant conflict is addressed can be a major contributor to rural peoples’ general lack of support for wider conservation efforts (Woodroffe et al., 2005).

In most human-elephant conflict incidents, the offending animal is a male (Sukumar, 1998; Smit et al., 2017; Stevens, 2018). For example, males are the primary crop foragers, likely owing to their propensity for high-risk, high-reward behaviour and tendency to roam further from protected areas (Hoare, 1999; Chiyo et al., 2011b; Chiyo et al., 2012; Smit et al., 2017). Understanding the ecological and social needs of male elephants is therefore of paramount importance, as this information can help us better guide our interactions with the species and inform management strategies to minimise negative impacts to both humans and elephants (Osborn & Parker, 2003a; Coltman et al., 2003). Genetic and demographic implications of poor male elephant management are known. For example, with intense selective harvesting of older males (owing to their greater body and tusk size, desired by hunters), paternity is highly skewed towards the few old males left in the population, leading to a loss of genetic diversity (Whitehouse & Harley, 2002; Ishengoma et al., 2008; Archie & Chiyo, 2011). Similarly, selective harvesting of males with large tusks has led to a reduction in tusk sizes of males in areas with hunting (Muposhi et al., 2016). However, of equal concern are the wide reaching, potentially long-term, behavioural consequences of human influences on this socially sensitive species. Research has come a long way from the times where adult male African elephants were considered asocial (Vidya & Sukumar, 2005; Morris-Drake & Mumby, 2018). The advent of applying social network analysis to animal societies has given us an improved toolkit for understanding the more temporally transitory, spatially wide-ranging relationships of animals with high fission-fusion grouping dynamics, such as male elephants (Chiyo et al., 2011a; Goldenberg et al., 2014; Murphy et al., 2019). Male elephants are suggested to be socially complex, connected to, and dependent on one another, as explored throughout this thesis.

Male elephants, as with their female counterparts, are likely highly sensitive to human influences disrupting natural processes relating to sociality, learning and communication (Shannon et al., 2013). Aspects of current elephant management techniques, which are of particular relevance owing to their potential to impact natural male social processes as well as to potentially exacerbate human-elephant conflicts, are introduced below.

Regulated trophy hunting of African elephants is permitted in several African nations and is argued to give local communities a benefit to living alongside the species through revenue generated from hunts and livelihood opportunities (DeMotts & Hoon, 2012; Naidoo et al., 2016; Mbaiwa, 2017). The oldest bulls are overwhelmingly targeted by trophy hunters, but also in illegal poaching activity (Moss, 1990; Archie et al., 2008; Boddington, 2013; Barnett & Patterson, 2005; Chiyo et al., 2015) because of their higher monetary value, owing to larger bodies and tusks (Hanks, 1972; Muposhi et al., 2016). Older males are rare resources throughout the range of African elephants (Wittemyer et al., 2013; Jones et al., 2018), and in many areas the hunting of older bulls under their current quotas is argued to be unsustainable (Selier et al., 2014). In this thesis, I explore the hypothesis that these older male elephants are important sources of social and ecological information to younger males (Chiyo et al., 2011a; Evans & Harris, 2008), the removal of which may have substantial knock-on effects on population viability. In **Chapter 2** I explore if older males are followed for their enhanced knowledge in navigating the landscape, and in **Chapter 4** I explore if older males are preferentially targeted with trunk-mediated “greeting” behaviours by same sex conspecifics. Family groups with younger matriarchs have less knowledge about forage and water in the extended environment compared to those with older matriarchs, and have lower calf survival in years of drought (Foley et al., 2008). If older males hold a similar role in transferring information about essential ecological resources (or at least guiding decision making as to where and when to travel) to younger, naïve, more recently dispersed males in the male society, their removal through selective harvesting may be widely disruptive as essential hubs of accumulated knowledge are lost. In the harshest environments, such a lack of access to knowledge could mean the difference between life and death for uninformed individuals (Foley et al., 2008).

Many advocates of trophy hunting that contend the activity has animal management value argue hunting can not only control animal numbers, but it can also manipulate animal behaviour and spatial distribution (Gaynor et al., 2020; Cromsigt et al., 2013; Le Saout et al., 2014; Little et al., 2016). “Hunting for fear” aims to divert the target species from certain areas where they are hunted, as animals learn they are in a high-risk area (Cromsigt et al., 2013). Sukumar (1998) coined this as “psychological warfare” with elephants, which is now best understood through the well-established “ecology of fear” literature (for review, Zanette & Clinchy, 2020). Over a certain threshold, elephants avoid habitats dominated by human activity (Hoare & du Toit, 1999) and it is argued that this is because of a certain level of disturbance or perception of being at risk on the elephant’s part (Guerbois et al., 2012). By this logic, controlled hunting of elephants in certain areas would act as a deterrent for future elephants to enter an area, in doing so protecting communities and crops. However, African elephants are not the typical ungulate on upon which the “hunting for fear” theory is based (Cromsigt et al., 2013). When sensing a threat, elephants can respond with lethal anti-predator responses (Dunham et al., 2010; DeMotts & Hoon, 2012). Elephants living in human dominated landscapes or in areas with historically high poaching risk demonstrate greater physiological stress (Hunninck et al., 2018; Gobush et al., 2008). Physiologically stressed elephants are more prone to aggression (Jachowski et al., 2012), and even the calls of distressed conspecifics can provoke aggressive behaviours in elephants (O' Connell-Rodwell et al., 2000). Furthermore, single traumatic events – such as exposure to culling and human induced death of conspecifics – can have long term negative impacts on the behaviour and development of individual elephants, including behaviours of high concern to humans such as hyper-aggression (Slotow & van Dyk, 2001; Bradshaw & Schore, 2007). It could be argued therefore that elephants are far too sensitive to social and psychological disturbance, and hold far too much potential to lethally impact humans to attempt at "psychological warfare". Creating environments where elephants widely perceive humans as a lethal risk could instead end up exacerbating human-elephant conflicts, with disaster for local human populations. In **Chapter 3** I explore social context influences on male elephant aggression and fear responses to non-elephant targets, as a proxy for elephants' perception of threat. I explore whether experienced older males play a role in assessing and communicating the environmental risk level in all-male groupings, hypothesising that increased older male presence at all-male aggregations in an area with moderate human presence will decrease elephants' performance of aggression and fear behaviours to non-elephant targets. If social and demographic factors impact on the prevalence of these behaviours that have the potential to be harmful for humans, it is crucial to identify these factors (Slotow & van Dyk, 2001, Slotow et al., 2000; Bradshaw & Schore, 2007).

In addition to potentially depending on older individuals in the immediate environment for information regarding location of ecological resources and effective assessment of risks, male elephants may also utilise social cues left behind by conspecifics in the environment to aid their movements, behaviours and decision making (Danchin, 2004). Of particular interest, and central to **Chapter 5** of this thesis, is the monitoring of social information left on elephant pathways. These pathways are largely fixed routes (position is unchanged year on year in landscape (Haynes, 2006)) used by elephants as paths of least resistance between critical resources in the environment (Von Gerhardt et al., 2014; Mutinda et al., 2011). Elephants are a highly olfactory focused species (Schulte et al., 2005) and it is suggested pathway networks act as sources of public social information through the urine and dung left by past travellers (Mutinda et al., 2011; Fishlock et al., 2016). A major factor contributing to the likelihood that a field has its crops foraged on by elephants, is its proximity to an elephant pathway (Songhurst & Coulson, 2014; Von Gerhardt et al., 2014). Whilst studies have explored, to varying success, exploiting elephants' olfactory sense to actively defend fields through chemical deterrents (predator odours (Valenta et al., 2020), chilli pepper (Hedges & Gunaryadi, 2010), temporal gland secretions (Gorman, 1986), bee pheromones (Wright et al., 2018)), to my knowledge no experiments have been conducted that use elephant olfactory cues to promote and encourage new or alternate movements. I open a discussion to this possibility in **Chapter 5**, where I explore the olfactory monitoring of pathways by elephants in relation to age and social grouping factors. For example, I hypothesise that elephants travelling alone will be more likely to respond to pathways compared to those travelling in groups, as they may be more reliant on olfactory cues on the pathway as an indicator of other elephants in the areas' movements. With olfactory stimuli accumulated from years of repeated use, pathways may hold potential to be a key tool in manipulating elephant movements, in the case that elephants use these stimuli as indicators of where to follow to find critical resources such as forage, water and refuge (Von Gerhardt et al., 2014; Fishlock et al., 2016). The majority of the African elephants' existing range is outside of protected areas in the anthropogenic dominated landscape, but some populations are restricted to protected areas in isolated, highly fragmented habitats (Thouless et al., 2016). Male elephants naturally have strong roving tendencies (Druce et al., 2006) and are critical components for gene flow across populations (Archie et al., 2007; 2008; Epps et al., 2013). Understanding and informing ways to promote movement of elephants (in particular of males) to improve connectivity of populations, whilst minimising contact with humans and their property (i.e., diverting movements away from fields and communities) is therefore of high priority to elephant management plans (Douglas-Hamilton et al., 2005; Epps et al., 2013; Van de Perre et al., 2014).

1.3 Thesis structure

In **Chapter 2** I analyse grouping patterns and order of processions of male elephants travelling on elephant pathways, asking:

(1) Does an elephant's age influence the likelihood that he travels in an all-male group as opposed to alone? Hypothesising younger adolescents will show a stronger preference for all-male group travel.

(2) Does an elephant’s age influence the likelihood of him occupying the lead position in all-male group processions? Hypothesising the oldest males will be more likely to lead all-male group processions.
(3) Does season affect tendency for elephants of certain age to lead all-male groups? Hypothesising older males will have divergent probabilities of leading all-male groups between the wet and dry season.

In **Chapter 3** I examine how rates of aggression and fear behaviours performed by male elephants at all-male aggregations vary with the social context, asking:

(1) Does social isolation differentially affect elephants of different age concerning the performance of fear and aggression behaviours to non-elephant targets? Hypothesising adolescents, but not adults will experience increases in these behaviours when in isolation compared to when in the company of other males.
(2) Does the increased presence of males from different age cohorts influence the likelihood of an elephant performing fear behaviours to non-elephant targets, or aggression behaviours to non-elephant targets or conspecifics? Hypothesising that increased older male presence will reduce the likelihood that elephants perform these three behaviours.

In **Chapter 4** I explore the choices male elephants make concerning the males targeted with trunk-mediated “greeting” behaviours at all-male aggregations, exploring three key hypotheses:

(1) Males will preferentially target age-matched males with trunk-mediated “greeting” behaviours.

(2) Males will preferentially target older males with trunk-mediated “greeting” behaviours.

(3) Males will preferentially target elephants met new at all-male aggregations, compared to those they arrived at aggregations in all-male groups with, with trunk-mediated “greeting” behaviours.

In **Chapter 5** I quantify the olfactory responses of male elephants utilising elephant pathways to both (i) the natural pathway substrate, and (ii) purposefully placed samples of conspecific male urine, asking:

(1) Do social grouping factors influence the olfactory responsiveness of males to elephant pathways? Hypothesising lone travellers will be more likely to pay olfactory responses to the pathway compared to those travelling in all-male groups, and those in the lead position of groups will be more likely to pay olfactory responses to pathways compared to those in following positions.

(2) Does a male’s age influence his olfactory responsiveness to elephant pathways? Hypothesising adolescents and adults will diverge in their tendency to pay olfactory responses to pathways.

(3) Do passing elephants pay focused olfactory responses to fresh male urine cues from conspecifics, and do these cues persist in the environment over time? Hypothesising focused olfactory responses will be paid to elephant urine samples over time, but not to a water control.

(4) Can male elephants distinguish between the remote urine cues of different aged same-sex conspecifics? Hypothesising that urine cues from adult males will be more likely to elicit vomeronasal system responses compared to urine cues from adolescent males.

In **Chapter 6** I take the key contributions of this thesis and discuss them within the wider literature of male sociality in social mammals. I discuss how the benefits afforded to male elephants by grouping with other males likely vary with age, and I discuss the potential social roles that older males may hold in non-reproductive all-male groupings. I also take my results and summarise how they might be applied to an improved conservation and management of African elephants, as well as discuss other potential directions of future research in the field of behavioural ecology.

1.6 Study area and general methods

1.6.1 Location, key landscape features and vegetation

The study was conducted in Makgadikgadi Pans National Park (MPNP), Botswana (Figure 1.1). A 2016 status report estimated Botswana is home to the largest African elephant population globally, with a population of 131,626 ± 12,508 (95% CI) elephants (Thouless et al., 2016), and a population spread concentrated heavily in the north of the country (Chase et al., 2018). For the tenure of the study (September 2015-September 2018) there was no culling or legal hunting of elephants practiced in Botswana (Mbaiwa, 2017). Furthermore, poaching levels of elephants were low in the country, although there is evidence to suggest this may have been on the rise (Schossberg et al., 2019). The MPNP lies at the south-eastern edge of the African elephants' range in the country, and the species' range is thought to be expanding southward to the Central Kalahari Game Reserve (Thouless et al., 2016). The MPNP can be described as a bull area for elephants (Lee et al., 2011), with the research group Elephants for Africa, based in the park since 2012, consistently reporting an overwhelmingly male predominance in the park (Evans, 2019).

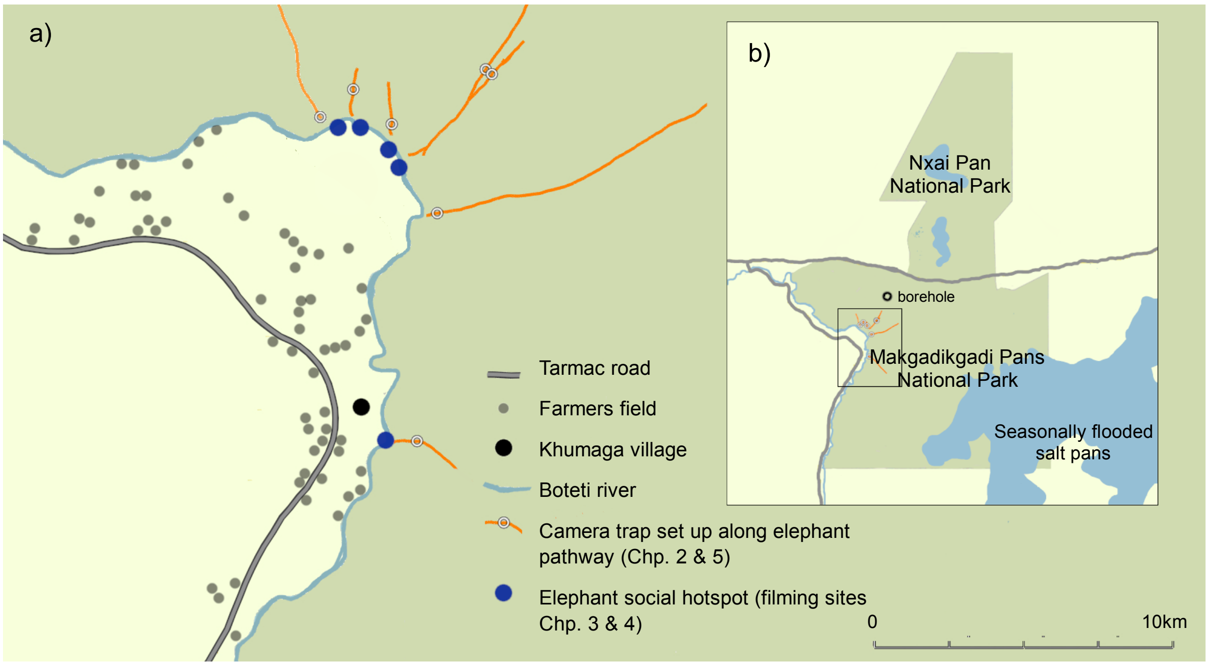

Figure 1.1: Map of the study area (a), and figure insert indicating location of study area in relation to the MPNP (b). Salt pans indicated (b) catch seasonal rainfall and inflow from rivers, and when flooded annually, provide important breeding grounds for birds, and sources of drinking water for migrating zebra and wildebeest (Brooks, 2005; Kgathi & Kalikawe, 1993). Dark green in both figures represents protected land, and light green, unprotected land, which within the study area was dominated by human activities, such as pastoral and arable farming (Stevens, 2018). Locations of sampled elephant pathways leading to the Boteti River, as well as locations of social hotspots are indicated.

Elephant movements are majorly influenced by availability of water (Wittemyer et al., 2008; Pittiglio et al., 2012). As obligatory drinkers, elephants drink at least every other day (Douglas-Hamilton et al., 2001; Chamaillé-Jammes et al., 2013; Fox, 2015), although desert dwelling elephants in Namibia can go longer periods without water and travel further from water resources (Viljoen, 1989; Leggett, 2006). The Boteti River is the major ecological feature in the MPNP influencing elephant movements in the study area (Evans, 2019; Figure 1.1), and the river roughly marks the current extremes of African elephant's range southward in the country concerning perennial water availability (Chase et al., 2018). The Boteti River was a central component in our research methods; data for **Chapters 2 and 5** was collected from camera traps placed on elephant pathways terminating at the Boteti River (utilised by elephants as paths of least resistance travelling to and from the river), and data for **Chapters 3 and 4** were collected from focal video recordings (Martin & Bateson, 1993) of male elephants aggregating at social hotspots along the river (Figure 1.1). Whilst water level in the river fluctuated throughout the study, with local rainfall and the seasonal flood waters of the Okavango Delta system (Vanderpost & Hancock, 2018), water was always present at all hotspots for the tenure of the study. Prior to 2009, the Boteti River had run dry for a 19-year period, and elephant numbers were far fewer in the region (Evans, 2019). The resurgence of the river, coincided with expanding elephant populations in northern Botswana led to an influx of elephants to the study area (Evans, 2019). Male elephants, with their natural exploratory tendencies (Osborn, 2004; Druce et al., 2008), make up the majority of this fringe population, as is common in founder populations and dispersing individuals in mammal species (Druce et al., 2008; Stephen Dobson, 1982).

The MPNP occupies 3,900km^2 within the 37,000km^2 Makgadikgadi basin (Figure 1.1b), with the Boteti River emptying into Ntwetwe Pan. Heading eastward from the Boteti River, the habitat in the study area is characterised by 2-5km of dense *Acacia* woodland, followed by an open *Acacia* savannah-type vegetation, *Schmidtia* grassland, halophytic grasslands, and eventually salt pans (Brookes, 2005; Figure 1.1). During the wet season, seasonal rainfall fills pans and temporary waterholes, and the eastern Makgadikgadi becomes the home range of migratory zebra (*Equus quagga*) and wildebeest (*Connochaetes taurinus*) ((Kgathi & Kalikawe, 1993). Wildlife is not as dependant on the Boteti River at this time, until these water sources dry up and species return to the western Makgadikgadi and the Boteti River once again (Kgathi & Kalikawe, 1993).

The Boteti River also represents the western boundary of the MPNP (Figure 1.1). In an attempt to reduce various human-wildlife conflicts and minimise disease transmission between cattle and wildlife, electrified fences were erected between 2004 and 2005 zig-zagging the riverbed, theoretically giving both people and livestock, and wild animals alternating access to the natural water pools and boreholes along the then dry riverbed (Ngaka et al., 2018; Brooks, 2005). The fence became un-electrified with the reflooding of the Boteti River in 2009, and for the duration of the study period the fence was at various stretches knocked down by elephants, with elephants and other species including cattle passing relatively uninhibited across the fence at various points (Kesch et al., 2015). The region to the west of the Boteti River consists of community, pastoral, and arable land, and with the increased elephant numbers since the return of the river there is increasing spatial overlap of elephants and communities to the west of the park (Stevens, 2018; Figure 1.1). The region surrounding the Boteti River suffers some of the highest rates of human-wildlife conflict in Botswana (Brooks & Bradley, 2010), with 64% of people interviewed in the communities surrounding the park stating that elephants hindered their access to drinking water and 71% stating elephants threatened their safety (Mayberry, 2015). The charity Elephants for

Africa, based in the park and surrounding area, works closely with communities to find solutions to human-elephant conflicts, such as improving safety for people sharing environments with elephants, and reducing elephant crop foraging events.

1.6.2 The elephant population, aging and identification methods

The elephant population in the MPNP is overwhelmingly male dominated, with around 98% of elephant sightings reported as males (Evans, 2019). Male elephants are non-territorial, roaming vast and variable distances over their lifetimes (Ngene et al., 2009). The elephant population of the study area is largely transitory, with individual bulls staying on average only 47 days in the area, followed by 238 outside the area (Pitfield, 2017). A total of 1229 individual males have been uniquely identified to utilise the MPNP within the study area (Evans, Personal communication), although aerial surveys estimate 1426 elephants utilise the wider western MPNP at any one time (dry season count; Chase et al., 2018). The male predominance in the MPNP is perhaps due to its location on the fringes of the African elephants' range in Botswana (Thouless et al., 2016). Males are able to move further from fixed water points and are less selective in their habitat choice, particularly in the dry season compared to female groups with dependent young (Stokke & du Toit, 2002). In bull areas, wide-ranging, sexually inactive bulls can coexist free from harassment from musth males that live in areas with females (Stokke & du Toit, 2002), and adult non-musth male elephants spend the majority of their time in such bull areas, spatially segregated from females (Lee et al., 2011). Also see **1.3.1** for further details on the proposed mechanisms behind formation of bull areas in African elephants in general.

Male elephants continue to grow throughout life, with age strongly associated with size (Lee & Moss, 1995). A combination of characteristics relating to size components such as overall body size, shoulder height, head shape and size, head size relative to body, and tusk girth and splay were used to determine a male elephant's age (Hanks, 1972; Lee & Moss, 1995; Moss, 1996; Black et al., 2019). For this study, males were categorised into age classes: adolescents, 10-15 years and 16-20 years and adults, 21-25 years and 26+ years. Concerning data collected from camera traps (**Chapters 2 & 5**), size assessment and age classification was greatly assisted by the fact that, in walking on fixed pathways in front camera traps, elephants could be observed occupying a uniform point in space, with a uniform head position in relation to the camera (Figure 1.2), allowing for easy comparison of relative body size between individuals. Aging of elephants observed at social hotspots (**Chapters 3 & 4**) is likely more prone to error. However at least 2 experienced researchers were always present in the field to discuss and mutually discern an accurate age class to elephants, and subsequent to data collection one researcher (CA) reviewed all footage and photographs to confirm a confidence in uniformity of age classification over the study period. Past research in this study population found the age of only a minority of elephants was disputed between researchers using blind presentation techniques (Pitfield, 2017). Analysis based on finer-scale categorisation of older bulls by age that is typical for male elephants in other study areas across Africa (26–35 years & 36 years+; Evans & Harris, 2008; 25–34.9 years, 35–49.9 years & 50+; Moss, 1996) was not possible in the current study due to a small sample size of individuals older than 36 years (Figure 1.3), which created limitations with statistical power and model convergence issues. Previous research in the study area also found very low numbers of bulls aged over 36 years (Stevens, 2018; King, 2019), and across other populations in Africa too, bulls aged over 36 years can represent a rare age cohort (Moss, 2001; Whyte, 2001; Wittemyer et al., 2013; Jones et al., 2018). We therefore set our older bull category as 26 years + and argue this is an appropriate categorisation because it represents the age where males begin exhibiting regular sexually active periods (musth periods), experiencing alterations to sexual and social interests and behaviours (Poole, 1989a,b; Poole et al., 2011; Lee et al., 2011), and achieving paternity success (Hollister-Smith et al., 2007).

Figure 1.2: Example images from camera traps for comparison of size and body characteristics of a 10-15 year old (top) and elephant aged 26+ years (bottom). Elephants in images are positioned at roughly the same point on the elephant pathway, in front of the same camera.

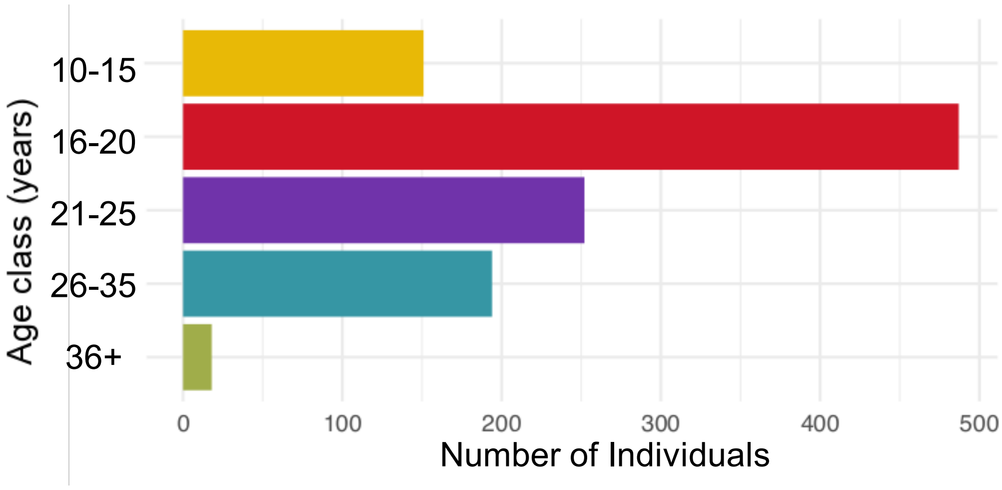

Figure 1.3: Ages of individually identified elephants observed travelling on elephant pathways in the MPNP between October 2017-September 2018. Only 18 individuals were sighted that were aged over 36 years of age, and were therefore pooled with the age class below (to create age class 26+ years) for all analyses in this thesis.

In all our models for statistical analyses, elephant ID was included as a random effect. This was to account for the possibility that independent of age, personality differences can exist between individual elephants (e.g. tendency to be solitary compared to with social companions, to have social influence over group members, to act aggressively (Lee et al., 2011; Lee & Moss, 2012; Seltmann et al., 2019)), which may influence results and must therefore be controlled for. Individuals were uniquely identified using distinguishing features such as ear notches, holes and tears (Douglas-Hamilton, 1972), tusk length, girth and shape, skin wrinkles and other abnormalities. Reliability of identification was validated by presenting footage of anonymised elephants to a blind researcher (Camera trap data footage). Using characteristics listed above, the researcher assigned the elephant to an ID in the data base. 100% of elephants were assigned their correct ID number (n = 30).

On rare occasion, females were sighted both in focal video sessions at social hotspots, as well as on camera traps. Furthermore, despite so few females present as mating opportunities in the study area, musth bulls were also occasionally sighted. Owing to their influence on male sexual and aggression behaviours (Poole, 1989a,b), both females and musth bulls are likely to affect the social behaviours of male elephants in their environment. Each chapter addresses separately how these two types of individual were accounted for in analyses.

1.6.3 Seasonality, climate and rainfall

Botswana has two main seasons, a “wet season” around November-May, and “dry season” from around June-October. Onset of rains varied from year to year in the study period, so season was determined by local rain records collected within the study period for our analyses. Rainfall was measured daily at the Elephants for Africa research camp (GPS coordinates: S: 20°27'28.67", E: 24°30'58.66”). Additional records were taken from entrance gates to the MPNP by the Botswana Department of Wildlife and National Parks (Khumaga gate: S: 20°28'19.94", E: 24°31'3.46", Phuduhudu Gate: S: 20°12'50.94", E: 24°35'40.53"). Together, these records helped determine the onset of wet and dry seasons for the course of the study. The onset of the wet season was determined by the first rainfall in the study area over 15mm, as in previous years this volume tended to signal the beginning of regular rainfall. The onset of the dry season was defined as 14 days after the last rainfall (regardless of volume), this lag was to account for the period following the last rains where vegetation was still of high quality (Mberego, 2017), and where water may hold in ephemeral pools away from the river. Elephants are more dependent on permanent water sources (such as the Boteti River) during the dry season (Wittemyer et al, 2008), whereas movements become more random in the wet season where water resources are more dispersed, for example in temporary pools.

In the semi-arid Kalahari of Botswana, rainfall has a large influence on vegetation abundance (Nicholson & Farrar, 1994), with natural forage abundance increasing in the short term soon after the onset of local rainfall (i.e., the same month; Mberego, 2017). Normalised difference vegetation index (NDVI) work is being undertaken in the study area (Figure 1.1) (Evans, Personal communication). In Botswana, vegetation cover declines rapidly with the cessation of rains (Mberego, 2017). Forage availability and season also have a strong influence on elephant movement patterns and group sizes (Chiyo et al., 2014; King, 2019), as well as on elephant body condition in the study area (Pitfield, 2017). Hence season, determined by rainfall was an important environmental factor to include in models throughout the study.

The MPNP has a semi-arid climate (Kgathi & Kalikawe, 1998). Using only recordings collected at the Elephants for Africa rain gauge, in the wet season of 2015-2016 a total of 182.7 mm was recorded, 515 mm was recorded in the 2016-2017 wet season, and 584.5 mm in the 2017-2018 wet season. Wet season temperatures can exceed 40 °C (Kgathi & Kalikawe, 1998), whilst the dry season has cooler temperatures, reaching daily maximums of around 28°C (Thomas & Shaw 1991).

1.6.4 Camera trap surveys along elephant pathways

Analyses for **Chapters 2 and 5** involved data collected from camera traps placed along well used pathways in the MPNP landscape (Figure 1.1). Elephants possess detailed spatial knowledge of their core range, within which they travel using a “Euclidean-cognitive map” (Presotto et al., 2019; Polansky et al., 2015). However, when navigating in the periphery of their range, elephants switch to using habitual routes to navigate (Presotto et al., 2019). Such habitual routes can after prolonged use lead to clear “elephant pathways” in the landscape (Mutinda et al., 2011; Songhurst et al., 2016; Von Gerhardt et al., 2014; Haynes, 2006; Figure 1.4). These regularly used routes are proposed to facilitate optimal foraging strategies by connecting predictable resources and landscape features such as drinking points (Von Gerhardt et al., 2014). In the MPNP such pathways are clearly identifiable (Figure 1.4) and terminate at easy access points on the Boteti River (Figure 1.1). Elephants travelled along the pathways with apparent purposeful movement, and upon arrival at the river, elephants immediately drank (personal observation) suggesting the river as a drinking resource is the key motivation for the traveling group moving towards the river. Elephants did however also use pathways for movements away from the river (N groups moving towards river=938, 63.81% of groups; N groups moving away from river = 521, 35.44% of groups). 11 additional groups were observed on camera traps, but not on the pathway, nor walking in any particular direction, presumably passing the camera trap by chance movement through the environment (0.75% of groups).

Figure 1.4: Example images of elephant pathways in the MPNP. Pathways measured on average 84.8 cm in width (SD= 6 cm, N pathways= 7, N measurements= 46, range N measurements per pathway= 5-16), with measurements taken at random points along the pathway within a safe 50m distance of a vehicle. Pathways are devoid of vegetation and maintained by repeated single file movement of elephants in both directions to and from the Boteti River.

Camera traps (2017 Bushnell Aggressor HD No-glow, set to record video) were positioned along 7 pathways in the MPNP (Figure 1.1). Pathways can also be seen from satellite images, with historical imagery available from the area in 2004 (Personal observation; GoogleEarth, n.d.) suggesting some routes have remained unchanged for at least 14 years. Aerial photographs in northern Zimbabwe suggest some elephant pathways in the area have been actively used for over 50 years (Haynes 2006). To ensure uniformity of camera trigger response, and to ensure as much of the animal was captured in the frame as possible, we placed cameras on 2m high poles positioned 9m, at an angle of 45°, either side of a central point on the pathway. By placing a camera facing inwards either side of the focal point, head on footage (essential for aging and identification purposes; Figure 1.2) was available for both elephants walking towards and away from the river. A total of 24 other mammal species were also observed to utilise elephant pathways (Table 1.1).

Table 1.1: Summary of species captured from the 7 camera traps on elephant pathways. Cameras were active for a cumulative 8942 study hours over the study period. "Total on main pathway" refers to species walking on the precise channel that marked the physical presence of the elephant pathway (Figure 1.4), rather than walking either side of this channel.

Species	**Total on camera traps**	**Total on main pathway**	**% on main pathway**
Elephant *Loxodonta africana*	3858	3365	87
Zebra *Equus quagga*	6787	875	13
Wildebeest *Connochaetes taurinus*	802	117	15
Giraffe *Giraffa giraffa*	118	65	55
Jackal *Canis mesomelas*	89	65	73
Porcupine *Hystrix africaeaustralis*	42	40	95
Lion *Panthera leo*	25	24	96
Steinbok *Raphicerus campestris*	61	23	38
Brown Hyena *Hyaena brunnea*	28	23	82
Kudu *Tragelaphus strepsiceros*	96	19	20
Cape Fox	14	10	71

Vulpus chama			
Impala *Aepyceros melampus*	16	7	44
Spotted Hyena *Crocuta crocuta*	6	6	100
Leopard *Panthera pardus*	6	5	83
Honey Badger *Mellivora capensis*	5	5	100
Common Duiker *Sylvicapra grimmia*	8	4	50
Bat Eared Fox *Otocyon megalotis*	4	3	75
Wild Cat *Felis lybica*	4	1	25
Caracal *Caracal caracal*	1	1	100
Hippo *Hippopotamus amphibius*	1	1	100
Serval *Leptailurus serval*	1	1	100
White Rhino *Ceratotherium simum*	1	1	100
Cattle *Bos taurus*	84	0	0
Zorilla *Ictonyx striatus*	3	0	0
Gemsbok *Oryx gazella*	1	0	0

For **Chapter 2**, camera traps were used to survey male elephant travelling groups in the MPNP. We analysed the tendency for different age classes of male elephants to travel alone or in all-male groups, as well as analysed the order of movement of different aged males within elephant travelling group processions on pathways. For **Chapter 5**, we exploited the tendency of male elephants to habitually walk along pathways to create an in-situ bioassay, whereby the olfactory responses of passing elephants were recorded to purposefully placed urine of donor elephants positioned on the main path.

A total of 3858 elephants were observed on camera traps over the cumulative 8942 study hours that cameras were active (Table 1.1). Due to time limitations, not all captured elephants were individually identified to be included in final analyses. Furthermore, various elephants or groups were excluded from analyses, for example due to female presence in groups, elephants not passing over samples directly (**Chapter 5**), previously passing elephants urinating or defecating in the sample area (**Chapter 5**). Consequently, **Chapters 2 and 5** have different overall sample sizes, with number of individual elephants, exclusions and final sample sizes outlined in each chapter separately.

1.6.5 Social hotspots along the Boteti River

Analyses for **Chapters 3 and 4** involved data collected from video recordings of focal elephants during their stay at social hotspots along the Boteti River (Figure 1.1). Hotspots were areas of river with easy access for elephants (no steep cliffs characteristic of stretches of the Boteti River) and were the terminal points of elephant pathways in the MPNP landscape (Figure 1.1). Hotspot boundaries were defined by natural landmarks in the environment, based on the general area in which the majority of elephants remained in during a visit to the river. On average, hotspots encompassed a 628.68m stretch of river (range=503.14m-793.34m) (Table 1.2).

Table 1.2: Locations and approximate sizes of social hotspots focal follows were sampled at.

Hotspot ID	**GPS most northern point**	**GPS most southern point**	**Approx. length (m)**	**Approx. area (km^2)**
1	20°28'55.68"S, 24°30'58.63"E	20°29'9.27"S, 24°30'54.68"E	503.14	0.069
2	20°23'45.22"S, 24°31'3.43"E	20°23'59.63"S, 24°31'12.14"E	527.21	0.169
3	20°23'28.69"S, 24°30'43.55"E	20°23'45.22"S, 24°31'3.43"E	763.04	0.195
4	20°23'17.60"S, 24°30'7.99"E	20°23'25.01"S, 24°30'34.75"E	793.34	0.185
5	20°19'19.80"S, 24°18'57.92"E	20°19'15.58"S, 24°19'14.30"E	556.68	0.052

As stated, the level of water in the river fluctuated at social hotspots throughout the study, as a result of local rainfall and the seasonal flood waters of the Okavango Delta system (Vanderpost & Hancock, 2018). Despite the fact that the river ran dry at various locations twice during the study's duration, deep water, enough to fully submerge an adult bull, was always present at all hotspots during the tenure of the study. Other key features of this study's social hotspots included dusting and mudhole sites for wallowing, and patches of dry riverbed from which elephants consumed dust/sand (presumably for mineral content (Weir, 2009)). On occasion, elephants were observed eating reeds growing in the river, or the sparse vegetation available on trees on the bank slope (Figure 1.5) – however, feeding on vegetation did not dominate behaviour of elephants at hotspots. Male elephants also utilised hotspots for social purposes, with time spent at hotspots often exceeding the amount of time needed for drinking, mud wallowing and feeding on minerals (average time spent at hotspot for focal elephants seen arriving and leaving via bank = 1h 13 min, range= 9min – 7 h 5 min, SD= 59 min, N focals= 217).

Figure 1.5: Example images of Boteti River social hotspots, demonstrating the good visibility of elephants. A hotspot consisted of the river (c), the surrounding flat, largely vegetation free sand that may be flooded during certain times of year (b), and a sandy slope leading down to the river (a & d), populated with riverine shrub and thorn savannah (Kgathi & Kalikawe, 1993). The majority of elephants arrived at hotspots at predictable points on the bank, having travelled on fixed elephant pathways to reach the river. The Boteti River marks the western boundary of the MPNP, whilst most elephants during the study arrived via the bank slope on the national park side (a) (N elephants= 2543, percent total= 65.42%), a minority arrived via the bank slope that leads out towards community owned land (d) (N elephants= 285, percent total= 7.33%). Furthermore, some elephants arrived having walked along the river from up or down stream of the hotspot (N elephants= 1059, percent total= 27.24%). These individuals were recorded when they crossed the defined hotspot boundaries.

Individual focal subjects were filmed for the entirety of their stay within social hotspots, starting either as the subject arrived over the bank slope, or as he entered the hotspot having moved from another stretch of river up or downstream, and terminating when similar boundaries were crossed during departure. Subjects of focal animal samples were filmed using a video cam-corder (JVC quad proof AVCHD) fixed to a tripod, with the subject kept central to the frame, but zoomed out enough to allow for behaviours of potential interactors to be captured. The research vehicle was parked at a safe distance (minimum 50m) from points expected to receive elephants (pathway arrival points, popular drinking points, mudholes). Non-musth males in the MPNP are largely relaxed around vehicles, and if the engine was off for the entire focal session, it was common for elephants to not look in the direction of the human observer. In the case that elephants would walk within 50m of the research vehicle, the standard protocol was to remain silently in place, as starting the vehicle may cause disturbance to elephants.

All video data was collected between 08:00 and 18:30. Individual recording sessions aimed to be a minimum of 4 hours long, but were extended when subjects were still present. To spread the distribution of subject arrival times across the day, we aimed to begin 1/3 of video sessions between 08:00-10:00, 1/3 between 10:00-12:00, and 1/3 between 12:00-14:00 (i.e., a session beginning at 14:00 would end around 18:00). The age class of subject to be recorded was randomly preselected, and the first elephant of the assigned age class to arrive at the hotspot since the start of the session was the subject of a focal animal sample. By recording the ages of and number of other elephants present at the focals arrival, and of the elephants arriving and departing hotspots during the focals stay, I produced a measure of the number of elephants present with focal subjects at social hotspots, and their ages, every 10-minutes. This provided the main measure for the social environment of elephant aggregations at social hotspots (Fishlock, 2010). Adolescent elephants had a greater presence than adults at social hotspots in this bull area (Figure 1.6). This is in interesting contrast to other study areas where adolescent males prefer to associate with females in family groups than in all-male groups, and use of bull areas is thought to increase with age (Lee et al., 2011). More elephants were present with focal elephants in focal follows conducted in the wet season than in the dry season (Figure 1.6).

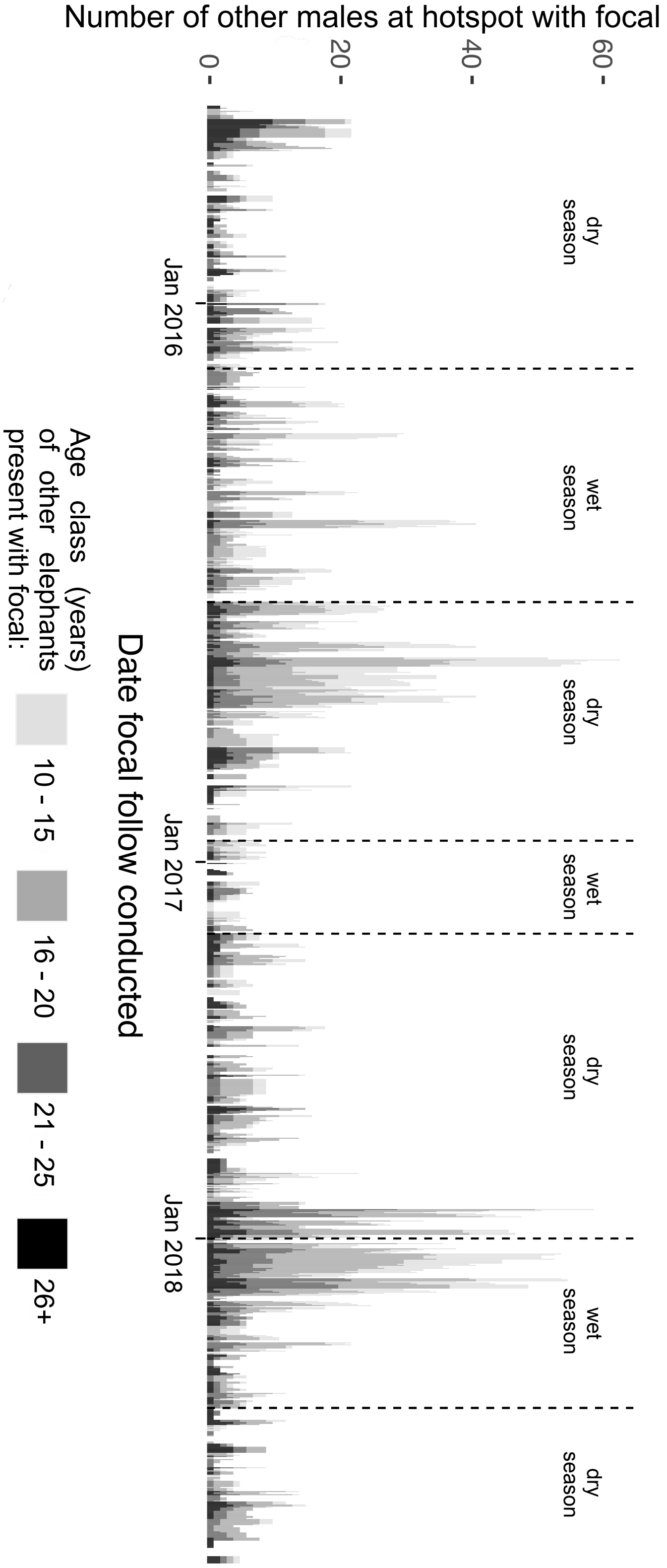

Figure 1.6: Number of elephants present at hotspots during focal follows, including ages (focal elephant's social context in 10-minute follow time window, excludes focal). Dry and wet season periods indicated. More elephants were

present at hotspot with focals in the wet season than in the dry season (average number of elephants present at hotspot with focal in dry season= 8.94, wet season= 10.35, Wilcoxon rank sum test with continuity correction: W= 209540, p= 0.038).

Elephants arriving via the bank slope (Figure 1.5) had been travelling on the kind of pathways sampled in our camera trap surveys (see **1.6.4**; Figure 1.1). Elephants arriving via the bank slope on either the national park side or community land side tended to arrive in single file and immediately line up together along the river and drink. In line with camera trap group determination methods, elephants that arrived within 10-minutes of one another were considered part of the same all-male group (see **Chapter 2** for method of discerning appropriate cut off times for group membership). Following initial arrival at the river however, there was considerable mixing of males, and elephants did not stick to particular associates or remain in particular proximity to their original group mates. As all-male groups continued to arrive throughout the day, hotspots became what I would describe as “aggregations” of males, and it was not possible to reliably discern who was in a group with one another at the hotspot (Figure 1.5). Our measure of social context for **Chapters 3 and 4** was therefore at the aggregation level, and represented the total potential interactors at the social hotspot for the focal male.

At departure from social hotspots however, elephants appeared to leave in more coordinated all-male groups again. Again, applying the 10-minute boundary of group membership (for the elephant passing over the bank slope), composition of all-male groups at departure was possible for 139 focal elephants. On average all ages departed in larger groups than they arrived in (Table 1.3). Only 14.39% of elephants left the hotspot with the identical group composition that they arrived at the river with (i.e the same individuals and no additional group members). In contrast, at mixed sex African forest elephant social aggregations in bais (forest clearings), despite males and females often associating with new individuals during their visit, 78.5% of elephants left with the same group composition that they arrived in (Fishlock & Lee, 2013). In the current study, 25.18% of elephants left the hotspot with completely new individuals. 26.62% of elephants left the hotspot alone. 33.81% of elephants left the hotspot with a combination of original group mates they arrived with and new elephants met at hotspots, or some but not all of their original group mates they arrived with. 48.20% of elephants left with at least 1 elephant that they had arrived at the river in a group with.

Table 1.3: Group sizes of arriving and leaving groups at social hotspots for each age class. Calculated only from focal elephants (video recorded for extraction of behaviours) observed both leaving and arriving via the bank slope. Includes solo arrivals and departures.

Age class (years), N	**Group size arrival (mean (SD, range))**	**Group size departure (mean (SD, range))**
10-15, N= 26	3.923 (2.448, 1-11)	4.615 (2.787, 1-11)
16-20, N= 41	2.732 (2.398, 1-13)	3.244 (2.634, 1-11)
21-25, N= 35	3.057 (2.520, 1-12)	3.743 (2.904, 1-13)
26+, N= 37	2.865 (1.988, 1-7)	4.622 (3.911, 1-15)

For **Chapter 3**, focal subjects' probability of performing aggression and fear behaviours was related to the social context he was in at the hotspot (i.e., the presence of other males and their ages). For **Chapter 4**, I analysed focal elephants' choices concerning partners targeted with trunk-mediated "greeting" behaviours during visits to social hotspots.

1.7 Ethics

This work received approval from the University of Exeter Research Ethics Committee (application ID: eCLESPsy000545 v3.2) and was conducted with permission of the Botswana Department of Wildlife and National Parks, under research permit EWT 8/36/4 XXXVI (57).

Chapter 2: Effect of Age on Lead and Following Positions in the Collective Movements of All-male Groups in African Elephants

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Author contributions: CRBA conceived the study, conducted field work, data extraction, statistical analysis and was the lead author in drafting the manuscript. DPC and LJBN participated in study design, statistical analysis and critically revised the manuscript. MW contributed to statistical analysis including writing of code. TM conducted field work.

2.1 Abstract

In long-lived social species, older individuals can provide fitness benefits to their groupmates through the imparting of ecological knowledge. Research in this area has largely focused on females in matrilineal societies where, for example, older female African elephants (*Loxodonta africana*) are most effective at making decisions crucial to herd survival, and old post-reproductive female resident killer whales (*Orcinus orca*) lead collective movements in hunting grounds. In contrast, little is known about the role of older males as leaders in long-lived social species. By analysing leadership patterns of all-male African elephant traveling groups along elephant pathways in Makgadikgadi Pans National Park, Botswana, we found that the oldest males were more likely to lead collective movements. Our results challenge the assumption that older male elephants are redundant in the population and raise concerns over the biased removal of old bulls that currently occurs in both legal trophy hunting and illegal poaching activity. Selective harvesting of older males could have detrimental effects on the wider elephant society through loss of leaders crucial to younger male navigation in unknown, ecologically unpredictable environments.

2.2 Introduction

During coordinated group movements certain individuals can consistently arise as “leaders” with a regular influence over group decisions, with high dominance rank (King et al., 2008), bold temperament (Harcourt et al., 2009) and greater age (often associated with an enhanced knowledge or experience (Maransky & Bildstein, 2001)) noted as common traits characterising leaders of groups (for review, see King et al., 2009). In the study of leadership in non-human animals, leadership can have various definitions, and refer to different social phenomena (Bourjade et al., 2015), such as individuals that are consistent in successfully recruiting their group members to move, those found at frontal “guiding” positions in groups, or individuals that make effective decisions most crucial to group survival (Brent et al., 2015; Pettit et al., 2015; Mutinda et al., 2011; Lee & Teichroeb, 2016). Whilst in some cases leadership can be a passive process, a consequence of simple consensus decisions to maintain group cohesion (Dyer et al., 2008), in other cases leaders actively communicate their intent to recruit followers (Lusseau & Conradt, 2009). In long-lived species, older individuals often respond more appropriately to complex, changing environments (Diamond, 2001; McComb et al., 2011a), providing substantial fitness benefits to younger group mates. For example, older matriarchs are more effective at appropriately mobilising groups in response to predation threats and conspecifics in female African elephants (*Loxodonta africana*) (McComb et al., 2001, 2011a), Similarly, in resident killer whale (*Orcinus orca*) groups there is a greater reliance on older, post-menopausal females as leaders of hunting groups in years of low salmon abundance (Brent et al., 2015).

Non-human research in this area has tended to focus on females and less attention has been given to the potential for old males to act as repositories of ecological knowledge and leaders in long-lived social species. In many social mammals, males are often assumed to be replaceable because they are typically the dispersing sex (Stephen Dobson, 1982), and old males may be reproductively redundant, which is commonly used as an argument to justify the legal trophy hunting of old males in many species (Baker, 1997; Hurt & Ravn, 2000). This combined with desirable features such as larger body size and ornaments, leads to selective harvesting of older males in many species, including the African elephant (Chiyo et al., 2015). However, there is no reason to assume there would be sex-based differences in the accumulation of information with age, and older males have the potential to occupy the same socio-cognitive role as older females, particularly in species where sexual segregation and all-male groupings occur, such as the African elephant.

Elephants possess detailed spatial knowledge of their core range, within which they travel using a “Euclidean-cognitive map” (Presotto et al., 2019). However, when navigating the periphery of their range, elephants switch to using habitual routes (Presotto et al., 2019). After prolonged use, these habitual routes can lead to “elephant pathways”, which are proposed to facilitate optimal foraging strategies by connecting predictable resources and landscape features such as drinking points (Von Gerhardt et al., 2014). Male elephants disperse from their natal herd between the age of 10-20 years and establish themselves in a separate bull society (Lee et al., 2011). Males roam vast distances during their lifetime (Ngene et al., 2009), and social associations among males are weaker and more transitory than among females (Archie et al., 2005; Chiyo et al., 2011a).

Between 25-30 years of age, males will begin experiencing reliable, stable 'musth' periods, annual cycles of a temporary heightened reproductive state where males seek out females for mating (Poole, 1987; Poole et al., 2011). Musth males are preferred by females, and up to 74% of calves are fathered by males in musth at the time of conception (Hollister-Smith et al., 2007). This temporal concentration of male sexual viability reduces intra-sexual conflict between males and opens the opportunity for male-male prosocial interactions among non-musth bulls (Goldenberg et al., 2014), including the opportunity for collective travel and potentially information transfer from leaders of groups to followers. Life expectancy including human-induced mortality has been estimated as 41 years for female African elephants, but just 24 years for males (Moss, 2001). Higher mortality could reflect the greater growth costs on adolescent males (Lee & Moss, 1995), their lower resistance to drought (Moss & Lee, 2011), males' greater involvement in wildlife conflict situations (Chiyo & Cochrane, 2005; Stevens, 2018; Obanda et al., 2008), or the general risks associated with adolescent male dispersal, such as lack of knowledge in navigating crucial resources in a new, complex and risky environment (Foley et al., 2008). Thus, young adolescent males may gain considerable fitness benefits by associating with older males, with potentially decades more experience of utilising their environment safely and effectively, and older male elephants may act as repositories of ecological knowledge to younger males.

Here we quantify grouping behaviour and patterns of leadership in all-male elephant groups traveling on elephant pathways to and from the Boteti River in the MPNP, Botswana. The MPNP is a “bull area”, with males representing 98% of elephant sightings (Evans, 2019). We first quantify the extent to which male elephants of different age classes travel alone versus in all-male groups, hypothesising that younger adolescent males show a preference for group travel. Second, we predict that mature adult bulls are more likely to lead all male groups, and will be observed occupying the front positions of all-male group processions. Finally, we compare leadership patterns between wet and dry seasons, hypothesising there may be a divergent dependency on older, mature males as leaders under particular ecological conditions. There may be greater leadership by older, more knowledgeable males in the dry season when resources are more scarce (Brent et al., 2015), or in the wet season, when widely spread, unpredictable resources, such as timings of sprouting of vegetation, may require experienced knowledge to locate (Shannon et al., 2010).

2.3 Methods

Elephant travelling groups were observed from camera traps positioned along elephant pathways that lead towards and away from the Boteti River (Figure 1.1) in the MPNP (See **1.6.4**). Due to the large volume of video collected, analysis was conducted on a subset of footage from the last seven sampled days of every sampled month (elephant sightings n=1264). Within this data set, a human observer identified individuals uniquely (n individuals=1097) and assigned age classes to individuals (See **1.6.2**). There was a considerable right skew in the data set in terms of number of times individual elephants were sighted, e.g., two individual males were sighted seven times (highest number of re-sightings), three individuals five times, and 95 individuals were sighted twice, but the majority of individual elephants were sighted only once (n individuals= 975). Repeat sightings were perhaps rare since footage was captured over only a 12-month period, with elephants staying on average 47 days in the area before 238 days outside the study area (Pitfield, 2017). Since we only identified elephants observed within the last week of each month, it is possible that during a week elephants do not commonly use the same pathway within that 7-day window, feasible considering the expanse of the park and the various pathway options available to elephants. It is likely if all elephants within the whole month were to be identified, repeat sightings would increase since elephants stay on average for a month and a half in the park (Pitfield, 2017). In addition, if the study was longer than 12 months, repeat sightings would also be likely to increase as elephants re-enter the park after on average 238 days (Pitfield, 2017).

Males were categorised as young adolescents, 10-15 years (N individuals= 150), older adolescents, 16-20 years (N individuals= 487), young adults, 21-25 years (N individuals= 252) and mature adults 26+years (N individuals= 208). Analysis based on finer-scale categorisation of older bulls by age as in other study areas across Africa (26-35 years & 36 years + (Evans & Harris, 2008); 25-34.9 years, 35-49.9 years & 50+ (Moss, 1996)) was not possible in our study due to a small sample size of individuals older than 36 years (n=18). We therefore set our older bull category as 26 years +, and argue this is an appropriate categorisation because (i) it represents the age where males begin exhibiting sexually active periods (musth) and experiencing alterations to sexual and social interests and behaviours (Poole et al., 2011), and (ii) male elephants over this age are the preferred targets of trophy hunting and poaching activity due to the size and weight of their ivory (Jones et al., 2018; DG Ecological Consulting, 2003; Pilgram & Western, 1986; De Villiers, 1994).

The vast majority of elephants walked in a single file procession along elephant pathways (Table 1.1), making order of travel easy to quantify. Existing studies use successful initiation of group movements, as well as positioning within group to indicate leadership in collective movements (Brent et al., 2015; Pettit et al., 2015; Mutinda et al., 2011; Lee & Teichroeb, 2016). Lacking information concerning initiations, we used the latter definition, assigning leadership to those at the front of single file processions. In processions of African elephant females in family groups, matriarchs are more likely to occupy the back of travelling groups, suggesting leadership from the rear (Mutinda et al., 2011). We also therefore analysed ages of elephants occupying middle and rear positions in all-male groups separately.

Group assignment was determined based on the time that an individual passed the camera trap in relation to the previous passing elephant moving in the same direction. Previous studies have defined elephant groups as individuals within 100m of each other, coordinated in their activities (Wittemyer et al., 2005; Murphey et al., 2019). Such large distances between socially coordinated individuals can be achieved due to the species' exceptional long-distance chemical, seismic and infrasonic communication abilities (Langbauer, 2000; O'Connell-Rodwell, 2007). Furthermore, the sparsely vegetated open *Acacia* savannah-type habitat of the MPNP study area (Brooks, 2005; Kgathi & Kalikawe, 1993) makes for a good visual range between individuals walking on pathways.

To assign group membership we plotted the time stamp differences of individual elephants from the previous individual to pass the camera trap on the pathway, traveling in the same direction, to discern appropriate cut-off times for group membership. The majority of following events occurred within 10 minutes, we therefore set an eleven-minute difference to the previous elephant to pass as the cut-off period to indicate the start of a new group (Figure 2.1). Using previous research, we estimate this 10 min cut-off period translates to an inter-individual distance of between 64 meters (if assuming average walking speed of elephants in protected areas (Douglas-Hamilton et al., 2005)) and 201 meters (if assuming faster walking speed of elephants in corridors (Douglas-Hamilton et al., 2005)), a reasonable distance over which elephants will be able to maintain a visual line of sight in the habitat and communicate.

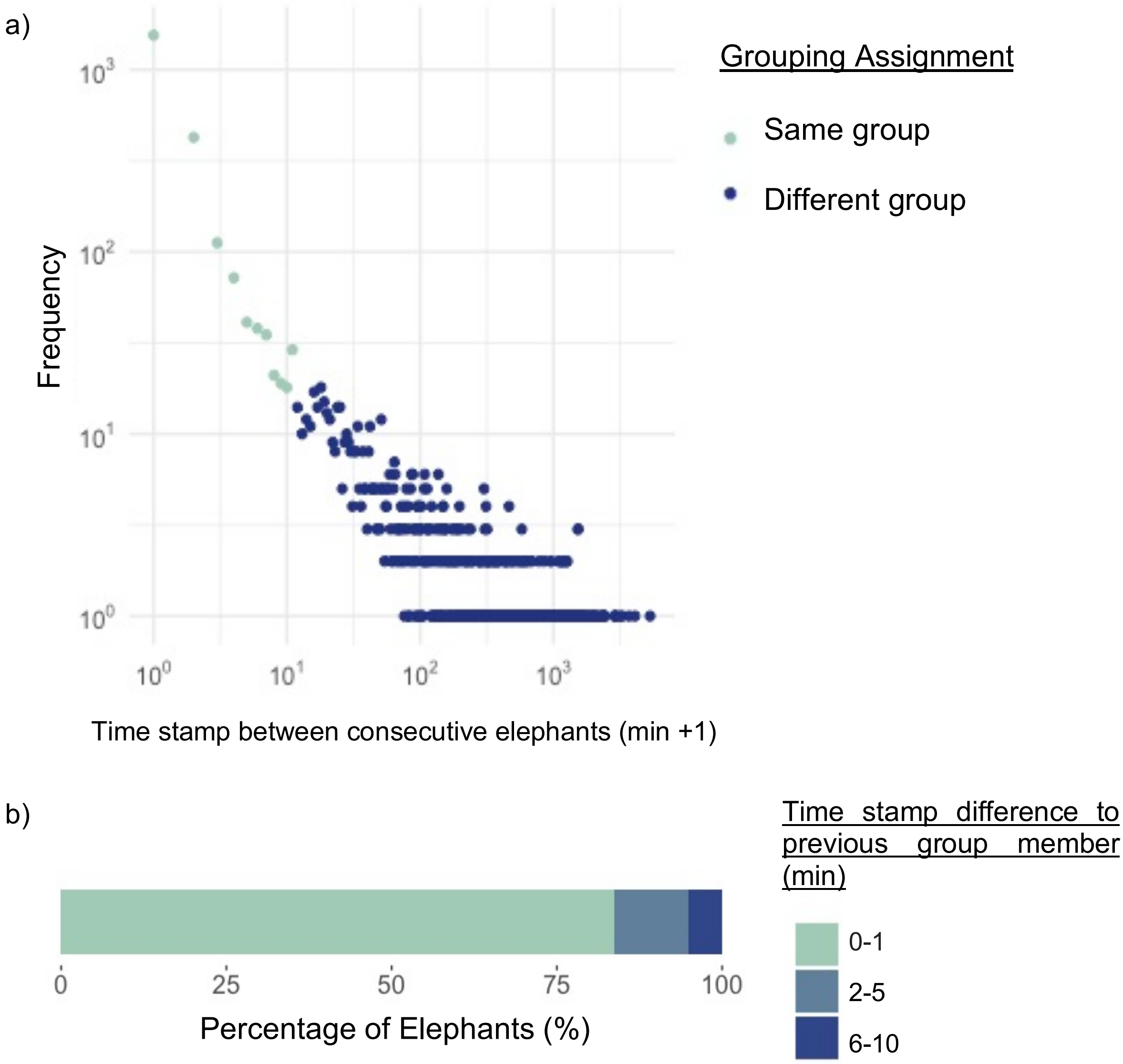

Figure 2.1: (a) Histogram (plotted on logarithmic scale) of the time difference between pairs of consecutive observations of elephants travelling on pathways. Groups were defined as individuals detected on the same pathway, moving in the same direction with a 10 minute or less time stamp to the previous passing individual. A time stamp difference of +1 min was added to all values to allow visualisation of 0-minute time stamp difference on a logarithmic scale. For between group recordings, only 10.21% of groups were separated by a 11-20 minute time stamp, with >20 minute differences separating groups in the majority of cases (range: 20-1437 minutes). (b) Percentage of elephants observed within certain time brackets of their previous group member.

Within groups, the majority of elephants in groups walked close to one another, with 83.65% of following events within groups occurring with a 0 or 1 minute time stamp difference to the previous elephant (Figure 2.1 b), we therefore further explored leadership patterns in these smaller, more tightly bunched “subgroups” and found qualitatively similar patterns to all our main analysis (**Supplementary Information 1**, Tables S1.1-S1.4, Figures S1.1-S1.4).

Statistical analysis

Patterns of male elephant grouping were analysed in R using generalized logistic mixed-effects models (GLMMs), with statistical significance assessed using permutation-based null models. We first investigated if males of adult age classes were more likely to travel alone (as opposed to in all-male groups), and adolescent age classes less likely than predicted by random chance. We fit a GLMM with a binomial error structure and a logit link function, predicting lone travel (dependent variable) by age class (independent variable), controlling for elephant ID as a random effect. We compared the estimates from this model to those generated from 20,000 permutations of the data in which we randomly re-assigned individuals to groups within the same season, maintaining the total number of times each individual was seen and the size of each group. A permutation approach allowed us to control for patterns in the data set owing to its inherent structure, including for example having a greater number of adolescents present in the population.

To test the prediction that mature bulls led all-male groups more than predicted by chance, groups containing at least 1 adult and 1 adolescent (n individuals=725, n groups=182) were assessed for the position of travel of individuals. Binomial GLMMs were fit, and the estimates obtained for the observed data set were compared to 20,000 randomised data sets, where age composition of individuals in each group was maintained, whilst position of individuals within groups were randomly shuffled in each permutation. Separate models were run predicting tendency to occupy front, middle and rear positions in groups (dependent variables) by age class (independent variable), again controlling for elephant ID as a random effect. The ages of elephants traveling in the middle of groups was assessed in all-male groups with a group size of at least 3 with at least 1 adult and 1 adolescent (n individuals=631, n groups=132).

The Boteti region has the greatest reported level of human-wildlife conflict in Botswana (Brooks & Bradley, 2010; Mayberry et al., 2017), and human conflict risk becomes higher for elephants closer to the Boteti River (Figure 1.1). Furthermore, lions in the area are at higher densities closer to the river (de Boer et al., 2010; Ngaka, 2015) Such threats may make the real or perceived risk (Bateson et al., 2011) of being at both the front and rear of groups greater for vulnerable individuals (King et al., 2012), which may affect patterns of positioning within groups. To test for these effects, we tested if distance of camera set up from the river modified elephants of different age classes tendency to hold certain position within groups, by running additional models to include distance as an interaction term in the above models. We similarly ran additional models to analyse any interaction of age class with season (wet vs. dry; see **1.6.3**) on models of lone travel and leadership, to explore whether there was variation in the tendency for elephants of certain ages to act as leaders between seasons.

Due to model convergence limitations, it was not possible to include both elephant ID and pathway location together as random effects in our main models. However mean size of traveling groups did not differ between pathways (Table 2.1 & 2.2), and the inclusion of pathway location as a random effect instead of elephant ID did not majorly alter the outputs of models (**Supplementary Information 1**, Table S1.5-S1.8). Data from the different pathways were therefore pooled for analyses.

Table 2.1: Summary statistics of all-male group sizes on the 7 sampled pathways, including lone male travellers. There was no significant difference between pathways for average group size of all-male groups observed on camera traps, lone travellers included (Kruskal Wallis $\chi2(6) = 9.445$, $p = 0.150$).

Pathway N.	**N. Groups**	**Mean Group Size**	**SD**	**Median**	**IQR**
1	179	2.58	2.22	2	2
2	31	2.32	2.14	1	2
3	110	2.39	2.88	1	1
4	144	2.28	1.70	2	2
5	47	2.36	1.47	2	2
6	22	2.32	1.91	2	2
7	15	1.87	0.92	2	2

Table 2.2: Summary statistics of all-male group sizes on the 7 sampled pathways, excluding lone male travellers. There was no significant difference between pathways for average group size of all-male groups observed on camera traps, lone travellers excluded (Kruskal Wallis χ2(6) = 4.064, p = 0.668).

Pathway N.	**N. Groups**	**Mean Group Size**	**SD**	**Median**	**IQR**
1	103	3.75	2.32	3	2
2	14	3.93	2.34	3	2.5
3	41	4.73	3.69	3	4
4	77	3.40	1.64	3	2
5	29	3.21	1.26	3	2
6	12	3.42	2.02	3	2
7	8	2.62	0.52	3	1

Addressing musth bulls and females in the data set

Musth bulls were identified by a combination of heavy temporal gland secretion, urine dribbling, and green staining around the penis (Poole, 1987). Musth bulls represented a small number of elephants observed in the study (n=19, 15 moving as lone travellers, and 4 in all-male groups). However, because musth affects only adult age classes, is likely to influence a males' grouping condition (Goldenberg et al., 2014), and because there were significantly more musth bulls in the wet season (2.5% of elephants) compared to dry season (0.9% of elephants) (Chi Square Goodness of Fit: X^2 (1) = 35.9, p < 0.001), we reran all permutation based GLMM's with musth bulls removed from the dataset and found qualitatively similar results in all models (**Supplementary Information 1**, Table S1.9-S1.21). Musth males do not therefore appear to be driving our results. Within the sampled period, an additional 19 mixed-sex groups were recorded containing a total of 38 females and 21 associated calves/ juveniles, these groups were excluded for analysis.

2.4 Results

Adolescent male elephants were less likely to be observed traveling alone

Lone travellers accounted for 20.8% of sightings on elephant pathways (N elephant sightings= 263/1264). Adolescent males were observed travelling alone significantly less than predicted by chance, whilst mature adult bulls travelled alone significantly more than predicted by chance (Permutation-based likelihood ratio test of GLMM, $\chi 2$ (3)= 9.02^{-7}, $p < 0.001$; Figure 2.2).

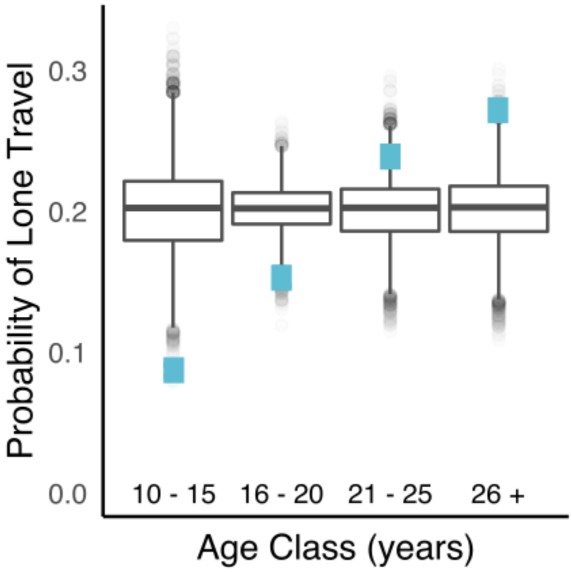

Figure 2.2: Observed probabilities of lone travel for the different age classes of male elephants (blue squares), plotted against randomly permuted probabilities of lone travel (boxplots with median, interquartile range, minimum and maximum values). Adolescent males were less likely to travel alone than expected by

chance. Observed probability of lone travel for ages: 10-15 years = 0.087, 95% CI random = (0.141-0.266), p = 0.001; 16-20 years = 0.153, 95% CI random = (0.166-0.232), p = 0.010; 21-25 years = 0.239, 95% CI random = (0.156-0.246), p = 0.105; 26+ years = 0.272, 95% CI random = (0.154-0.248), p = 0.004.

Older males occupied lead positions in all-male groups

Adolescents were significantly less likely than predicted by chance to travel at the front of all-male groups and adult age classes were significantly more likely than predicted by chance to travel at the front of all-male groups (Permutation-based likelihood ratio test of GLMM, χ2 (3)= 7.83^{-7}, p<0.001; Figure 2.3a). Adolescents were significantly more likely than predicted by chance to occupy middle positions in all-male groups, and adult age classes significantly less likely (Permutation-based likelihood ratio test of GLMM, χ2 (3)= 3.69^{-10}, p<0.001; Figure 2.3b). No age class differed from random chance in their probability of being located at the rear of an all-male traveling group (Permutation-based likelihood ratio test of GLMM, χ2 (3)=0.087, p=0.185; Figure 2.3c).

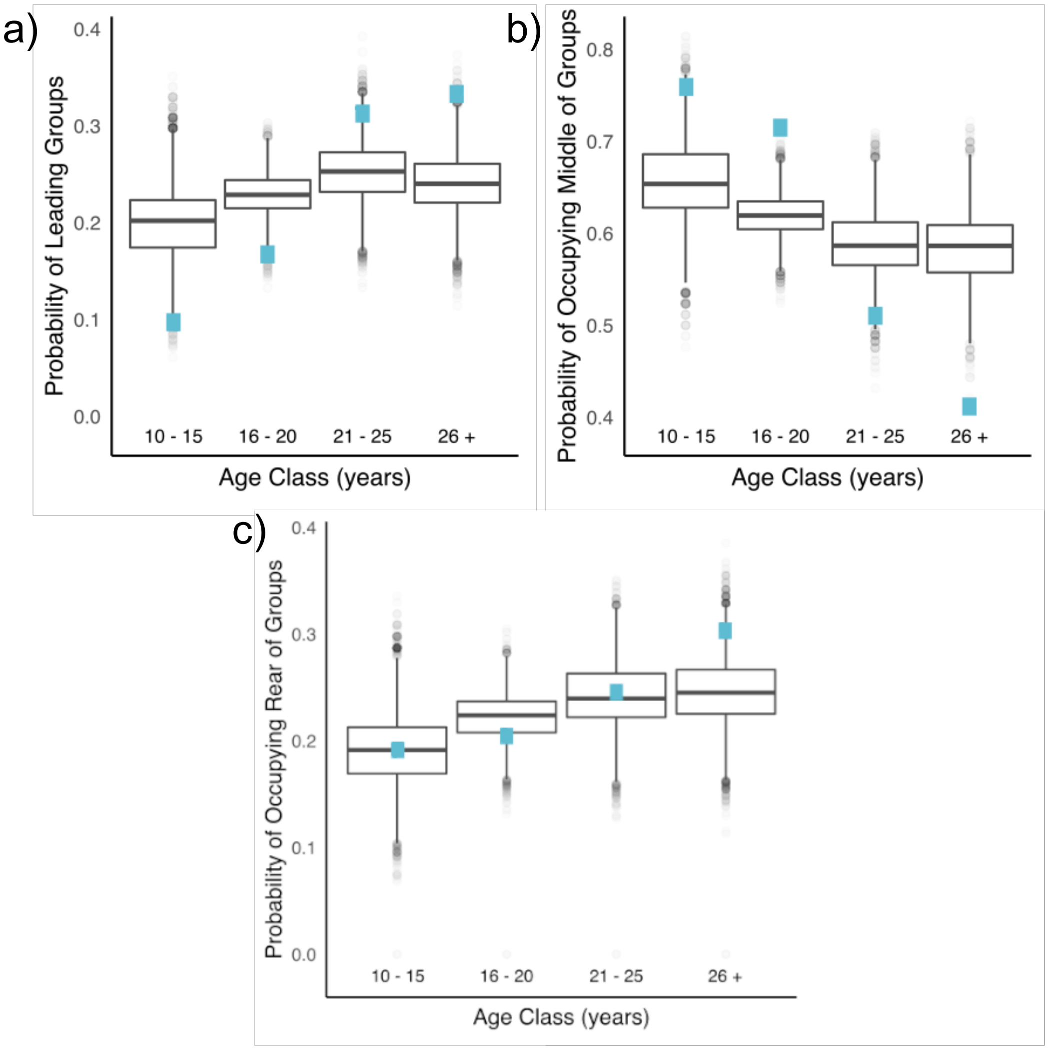

Figure 2.3: Observed probabilities of elephants occupying certain positions within all-male travelling groups. Blue squares represent observed probabilities of occupying a certain position, plotted against box plots (with median, interquartile range, minimum and maximum values) of randomly permuted probabilities of occupying certain positions. a) Older, mature males were more likely to lead groups than expected by chance, and had the greatest probability of being observed at the front of all-male travelling groups. Observed probability for ages: 10-15 years = 0.097, 95% CI random = (0.128-0.277), p = 0.004; 16-20 years = 0.167, 95% CI random = (0.187-0.270), p = 0.005; 21-25 years = 0.313, 95% CI random = (0.194-0.312), p = 0.045; 26+ years = 0.333, 95% CI random = (0.180-0.305), p = 0.004. b) Adult males were less likely to occupy the middle position in

all-male traveling groups, and adolescents more likely than expected by chance. Observed probability for ages: 10-15 years = 0.759, 95% CI random = (0.570-0.736), p = 0.012; 16-20 years = 0.715, 95% CI random = (0.577-0.663), p < 0.001; 21-25 years = 0.510, 95% CI random = (0.518-0.655), p = 0.028; 26+ years = 0.412, 95% CI random = (0.511-0.654), p < 0.001. c) Males of no age-class were more or less likely compared to chance to occupy the rear position in all-male traveling groups. All observed probabilities (blue squares) fell within range of randomly permuted probabilities of occupying the rear of groups (boxplots).

Distance of the group from the river did not differentially modify the tendency of any age class to hold the front (Permutation-based likelihood ratio test of GLMM, Age Class*Distance: χ2 (3)= 0.664, p= 0.645), middle (Permutation-based likelihood ratio test of GLMM, Age Class*Distance: χ2 (3)= 0.593, p= 0.591) or rear position of groups (Permutation-based likelihood ratio test of GLMM, Age Class*Distance: χ2 (3)= 0.417, p= 0.375) outside the range predicted by random chance.

Season did not differentially affect lone travel and leadership patterns of the age classes

There was no differential effect of season on tendency for males of different age classes to travel alone (Permutation-based likelihood ratio test GLMM, Age Class*Season: χ2 (3)= 0.382, p= 0.383), nor was there a differential effect of season on the tendency of different age classes to lead groups (Permutation-based likelihood ratio test of GLMM; Age Class*Season: χ2 (3)= 0.962, p= 0.965).

2.5 Discussion

Adolescents travelled alone on elephant pathways less than expected by chance, supporting our hypothesis that lone travel is riskier for younger, newly independent and less experienced individuals. In support of the hypothesis that mature adult bulls act as repositories for ecological knowledge, we found mature adult males were more likely to lead group movements, by occupying the front of all-male travelling groups. This age-related leadership pattern is consistent with findings in other species where older individuals have been shown to occupy leadership positions along migration routes, and during group-based foraging (whooping cranes, *Grus americana*, (Mueller et al., 2013); resident killer whales, *Orcinus orca*, (Brent et al., 2015)). Contrary to our prediction, leadership by mature adult bulls did not vary between the wet and dry season suggesting that adult bulls play a key role in leading all-male groups, regardless of season.

In addition to enhanced experience, other mechanisms could lead to the observed age structuring of leadership patterns in this study. For example, leadership patterns could emerge due to a gradient of differences in walking speeds of different age classes, with adults walking faster than adolescents due to their larger size (Pettit et al., 2015). However, despite smaller absolute stride lengths in younger elephants, young African elephants can move as efficiently and as fast as older adults (Hutchinson et al., 2006), and on the contrary, non-musth bulls have been shown to decrease their average walking speed with increasing age (Taylor et al., 2020). We found little evidence that size differences were driving our results. There was no observed size (age) gradient with position in groups, with neither the smallest nor largest bodied age class occupying the rear of groups more than chance.

Predation risk is also known to differ depending on the spatial position of individuals in groups with those at the periphery being more vulnerable to predation (King et al., 2012). Whilst a healthy adult bull has no natural predators, lions in Botswana's Savute region predate young adolescent elephants at a 50% success rate and tend to attack elephants from the rear (Joubert, 2006). Adolescents did not avoid vulnerable rear positions of processions in our study, suggesting that predation risk is not a major factor in determining the position of animals in these traveling groups. Furthermore, closer to the river, there is an increased threat of predation from lions (de Boer et al., 2010) and chance of human encounter (Figure 1.1) both of which have the potential to affect male mortality, with human activity being the leading cause of adult male mortality in many populations (Moss, 2001; Wittemyer et al., 2013; Jones et al., 2018). However, we found no effect of distance from the river on traveling positions, further suggesting that such mortality risks are not driving the observed leadership patterns.

Leadership patterns can also emerge in animal groups due to variation among individuals in motivational state (Conradt et al., 2009) with individuals most incentivised to change the environment or attain a goal often arising as leaders (e.g. food deprived fish leading shoals (Hoare et al., 1998), lactating zebra mares, *Equus burchellii*, leading groups to water (Fischhoff et al., 2007). Various studies suggest that smaller bodied adolescent elephants have greater drinking needs (Leggett, 2006), and require higher quality forage relative to older males

(Bell, 1982; Mramba et al., 2019); suggesting that younger adolescents should be the most motivated to travel at the front of groups in order to reach foraging and drinking locations connected by pathways. Such patterns were not observed in the current study, suggesting internal condition was not the key determinant of which individuals arose as leaders in groups.

As stated, in many species, it is common for older members of groups to be found at the front of groups processions, or to initiate group movements (Dumont et al., 2005; Berry & Bercovitch, 2014; Brent et al., 2015; Lee & Teichroeb, 2016; Tokuyama & Furuichi, 2017). In many cases, this leadership is argued to be linked with the dominance of older individuals asserting their will on subordinates (e.g. in gorillas, *Gorilla g. beringei* (Schaller, 1963), and mountain baboons*, Papio h. ursinus* (Byrne et al., 1990) top ranking males regulate their groups' movements). In male elephants too, dominance is linear with age, and older elephants have superior positions in the dominance hierarchy (Lee et al., 2011; O'Connell-Rodwell et al., 2011). However male elephant groups are high in fission-fusion dynamics, and group membership is not fixed in the same way as say primate groups, with males rarely spending more than 10% of their time with any one particular individual male (Archie & Chiyo, 2011). It is therefore unlikely that dominant males assert a despotic control over all-male group movements and decision making, as animals in conflict are free to break away from one another. Adolescent males following older males is more likely to represent a motivation to stay associated with a desired, high status individual perceived to have a better knowledge about the environment than themselves (Mutinda et al., 2011; McComb et al., 2011a,b; Lee & Moss, 2012), rather than older males asserting will on group members owing to greater dominance status. In African elephants in general, it is argued that qualities of “leadership” are more associated with how an individual is perceived and “respected” by conspecifics for their superior problem solving abilities, rather than on how well an individual is able to assert power over others (Lee & Moss, 2012).

Our finding that mature bulls held leading positions at the front of groups, and that no age class occupied the rear more than chance is in stark contrast to matriarchs in female family groups of African elephants, who have been observed to initiate group movements and indicate the direction of travel before retreating to the back positions of groups (Mutinda et al., 2011). This may point to the different motivations for group-travel and different leader-follower dynamics in all-male groups compared to family groups. Whilst male African elephants are “atomistic” in their community structure, with each individual male representing a unit that can choose to break off or join with other males based on current pressures and motivations; females in African elephant female groups are “molecular” (Aureli et al., 2008), with the smallest unit consisting of a tightly bonded stable family group, led by a matriarch, that can join and break off with other families in increasing levels of social organisation (Moss & Poole, 1983; Wittemyer et al., 2005). Whilst male elephants in all-male groups are flexible to break up or fuse based on immediate, individual needs, female family groups are principally held together by inclusive fitness and kin selection (Archie et al., 2005). A matriarch is therefore more likely to benefit from monitoring group members and their safety (Bates et al., 2008) compared to any individual male in an all-male group. If matriarchs benefit by actively maintaining their followers, traveling at the rear of groups where family members can be monitored, may be more effective than traveling at the front (Bates et al., 2008; Mutinda et al., 2011). In contrast, the leadership role of older male elephants' may be a far more passive process, and an example of the assignment and role of a "leader" being principally determined by the behaviour of followers (King, 2010); with older individuals making choices (based on enhanced experience and their own needs) and being tolerant to the active followers that target and trail behind them (King et al., 2009; Couzin et al., 2005). It is unlikely older males are highly concerned with maintaining contact with any younger males trailing behind them, as preferred, reoccurring associates are most often age-mates (Lee et al., 2011; Chiyo et al., 2011a). Similarly in giraffes, older dominant bulls are also thought to be targeted by younger males for their enhanced knowledge of habitat and resources (Bercovitch & Berry, 2014). These older males also tolerate younger male presence despite no obvious benefits for them in the association, as the cost of repeatedly driving away young males would be too great (Bercovitch & Berry, 2014).

Across their geographic range, mature bulls represent a minority in the population (Moss, 2001). Exacerbating this, older bull elephants are preferentially targeted in both illegal poaching and legal trophy hunting activity (Chiyo et al., 2015; Jones et al., 2018), because of their larger body size and increased trophy size (ivory tusks) with age (Hanks, 1972; Muposhi et al., 2016). Mostly only male elephants are targeted for trophy hunting, and operators often put minimum ages, corresponding with greater tusk weights, on targeted animals (DG Ecological Consulting, 2003; Pilgram & Western, 1986; De Villiers, 1994). Poaching, conflict with communities, and hunting activity are leading causes of mortality for mature bulls, and their numbers are declining at a rapid and arguably unsustainable rate (Wittemyer et al., 2013; Selier et al., 2014). Trophy hunting divides conservationists for its potential benefits and negative impacts (Lindsey et al., 2007; Selier et al., 2014). Supporters argue when a quota system for trophies is managed carefully following ecological theory, trophy hunting only removes a few older males with low reproductive value from a population, which should have a negligible effect on the wider environment (Baker, 1997; Hurt & Ravn, 2000). However, there is concern that this model fails to consider the mating and social system of the species of interest when applied to African elephants (Lee et al., 2011; Selier et al., 2014; Archie et al., 2008). Our finding that mature adult bulls act as leaders during all-male collective movements complements existing research that highlights the central role of mature bulls in all-male African elephant societies. For example, older bulls are most commonly targeted as nearest neighbours by males of all ages (Evans & Harris, 2008), and have a greater number of associates than younger males (Chiyo et al., 2011a). Removal of older mature bulls not only removes the prime breeders (the oldest individuals in the population sire the most offspring (Poole, 1987; Hollister-Smith et al., 2007; Poole et al., 2011)), but, as our study suggests, it also removes individuals with a central role in the male society, particularly in the context of their role in potentially leading younger naïve males between critical resources.

2.6 Conclusion

In this chapter, I showed how males of different life history stages have different probabilities of being observed travelling alone, compared to in all-male groups, in a sexually segregated area. Mature adults were more likely than chance to be observed travelling alone, and adolescents, less likely. The selective pressures on males during adolescence are likely more favouring of all-male grouping, with greater benefits e.g., increased predator protection (Joubert, 2006), better access to informed individuals (Evans & Harris, 2008), and lower costs, i.e., adolescent males are not competitive for mating opportunities until their mid-twenties, hence have a lower sexual competition with fellow males (Poole et al., 2011).

Within all-male groups, older individuals were more likely to be observed in front positions of all-male travelling groups on pathways connecting critical resources in the environment. I argue this is due to their enhanced ecological experience that comes with age, making these individuals desirable targets for younger males to follow. I did not provide any evidence that older males actively recruit and purposefully maintain followers in all-male groups, but rather I suggest they are tolerant to the needy, less informed followers that trail behind them. These results highlight the importance of older, experienced males outside of a mating context, and the potential roles they play as reservoirs of accumulated knowledge and experience to other males associating with them in all-male groups.

At the time of writing, Botswana had recently announced a decision to recommence elephant trophy hunting, and has been issued export quotas for tusks from trophies of 400 elephants by CITES for 2020 and 2021 (CITES, 2020; 2021). An article supporting a return to trophy hunting in Botswana, reported of an effective quota system that “is regulated such that only old male animals were killed” (Mbaiwa, 2017). I argue that such age-selective hunting would not be sustainable applied to African elephants, and removal of older mature bulls from the population could disrupt the wider bull society and potentially the inter-generational flow of information concerning decades of accumulated ecological knowledge, including on effective navigation and location of critical resources. I suggest mature bulls may occupy a similar social role in male elephant society as old female matriarchs do in female groups (McComb et al., 2001; 2011a) and may require equal protection.

Chapter 3: Reduced Older Male Presence is Associated with Increased Aggression to Non-elephant Targets, but not Conspecifics, in Male African Elephants

A peer reviewed, adapted version of this chapter is published in the journal Proceedings of the Royal Society B under the following details:

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Author contributions: CRBA conceived the study, conducted field work, data extraction, statistical analysis and was the lead author in drafting the manuscript. DPC and LJBN participated in study design, statistical analysis and critically revised the manuscript.

3.1 Abstract

Males in many large mammal species spend a considerable portion of their lives in all-male groups segregated from females. In long-lived species, these all-male groups may contain individuals of vastly different ages, providing the possibility that behaviours such as aggression vary with the age demographic of the social environment, as well as an individual's own age. Here, we explore social factors affecting aggression and fear behaviours in non-musth male African elephants (*Loxodonta africana*) aggregating in an all-male area. Adolescent males had greater probabilities of directing aggressive and fearful behaviours to non-elephant targets when alone compared to when with other males. All males, regardless of age, were less aggressive toward non-elephant targets, e.g., vehicles and non-elephant animals, when larger numbers of males from the oldest age cohort were present. Presence of older males did not influence the probability that other males were aggressive to conspecifics or expressed fearful behaviours toward non-elephant targets. Older bulls may police aggression directed toward non-elephant targets, or may lower other elephants' perception of their current threat level. Our results suggest male elephants may pose an enhanced threat to humans and livestock when adolescents are socially isolated, and when fewer older bulls are nearby.

3.2 Introduction

Since male fitness is mainly driven by the number of successful fertilisations (Trivers, 1972), aggression in males is typically viewed through the lens of sexual competition, with a focus on direct mate guarding (Schubert et al., 2009), defence of territory and resources to gain access to females (Sperry et al., 2010), or establishment of dominance hierarchies in order to monopolise mating (Clutton-Brock et al., 1979). However sexual segregation and bachelor groups occur in many large mammal species (Chiyo et al., 2014; Ruckstuhl & Neuhaus, 2002), providing potential for aggressive behaviours by males in the absence of females to directly contend for. Currently, we know comparatively little about the factors that influence aggressive behaviours in all-male groups. This represents an important gap in knowledge as many males spend the majority of their lives in such all-male groups. Additionally, in long-lived species with distinct life history stages (e.g. prolonged adolescent periods with higher investment in learning and development, and lower investment in reproductive activities (Evans & Harris, 2008)) the possibility arises that differences in the ages of males in all-male groups may influence the aggressive behaviours that are performed by members (Slotow et al., 2000; Slotow & van Dyk, 2001; Bourjade et al., 2009; Henry et al., 2012).

Male African savannah elephants (*Loxodonta africana*) dispersed from their natal herd spend most of their lives sexually segregated from females (Lee et al., 2011), with males spending 63% of their time in all-male groups, and 18% of their time alone (Chiyo et al., 2011a). The species is also one of the few non-predatory species whose aggressive behaviours can potentially serve an immediate lethal threat to humans and their livelihoods (DeMotts & Hoon, 2012; Dunham et al., 2010), and males are disproportionately involved in human-elephant conflicts compared to females (Von Gerhardt et al., 2014). Social disruptions during development in African elephants can lead to negative behavioural outcomes, including abnormal hyper-aggression (Bradshaw & Schore, 2007). Mature bulls appear to have a role in inhibiting musth (sexually active state in male elephants, characterised by high rates of aggression (Poole, 1987)) in younger males (Slotow et al., 2000; Slotow & van Dyk, 2001), suggesting both an individual's life history stage and the social environment can influence aggression in this species. Understanding the patterns of aggression in male elephants, including the nature and targets of this aggression, and how factors such as age and social context within all-male groups can influence these behaviours is therefore of paramount importance owing to its relevance to human safety and well-being.

Here, we quantify the agonistic behaviours of non-musth male African elephants in a male-dominated area under different social contexts. We first examined how social isolation was linked to elephants of different ages' expressing "flight or fight" (fear and aggression behaviours respectively) responses towards non-elephant targets. Whilst directing aggression to a perceived threat may be one reactive response for elephants under stress ("fight" response), they may also respond with more "flight" type fearful anti-predator responses, i.e., running away from the perceived threat (Von Holst, 1998; Stankowich & Blumstain, 2005; Bates et al., 2007). Male elephants form larger groups when in higher risk environments, for example when outside of protected areas (Chiyo et al., 2014). We therefore predicted, both due to their lack of previous experience in assessing and responding appropriately to real risk (Lee et al., 2011; Delville et al., 2005), as well as a greater genuine vulnerability (e,g, predation risk (Joubert, 2006), and dispersal risks in a novel environment (Alberts & Altmann, 1995)), that adolescents would be more likely to perform fear-related behaviours when alone compared to when in the company of other males. In contrast, being alone was not expected to represent as severe a threat for adults, who are more experienced and physically larger (Lee & Moss, 1995; Lee et al., 2011). We therefore predicted adult males that were socially isolated would express fear and aggression behaviours to non-elephant targets at equal rates to those in the company of other males.

Secondly, we tested if the number of males of different age classes present in the immediate environment was associated with performance of agonistic behaviours (both to conspecifics and non-elephant targets). Specifically, we hypothesised greater number of mature males in the immediate environment would reduce the expression of aggressive and fear behaviours in male elephants.

In a prominent case study of “delinquent” young male elephants in Pilanesberg National Park (South Africa), abnormal aggression and premature musth in young males was corrected once mature bulls were introduced to the population (Slotow et al., 2000; Slotow & van Dyk, 2001). This observation is reminiscent to the finding that dominant individuals act as policers of subordinates’ conflicts in primates (Flack et al., 2005a), and that lower adult-young ratios in horse groups leads to greater aggression in young horses due to adult regulation of young horse’s aggression behaviours (Bourjade et al., 2009). It is likely that aggression directed to conspecifics differs in function to the aggression directed to non-elephant targets and relates more to dominance hierarchy establishment and access to resources, as opposed to a reactive response to a perceived threat or irritant (Wingfield et al., 2005). We predicted there would be increases in aggression to conspecifics with reduced mature male presence, which may indicate disruptions to the linear dominance hierarchy (Slotow et al., 2000; Slotow & van Dyk, 2001; O'Connell-Rodwell et al., 2011), and/or a potential policing influence of mature males on younger male's conflicts (Flack et al., 2005a,b). Additionally, mature males may also police aggression behaviours to non-elephant targets as a behaviour that is also potentially detrimental to group cohesion (Flack et al., 2005a), and we also predict elephants will direct less aggression to non-elephant targets with increased mature male presence in the environment.

Alternatively, elephants may be more likely to direct aggression to non-elephant targets with decreased mature bull presence as they may perceive themselves to be at greater risk in the absence of experienced individuals in the environment (Bateson et al., 2011). Increases in elephants performing fear behaviours to non-elephant targets with decreased mature bull presence would also support this risk perception hypothesis. In horses, informed (often older) individuals appear to play an important role in transmitting information to group mates regarding safety, for example, naïve horses have reduced fear responses when paired with informed demonstrators (Christensen et al., 2008), and young foals weaned without adults express increased aggression and behavioural and physiological stress (Henry et al., 2012). An age structured effect on risk assessment has been in shown in female groups of African elephants, for example, where older matriarchs make better assessments about risk, which they communicate to group mates (McComb et al., 2011a). Such findings would highlight the need to investigate the social role of mature individuals in all-male groups, and would provide new insights to the importance of older individuals from a wildlife management perspective.

3.3 Methods

The study was conducted within, but at the border of Makgadikgadi Pans National Park (MPNP), Botswana (Figure 1.1), a bull area where 98% of elephant sightings are sexed as male (Evans, 2019). The region adjacent to the site of data collection has the highest reported rate of human-wildlife conflict in Botswana (Brooks & Bradley, 2010), with 71% of residents in Greater Khumaga interviewed stating that elephants threatened their safety (Mayberry, 2015). We conducted focal sampling of male African elephants aggregating at hotspots of elephant social activity along the Boteti River, which marks the border of the MPNP (See **1.6.5** for details regarding features of hotspots and general data collection methods). Hotspots were areas of river with easy access for elephants and were the terminal points of elephant pathways in the MPNP landscape (Figure 1.1).

Data collection

Individual subjects were filmed for the entirety of their stay within social hotspots, starting either as the subject arrived over the bank, or as he entered the hotspot having moved from another stretch of river up or downstream, and terminating when similar boundaries were crossed during departure. Elephants arrived at hotspots alone, or in coordinated all-male group processions (see **Chapter 2**).

However, following arrival, considerable mixing of males occurred from multiple arriving groups and original groupings became indiscriminate from the larger all-male aggregation. Males were categorised into 4 age classes, adolescents, 10-15 years & 16-20 years, and adults, 21-25 & 26+ years, based on body size, shoulder height (Lee & Moss, 1995), head size and shape, and tusk girth and splay (Hanks, 1972) (See **1.6.2**). The age class 26+ years represents an age where males are largely considered sexually and socially mature (Poole et al., 2011; Lee et al., 2011), begin experiencing regular annual musth periods, and achieving mating success (Hollister-Smith et al., 2007; Poole et al., 2011). The age class of focal subject to be recorded was randomly preselected, and the first elephant of the assigned age class to arrive at the hotspot since the start of the session was the subject of a focal animal sample (elephants were aged in the field, if the arrival group had multiple individuals from the preselected age class, the focal was selected at random from the choice). Recordings of visits to hotspots were taken from focal individuals only once over the study period. Individuals were identified by distinguishing features (outlined in **1.6.2**).

Subjects of focal animal samples were filmed using a video cam-corder (JVC quad proof AVCHD) fixed to a tripod, with the subject kept central to the frame, but zoomed out enough to allow for potential interactors to be captured. The research vehicle was parked at a safe distance (minimum 50m) from points expected to receive elephants (pathway arrival points, popular drinking points, mudholes). Non-musth males in the MPNP are largely relaxed around vehicles, and if the engine was off for the entire focal session, it was common for elephants to not look in the direction of the human observer (**Supplementary Information 2**, Note S2.1 for methods for addressing vehicle presence in the study).

Focals could stay at social hotspots for several hours (average time spent at hotspot for focal elephants seen arriving and leaving via bank = 1h 13min, range= 9min – 7h 5min, SD= 59min), over which time, the males present at aggregations with focals could be highly dynamic. No existing research protocols provide a reference for an appropriate break point between successive samples that would give a suitable resolution of the changing social environment at social aggregations of male elephants, so time windows of focal follows and the associated social context within that follow was determined based on personal expertise. Since individuals arriving in all-male groups tend to arrive within 10 minutes of one another (Figure 2.1), focal follows were subdivided into 10-minute follows (e.g., a focal follow of an elephant staying 40 minutes at the hotspot, would produce four 10-minute focal follows), to which a corresponding social context was assigned (see below), in order to capture the temporally dynamic nature of male aggregations at the hotspots.

In 15 10-minute follows (from 6 individuals), females were also present at the hotspot. Presence of females was rare in this bull area, so it is possible this could impact on aggressive interactions between males. Presence of females did not predict the expression of any behaviours of interest by males in the study (**Supplementary Information 2;** Table S2.1). Nevertheless, to be conservative, the 15 focal samples where females were present were excluded from our analyses. Additionally, 52 focal animal samples (from 10 individuals), were collected on elephants in musth. Due to the established consensus that bulls act differently in musth state, with greater aggression to same-sex conspecifics (Poole, 1989a), we excluded musth bull focals from our data set. The supplementary materials (**Supplementary Information 2**; Figure S2.1) provide a comparison of aggressive behaviours of musth compared to non-musth males in this study. Finally, if a subject was out of view for over 2 minutes within a follow, i.e. over 20% of time, the 10-minute focal follow was excluded from analysis (N 10-min follows excluded= 201). For 126 10-minute focal follows the focal elephant was out of view for 00.01 – 01:59 minutes, however, for most cases (N 10-min focal follows =1401) the subject was in view for the full 10 minutes. This gave an overall final sample size of 1527 10-minute focal follows, from 281 different individual elephants (range 10-minute focal follows per individual = 1-24, mean = 5.676).

Scoring of behaviours

Focal follow videos were scored by one researcher (CA) to standardise scoring of behaviours, with each follow observed for behaviours 3 times. Behaviours of interest (aggression directed to conspecific, aggression to non-elephant target, fear to non-elephant target) were scored as number of events per 10-minute focal follow (Tables 3.1 – 3.3).

Table 3.1: Behaviours recorded as events of “conspecific aggression” directed by focal elephants. Over the accumulative approximate 273 hours of focal follow observation only 6 events of escalated aggression were observed in the form of “charges” (no observations of parallel walk, ramming, duelling (Poole & Granli, 2011)). Due to this low occurrence, escalated aggression was included together with all conspecific aggression, alongside more subtle dominance and threat displays between males. Elephant behaviours compiled from the work of Poole & Granli (2011; 2021) and Estes (2004) as well as our own observations:

Behaviour	Description
Spreading ears	Ears spread out perpendicular to body in direction of opponent, from the front view the elephant appears larger
Head high	Head held above shoulders, with chin tucked in
Folding ears	Pressing lower portion of ears towards body, leading to a distinct ridge to appear across ear
Standing tall	Head held above shoulders, tusks raised, often looking down towards opponent
Throw trunk toward	Swinging trunk in direction of opponent
Head jerk	Rapid upward movement of the head towards opponent
Head shake	Twisting of head to one side, followed by rapid shake/ rotation of head from side to side, with the contact of ears to neck skin causing a load slap. Recorded as threat to conspecific when the performers focus was orientated toward another elephant prior or latter to performing the behaviour
Turn toward	Orienting body in the direction of opponent (combined with other aggression behaviours that indicate behavioural context is hostile intent)
Advance toward	Purposed walking toward opponent (combined with other aggression behaviours that indicate behavioural context is hostile intent)
Pursuit	Aggressively following or chasing an opponent. Often following after another agonistic interaction – the victor pursues the defeated elephant

Charge	Running toward opponent (combined with spread ears and raised head), may stop abruptly (mock charge) or follow through to physical contact with opponent, tusks first (real charge)
Pushing	Physically pushing another elephant off a resource (e.g. mudhole) or out of a desired location (e.g. point where conspecific is drinking), typically with the head, outside context of play
Tusking	More aggressive form of pushing, the tusks are used to poke another elephant off a resource or desired location, outside context of play
It was rare that the behaviours listed above were performed in isolation, many behaviours were often used in combination or routine succession from one another, E.g. elephants may (1) advance toward a conspecific, with (2) head held high and (3) ears spread. In the case where multiple behaviours were recruited in the overall aggressive act, the event was still only recorded as 1 event, for example the example given above would be 1 event. A new aggressive event was only recorded if between there had been a cessation of previous aggressive behaviours (e.g., advance towards halted, and ears returned to relaxed posture), or there was a drastic change in intensity of the aggressive act. For example, an elephant performing “standing tall” posture in the direction of an opponent, transitioning to a sudden charge would be recorded as 2 events. Most aggressive acts were however short, distinct and easy to quantify as individual events, with elephants quickly returning to a relaxed state following temporary conflict.	

Table 3.2: Behaviours recorded as events of “aggression to non-elephant targets” directed by focal elephants. Targets of non-elephant aggression included other species (e.g. ungulates, carnivores, reptiles and birds), vegetation and tourist vehicles, but in most cases the target of the aggressive behaviour was unidentifiable (**Supplementary Information 2**; Figure 2.2). Over the accumulative approximate 273 hours of focal follow observation most aggression

to non-elephant targets was of a display nature, physical contact with the target was only observed in a few instances of bush-bashing behaviour. Elephant behaviours compiled from the work of Poole & Granli (2011; 2021) and Estes (2004) as well as own observations:

Behaviour	**Description**
Head high	Head held above shoulders, with chin tucked in
Spreading ears	Ears spread out perpendicular to body in direction of threat or irritant
Folding ears	Pressing lower portion of ears towards body, leading to a distinct ridge to appear across ear
Standing tall	Head held above shoulders, tusks raised, often looking down towards threat or irritant
Throwing trunk toward	Swinging trunk in direction of irritant or threat, may be combined with throwing of objects and debris
Head jerk	Rapid upward movement of the head towards threat or irritant
Head shake	Twisting of head to one side, followed by rapid shake/ rotation of head from side to side, with the contact of ears to neck skin causing a load slap. Most typical of the recorded aggression directed at “unknown” target, whilst suggested to be a behaviour performed out of elephant experiencing annoyance or irritation over current situation, headshakes were often performed towards no obvious threatening target or irritant
Mock charge	Running toward threat or irritant, combined with spread ears and raised head, halting abruptly ahead of making physical contact
Turn toward	Orienting body in the direction of threat or irritant (combined with other aggression behaviours that indicate behavioural context is hostile intent)

Advance toward	Purposed walking toward threat or irritant (combined with other aggression behaviours that indicate behavioural context is hostile intent)
Pursuit	Aggressively following or chasing a threat or irritant
Tusking vegetation/ Bush-bashing	Violent thrashing of vegetation with head and tusks in non-playful context
See Table 3.1 for details on how individual events recorded, as individual aggression events typically employ a combination of listed behaviours performed together.	

Table 3.3: Behaviours recorded as events of “fear to non-elephant targets” directed by focal elephants. Targets of (or rather, the triggers of) these defensive and fearful behaviours included other species (e.g. ungulates, carnivores, reptiles and birds) and tourist vehicles, but in most cases the triggers of these behaviours were unidentifiable (**Supplementary Information 2**; Figure S2.2). Elephant behaviours compiled from the work of Poole & Granli (2011; 2021) and Estes (2004) as well as own observations:

Behaviour	**Description**
Tail raised	Holding tail erect, typically to horizontal position, may wrap to one side around the body
Flattening ears	Ears flattened against the body
Jaw tilted upward	Lifted jaw posture, with ears slightly spread. When combined with moving away from threat, elephant may look back over shoulder to threat
Turn away	Rapid turning away from perceived threat (combined with other fear behaviours that indicate behavioural context is fearful)

Backing away/ retreat	Moving away from perceived threat (combined with other fear behaviours that indicate behavioural context is fearful)
Running away	Fleeing from perceived threat with fast pace
As with aggressive behaviours, it was rare that the behaviours listed above were performed in isolation, often many of the behaviours listed were performed in combination or in succession from one another and treated as one event for analysis. A new fearful event was only recorded if there had been a cessation of previous fearful behaviours (e.g. retreat halted, and body returned to relaxed posture), or there was a drastic change in intensity of the fearful behaviour. For example, an elephant backing from a non-elephant threat with ears held flat and head low, transitioning to running away with tail raised would be recorded as 2 events. We excluded apprehensive behaviours discussed in the literature (Poole & Granli, 2011), such as displacement feeding, displacement grooming, touching face etc. due to ambiguity in quantifying these behaviours.	

Social Context

During field observations, data were collected on the number of, and ages of, all other elephants present at the hotspot with the subject elephant, such that for every 10-minute focal follow there was a corresponding recording of all ages observed as present with the focal within that time window (Figure 1.6). The social context at social hotspot was unknown to researcher scoring behaviours from videos and was only matched to corresponding focals subsequent to all videos being coded for behaviours.

Statistical Analyses

For our analyses we ran generalized logistic mixed-effects models (GLMMs) in R. Within each 10-minute focal follow, each of the 3 behaviours of interest (Tables 3.1-3.3) were transformed to a binary 1/0 (present/absent) term due to a considerable right skew in the data set. Due to a small sample size for 10-15 year old focals sighted alone (eight 10-min focal follows), we merged age classes of focal elephants into the categories “adult” (21+ years; N=846 10-min focal follows from 147 individuals) and “adolescent” (10-20 years; N=681 10-min focal follows from 134 individuals) to test the effect of social context on the behaviours of subjects.

Firstly, we explored if social isolation was related to elephants’ (i) expression of aggressive behaviours to non-elephant targets, and (ii) expression of fear behaviours to non-elephant targets. For these GLMM’s, each behaviour (dependent variables) was modelled in relation to season, hotspot location, age category (adult or adolescent), social isolation condition (where 1 represented a subject being alone at a hotspot, and 0 represented other elephants being present with the subject), and the interaction between age category and social isolation condition (whereby reference class of age category was switched to explore the influence of social isolation on the aggression and fear behaviours for adolescent and adult bulls separately). Elephant ID was included as a random effect in both models.

Secondly, we investigated if the number of mature bulls (26+ years) at the hotspot was related to the probability that a subject directed aggressive behaviours at (i) conspecific targets and (ii) non-elephant targets, and (iii) fear behaviours at non-elephant targets. For these models, only males observed with other elephants at the hotspot were included (lone subjects were excluded). We fit GLMMs predicting each behaviour (dependent variable) by focal age category (adult or adolescent), season, hotspot location and number of each age class present during the 10-minute focal follow (i.e. number of each age class 10-15, 16-20, 21-25 and 26+ years were included as separate predicting variables). This allowed us to compare whether the number of other age classes present also influenced behaviours. In cases where the expression of a behaviour was only predicted by number of mature bulls and not the presence of individuals from other age classes, we re-ran this analysis to include interaction terms between focal age category and number of mature bulls, to test if the number of mature bulls in the environment had a different effect on adolescents compared to adults. All non-significant fixed effects from the initial model were excluded in this second interaction model. Elephant ID was again included as a random effect in all models.

In all the above analyses, we also included a fixed effect of whether this type of behaviour had also been performed in the preceding 10-minute follow to control for the potential influence of temporal autocorrelation (**Supplementary Information 2**; Note S2.2). We also included season in all our GLMMs because availability of resources, and potentially body condition, are linked to season (Pitfield, 2017) which may influence elephants' tolerance in sharing limited resources, or influence linear dominance hierarchies (O'Connell-Rodwell et al., 2011) (See **1.6.3** for season determination methods). Furthermore, focal observations conducted in the wet season had higher numbers of other elephants present at the hotspot compared to the dry season (Figure 1.6) and we wanted to account for this seasonal difference in aggregation sizes. Lastly, season also represented the best indicator of numbers of other species (potential targets of behaviours) sharing the hotspot resource with elephants, with some 20,000 zebra and wildebeest frequenting the Boteti River over the dry season, but absent in the wet season (Kgathi & Kalikawe, 1993). As a control, hotspot location was also included as a fixed effect in all models, since the 5 hotspot locations differed in factors such as proximity to human-dominated landscapes and tourist presence, which may influence behaviours.

3.4 Results

Adolescents performed more fear and aggression behaviours when socially isolated, compared to when with other males

Social isolation significantly predicted the likelihood of adolescents, but not adults, performing both aggression and fear-based behaviours to non-elephant targets, with adolescent males more likely to perform both these behaviours when alone compared to when observed with other elephants (Figure 3.1; Adjusted odds ratio (aOR) for directing fear behaviours to non-elephant targets when alone compared to with other elephants: adolescents= 2.775, p= 0.013; adults= 1.206, p= 0.736. aOR for directing aggression behaviours to non-elephant targets when alone compared to with other elephants: adolescents= 2.624, p= 0.021; adults= 1.387, p= 0.400; Tables 3.4 & 3.5 for full outputs of GLMMs including 95% confidence intervals).

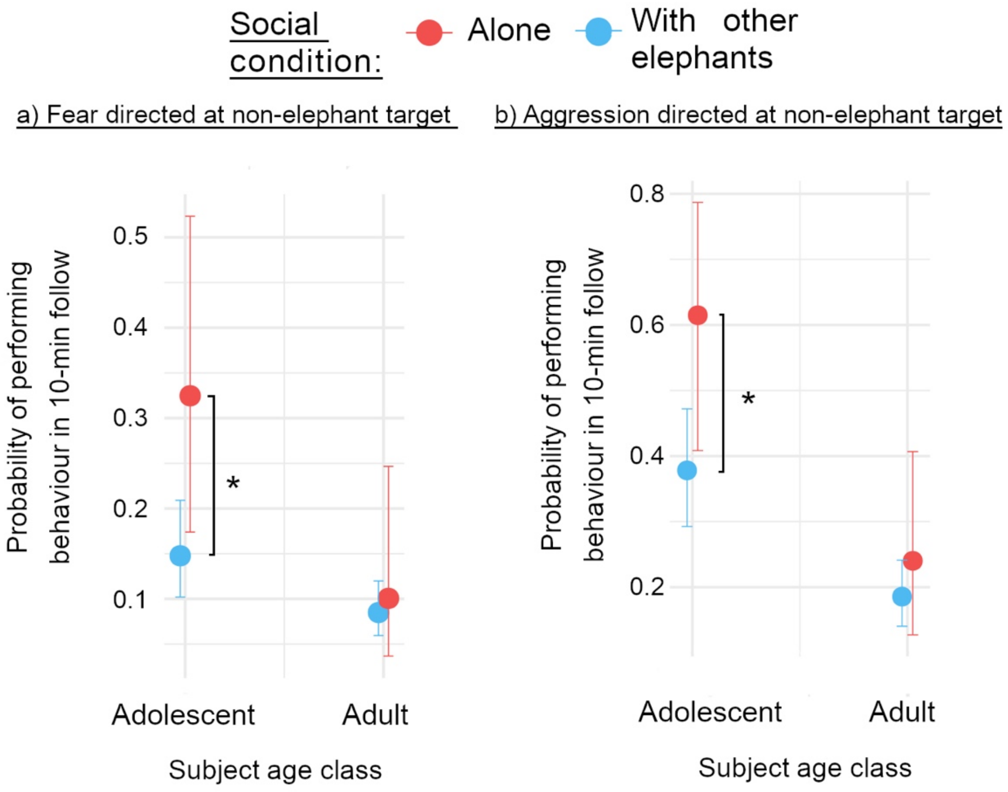

Figure 3.1: Probabilities of male elephants performing fear and aggression behaviours to non-elephant targets when alone vs. with other male elephants at social hotspots. a) Being alone significantly predicted the likelihood of adolescents performing fear behaviours to non-elephant targets, but not adult elephants (Table 3.4 for full output of GLMM). b) Being alone significantly predicted the likelihood of adolescents performing aggression behaviours to non-elephant targets, but not adult elephants (Table 3.5 for full output of GLMM). Significant regression coefficients indicated with (*), 95% confidence intervals indicated.

Table 3.4: Output of GLMM: focal age category, season, hotspot location, previously directed fear, social isolation, and interaction between focal age category and social isolation conditions' effect on likelihood of elephant subject directing fear behaviours to non-elephant targets during a 10-min focal follow.

Focal ID included as random effect. Reference class of age category switched to obtain effect of social condition on adolescents and adults.

Dependent variable: Fear directed at non-elephant target **Reference Class - Adolescent**				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-1.753	0.173 (0.113-0.264)	**<0.001**
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.625	0.535 (0.350-0.819)	**0.004**
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	1.021	2.775 (1.236-6.230)	**0.013**
Season	Dry	*Ref*	*Ref*	
	Wet	-0.434	0.648 (0.408-1.027)	0.065
Hotspot location	1	*Ref*	*Ref*	
	2	-0.395	0.674 (0.413-1.097)	0.113
	3	-0.353	0.703 (0.224-2.203)	0.545
	4	-0.272	0.762 (0.404-1.436)	0.400
	5	-0.282	0.754 (0.250-3.799)	0.616
Fear to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.857	2.357 (1.462-3.799)	**0.004**
Social Condition* Age category	Adult*Alone	-0.834	0.434 (0.112-1.676)	0.226
Reference Class – Adult				
Intercept		-2.378	0.093 (0.063-0.136)	**<0.001**
Age category	Adolescent	0.625	1.868 (1.221-2.857)	**0.004**
	Adult	*Ref*	*Ref*	
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	0.187	1.206 (0.407-3.570)	0.736
Season	Dry	*Ref*	*Ref*	
	Wet	-0.434	0.648 (0.408-1.027)	0.065

Hotspot location	1	*Ref*	*Ref*	
	2	-0.395	0.674 (0.413-1.097)	0.113
	3	-0.353	0.703 (0.224-2.203)	0.545
	4	-0.272	0.762 (0.404-1.436)	0.400
	5	-0.282	0.754 (0.250-3.799)	0.616
Fear to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.857	2.357 (1.462-3.799)	**0.004**
Social Condition* Age category	Adolescent *Alone	0.834	2.302 (0.597-8.880)	0.226

Table 3.5: Output of GLMM – focal age category, season, hotspot location, previously directed aggression, social isolation, and interaction between focal age category and social isolation conditions' effect on likelihood of elephant subject directing aggression behaviours to non-elephant targets during a 10-min focal follow. Focal ID included as random effect. Reference class of age category switched to obtain effect of social condition on adolescents and adults.

Dependent variable: Aggression directed at non-elephant target **Reference Class – Adolescent**				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-0.498	0.608 (0.414-0.894)	**0.011**
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.982	0.375 (0.265-0.530)	**<0.001**
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	0.965	2.624 (1.157-5.955)	**0.021**
Season	Dry	*Ref*	*Ref*	
	Wet	0.122	1.130 (0.777-1.643)	0.523
Hotspot location	1	*Ref*	*Ref*	
	2	-0.194	0.824 (0.550-1.235)	0.348

	3	-0.127	0.880 (0.352-2.202)	0.786
	4	-0.383	0.682 (0.408-1.138)	0.143
	5	0.372	1.450 (0.634-3.316)	0.379
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.627	1.871 (1.405-2.492)	**<0.001**
Social Condition* Age category	Adult*Alone	-0.638	0.529 (0.173-1.617)	0.264
Reference Class – Adult				
Intercept		-1.479	0.228 (0.163-0.318)	**<0.001**
Age category	Adolescent	0.982	2.669 (1.886-3.776)	**<0.001**
	Adult	*Ref*	*Ref*	
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	0.327	1.387 (0.647-2.974)	0.400
Season	Dry	*Ref*	*Ref*	
	Wet	0.122	1.130 (0.777-1.643)	0.523
Hotspot location	1	*Ref*	*Ref*	
	2	-0.194	0.824 (0.550-1.235)	0.348
	3	-0.127	0.880 (0.352-2.202)	0.786
	4	-0.383	0.682 (0.408-1.138)	0.143
	5	0.372	1.450 (0.634-3.316)	0.379
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.627	1.871 (1.405-2.492)	**<0.001**
Social Condition* Age category	Adolescent *Alone	0.638	1.892 (0.619-5.787)	0.264

Males were less likely to direct aggression to non-elephant targets, with increased older male presence at male aggregations

Excluding subjects alone at hotspots, 10-minute focal follows had on average 2.85 (SD=3.98, Max=22) 10-15 year olds, 4.22 (SD=4.88, Max=28) 16-20 year olds, 2.15 (SD=2.44, Max=21) 21-25 year olds and 1.04 (SD=1.48, Max=10) 26+ year olds present with the focal subject. However, there were differences between adolescent and adult subjects concerning the mean number of other age classes present with them. Adolescent subjects had more 10-15 year olds present with them at hotspots than adult subjects did, and adult subjects had more elephants aged 16-20, 21-25 and 26+ years present with them at hotspots than adolescent subjects did (Table 3.6).

Table 3.6: Means and standard deviations of the number of each age class present at hotspots with adult and adolescent focal elephants (excludes elephants sighted alone). The mean number of other elephants of each age class present during focal follows significantly differed between adolescent and adult subjects (Wilcoxon rank sum tests with continuity correction; Mean N of 10-15 years males present at hotspot with focal: W= 252610, p<0.001; Mean N of 16-20 years males present at hotspot with focal: W=195972, p<0.001; Mean N of 21-25 years males present at hotspot with focal: W=182296, p<0.001; Mean N of 26+ years males present at hotspot with focal: W=175750, p<0.001).

Age category of subject	**Mean (Standard deviation) number of other age classes of male elephants at hotspot with focal**			
	10-15 years	**16-20 years**	**21-25 years**	**26 + years**
Adolescent (10-20 years)	3.50 (4.47)	4.12 (4.88)	2.00 (2.47)	0.850 (1.43)
Adult (21+ years)	2.29 (3.41)	4.32 (4.87)	2.30 (2.40)	1.21 (1.51)

Adults were more likely to direct aggression to conspecifics compared to adolescents (aOR adult compared to adolescent= 1.686, p=0.014; Table 3.7). The number of elephants of each age class present at a hotspot did not predict the likelihood of subjects directing aggression to conspecifics (Table 3.7).

Table 3.7: Output of GLMM: focal age category, season, hotspot location, previous aggression directed and number of elephants of each class present at hotspot with focals' effect on likelihood of focal subject directing aggression to conspecific target. Focal ID included as random effect.

Dependent variable: Aggression directed at conspecific				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-2.029	0.131 (0.077-0.224)	**<0.001**
Age category	Adolescent	*Ref*	*Ref*	
	Adult	0.522	1.686 (1.113-2.555)	**0.014**
Season	Dry	*Ref*	*Ref*	
	Wet	0.048	1.049 (0.667-1.648)	0.836
Hotspot location	1	*Ref*	*Ref*	
	2	-0.341	0.711 (0.428-1.183)	0.190
	3	0.137	1.147 (0.391-3.362)	0.803
	4	-0.513	0.599 (0.310-1.157)	0.127
	5	0.809	2.245 (1.235-2.733)	0.060
Aggression to conspecific target in 10-minute follow previous (control for temporal autocorrelation)		0.608	1.837 (1.235-2.733)	**0.003**
Number 10-15 year olds present		0.059	1.061 (0.983-1.146)	0.131
Number 16-20 year olds present		-0.026	0.975 (0.901-1.054)	0.516
Number 21-25 year olds present		0.021	1.021 (0.904-1.153)	0.736
Number 26+ years present		-0.103	0.902 (0.764-1.064)	0.222

Adults were less likely to direct fear behaviours to non-elephant targets compared to adolescents (aOR adult compared to adolescent= 0.556, p=0.016; Table 3.8). Only the number of 10-15 year olds present at a hotspot predicted the likelihood of subjects directing fear behaviours to non-elephant targets, with elephants directing more fear to non-elephant targets when greater number of 10-15 year olds were present (Regression coefficient: 0.113, p=0.015; Table 3.8).

Table 3.8: Output of GLMM: focal age category, season, hotspot location, previous fear directed and number of elephants of each class present at hotspot with focals' effect on likelihood of focal subject directing fear to non-elephant target. Focal ID included as random effect.

Dependent variable: Fear directed at non-elephant target				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-1.575	0.207 (0.116-0.369)	**<0.001**
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.586	0.556 (0.345-0.897)	**0.016**
Season	Dry	*Ref*	*Ref*	
	Wet	-0.303	0.739 (0.436-1.251)	0.260
Hotspot location	1	*Ref*	*Ref*	
	2	-0.406	0.667 (0.370-1.202)	0.178
	3	-0.362	0.696 (0.184-2.639)	0.595
	4	-0.155	0.856 (0.424-1.732)	0.666
	5	0.001	1.001 (0.311-3.221)	0.998
Fear to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.327	1.387 (0.774-2.486)	0.272
Number 10-15 year olds present		0.113	1.120 (1.023-1.226)	**0.015**
Number 16-20 year olds present		-0.082	0.922 (0.831-1.022)	0.123

Number 21-25 year olds present	-0.127	0.881 (0.735-1.056)	0.171
Number 26+ years present	0.050	1.051 (0.874-1.265)	0.595

The number of 26+ year olds present at a hotspot did predict the probability of a subject directing aggression to non-elephant targets. As the numbers of mature bulls present increased, the likelihood of subjects directing aggression to non-elephant targets decreased (Regression coefficient: -0.242, p =0.001; Figure 3.2). No relationship was found between the likelihood of a subject directing aggression to non-elephant targets and the number of elephants present of all the other age classes (Table 3.9). Adults were less likely to direct aggression to non-elephant targets than adolescents (aOR adult compared to adolescent= 0.378, p <0.001; Table 3.9), but there was no interaction between age category of the subject and the number of 26+ year olds present at a hotspot in predicting the likelihood of the subject directing aggression to non-elephant targets (Table 3.10). That is, when greater numbers of mature bulls were present, the probability of males of any age acting aggressively to non-elephant targets decreased.

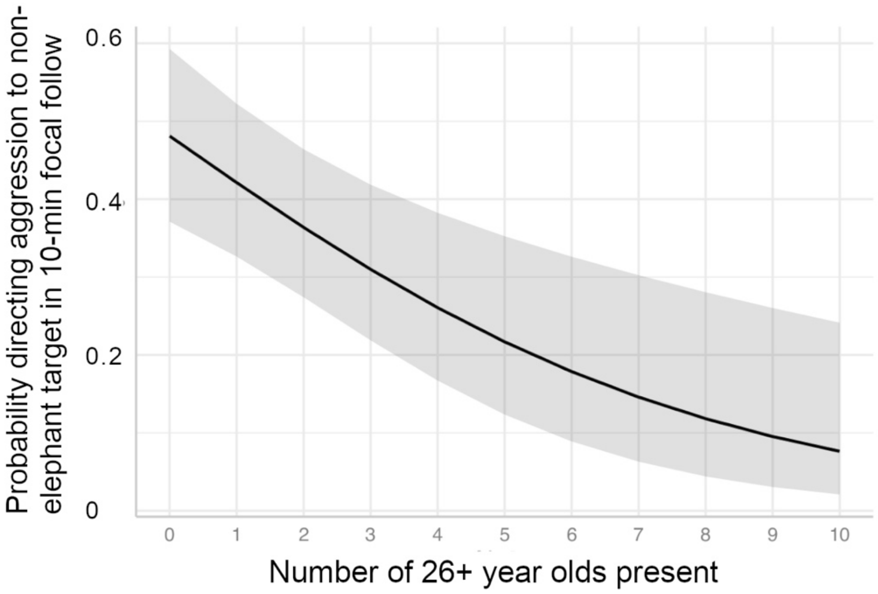

Figure 3.2: Elephants were less likely to direct aggression to non-elephant targets with greater numbers of 26+ year olds present at social hotspots. Grey area represents 95% confidence intervals based on standard errors (Table 3.9 for output of GLMM).

Table 3.9: Output of GLMM: focal age category, season, hotspot location, previous aggression directed and number of elephants of each class present at hotspot with focals' effect on likelihood of focal subject directing aggression to non-elephant target. Focal ID included as random effect.

Dependent variable: Aggression directed at non-elephant targets.				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-0.142	0.868 (0.542-1.389)	0.554
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.972	0.378 (0.263-0.544)	**<0.001**
Season	Dry	*Ref*	*Ref*	
	Wet	-0.000	1.000 (0.671-1.490)	0.999
Hotspot location	1	*Ref*	*Ref*	
	2	-0.401	0.670 (0.431-1.041)	0.075
	3	-0.232	0.793 (0.297-2.116)	0.643
	4	-0.559	0.572 (0.331-2.116)	**0.045**
	5	0.016	1.017 (0.422-2.448)	0.971

Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)	0.631	1.879 (1.382-2.555)	**<0.001**
Number 10-15 year olds present	-0.029	0.971 (0.906-1.041)	0.409
Number 16-20 year olds present	-0.007	0.993 (0.925-1.067)	0.852
Number 21-25 year olds present	-0.081	1.084 (0.970-1.211)	0.154
Number 26+ years present	-0.242	0.785 (0.677-0.911)	**0.001**

Table 3.10: Output of GLMM: hotspot location, previous aggression directed, focal age category and number of 26+ year olds present at hotspot with focals, and interaction between the latter two predictors' effect on likelihood of focal subject directing aggression to a non-elephant target. Focal ID included as random effect.

Dependent variable: Aggression directed at non-elephant target				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-0.163	0.850 (0.584-1.237)	0.396
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.950	0.387 (0.255-0.585)	**<0.001**
Number 26+ years present		-2.080	0.812 (0.685-0.963)	**0.017**
Age category* Number 26+ years present		0.035	1.035 (0.816-1.314)	0.775
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.639	1.894 (1.393-2.574)	**<0.001**
Hotspot location	1	*Ref*	*Ref*	
	2	-0.370	0.691 (0.461-1.035)	0.073
	3	-0.185	0.831 (0.322-2.144)	0.702
	4	-0.503	0.605 (0.356-1.027)	0.063
	5	0.025	1.025 (0.441-2.385)	0.953

Season had no influence on the probability of an elephant directing aggression to either conspecific targets (Table 3.7) or non-elephant targets (Tables 3.5 & 3.9), nor on probability of directing fear behaviours to non-elephant targets (Tables 3.4 & 3.8). Hotspot location did not predict likelihood of behaviours being performed in any of our models, apart from in the main effects model predicting aggression directed to non-elephant targets by numbers of each age class present, whereby aggression was more likely to be performed at hotspot 1 compared to hotspot 4 (Table 3.9). In all models, performance of behaviours in a 10-min follow were also predicted by whether that type of behaviour had also been performed in the 10-min follow immediately previous, apart from the model predicting fear directed to non-elephant targets by numbers of each age class present (Table 3.4-3.10).

3.5 Discussion

When alone, adolescents were more likely to perform aggression and fear behaviours to non-elephant targets compared to when with other males at hotspots, and overall, adolescent male elephants were more likely to direct aggression and fear behaviours to non-elephant targets than adult males. These “fight or flight” type responses to non-elephant targets may be a reflection of the physiological and psychological state of elephants, driven by their perception of their current risk and threat level (Wingfield et al., 2005; Bateson et al., 2011). Aside from human threats, adult bulls have no other natural predators (Wittemyer et al., 2013). Adult elephants may be less fearful in the exposed habitat of the riverbed hotspot environment that they may have frequented multiple times over their lifetime and thus have a greater level of familiarity with (Lee et al., 2011).

Adolescents, on the other hand, are still vulnerable to a real threat of predation from lions (Joubert, 2006). Adolescents are also more likely to be recently dispersed from their natal herd and may be more sensitive to perceive the potentially novel, unknown environment as risky (Alberts & Altmann, 1995; Lee et al., 2011; Boonstra, 2012; Srinivasaiah et al., 2019). Less experienced adolescents may also perceive the social hotspots as dangerous due to their close proximity to human settlements, to which they are not yet habituated (the hotspots mark the boundary of a protected area and a human-dominated landscape (Evans, 2019)) (Tingvold et al., 2013). Indeed, elephants are very sensitive to human scent (Bates et al., 2007), and adolescents may additionally be less habituated to tourist presence, hence more likely to perform self-defence type fight-or-flight behaviours in the national park (Wingfield et al., 2005; Szott et al., 2019). Animals adjust vigilance rates in response to group size and respond with flexible heightened anti-predator and flight behaviour when they perceive human or predatory threats (Creel et al., 2014; Zanette & Clinchy, 2020). When socially isolated, the real and perceived risks described are likely exacerbated (e.g. individual risk of predation is greater (Joubert, 2006)) and younger males may experience a further lowered threshold of risk perception (Wingfield et al., 2005; Srinivasaiah et al., 2019; Zanette & Clinchy, 2020), demonstrated by their increases in fear and aggression behaviours to non-elephant targets. In contrast, the behaviour of adult males did not appear to be influenced by social isolation, suggesting that physically larger, and more socially experienced adults do not experience a change to their real or perceived threat level when alone (Boonstra, 2012).

In many species that experience an adolescent life history stage, where individuals are not fully socially mature, hormones in the adolescent's physiology can drive exploratory tendencies, novelty seeking and motivation for risk-taking behaviours that could be more likely to put the individual in dangerous situations (Laviola et al., 2003; Peper & Dahl, 2013). This highlights a potential dilemma of cause and effect in our findings. It may not be possible to discern whether adolescents are more prone to social context influencing their behaviour compared to adults (i.e. their increased sensitivity in performing more agonistic behaviours to non-elephant targets when alone), or alternatively whether adolescents with temporary hormonal and aggressive "surges" separate themselves and choose to be alone, or are excluded from groups owing to their disruptive hyper-aggressive and fearful behaviours. Furthermore, the observed lack of variation in adult agonistic behaviours to non-elephant targets depending on grouping condition may be due to selective disappearance of the individuals that are overly fearful and aggressive when alone (Hämäläinen et al., 2014) (i.e. individuals that express heightened fear and aggression behaviours when alone don't reach adulthood). Whilst a longer-term study would be needed to address the potential of selective disappearance of individuals with a low threshold to coping with risk in adulthood, we believe it is unlikely that the sample of lone elephants represented individuals that were actively excluded from groups, or choosing to be alone. Hotspots were routinely visited by large numbers of elephants, and our method of scoring social context quantified the presence of all elephants at the hotspot, not necessarily reflecting the individuals' preferred choice of social companions. Whilst it is possible that individuals excluded from groups or choosing to be alone can fissure from groups out in the larger landscape of the MPNP, the hotspots are a large, shared and popular resource, and elephants have no control over the arrival of conspecifics.

For both adult and adolescent elephants, the probability of performing aggressive behaviours to non-elephant targets was greater when there were fewer older male elephants in the immediate environment. One interpretation of this result could be that elephants perceived themselves to be at higher risk in these cases. Male elephants of all ages prefer to have the oldest males in a population as their nearest neighbours, potentially to reap benefits from their heightened ecological knowledge (Evans & Harris, 2008), which could include knowledge regarding environmental risk assessment. Some researchers suggest that due to their heightened experience with age, older males hold a similar role as matriarchs do in female family groups in their importance to the wider bull society (Evans & Harris, 2008; Chiyo et al, 2011a; McComb et al., 2011a). In elephant family groups, older matriarchs are better at assessing risks in the environment, which provides survival benefits to their group mates (McComb et al., 2011a). We suggest that, for males too, with fewer older mature males present in environment, males may perceive themselves to be at higher risk, and experience lower levels of certainty about their safety (Bateson et al., 2011), which is expressed though the observed increases in aggression to non-elephant targets. In other words, older males may act as particularly effective partners in social buffering (Kikusui et al., 2006), relieving stress and anxiety in group mates. In addition, we also found elephants were more likely to direct fear behaviours to non-elephant targets when greater numbers of 10-15 year olds were present, this may reflect a social contagion and spread of fear behaviours triggered by greater numbers of more skittish, fearful young adolescents being present.

Whilst the increased probability of performing aggressive behaviours to non-elephant targets when in higher-risk social contexts may represent responses to targets actually perceived as threatening by elephants with a heightened sensitivity, this aggression may alternatively or additionally be a form of re-directed or displaced aggression linked to an acute stress response induced by a perceived threatful social condition (Virgin & Sapolsky, 1997; Poole & Granli, 2011). Indeed, aggression to non-elephant targets often appeared not to be a true anti-predator defence because it was directed at non-threatening objects or bystanders (for example bashing of vegetation, charging of birds or smaller ungulates) or had no obvious target (target was unidentifiable, **Supplementary Information 2**; Figure S2.2). In many social mammals, following a stressful experience, redirecting aggression to third parties of their own species is thought to represent a stress-reducing behavioural outlet (Virgin & Sapolsky, 1997; Kazem & Aureli, 2005). However, we suggest in such a large and weaponised species, displacing aggression to a conspecific carries too much risk due to potential for escalated conflict, which can potentially turn lethal. African elephants may therefore tend to displace aggression to non-elephant targets. Whilst in the case of the “delinquent” males of Pilanesberg national park, young males were far more isolated from mature bulls than our current study, with total absence of mature bulls in the environment leading to a pre-mature musth in young males (Slotow et al., 2000), we find it interesting to note that there too, in the absence of mature bull influence, elephants directed lethal aggression to rhinos, not conspecifics (Slotow & van Dyk, 2001).

Finally, mature bulls may also act as policers of aggressive behaviour directed at non-elephant targets. Reduced presence of mature bulls in the environment may have led to an uninhibited expression of these behaviours (Slotow et al., 2000; Flack et al., 2005a). These aggressive behaviours are potentially highly disruptive to the social groups activities, cohesion and stability (Judge & Mullen, 2005), as well as run risk of escalating and spreading further in the group as bystanders become affected and themselves anxious (personal observation, Flack et al., 2005b). For example, the calls of distressed elephants can make elephants act aggressively (O'Connell-Rodwell et al., 2000). Mature bulls may have a role in regulating such behaviours that are disruptive to all-male groups (Flack et al., 2005a). Future research should focus on whether mature bulls are actively policing the aggressive behaviours of other males through ongoing punishment (our results might suggest this is not the case, as whilst adults performed more aggression behaviours to conspecifics compared to adolescents, elephants did not increase their aggression to conspecifics with the increased presence of any age class) (Flack et al., 2005a,b; de Waal, 1989). Alternatively, it was often observed that approaches of mature bulls to younger elephants evoked submissive responses even in the absence of dominance and aggressive signalling from the older male (although we cannot exclude the possibility that aggressive vocalisations could be being performed by the older male). Older elephants, with their clear dominance owing to greater size (Lee & Moss, 1995) and greater potential to inflict harm obvious to younger males, may have a more passive policing influence on other males, i.e, elephants may simply "behave better" when mature bulls are around without receiving particular policing behaviours (Semple et al., 2009).

3.6 Conclusion

In this chapter I demonstrated not only how agonistic behaviours can vary across life history stages in a sexually segregated population of males, but also how the age structure of the males in an individual’s environment can influence the expression of agonistic behaviours.

Adolescents were affected by social isolation, and experienced increases in expression of flight or fight type behaviours towards non-conspecific targets when alone, compared to when in the company of other males. For smaller, younger and less experienced adolescents, associating in all male groups may reduce an individual’s perception of his current risk level, and associating with other males appeared to have a strong social buffering effect (Kikusui et al., 2006). For adults on the other hand, social isolation did not affect likelihood of performing flight or fight type behaviours towards non-conspecific targets. This suggests for more socially mature, larger and more experienced males, the motivation for associating with other males in all male groups is not as strongly influenced by social buffering influences on risk perception, or an improved certainty about safety.

I also provide evidence that the oldest age cohort may have a particularly strong social buffering effect on other males, as increased presence of older males in the environment was associated with both adults and adolescents directing aggression to non-conspecific targets at reduced rates. This may be due to the increased ecological experience that comes with age, and males may experience reduced anxiety when more old, experienced males are nearby. Alternatively, seeming as we saw no corresponding relationship between the rate of fear responses to non-elephant targets increasing with lower mature male presence, it may not be that the higher rates of aggression observed are linked to male's perception of risk level, but rather that older mature males act as policers of aggression behaviours to non-conspecific targets.

Overall, only agonism related to non-conspecific targets was influenced by a focal male's social context at all-male aggregations in this sexually segregated society. Whilst overall adults were more likely to perform aggressive behaviours to conspecifics compared to adolescents, we found that aggression directed to other males was unaffected by the increased presence of any age class in an individual's environment.

Understanding elephant aggression is essential for protecting the lives and livelihoods of people that live alongside the species (DeMotts & Hoon, 2012; Dunham et al., 2010). Whilst this study was conducted in an area with only moderate tourist presence with humans outside of vehicles absent, the aggressive behaviours observed by elephants have the potential to also be performed in areas with greater human presence, including where people move without the protection of vehicles. Globally, elephants are responsible for a significant proportion of large-mammal caused injury and fatality to humans (Acharya et al., 2016), and previous research has suggested physiologically stressed elephants may be more prone to aggressive encounters with humans (Jachowski et al., 2012). Our results suggest wildlife managers should be careful to ensure mature bulls are present in elephant populations, as their increased presence was associated with decreased rates of male elephant aggression to non-elephant targets. Adolescent male elephants that are socially isolated, or all ages that are unable to associate with mature males may serve as a greater threat to humans and livestock. These results, like the conclusions of **Chapter 2** suggest that older males may be inappropriate targets of selective trophy hunting activity, and additionally highlight the importance of considering male age demographics of populations when implementing translocation and reintroduction schemes of elephants (Slotow et al., 2000; Slotow & van Dyk, 2001).

Chapter 4: Effects of Age on Trunk-mediated “Greeting” Behaviours in Male African Elephants

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4.1 Abstract

A common behavioural interaction between male elephants is for an actor to direct his trunk to contact a same sex conspecifics' mouth, temporal gland, or genital region. Such behaviours are often referred to as "greetings". Along with its inherent tactile element, these behaviours also likely provide olfactory information to actors concerning aspects of the target's phenotype, including sexual status, feeding history, individual identity, and emotional state. Here we explore whether the age and novelty of potential interactors affect the choice of individuals targeted by male elephants for these trunk to scent emitting organ (SEO) behaviours at social hotspots in a male dominated area. Male elephants of all ages, except older adolescents aged 16-20 years, preferentially targeted elephants of the same age class with trunk-to-SEO behaviours. Elephants younger than 26 years did not direct trunk-to-SEO behaviours to mature bulls (26+ years) more than expected by chance, suggesting these behaviours are not primarily used for younger males to establish contact with, or obtain information from or about older, more experienced individuals. We also found no evidence that males directed these behaviours preferentially to new individuals they encountered at male aggregations (compared to those they arrived in all-male groups with), suggesting these behaviours are not primarily employed by males as a reunion display to establish relationships between new individuals or update relationships between familiar individuals separated over time. Age-mates may be preferentially targeted with these behaviours as a means to facilitate further interaction with beneficial partners (e.g., for sparring activity), or as a safe way to assess relative dominance rank in similarly aged and hence, size and strength, matched dyads. Our results suggest male elephants use trunk-to-SEO

behaviours continuously over time, to facilitate positive relationships, test willingness to interact, and assess aspects of phenotype, between males occupying the same ecological space.

4.2 Introduction

The chemical products released by animals play an important role in communication in animal societies (Eisenberg & Kleiman, 1972; Kelliher, 2007). Often, owing to the ability for chemical cues and signals to remain long after the depositor has departed, such communication can occur remotely between individuals, for example, in scent marking of territory (Gazit et al., 1997; Gosling & Roberts, 2001) and sexual advertising (Ferkin et al., 2004). However, many species also engage in close contact olfactory assessments of conspecifics which, considering the potential risks of close proximity, even tactile contact between individuals, may also overlap with other social messages, e.g. tests of dominance, relationship strength, or willingness to interact (East et al., 1993; Dias et al., 2008; Bos & Buning, 2010; Baan et al., 2014). Sniffing behaviours in rats, for example, are not solely used for obtaining olfactory information, but also to convey appeasement during social interactions (Wesson, 2013). Such tactile behaviours are observed in elephant species, whereby close physical contact is initiated by the subject directing its trunk towards a target elephants' mouth, temporal gland or genitals (Poole & Granli, 2011). These behaviours are performed in a diverse range of contexts, including during reunion, social play, conciliation and coalition building (Poole & Granli, 2021). The mouth, temporal glands and genitals of elephants are known to emit chemical products, so it is likely an element of olfactory assessment can also be conducted by the actor

(Schulte et al., 2005). The secretions of these organs in elephants may encode various aspects of phenotype, such as sexual status (Poole, 1987; Hollister-Smith et al., 2008), feeding history (Lee & Moss, 1999; 2011), individual identity (Bates et al., 2008), and potentially age and emotional state (Rasmussen & Wittemyer, 2002; Poole & Granli, 2011). The adaptive function of these trunk behaviours between males is particularly interesting because it involves risky close contact between potential competitors (Andersson & Iwasa, 1996), as well as a risk of disease transmission owing to close or direct contact of body orifices (Wobeser, 2005). This study aims to provide new insights into the function of trunk to scent emitting organ (SEO) behaviours in male African savannah elephants (*Loxodonta africana*), particularly concerning their occurrence between partners of similar or divergent age in this long-lived mammal.

Male African elephants live in societies with a high degree of fission-fusion dynamics, whereby individuals maintain diverse and loose associations with other males of mixed age and level of maturity (Aureli et al., 2008; Chiyo et al., 2011a; Lee et al., 2011). This is in contrast to the more tightly bonded groups of females that are primarily held together by strong kinship ties, within higher levels of social organisation (Wittemyer et al., 2005; Archie et al., 2005). Outside of sexually active “musth” periods, males are generally gregarious (Poole, 1987; Goldenberg et al., 2014), spending around 63% of their time in all-male groups (Chiyo et al., 2011a). Male African elephants have an adolescent life history stage between the ages of 10-20 years (Lee et al., 2011; Evans & Harris, 2008), and full sexual maturity, and first paternity is in general not achieved till the age of 25-30 years (Hollister-Smith et al., 2007; Lee et al., 2011; Poole et al., 2011). There is evidence that males can hold stable relationships over time, although the long-term time scale for these relationships is not yet clear (Lee et al., 2011; Murphy et al., 2019). Whilst a number of studies have looked at the patterns of social associations within male African elephant society (Chiyo et al., 2011a; Goldenberg et al., 2014; Murphy et al., 2019), the specific behavioural interactions between males in all-male groups has less often been the focus of research (but on aggression see (Poole, 1987; O'Connell-Rodwell et al., 2011; **Chapter 3**), and on sparring (Chiyo et al., 2011a; Evans & Harris, 2008).

In male African elephant communication, the trunk-to-SEO behaviours described are often labelled as "greetings" (Poole & Granli, 2011; 2021). Greeting behaviours in other species similarly can involve an aspect of inspection of sources of scent (e.g. armpit and genital sniffing in howler monkeys, *Alouatta palliata* (Dias et al., 2008); inspection of anogenital region in wolves, *Canis lupus* (Harrington & Asa, 2013) and spotted hyenas, *Crocuta crocuta* (Smith et al., 2011)), as well as intimate tactile contact (e.g. genital fondling in baboons, *Papio sp.* (Whitham & Maestripieri, 2003); embraces in spider monkeys, *Ateles geoffroyi* (Aureli & Schaffner, 2007)). Greeting behaviours are frequently performed in the context of reunion (although not exclusively (Dal Pesco & Fischer, 2018)), and one proposed function of greetings is to update uncertain relationships between individuals following prolonged periods without social contact, and greetings are often observed in species that demonstrate a high degree of fission-fusion dynamics, such as male African elephants (Aureli & Schaffner, 2007; Aureli et al., 2008; Smith et al., 2011). The tension and potential conflict of reunion (or meeting of completely novel individuals) during group fusion events is thought to be resolved by greeting behaviours, and individuals can communicate their intention to interact in an affiliative manor, as well as update previously insecure relationships (e.g., establish relative dominance status) via close contact assessments (Colmenares et al., 2000; Aureli & Schaffner, 2007). Greetings are also argued to serve other functions in other species, which may similarly apply to male African elephants. For example, greeting behaviours can be a mechanism to reconcile and diffuse conflicts (Aureli et al., 2002; Smith et al, 2011; Poole & Granli, 2021), a means for individuals to communicate their awareness of dominance asymmetries (e.g., appeasement behaviours from subordinates to dominants (Laporte & Zuberbühler, 2010)), and as a means of maintaining cooperation and reinforcing social bonds among members of groups (Smith et al., 2011; Dal Pesco & Fischer, 2018; Rütten & Fleissner, 2004).

This study explores trunk-to-SEO behaviours performed by male African elephants aggregating at hotspots of social activity along a river in an area spatially segregated from females. African elephants are a long-lived species and males aggregate in mixed age groups (Chiyo et al., 2011a; Lee et al., 2011). Localised, but shareable resources in the environment such as these river hotspots provide aggregating males exposure to different ages of potential interactors, and hence opportunities for information exchange and social contact with a diverse set of new associates (Fishlock & Lee, 2013; Fishlock et al., 2016). We were first interested in exploring how differences in age affect the rate at which male elephants perform trunk-to-SEO behaviours, hypothesising that (i) males of different age will perform trunk-to-SEO behaviours at divergent rates. Adolescents are in general more sociable than adult male elephants; they are found in larger groups (Evans & Harris, 2008), and are less likely to travel alone (**Chapter 2;** Lee et al., 2011). If adolescents perform more trunk-to-SEO behaviours compared to adults, it may be that these behaviours are used to facilitate further social connections and interactions, or to obtain information about other males in the male social network to which adolescents are more recently dispersed and less stably established in (Lee et al., 2011; Murphy et al., 2019). Alternatively, if breeding age adult males perform more trunk-to-SEO behaviours than non-breeding age adolescents, it may be that the main function of these behaviours is for evaluation of sexual status of potential competitors, for example proximity to transmission to musth state (Hollister-Smith et al., 2008). Throughout this study, we also consider the organs targeted by the trunk separately from one another. The mouth, temporal gland, and genitals may carry different olfactory information, and may therefore provide different information about a conspecific (Lee & Moss, 1999; 2011; Rasmussen & Wittemyer, 2002; Rasmussen & Riddle, 2004; Bates et al., 2008; Hollister-Smith et al., 2008; Poole & Granli, 2011). In addition, trunk-to-SEO behaviours can also be reciprocated back to the subject (Poole & Granli, 2011), we therefore also explored whether age class influenced the likelihood of a subject's trunk-to-SEO behaviour being a reciprocated event.

Secondly, we explored to what age targets trunk-to-SEO behaviours are directed, as an indicator of the potential function of these behaviours in male African elephant communication. We tested two alternative hypotheses. From adolescence through to adulthood, male African elephants grow drastically (Lee & Moss, 1995), making relative dominance easy to establish between individuals separated by large age gaps. For males that are of similar age, we predicted that trunk-to-SEO behaviours may be important for clarifying less obvious dominance relationships (Dias et al., 2008) and we thus hypothesised that (ii) elephants will target age-matched elephants more with trunk-to-SEO behaviours than predicted by chance. Males may also prefer to associate with age-matched partners for cooperative benefits, such as access to size and strength matched sparring partners (Evans & Harris, 2008; Chiyo et al., 2011a) and trunk-to-SEO behaviours between age-mates may also be used to facilitate new connections and communicate affiliative intent towards such partners. For our alternate hypothesis, we predicted that (iii) elephants will target the oldest males in the population with trunk-to-SEO behaviours more than predicted by chance. There is evidence that older males are the preferred nearest neighbours of males of all ages (Evans & Harris, 2008) and older males have a greater number of associates, and higher centrality in male social networks (Chiyo et al., 2011a). In fusion events of hyenas, high ranking females are preferentially targeted with close contact greeting behaviours of the genitals, reflecting a preference for powerful allies and popular social contacts (Smith et al., 2011). Similarly, as with older matriarchs in African elephant female groups, older bulls may represent desirable contacts owing to their potentially enhanced ecological and social experience and knowledge (McComb et al., 2001; 2011a; Chiyo et al., 2011a), and elephants may benefit from directing trunk-to-SEO behaviours to these high-value targets to initiate further contact with them, or to obtain information on, for example, their individual identity or feeding behaviour (Lee & Moss, 1999; 2011; Evans & Harris, 2008). Alternatively, male elephants may also preferentially direct trunk-to-SEO behaviours to older bulls in the case that this behaviour is primarily an appeasement gesture performed by subordinates to dominants to signal awareness of dominance asymmetry (Preuschoft, 1999; Laporte & Zuberbühler, 2010; Baan et al., 2014).

Finally, we compared how male African elephants' direct trunk-to-SEO behaviours to targets based on their relative novelty to the actor. In societies with a high degree of fission-fusion dynamics such as male African elephants, these trunk behaviours could be used for reaffirming relationships following separations, or obtaining information about new, unknown individuals in a safe, ritualised context (Aureli & Schaffner, 2007; Dias et al, 2008). Hence, we hypothesised that (iv) elephants will be more likely to direct trunk-to-SEO behaviours towards individuals met new at all-male aggregations at social hotspots, compared to elephants that they arrived at the hotspot in an all-male group with.

4.3 Methods

Subjects of the study were male African elephants aggregating at hotspots of male elephant social activity along the Boteti River, in MPNP (Figure 1.1), Botswana, a recognised bull area with 98% male sightings (Evans, 2019). Details regarding the nature (size, location, resources present) of these "social hotspots" can be found in **1.6.5.**

Focal subjects were recorded for the duration of their stay within defined social hotspots using a video cam-corder (JVC quad proof AVCHD). Male elephants were categorised into 4 age classes: adolescents, 10-15 years & 16-20 years, and adults, 21-25 & 26+ years (see **1.6.2**). We randomly preselected the age class of the subject to be recorded for a particular follow, and the first elephant of the assigned age class to arrive at the hotspot since observers started the session, would be the subject of a focal animal sample. If more than 1 elephant arrived of the predetermined age class in the same group, the focal was selected at random from the choice of elephants. Video focal follow recordings of visits to the river were taken from individual elephants only once over the course of the study, with an individual's identity determined using characteristics such as notches, tears, holes and venation in the ears, morphology of tusks, folds and wrinkles of the skin, and other body abnormalities (Douglas-Hamilton, 1972; **1.6.2**).

A focal follow began either as the subject arrived over the bank slope, or as he entered the hotspot having moved from another stretch of river up or downstream of the hotspot. Focal follows were terminated when similar boundaries were crossed during departure. Focals could stay at social hotspots for several hours (average time spent at hotspot for focal elephants seen arriving and leaving via bank = 1h 13 min, range= 9min – 7 h 5 min, SD= 59 min), over which time, the males present at aggregations with focals could be highly dynamic. Since individuals arriving in all-male groups tend to arrive within 10 minutes of one another (Figure 2.1), focal follows were subdivided into 10-minute follows (e.g. a focal follow of an elephant staying 50 minutes at the hotspot, would produce five 10-minute focal follows), to which a corresponding social context was assigned (see below), in order to capture the temporally dynamic nature of male aggregations at the hotspots. Only focal follows where the subject was exposed to at least 1 potential interactor during his stay at the river were used for the study.

Data collection methods allowed for good visibility of focal elephants (**Chapter 1**; Figure 1.5). However, if a subject was out of view from the camera for over 2 minutes of a 10-minute focal animal follow, i.e. over 20% of time, the focal follow was excluded from analyses (N 10-min follows excluded= 152). This gave a total sample size of 1223 10-minute focal follows for analysis (N 10-15 years= 246, N 16-20 years= 320, N 21-25 years= 319, N 26+ years= 338), from 240 individuals (range 10-minute focal follows per individual = 1-17, mean = 4.903).

Scoring of trunk to scent-emitting-organ behaviours

Video footage of focal follows was scored for behaviours by one researcher (CA) to standardise scoring. Focal follows were watched 3 times to verify behaviours. We recorded trunk behaviours performed by focal elephants that involved the direction of the trunk towards a target elephants' temporal glands, genitals, or mouth (Poole & Granli, 2011; Figure 4.1).

We recorded trunk behaviours as events, recording the time each behaviour was performed, the target organ of the behaviour (Figure 4.1), the age class of the elephant targeted, and whether he was an elephant the focal arrived at the river with, or met new at the river (did not arrive in a group at the hotspot with).

Trunk-to-SEO behaviours can be one-way, or reciprocated events between dyads (Poole & Granli, 2011). We therefore also recorded whether a trunk-to-SEO behaviour directed by a focal to an individual was reciprocated or not. Defining a cut-off to reciprocate a trunk-to-SEO behaviour as both 1 or 5 minutes before or after the focal contacted the target, or as being performed within the time spent continuously within one body length of the target of the behaviour, all produced identical results. Most reciprocated a trunk-to-SEO behaviours occurred immediately alongside each other (personal observation).

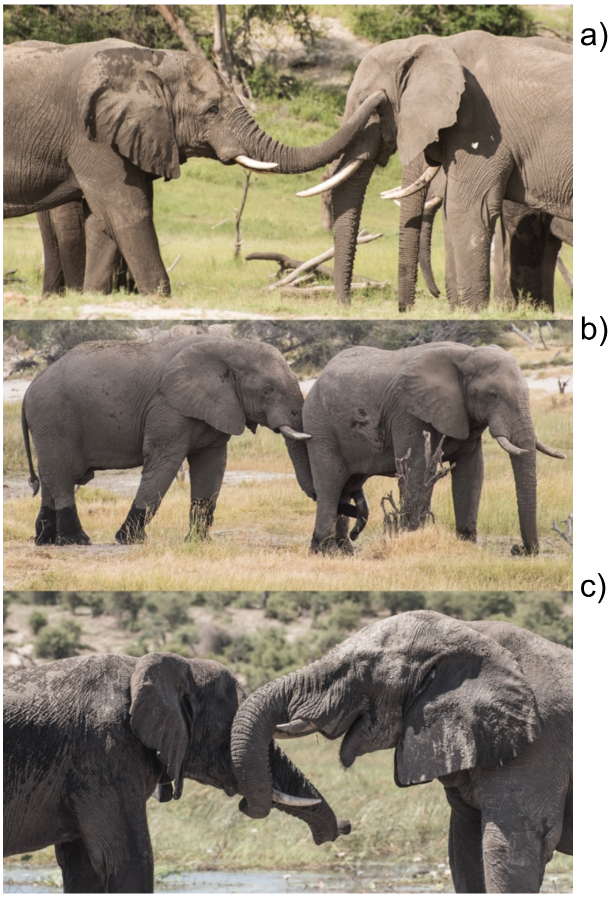

Figure 4.1: Example photos of close contact trunk-to-SEO behaviours, with trunk of the focal elephant directed to a target elephants a) temporal gland, b) genitals, and c) mouth.

Determination of social context

The number of other elephants already present aggregating at the hotspot and their age classes were recorded at the time of a focal elephant’s arrival, as were the ages of those he arrived at the river with in a group. Furthermore, we continuously recorded elephants that arrived and left the hotspot by the river bank or hotspot boundaries up or down stream during a focals stay, such that for every 10-minute focal follow, there was a corresponding recording of the number of other elephants present at the hotspot with a subject as a potential interactor in that 10-minute follow, and their age classes.

No focal follows were collected from elephants identified to be in musth (Poole, 1987). Furthermore, we excluded focal follows where a musth bull was present as a potential interactor at the hotspot (N 10-min follows= 11), due to the established consensus that males act differently when in the musth state, and that non-musth males overall have a tendency to avoid close contact with musth males (Poole, 1987). We also excluded a small number of follows where females were present as potential interactors (N 10-min follows= 11), since presence of females was a rare event in this bull area and was likely to influence the choice of targets of, and rates given of trunk-to-SEO behaviours.

Statistical analysis

To determine how (i) rate of performing trunk-to-SEO behaviours varied with age class, Kruskal Wallis H tests were run, and where significant results were found, post hoc pairwise comparisons were made using Wilcoxon rank sum tests with corrections for multiple comparisons, to identify between which age classes these differences were driven. Rates of performing trunk-to-SEO behaviours were explored through number of behaviours made by subjects/ hour, number of individuals targeted with behaviours/ hour, number of individuals targeted with behaviours/ potential interactor exposed to during a hotspot visit, and number of individuals targeted with behaviours/ potential interactor/ hour, as there are multiple ways to meaningfully measure the rate at which trunk-to-SEO behaviours are performed, which may need to be controlled for by number of potential interactors present, and sample duration. We similarly compared all these measures for the specific organ targeted separately, in case age classes differed in their targeting of the different organs with trunk contacts.

As a control, we also ran a generalised logistic mixed-effects model (GLMM) to explore whether number of other elephants present at hotspots with subjects predicted the likelihood of directing a trunk-to-SEO behaviour toward another animal during a 10-minute focal follow. In this model “trunk-to-SEO behaviour performed in 10-min follow” (yes or no, dependent variable) was predicted by focal age class, the number of other elephants present at the male aggregation and the interaction term between the two (independent variables). Another GLMM explored whether a focal elephants’ age class predicted whether a trunk-to-SEO behaviour was reciprocated by the target back to the focal. In this model, the independent variable was “trunk-to-SEO behaviour reciprocated” (yes or no), and independent variable was focal age class. Focal ID was included as a random effect in both these GLMMs.

We ran GLMMs to determine whether elephants directed trunk-to-SEO behaviours to particular age cohorts more than would be predicted by random assignment of these behaviours to elephants present in a subjects’ social environment at the hotspot (all-male aggregations), with statistical significance determined using permutation-based null models. Only focal follows that had at least 1 individual from both categories of potential interactors present (see each hypothesis below), and had no more than 30 elephants present as potential interactors were included in models to assist with model convergence.

We first investigated if (ii) elephants directed trunk-to-SEO behaviours to age-matched elephants at social hotspots more than predicted by random chance assignment of these behaviours to the elephants present with subjects at hotspots. We fit a GLMM with a binomial error structure and a logit link function, predicting “trunk-to-SEO behaviour given to individual” (dependent variable, yes or no) by whether a potential interactor (present in that 10-minute focal follow) was age-matched or not to the focal elephant (independent variable). We ran four separate models: one including all trunk-to-SEO behaviours directed (3 target organs combined), as well as individually for the particular organ targeted (mouth, temporal gland, genitals). Binomial GLMMs were fit, and estimates obtained for the observed data set were compared to 10,000 randomised data sets. In these permutations the age composition of the social environment was maintained (number of age-matched and non-age-matched present at the hotspot) in each 10-minute follow, but trunk-to-SEO behaviours given were randomly shuffled between the individuals present in each permutation. We then ran the same models again, this time including focal age class as an interaction term, to investigate whether different age classes differed in their tendency to target age-matched males with trunk-to-SEO behaviours. In all models, focal ID was included as a random effect.

For our alternative hypothesis, we investigated whether (iii) elephants directed trunk-to-SEO behaviours to older, mature individuals (aged 26+ years) more than younger age classes of elephants. The structure of these GLMM’s, and methodology was identical to the above models concerning age-matched status, however the independent variable was the age of the potential target of interaction (either aged 26+ years or not).

Finally, we explored whether (iv) elephants preferentially directed trunk-to-SEO behaviours to individuals that they did not arrive at the hotspot with compared to those with whom they did. These GLMMs predicted “trunk-to-SEO behaviour given to individual” (dependent variable, yes or no) by the “novelty” status of the elephants present during a focals stay at the river hotspot (arrived at the river in a travelling group with the focal, or was a new interactor met at the all-male aggregation). In these permutations, only elephants that were observed leaving and arriving via the riverbank (no arrival or departure from up or downstream of hotspot) were used for analysis. The “novelty” status of elephants was maintained in each permutation (number of elephants met new versus arrived with exposed to), but trunk-to-SEO behaviours were randomly shuffled amongst the individuals present in each permutation. Binomial GLMMs were fit, and estimates obtained for the observed data set were compared to 10,000 randomised data sets. Again, models were also run for the target organs separately, and rerun to include age class of the subject elephant as an interaction term. Focal ID was included as a random effect in all models.

4.4 Results

Considering all trunk-to-SEO behaviours together, males of divergent age classes performed trunk behaviours at different rates (Table 4.1 for Kruskal-Wallis H test results, Table 4.2 for means and standard deviations of trunk-to-SEO behaviours performed by the different age classes). This was driven in all cases by the two adolescent age classes performing trunk-to-SEO behaviours of conspecifics at significantly higher rates than the two adult age classes

(**Supplementary Information 3**; Tables S3.1-S3.4 for significant pairwise comparisons using Wilcoxon rank sum tests).

Table 4.1: Output of Kruskal-Wallis H tests for each method of measuring differences in rate of performing trunk-to-SEO behaviours between the four age classes of focal.

Behavioural measure	**Result Kruskal-Wallis H test**	
	χ^2 (3)	**P**
Trunk to scent emitting organ (any of 3 organs)		
Behaviour performed/ hour	28.697	**< 0.001**
Individuals targeted with behaviour/ hour	28.009	**< 0.001**
Individuals targeted with behaviour/ potential interactor	29.517	**< 0.001**
Individuals targeted with behaviour/ potential interactor/ hour	28.913	**< 0.001**
Trunk-to-mouth		
Behaviour performed/ hour	26.890	**< 0.001**
Individuals targeted with behaviour/ hour	26.493	**< 0.001**
Individuals targeted with behaviour/ potential interactor	27.456	**< 0.001**
Individuals targeted with behaviour/ potential interactor/ hour	26.545	**<0.001**
Trunk-to-temporal-gland		
Behaviour performed/ hour	6.957	0.073
Individuals targeted with behaviour/ hour	6.957	0.073
Individuals targeted with behaviour/ potential interactor	7.685	0.053
Individuals targeted with behaviour/ potential interactor/ hour	7.427	0.059
Trunk-to-genitals		
Behaviour performed/ hour	2.414	0.491
Individuals targeted with behaviour/ hour	2.483	0.479
Individuals targeted with behaviour/ potential interactor	1.768	0.622
Individuals targeted with behaviour/ potential interactor/ hour	2.015	0.569

Table 4.2: Table of means and standard deviations of trunk-to-SEO behaviours performed by focals of different age classes during a visit to a social hotspot.

	Age class of focal			
	10-15 years (N=50)	*16-20 years (N=63)*	*21-25 years (N=67)*	*26+ years (N=60)*
Trunk-to-SEO behaviours performed/ hour:	4.71 (4.39)	3.84 (4.27)	2.17 (2.84)	1.43 (2.17)
Individuals targeted with trunk-to-SEO behaviours/ hour:	3.15 (2.77)	2.71 (3.50)	1.56 (1.94)	1.04 (1.55)
Individuals targeted with trunk-to-SEO behaviours/ potential interactor:	0.26 (0.24)	0.27 (0.27)	0.13 (0.16)	0.10 (0.18)
Individuals targeted with trunk-to-SEO behaviours/ potential interactor/ hour:	0.34 (0.40)	0.37 (0.50)	0.16 (0.24)	0.10 (0.21)

Trunk-to-SEO behaviours were largely dominated by trunk-to-mouth behaviours (Figure 4.2). Considering only trunk-to-mouth behaviours, males of divergent age classes performed this behaviour at different rates (Table 4.1 for Kruskal-Wallis H test results, Table 4.3 for means and standard deviations of trunk-to-mouth behaviours performed by the different age classes). This was again driven in all cases by males from both the adolescent age classes performing trunk-to-mouth behaviours at significantly higher rates than males from both adult age classes (**Supplementary Information 3**; Tables S3.5-S3.8 for significant pairwise comparisons using Wilcoxon rank sum tests). The subject elephant's age class had no effect on the rates at which elephants directed the trunk to conspecifics' temporal glands or genitals (Table 4.1 for Kruskal-Wallis H test results, Tables 4.4 & 4.5 for means and standard deviations of trunk-to-temporal-gland and trunk-to-genital behaviours performed by the different age classes respectively).

Table 4.3: Table of means and standard deviations of trunk-to-mouth behaviours performed by focals of different age classes during a visit to a social hotspot.

	Age class of focal			
	10-15 years (N=50)	*16-20 years (N=63)*	*21-25 years (N=67)*	*26+ years (N=60)*
Trunk-to-mouth performed/ hour:	3.61 (3.79)	2.74 (3.42)	1.33 (1.75)	0.979 (1.94)
Individuals targeted with trunk-to-mouth / hour:	2.56 (2.55)	2.10 (3.05)	1.03 (1.32)	0.726 (1.27)
Individuals targeted with trunk-to-mouth / potential interactor:	0.221 (0.234)	0.212 (0.251)	0.086 (0.111)	0.066 (0.116)
Individuals targeted with trunk-to-mouth / potential interactor/ hour:	0.297 (0.366)	0.293 (0.416)	0.112 (0.197)	0.072 (0.161)

Table 4.4: Table of means and standard deviations of trunk-to-temporal-gland behaviours performed by focals of different age classes during a visit to a social hotspot.

	Age class of focal			
	10-15 years (N=50)	*16-20 years (N=63)*	*21-25 years (N=67)*	*26+ years (N=60)*
Trunk-to-temporal-gland performed/ hour:	0.200 (0.603)	0.502 (1.030)	0.389 (0.868)	0.197 (0.523)
Individuals targeted with trunk-to-temporal-gland/ hour:	0.200 (0.603)	0.406 (0.746)	0.361 (0.802)	0.197 (0.523)
Individuals targeted with trunk-to-temporal-gland/ potential interactor:	0.015 (0.044)	0.066 (0.145)	0.029 (0.066)	0.021 (0.064)
Individuals targeted with trunk-to-temporal-gland/ potential interactor/ hour:	0.016 (0.049)	0.061 (0.159)	0.030 (0.076)	0.018 (0.064)

Table 4.5: Table of means and standard deviations of trunk-to-genitals behaviours performed by focals of different age classes during a visit to a social hotspot.

	Age class of focal			
	10-15 years (N=50)	*16-20 years (N=63)*	*21-25 years (N=67)*	*26+ years (N=60)*
Trunk-to-genitals performed/ hour:	0.677 (1.20)	0.496 (1.17)	0.454 (0.12)	0.238 (0.526)

Individuals targeted with trunk-to-genitals/ hour:	0.617 (1.08)	0.465 (1.13)	0.381 (0.928)	0.227 (0.508)
Individuals targeted with trunk-to-genitals/ potential interactor:	0.048 (0.090)	0.047 (0.120)	0.027 (0.064)	0.034 (0.091)
Individuals targeted with trunk-to-genitals/ potential interactor/ hour:	0.079 (0.180)	0.076 (0.237)	0.037 (0.098)	0.030 (0.089)

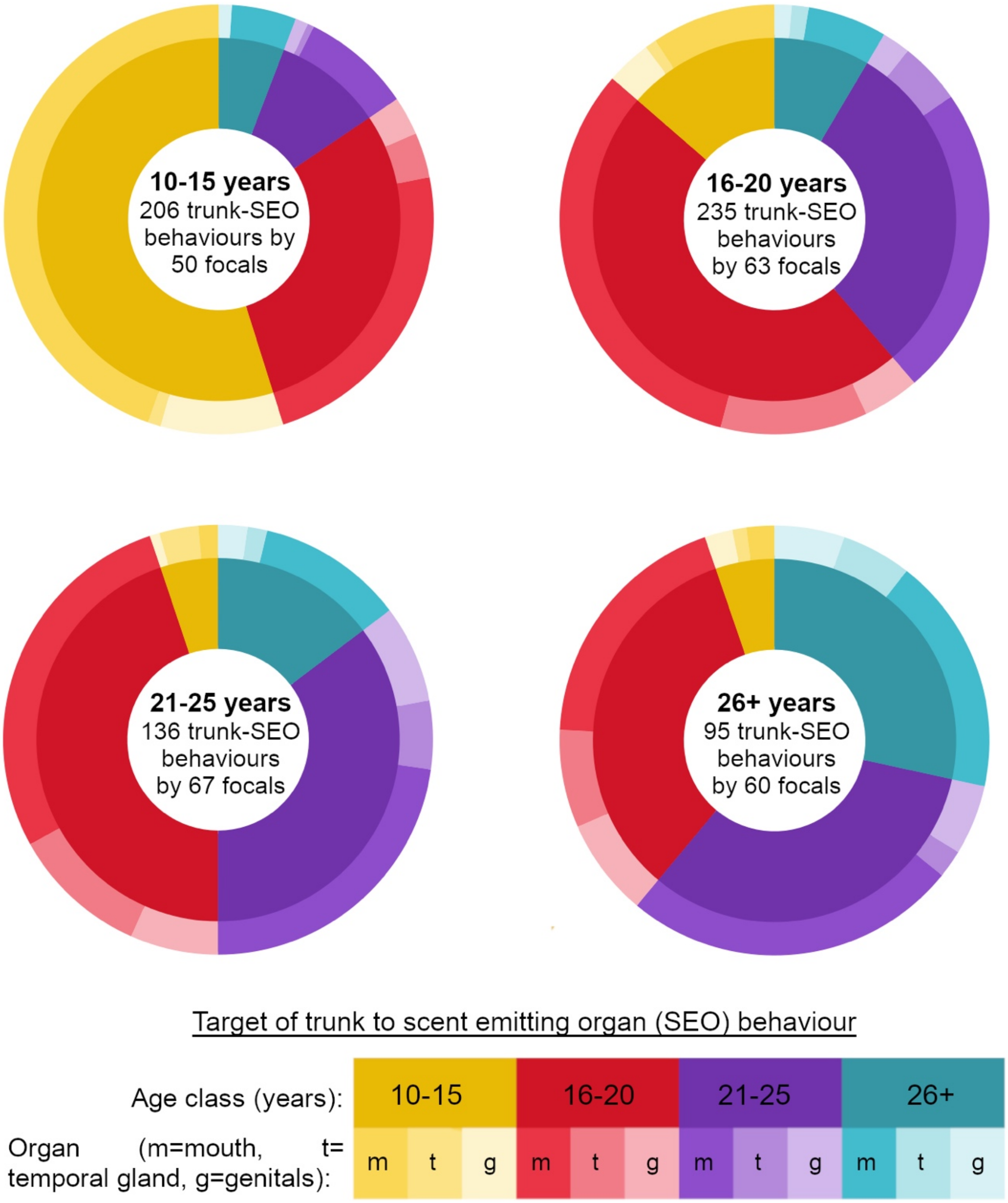

Figure 4.2: Donut charts summarising all observed trunk-to-SEO behaviours directed by focal elephants of different ages. Inner rings indicate age class targeted for behaviour, and outer rings the target organ.

For all age classes, the likelihood that a trunk-to-SEO behaviour was performed in a 10-minute follow was unaffected by the total number of elephants present with the subject at all-male aggregations at hotspots (Figure 4.3).

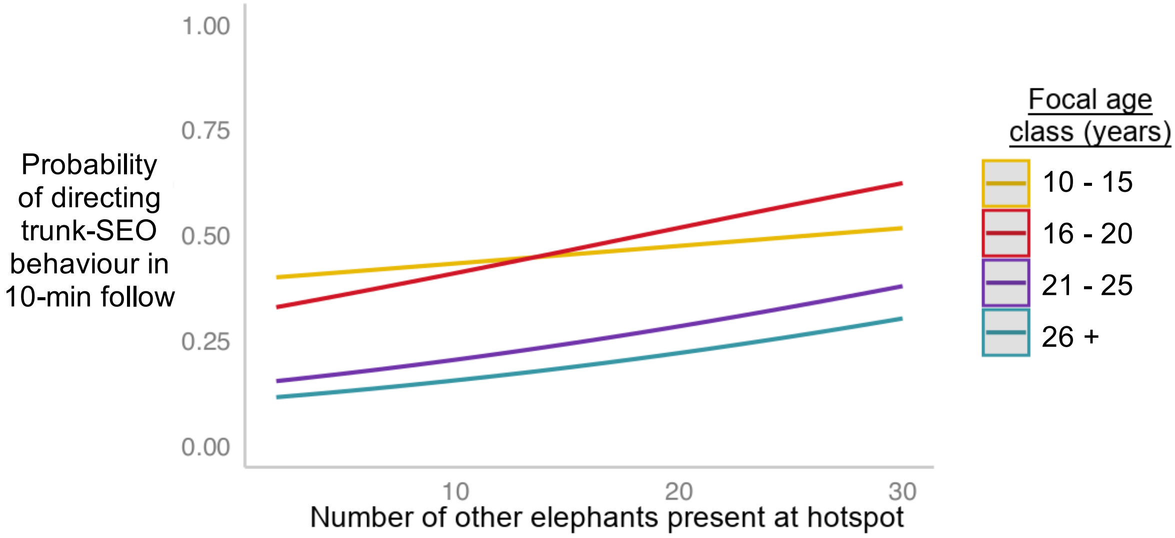

Figure 4.3: The number of other elephants present with the focal did not significantly affect probability of directing a trunk-to-SEO behaviour in a 10-minute focal follow (GLMM of “trunk-to-SEO behaviour directed in 10-min follow” predicted by interaction of focal age class and “Number of other elephants present with focal at hotspot”: Regression coefficients, adjusted odds ratios (aOR), 95% confidence intervals and significances of “Number of other elephants present with focal at hotspot”: 10-15 years as reference class: 0.017, 1.017 (0.972-1.064), p = 0.462; 16-20 years as reference class: 0.043, 1.044 (0.991-1.101), p = 0.104; 21-25 years as reference class: 0.043, 1.044 (0.990-1.102), p =0.115; 26+ years as reference class: 0.043, 1.044 (0.982-1.109), p = 0.169.

A subject elephant’s age class significantly predicted whether a trunk-to-SEO behaviour was reciprocated. Higher probabilities of reciprocation were observed in adult age classes, with 10-15 year olds having significantly lower probabilities of these trunk behaviours being reciprocated events than all other age classes

(Probability of trunk-to-SEO behaviour being a reciprocated event: 10-15 years: 0.298; 16-20 years: 0.432; 21-25 years: 0.568; 26+ years: 0.537; Table 4.6 for GLMM output, for significant differences between age classes).

Table 4.6: Output of GLMM: likelihood of a trunk-to-SEO behaviour being a reciprocated event, predicted by age class of the focal subject. Reference class releveled to show differences between the different age classes concerning likelihood of trunk-to-SEO behaviour being a reciprocated event.

Reference class	**Predictor**	**Coefficient**	**aOR (+95% CI)**	**P**
10 – 15 years	16 – 20 years	0.579	1.785 (1.070 - 2.977)	**0.026**
	21 – 25 years	1.127	3.088 (1.750 - 5.446)	**< 0.001**
	26 + years	1.002	2.722 (1.470 - 5.041)	**0.001**
16 – 20 years	10 – 15 years	-0.579	0.560 (0.336 - 0.934)	**0.027**
	21 – 25 years	0.548	1.730 (1.022 - 2.927)	**0.041**
	26 + years	0.422	1.525 (0.852 - 2.730)	0.155
21 – 25 years	10 – 15 years	-1.127	0.324 (0.184 - 0.571)	**<0.001**
	16 – 20 years	-0.548	0.578 (0.342 - 0.978)	**0.041**
	26 + years	-0.126	0.882 (0.473 - 1.643)	0.692
26 + years	10 - 15 years	-1.002	0.367 (0.198 - 0.680)	**0.001**
	16 - 20 years	-0.422	0.656 (0.366 - 1.174)	0.155
	21 - 25 years	0.126	1.134 (0.609 - 2.113)	0.692

The age class of the focal subject predicted whether a trunk-to-SEO behaviour was a reciprocated, as opposed to a one-way event. 10-15 year olds had a lower probability of a directed trunk-to-SEO behaviour being a reciprocated event than all other age classes. 16-20 year olds had a higher probability of being in a reciprocated trunk-to-SEO behaviour event than 10-15 year olds, but lower probability than 21-25 year olds. 21-25 year olds and 26+ years olds did not differ from one another concerning whether their trunk-to-SEO behaviours were reciprocated events or not.

Elephants preferentially targeted age-matched individuals with trunk to scent emitting organ behaviours at all-male aggregations

Whether a potential interactor was age-matched to the subject elephant predicted the likelihood of the subject directing a trunk-to-SEO behaviour to him (Permutation-based likelihood ratio test of GLMM, $\chi2$ (1) = 5.485^{-12} , $p < 0.001$), with elephants directing these behaviours to age-matched individuals more than predicted by chance (Table 4.7). Considering the target organs independently, whether a potential interactor was age-matched to the subject elephant predicted the likelihood of the subject directing a trunk-to-mouth and trunk-to-genital behaviour to him (Permutation-based likelihood ratio test of GLMM, trunk-to-mouth: $\chi2$ (1) =4.803^{-10} , $p < 0.001$, trunk-to-genitals $\chi2$ (1) =0.004, $p = 0.005$), but not a trunk-to-temporal-gland behaviour (Permutation-based likelihood ratio test of GLMM: $\chi2$ (1)= 0.134 , $p = 0.198$), with elephants preferably targeting age-matched elephants with trunk-to-mouth and trunk-to-genital behaviours (Table 4.7).

Table 4.7: Observed odds ratios and permutation-based significances of elephants targeting an age-matched individual relative to non-age-matched individual with trunk-to-SEO behaviours of different target organs.

Behaviour directed to conspecific	**Observed odds ratio of directing behaviour to age-matched relative to non-age-matched individual**	**95% CI Randomised odds ratios**	**Randomised P**
Trunk-to-SEO behaviour (all organs combined)	2.275	0.887-1.419	**<0.001**
Trunk-to-mouth	2.374	0.980-1.646	**<0.001**
Trunk-to-temporal gland	1.569	0.632-2.037	0.373
Trunk-to-genitals	2.390	0.580-2.000	**0.012**

All ages targeted age-matched individuals with trunk-to-SEO behaviours more than predicted by random assignment of these behaviours to individuals present, apart from 16-20 year olds, who targeted age-matched individuals with trunk-to-SEO behaviours as expected by random chance (Figure 4.4). Considering the target organs independently, 10-15 year olds directed trunk-to-mouth behaviours to age-matched elephants, and 21-25 year olds directed trunk-to-genitals to age-matched males more than expected by random chance (Figure 4.4).

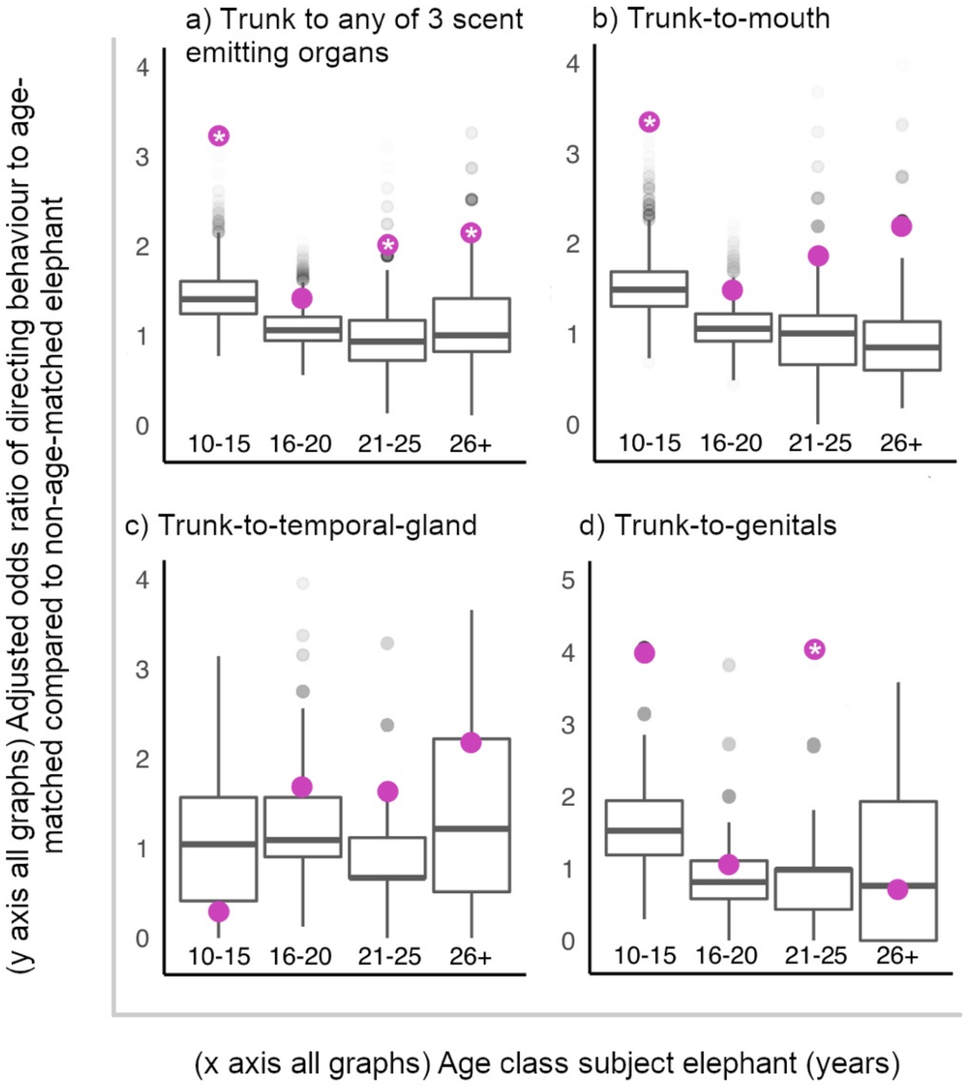

Figure 4.4: Observed adjusted odds ratios of elephants directing a trunk-to-SEO behaviour to an age-matched elephant relative to non-age-matched elephant (purple circles), plotted against randomly permuted adjusted odds ratios of directing a trunk-to-SEO behaviour to an age-matched relative to non-age-matched elephant (boxplots with median, interquartile range, minimum and maximum values). Significant permutation based adjusted odds ratios indicated with “*”. (a) Considering all target organs together, all ages were more likely to target age-matched elephants relative to non-age-matched elephants with trunk-to-SEO behaviours than expected by chance, except older adolescents (16-20

years), who targeted age-matched elephants as expected by random chance (Permutation based observed adjusted odds ratio of targeting age-matched relative to non-age-matched elephant with trunk-to-SEO behaviour: 10-15 years= 3.268, p <0.001; 16-20 years= 1.454, p= 0.085; 21-25 years= 2.056, p = 0.014; 26+ years= 2.185, p= 0.048 (**Supplementary Information 3**; Table S3.9 for randomised 95% confidence intervals)). (c) All age classes directed trunk-to-temporal-gland behaviours to age-matched elephants as expected by random chance, (b) 10-15 year olds directed trunk-to-mouth behaviours to age-matched elephants more than expected by random chance, and (d) 21-25 year olds directed trunk-to-genitals behaviours to age-matched males more than expected by random chance (**Supplementary Information 3**; Tables S3.9 for observed adjusted odds ratios, 95% confidence intervals and p values for each age class and target organ).

Elephants did not preferentially target older individuals with trunk to scent emitting organ behaviours at all-male aggregations

Whether an elephant target was aged 26+ or not did not predict the likelihood of a subject elephant directing a trunk-to-SEO behaviour to him (Permutation-based likelihood ratio test of GLMM, $\chi2$ (1) = 0.212, p = 0.199). Considering the organs targeted separately, whether an elephant was aged 26+ or not did not predict the likelihood of the subject directing his trunk to the target elephant's genitals (Permutation-based likelihood ratio test of GLMM: $\chi2$ (1)= 0.295, p = 0.336), temporal gland ($\chi2$ (1)= 0.949, p = 0.960), or mouth ($\chi2$ (1)= 0.225, p = 0.214). Elephants directed all trunk-to-SEO behaviours to elephants aged 26+ years as predicted by random assignment of these behaviours to elephants present at all-male aggregations in the social hotspot environment (Table 4.8).

Table 4.8: Observed odds ratios and permutation-based significances of elephants targeting an elephant aged 26+ years relative to a younger male with trunk-to-SEO behaviours of different target organs.

Behaviour directed to conspecific	**Observed adjusted odds ratio of directing behaviour to elephant aged 26+ years relative to a younger male**	**95% CI randomised odds ratios**	**Randomised P**
Trunk-to-SEO behaviour (all 3 target organs combined)	1.276	0.688-1.512	0.322
Trunk-to-mouth	1.327	0.646-1.532	0.283
Trunk-to-temporal gland	0.970	0.431-3.066	0.614
Trunk-to-genitals	1.560	0.265-2.078	0.208

Concerning individual age classes, in line with age-matched models, 26+ year olds directed trunk-to-SEO behaviours to fellow 26+ year olds more than predicted by chance per 10-minute opportunity (Figure 4.5). All other age classes targeted 26+ year olds with trunk-to-SEO behaviours within the range predicted by random chance (Figure 4.5). Considering the target organs separately, all age classes directed trunk behaviours to the mouth, temporal glands and mouth of elephants aged 26+ years as expected by random chance (**Supplementary Information 3**; Figure S3.1 & Table S3.10).

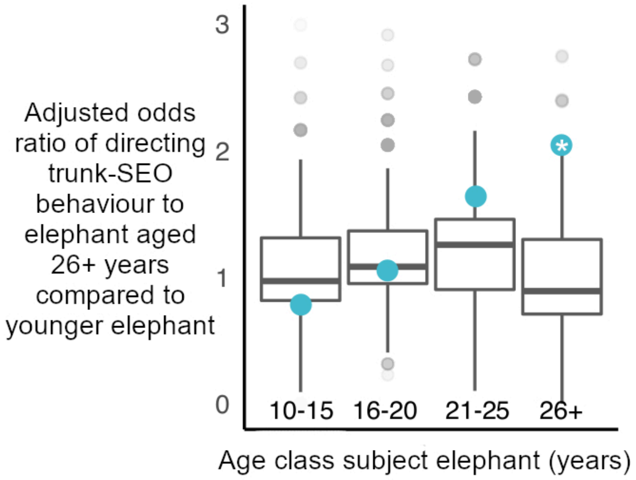

Figure 4.5: Observed adjusted odds ratios of elephants directing a trunk-to-SEO behaviour to a mature bull (26+ years) relative to younger elephant (blue circles), plotted against randomly permuted adjusted odds ratios of directing a trunk-to-SEO behaviour to a mature bull relative to younger elephant (boxplots with median, interquartile range, minimum and maximum values). Only 26+ year old elephants directed these behaviours to fellow mature bulls more than expected by chance (Significant permutation-based adjusted odds ratio (*): 2.077, p =0.042 (**Supplementary Information 3**; Table S3.10 for observed adjusted odds ratios, 95% confidence intervals and p values for all ages)).

Elephants did not preferentially target new individuals with trunk to scent emitting organ behaviours at all-male aggregations

There was no change in an elephant’s probability of directing a trunk-to-SEO behaviour over the time course of his stay at a hotspot, nor any evidence that elephants directed these behaviours more upon their initial arrival at hotspots (Table 4.9, Figure 4.6).

Table 4.9: Output of GLMM: likelihood of an elephant directing a trunk-to-SEO behaviour to conspecific during a 10-minute focal follow predicted by different time conditions that the follow represented within the focal's full hotspot visit.

Predictor	**Coefficient**		**aOR (+95% CI)**	**P**
Intercept	-1.202		0.301 (0.175-0.516)	**<0.001**
% Time progression within total focal follow	< - 0.001		1 (0.993-1.009)	0.815
Is first 10-minutes of full focal follow	No	*Ref*	*Ref*	
	Yes	-0.510	0.600 (0.346-1.041)	0.069
Is last 10-minutes of full focal follow	No	*Ref*	*Ref*	
	Yes	-0.385	0.680 (0.380-1.217)	0.194

The percent of time progressed within a focal follow that a particular 10-minute follow occupied did not predict likelihood of a trunk-to-SEO behaviour being performed by a focal. There was no difference between likelihood of focals directing trunk-to-SEO behaviours to conspecifics in their last 10-minutes at hotspots, compared to earlier 10-minute follows, nor in their first 10-minutes at hotspots compared to later follows. Focal ID included as random effect.

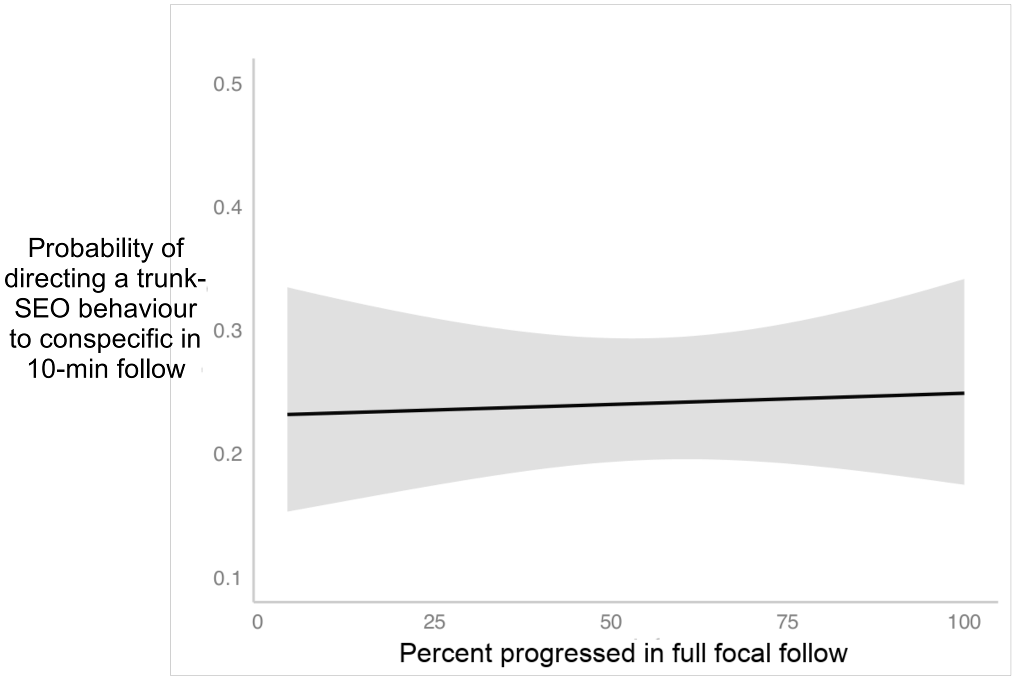

Figure 4.6: There was no change in a focals probability of directing a trunk-to-SEO behaviour to a conspecific over the course of his stay at a social hotspot. The percent of time progressed within a focal follow that a particular 10-minute follow occupied did not predict likelihood of trunk-to-SEO behaviours being performed by focals (aOR (95% CI)= 1 (0.993-1.009), p = 0.815).

Whether an elephant arrived at the river in a group with the subject elephant, or whether the subject was exposed to an elephant as a new potential interactor at the river did not predict the likelihood of the subject directing a trunk-to-SEO behaviour to him (Permutation-based likelihood ratio test of GLMM, χ2 (1) = 0.135, p = 0.107; Figure 4.7). The observed odds of targeting new individuals with trunk-to-SEO behaviours compared to elephants arrived with at the river fell within the range predicted by random assignment of behaviours to elephants present for all age classes of focal elephants (**Supplementary Information 3**; Figure S3.2).

Considering the organs targeted with trunk-to-SEO behaviours individually, whether an elephant arrived at the river in a group with the subject elephant, or whether the subject was exposed to an elephant as a new potential interactor at the river did not predict the likelihood of the subject directing his trunk to a target's mouth (Permutation-based likelihood ratio test of GLMM, χ2 (1) = 0.120, p = 0.116; Figure 4.7), temporal glands (Permutation-based likelihood ratio test of GLMM, χ2 (1) = 0.535, p = 0.525, Figure 4.7) or genitals (Permutation-based likelihood ratio test of GLMM, χ2 (1) = 0.868, p = 0.843, Figure 4.7). Elephants directed all trunk-to-SEO behaviours to elephants met new at aggregations as predicted by random assignment of these behaviours to elephants present in the social hotspot environment (Table 4.10).

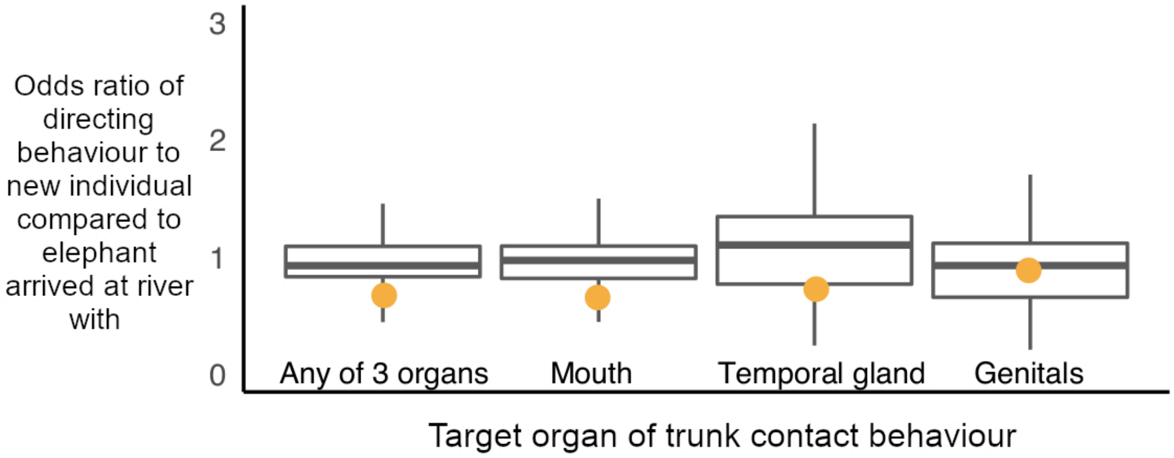

Figure 4.7: Observed odds ratio of directing trunk-to-SEO behaviours to new individuals encountered at the river compared to individuals the subject arrived with during a social hotspot visit (orange circles), plotted against the randomly permuted odds ratios of directing a trunk-to-SEO behaviour to elephants met new compared to arrived with at hotspot (boxplots with median, interquartile range, minimum and maximum values). Elephants directed trunk-to-SEO behaviours to new elephants as predicted by random assignment of behaviours to elephants present during a social hotspot visit (Permutation-based observed odds ratios:

trunk to any of 3 organs (trunk-to-SEO) = 0.711, p= 0.182; trunk-to-mouth= 0.693, p= 0.145; trunk-to-temporal-gland= 0.770, p= 0.521; trunk-to-genitals= 0.929, p= 0.947 (Table 4.10 for randomised 95% confidence intervals)).

Table 4.10: Observed odds ratios and permutation-based significances of elephants targeting an elephant met new at the river relative to elephant arrived at river with, with trunk-to-SEO behaviours of different target organs.

Behaviour directed to conspecific	**Observed odds ratio of directing behaviour to new elephant relative to elephant arrived at river in a group with**	**95% CI randomised odds ratios**	**Randomised P**
Trunk-to-SEO behaviours (all 3 target organs combined)	0.711	0.642-1.457	0.182
Trunk-to-mouth	0.693	0.621-1.500	0.145
Trunk-to-temporal-gland	0.770	0.472-2.141	0.521
Trunk-to-genitals	0.929	0.477-2.185	0.947

4.5 Discussion

Adolescent male elephants directed trunk-to-SEO behaviours to conspecifics at higher rates than adult elephants did. Adolescents are more likely to be recently dispersed from their natal herd (Lee et al., 2011), and they may use trunk-to-SEO behaviours for obtaining information about other males in the male social network, including identities of individuals (Johnston, 2008), and relative dominance rank (Ganswindt et al., 2002; Rasmussen & Wittemyer, 2002), whereas adults that may be more established and stable in the social network and hence have less need to perform these investigatory behaviours (Murphy et al., 2019). Similarly, adolescent males are more sociable in general than adults (Evans & Harris, 2008), and may perform more of these trunk behaviours to assist in establishing new contacts and facilitating further affiliative interactions with social companions, a pattern also seen in other species that perform greeting behaviours (Colmenares et al., 2000). Adolescent male African elephants also assess urine cues of conspecifics in the environment at greater rates than adults (Schulte et al., 2012). As part of the intense learning that is undergone in adolescence, adolescents may need to map phenotype features as well as individual identities (there is evidence elephants hold long term memory of individuals by their unique chemical signatures (Buss et al., 1976; Rasmussen, 1995; Bates et al., 2008)) of particular same-sex conspecifics to their corresponding chemosignals via close contact olfactory assessments (trunk-to-SEO behaviours). In other words, as part of the recognition process, adolescents may need to learn which olfactory features belong to which individuals and phenotypes when forming mental templates, whilst adults may have already learnt this (Sherman et al., 2003; Brennan & Kendrick, 2006).

However, of the organs targeted, adolescents only directed trunk-to-SEO behaviours to the mouth at greater rates than adults. Trunk-to-genitals and trunk-to-temporal-gland behaviours appeared to be equally important to elephants of all ages. African elephant calves and juveniles commonly place their trunks in the mouth of their mothers and other females in their natal families as a conciliatory gesture, or to solicit, sample or steal food items (Lee & Moss, 1999; 2011; Poole et al., 2011). Among females in female groups, trunk-to-mouth is the most common component of affiliative interactions (Poole & Granli, 2021) and adolescent males may continue to perform this familial behaviour post dispersal, with the rate declining with age as the male adopts more adult male behaviour. Furthermore, since only trunk-to-mouth behaviours were influenced by the age class of our subjects, it is possible that trunk-to-genitals and trunk-to-temporal-gland behaviours may communicate information on different aspects of phenotype, or as tactile and gestural signals may be used to communicate divergent social messages to that of trunk-to-mouth behaviours. Similarly, in rats, facial sniffing is thought to be an appeasement signal, but not genital or flank sniffing (Wesson, 2013).

Our results suggest that at least in bull areas segregated from females, trunk-to-SEO behaviours are not primarily used for monitoring the sexual status of potential competitors, since none of the target organs were contacted at greater rates by breeding age adult males (adolescents are unlikely to be of a competitive age for mating (Hollister-Smith et al., 2007; Poole et al., 2011). Musth (and hence sexual) status, as well as proximity to transitioning to musth state, is believed to be signalled in the urine, temporal glands and breath, i.e. all the target organs (Rasmussen & Schulte, 1998; Rasmussen & Riddle, 2004; Rasmussen & Wittemyer, 2002), although receivers ability to detect musth has only been confirmed in urine (Hollister-Smith et al., 2008). Whilst adolescent males can show a particular interest in musth males, watching and following them, perhaps for learning of sex-specific behaviours (Personal communication, Reviewer 2), our later findings concerning mature males not being preferentially targeted with trunk behaviours to any organs suggests the individuals most likely to be transitioning to a sexual, musth state were not those preferentially targeted with trunk behaviours, providing further support for our argument that sexual assessment of same-sex conspecifics is not the prime motive of these behaviours.

Previous research found that the decline in olfactory investigation of urine cues in the environment from adolescence to adulthood in male African elephants is compensated for by adults only investigating relevant cues (Schulte et al., 2012). This was also supported in our study – most notably by the very low numbers of trunk-to-SEO behaviours being made of 10-15 year olds by adult males. These young adolescents are likely to represent both a low threat to adult males, as well as non-valuable social companions concerning learning opportunities or sparring partners. Similarly, the fact that young adolescents, 10-15 were less likely than all other ages to have their trunk-to-SEO behaviours reciprocated also suggests their low value as social contacts/ sources of information to age classes older than their own.

Alternatively, because with increasing age males have greater distances to their nearest neighbours on average (Evans & Harris, 2008), adults may perform less trunk-to-SEO behaviours simply because adult males had less opportunities to perform such close contact behaviours. Similarly, adult males may be less likely to engage in the intimate behaviours that provide opportunity for these trunk directed contacts to be performed. For example, trunk-to-mouth and trunk-to-temporal-gland behaviours were sometimes performed during sparring bouts, an activity engaged in more by adolescents than adults (Evans & Harris, 2008). However, the importance of these features seems small considering only trunk-to-mouth behaviours were affected by age. If lack of opportunities for close contact behaviours explained our results, we would also expect an influence of age class on trunk behaviours directed to the temporal glands and genitals, which we did not find.

In the current study, it was observed that when an elephant received a trunk-to-genital behaviour, he sometimes ceased movement and “allowed” himself to be assessed in the case where he was younger than the director of the behaviour. In contrast, where the targeted individual was an adult, and older or age-matched to the subject, trunk-to-genital behaviours were sometimes responded to with kick-backs and tail swatting behaviour to the subject, suggesting dominance related interactions occur alongside this behaviour. Trunk contacts directed to the mouth and temporal gland did not appear to trigger any dominance related behaviours between males and appeared to have a far more benign and mutual reception, and were performed in a variety of contexts from during drinking and feeding on riverbed substrate, to during sparring bouts. In a recently formulated ethogram of elephant behaviour and communication, a large emphasis was drawn to the multiple contexts in which trunk-to-SEO behaviours are performed (Poole & Granli, 2021). We suggest future studies consider the behaviours of elephants in the interaction immediately prior to and after the trunk-to-SEO behaviour is performed, as signals can vary in meaning depending on the context in which they are performed (Flack & de Waal, 2007).

All ages of elephants preferentially directed trunk-to-SEO behaviours to age-matched males at male-aggregations, except older adolescents, aged 16-20 years. If considering these tactile and olfactory behaviours as greeting behaviours between males, a suggested function may be that these behaviours are used to initiate and facilitate further association and interaction with partners, e.g. for future sparring activity, a behaviour important for testing and developing skills for competitive fighting (Miller & Byers, 1998). Males in many species, including African elephants, prefer to spar with age-matched individuals (Chiyo et al., 2011a; Granweiler et al., 2021). Alternatively, these greeting type behaviours may be used to assess individuals similar in dominance rank in a safe and ritualised context. Trunk-to-SEO behaviours may assist in discerning relative dominance through assessment of olfactory cues (for example levels of hormones and other volatile compounds that reflect social dominance, such as androgens like testosterone (Gosling & Roberts, 2001; Ganswindt et al., 2002; Rasmussen & Wittemyer, 2002) in otherwise similarly sized and strength matched individuals. Male hamadryas baboons *Papio hamadryas* also use greetings as an assessment strategy, with rivals matched in dominance and competitive abilities exchanging more greetings than those un-matched in competitive ability (Colmenares, 1991), and male mantled howlers *Alouatta palliata* are more likely to greet conspecific males close in dominance rank to themselves (Dias et al., 2008).

16-20 year olds targeted age-matched males with trunk-to-SEO behaviours within the range predicted by random chance. In addition, 16-20 had the lowest odds of directing these behaviours to age-matched compared to non-age-matched males out of all the 4 age classes. This may represent a widening of interests concerning beneficial social partners in late adolescence, and a period where elephants are not so focused on peer specific relationships, and are less selective of who they target for obtaining information on or initiating interaction with. This compliments findings of Chiyo et al. (2011a), that found whilst adult age classes of African elephants associated with age-mates preferentially, adolescents associated with their own age class at random. Alternatively, this result may reflect the fact that age was recorded categorically rather than continuously. Elephants at the older end of 16-20 years may be closer in age (hence better “age-matched”) to the youngest individuals in the category 21-25 years than to some members of their own age class, and vice versa, elephants at the younger end of 16-20 years may be closer in age to the oldest individuals in the 10-15 years category than to some members of their own age class. In this way, elephants within the 16-20 year old class may have experienced a diffusing of the effect of targeting age-mates with trunk-to-SEO behaviours. At least that is in comparison to the youngest (10-15 years) and oldest (26+ years) age classes, who are only affected on one end of their category by the possibility that a similar aged interactor is in fact categorised into an adjacent age category. However, by this logic, elephants aged 21-25 years would also direct trunk-to-SEO behaviours to age-matched males as random chance, which we did not find. Regardless, future study may wish to consider age as a continuous variable, with age-match status measured continuously as absolute age difference, to avoid such uncertainty with interpreting results.

The oldest elephants at all-male aggregations at social hotspots were not preferentially targeted with trunk-to-SEO behaviours by younger males. This suggests male African elephants are not primarily using these trunk behaviours to initiate contact with or obtain information such as identity and feeding history from older, more experienced individuals that may be high value social partners. Furthermore, these behaviours do not appear to be appeasement gestures directed to dominants (Preuschoft, 1999). Despite a preference to maintain close proximity to older males (Evans & Harris, 2008), we found no evidence that

African elephants preferentially targeted them with trunk-to-SEO behaviours, suggesting males learn from older, experienced males via other modalities and not close contact trunk-to-SEO behaviours. We recommend exploring whether more “eavesdropping” type methods are used for learning from older males (Bonnie & Earley, 2007). Visual cues (observing older males), and auditory cues (listening to older males) may be more likely to be important modes of inter-generational social learning in male African elephants (Langbauer, 2000; Soltis et al., 2005; McComb et al., 2011b).

Finally, contrary to our hypothesis, males did not preferentially target new social companions met at the hotspot compared to those they had been seen to have been associating with, having arrived in a group together to the hotspot, with trunk-to-SEO behaviours. Trunk-to-SEO behaviours thus do not seem to be primarily used by male African elephants as a way to peacefully initiate contact between, or obtain information on, unknown individuals, or individuals that have been separated for prolonged periods of time in this fission-fusion society (Aureli & Schaffner, 2007; Dias et al., 2008). Additionally, over the time period of an elephant’s stay at the river, there were no changes in his probability of performing these behaviours, suggesting trunk-to-SEO behaviours are general, continuous olfactory assessments and/ or tactile contacts between individuals sharing the same ecological space. This is in stark contrast to the vivid and high-energy reunion events that can occur at fusion events of female African elephants in family groups (Poole & Granli, 2021). If viewed as a greeting behaviour, the performance of these trunk-to-SEO behaviours better matches the putative function for spatially tolerant gregarious males of testing willingness to interact, facilitating positive relationships, and assessing aspects of phenotype of same-sex conspecifics (Dal Pesco & Fischer, 2018; De Marco et al., 2014).

4.6 Conclusions

In this chapter I explored the choices male African elephants make regarding the individuals targeted with trunk-to-SEO behaviours as an indicator of their potential function in this highly fission-fusion male society. In this male dominated area, it is unlikely males primarily use trunk-to-SEO behaviours to assess reproductive condition of potential competitors. Trunk-to-mouth behaviours were performed more often by adolescent than adult subjects, and likely communicate different information between signaller and receiver than trunk-to-genitals and trunk-to-temporal-gland behaviours. Male African elephants of all ages, apart from older adolescents, preferentially targeted age-mates for trunk-to-SEO behaviours, and I found no evidence that males directed trunk-to-SEO behaviours preferentially to less familiar individuals at social hotspots. My results suggest male African elephants may use trunk-to-SEO behaviours to facilitate further positive interaction with other males, or to assess aspects of phenotype (such as relative dominance) between males generally occupying the same ecological space, rather than as a benign “first contact” or “reunion” signal directed at novel partners.

Furthermore, I found no evidence that males preferentially directed trunk-to-SEO behaviours to older males, suggesting the function of such behaviours is not primarily for facilitating contact with, or obtaining information from informed, experienced individuals. For future study concerning social learning from older to younger male elephants, I recommend pursuing research techniques concerning younger males watching or listening to older males.

Chapter 5: Field Evidence Supporting Monitoring of Chemical Information on Pathways by Male African Elephants

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Author contributions: CRBA conceived the study, conducted field work, data extraction, statistical analysis and was the lead author in drafting the manuscript. DPC and LJBN participated in study design, statistical analysis and critically revised the manuscript. TM conducted field work.

5.1 Abstract

When animals move along well-established pathways, sensory cues along the path may provide valuable information concerning other individuals that have used the same route. Yet the extent to which animals use pathways as sources of public social information is poorly understood. Here we quantified the responses of wild African elephants, *Loxodonta africana*, to olfactory information along natural elephant pathways, habitual routes that link predictable critical resources in the environment. By monitoring the behaviour of elephants travelling on pathways in a predominantly male study population, we found that elephants were highly olfactorily responsive to pathway substrate. Lone travellers were more responsive than elephants travelling in groups, suggesting elephants without social companions may be more dependent on olfactory cues on pathways during navigation. Furthermore, by experimentally presenting olfactory urine cues on pathways we provide evidence that male African elephants exhibit focused olfactory responses to urine cues of same-sex conspecifics for at least 48 hours from time of deposition, and found that urine from adult elephants was more likely to elicit vomeronasal system responses compared to adolescent urine. African elephants may therefore potentially be able to discern the age of individuals they can expect to encounter in the environment from remote urine deposits on pathways. We suggest elephant pathways act as a public information resource, assisting navigating elephants via the deposition of urine and dung by previous travellers on the route. These results could help inform elephant management, which may manipulate olfactory information on pathways in high human-wildlife conflict areas, or could use olfactory urine cues to improve the efficiency of corridors that link protected areas for elephants.

5.2 Introduction

Detection and use of olfactory information produced from conspecifics is a widespread and ancient adaptation in mammals (Eisenberg & Kleiman, 1972; Eisthen, 1997). Olfactory products can be classified as signals when they have evolved for the purpose of communication, hence evoking adaptive behavioural changes in the receiver (Maynard Smith & Harper, 2003), or as cues when the products have not evolved for the purpose of communication but are still used by conspecifics to guide behaviour (Thomas, 2011). Such cues can act as public social information, potentially assisting conspecifics in acquiring useful information regarding, for example, habitat selection and foraging decisions (Deutsch & Nefdt, 1992; Galef, 1990; Danchin et al., 2004; Bonnie & Earley, 2007).

In mammals, compounds present in urine can provide conspecifics with information on a range of phenotypic traits including sex, dominance, reproductive state, stress level, and even individual identity (Laska & Hudson, 2010; Rajagopal et al., 2010; Nodari et al., 2008; He et al., 2008; Bates et al., 2008). In many species, both the main olfactory system and vomeronasal system are involved in the detection of pheromones and other odorant molecules present in urine (Verberne, 1976; He et al., 2008; Tirindelli et al., 2009). Similar to visual information left behind by conspecifics, olfactory cues and signals have a greater potential to be long lasting in comparison to tactile and auditory information, remaining after an individual has departed and long after the information was first created (e.g. visual cues can assist in habitat copying of nesting sites, Parejo et al., 2005). Furthermore, in comparison to other sensory informing modalities, olfactory information can convey more information concerning an individual's phenotype in the absence of the depositor, as well as potentially information about the depositor's proximity, due to microbially-mediated modifications to compounds over time, or slow releases of molecules from carrier proteins (Albone et al., 1977; Hurst et al., 1998; Archie & Theis, 2011). However, despite its importance to many mammals, the potential of olfactory information as a tool in wildlife conservation and management remains relatively untapped (Campbell-Palmer & Rosell, 2011), which may reflect both methodological challenges and perhaps researcher bias (Heymann, 2006).

The African elephant (*Loxodonta africana*) has the largest olfactory receptor gene repertoire of any species reported to date (Niimura et al., 2014). Elephant species indisputably have remarkable olfactory abilities, with the Asian elephant (*Elephas maximus*) able to discriminate odours differing in only one carbon chain length and retain information of the identity of trained odours 16 weeks after exposure (Arvidsson et al., 2012). A primary use of the highly developed olfactory sense in elephants is in locating critical ecological resources such as water, as well as for habitat and food selection (Plotnik et al., 2014; Rasmussen & Krishnamurthy, 2000). Furthermore, behavioural studies both in captivity (Meyer et al., 2008; Rasmussen & Schulte, 1998) and in the wild (Schulte et al., 2012; Bates et al., 2008), provide evidence for an extensive use of chemical cues and signals in elephant social communication. For example, the continuous urine dribbling during musth (a temporary heightened sexual state experienced by mature adult male elephants (Poole 1987, **1.3.1**)) contains compounds signalling sexual status, with males able to discern musth from non-musth urine (Hollister-Smith et al., 2008), and female African elephants monitor the location of family members in relation to themselves from urine deposits (Bates et al., 2008). In the wild, male African elephants are often observed making olfactory assessments of conspecifics genitals, temporal gland secretions and breath (Poole & Granli, 2011; **Chapter 4**). Similarly, focused olfactory responses are often directed toward sources of scent in communal areas, with males investigating dung and urine more than females (Loizi et al., 2009). This may be because for polygynous males such as elephants, both odors from females (to assess reproductive receptibility) and males (to assess potential competitors) may be of interest (Merte et al., 2010). The chemical composition of urine from wild male African elephants is known to change with age and maturity, younger male urine is characterised by high levels of acids and esters, and older males by alcohols and ketones (Rasmussen & Wittemyer, 2002). For male African elephants, olfactory assessment of the urine cues of same-sex conspecifics, may therefore provide important information about the age, reproductive status and location of potential competitors and affiliates (LaDue et al., 2018; Hollister-Smith et al., 2008).

Elephant pathways, regular routes utilised by elephants that connect valuable, predictable resources such as feeding sites and waterholes (Von Gerhardt et al., 2014; Mutinda et al., 2011), are multifunctional in elephant ecology, assisting in both improved usage of the environment, and possibly providing an opportunity to monitor conspecifics that have previously utilised the route through their urine and dung deposits (Mutinda et al., 2011; Croze & Moss, 2011). In a previous study on African elephant pathways, Shannon et al. (2009) found that the most heavily used pathways were characterised by the presence of dung piles every 10-50 m. It is also estimated that elephants produce between 45-60 litres of urine daily, in bouts of 5-11 litres at a time (Miller, 2006; Benedict, 1936). As a result, elephants are likely to continuously encounter urine and dung deposits from previous users of a pathway, which may provide a valuable source of social information. Indeed, it has been previously proposed that elephant pathways act as sources of public information, potentially allowing for remote communication between individuals or groups concerning age, identity, sexual state, or quality of previously used habitat (Mutinda et al., 2011). However, to date no in-situ experiments have been conducted that investigate the sensory responsiveness of male elephants to olfactory cues on elephant pathways, or that quantify their ability to discern the phenotypes of the animals leaving urine deposits.

Here we use an in-situ experiment to examine the importance of olfactory cues as inadvertent public social information on well-established pathways that are a characteristic of many mammal species (Edelstein-Keshet, 1994; Able, 1981; Jamon, 1994). Specifically, we asked whether passing elephants respond to the olfactory cues of conspecifics on elephant pathways, and whether their responses differ depending on the receiver's age and social condition, as well as the age of the conspecifics who's cues they encounter. First, we quantified the general olfactory responsiveness of male African elephants traveling along elephant pathways. We quantified how general olfactory responsiveness is influenced by the age class (adolescent/ adult) of the focal individual, predicting that adolescents and adults will have divergent levels of olfactory responsiveness. Owing to their greater age, adults may be more experienced at utilising elephant pathways effectively and thus more responsive to olfactory information compared to adolescents. Alternatively, adolescents may be more responsive, in line with previous research on male elephant olfactory investigations of urine at waterholes that found that olfactory investigation peaked in adolescence and receded in adulthood (Schulte et al., 2012). We also hypothesized that social factors, such as whether the subject elephant is travelling alone or in an all-male group, and spatial position within a travelling group will influence olfactory responsiveness, predicting that elephants traveling in all-male groups, and those not at the front of groups would be less responsive to olfactory cues. Elephants travelling in groups, and following behind other travellers, may depend more on other group members to detect threats, or to navigate pathways using olfactory information, similar to the tendency of many group living vertebrates to reduce vigilance behaviours in larger groups (e.g. Tibetan antelope, *Pantholops hodgsonii* (Lian et al., 2007); ring-tailed coati, *Nasua nasua* (Di Blanco et al., 2006)), and to depend on informed leaders during group movements (resident killer whales, *Orcinus orca* (Brent et al., 2015); whooping cranes, *Grus americana* (Mueller et al., 2013)).

Second, we quantified how male elephants monitor fresh urine cues from other males of different age classes (adolescent and adult males). We predicted olfactory information from elephant urine samples, compared with a water control, will last longer in the environment, indicated by continuing to elicit focused olfactory responses from passing elephants for longer since being deposited. While elephants may first respond to water controls due to the odour of water, to which elephants are highly sensitive (Plotnik et al., 2014; Ramey et al., 2013), and potentially due to the visual stimulus of a darkened spot of sand, we predicted these responses will diminish as water dries up over time, whereas urine samples will continue to emit odours that elicit responses even when dried. We predicted responses to adult and adolescent urine will be differentially affected by time because the chemical profiles of urine from males of different developmental stages are expected to be different (Rasmussen & Wittemyer, 2002), which may affect microbial action and the release of odorous chemicals over time (Goodwin et al., 2012). Moreover, concerning vomeronasal system responses (indicative of heightened interest in samples) we predicted age class of the receiver will influence an elephant's likelihood of responding to urine deposits, as the information contained within chemical cues, as well as their detection ability and relevance, varies with the condition of both the depositor and the receiver (Schulte et al., 2007). We also hypothesized that urine carries information concerning the depositor's age, and that adolescent and adult urine will elicit different levels of vomeronasal system responses in receivers. Urine is likely to be a largely honest indicator of depositor characteristics, such as age (Schulte et al., 2007), as chemical cues in urine are directly linked to phenotype and physiological condition (Gosling & Roberts, 2001). We tested these hypotheses through a bioassay protocol, using readily observable responses to urine samples to discern chemical reception of the receiver to the deposits of varying depositor characteristics in a natural context (Mackintosh, 1985).

5.3 Methods

In-situ bio-assay design

Data collection was conducted between October 2017 – September 2018, in MPNP, Botswana, from camera traps, as described in **1.6.4**. We exploited the tendency of male elephants to habitually walk along identified elephant pathways in the MPNP (Figure 1.1 & 1.4) to create an in-situ bio-assay, whereby passing elephants were exposed to purposefully placed urine of donor elephants positioned on the main path (Figure 1.4).

Cameras, set to record video, were placed on 2m high poles positioned 9m away, at an angle of 45°, on either side of a central “presentation zone” measuring 1m in length along the pathway. During different trials, samples were presented at random points within this presentation zone. By placing a camera facing inwards on either side of the sample, head on footage (essential for aging and identification purposes), as well as an unobscured view of responses to pathways and samples, was available for both elephants walking towards and away from the river.

Trial type consisted of either no sample, a male elephant urine sample (from an adolescent or adult elephant), or a water control sample presented (see sample collection below). For our first hypothesis we wanted to explore the general olfactory responsiveness of elephants to the pathway substrate. To do so, we observed the behaviour of elephants traveling on pathways, exposed to no sample. We monitored the olfactory responses of elephants to a fixed point within the presentation zone, the location of which was assigned randomly per trial. Responses were scored based on an ethogram of olfactory responses (Figure 5.1; Table 5.1). For later hypotheses concerning the responses of male elephants to fresh urine cues, we presented male elephant urine samples, or water control samples within the presentation zone, and scored elephant’s responses to the sample (Table 5.1).

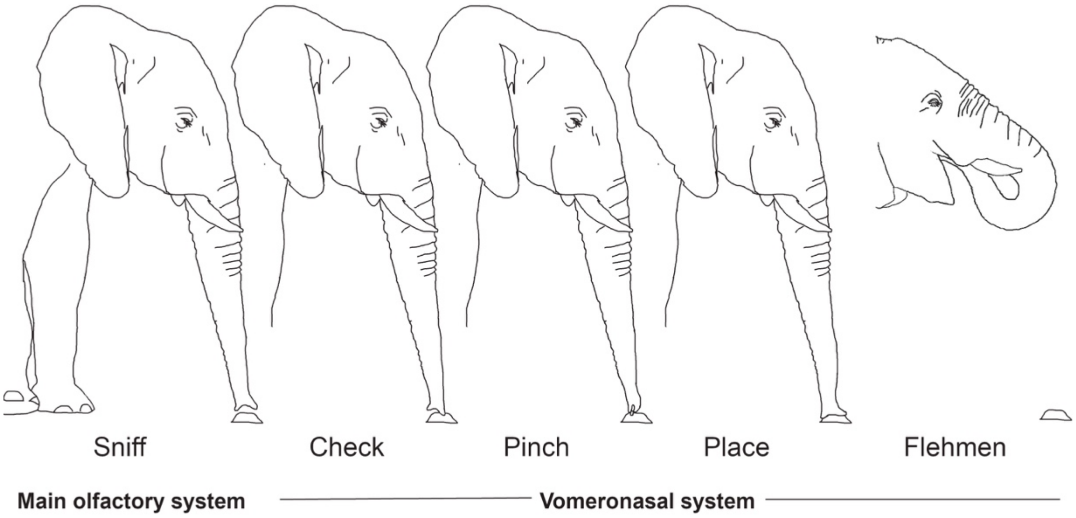


Figure 5.1: Example images of focused olfactory responses performed by elephants to samples in the study.

Table 5.1: Ethogram of olfactory responses to elephant pathway substrate and presented samples. Assembled using information from Schulte et al. (2005), Poole & Granli (2011), as well as our own observations. Elephants detect odorant molecules and pheromones through both the main olfactory and vomeronasal system (Schulte et al., 2005; Lledo et al., 2005). The trunk acts as the key organ both for detecting airborne chemical compounds (main olfactory system), as well as for physically transporting less volatile chemicals of heightened interest to the vomeronasal organ, in the dorsal anterior roof of the mouth (vomeronasal system) (Rasmussen et al., 1982; Schulte et al., 2005). A supplementary video is available online demonstrating examples of responses (**Supplementary Information 4**; Note S4.1)

	Response	Behaviours included	Description
Non-olfactory	**None**	Trunk drag	Dragging trunk along pathway substrate
		Trunk suck	Sucking trunk
		Trunk swing	Swinging trunk
		None – other	Trunk held in other postures not indicative to be for the purpose of olfaction. E.g. Two “fingers” of trunk held clenched, trunk rolled up, pulling ear, trunk held floppy etc.
		Periscope	Holding the trunk raised above head in an ‘S’ shape, for detection of airborne scents. Whilst indicative that elephant is using olfactory information – focus is not principally to the pathway substrate
		Hover ahead	Holding trunk ahead in a posture indicating response to olfactory information, but not directed at the pathway substrate in particular. Also includes observed posture to curl trunk over at tip to point ahead
Non-focused olfactory	**General olfactory response to pathway substrate.** **(main olfactory system)**	Tracking	The trunk is held either with the anterior “finger” directed at the ground, or with the entire surface of tip of the trunk (nasal openings) hovering flat over the ground surface. The trunk moves continuously “tracking” the surface of the pathway (no physical contact), with no suspended movement or focused response to any particular point on the pathway
		J sniff	The trunk is held in a sniff posture just above the ground substrate, with the trunk curled towards the elephant at the tip in a “J” shape, with no suspended

			movement or focused response to any particular point on the pathway
Focused olfactory	**Sniff** **(main olfactory system)**	Sniff	Trunk nasal openings purposefully point toward the sample in an extended sniff posture. The trunk is held focused over the sample substrate, rather than moving continuously with the natural gait of the elephant. Elephant may seize movement and continue smelling sample, however no physical contact made (Figure 5.1)
	Accessory trunk behaviours **(accessory behaviours)**	Trunk shake	Rapid “wriggling” of the trunk up/down or side/side, proposed to be for purpose of clearing nasal pathways to improve olfaction
		Blow	Forced exhalation through the trunk, often audible with substrate visibly scattered by force. Proposed to be for purpose of clearing nasal pathways to improve olfaction
	Pre-flehmen & flehmen behaviours **(vomeronasal system)**	Check	Placing the trunk anterior “finger” in physical contact with the sample substrate (Figure 5.1)
		Pinch	Pinching the sample substrate between the two trunk “fingers” (Figure 5.1)
		Place	Placing the entire tip of trunk nasal opening surface flush with the sample substrate (Figure 5.1)
		Flehmen	Subsequent to physical contact with the sample substrate, curling the trunk into the mouth to touch the vomeronasal organ on the roof of the mouth (Figure 5.1)

A total of 665 responses were recorded from male elephants traveling alone or in all-male groups along elephant pathways (123 lone travellers, 542 elephants in 186 groups; group determination methodology as in **Chapter 2**; Figure 2.1). Within this dataset, all individuals were uniquely identified (*N* individuals=594), and age classes assigned to elephants following **1.6.2**, to the resolution of adult and adolescent. The supplementary materials provide a summary of distribution of sample sizes by age, social grouping, and climatic variables (**Supplementary Information 4**; Figure S4.1, Table S4.1). Elephants that were not walking in single file on the main pathway (Figure 1.4; Table 1.1) were not included for analysis as they did not pass over samples, however their presence was accounted for concerning the grouping condition and position of any group-mates whose responses were captured.

Seven responses were from elephants identified to be in musth (Poole, 1987), but due to their low numbers (1.05% of total responses) we included these responses in analysis. An additional 11 mixed-sex groups were recorded containing a total of 26 females and 8 calves/ juveniles, these groups were removed from analysis. We did however test for any significant effect on olfactory responsiveness of elephants to pathways in the case that a musth male, or female had walked on the pathway before them in a given trial. This was to account for musth male urine dribbling and elephants' known ability to detect musth males by odour (Hollister-Smith et al., 2008; Poole, 1989), and observation that males monitor female urine cues for estrous state (Poole & Granli, 2011; Bagley et al., 2006), which both may influence olfactory responsiveness to pathways.

Urine samples were collected from age-classed male elephants aggregating along the Boteti River in MPNP. When an elephant was observed urinating, a timer was started and a sample of urine-soaked sand was collected within 20 min of urination (time taken from beginning of urination to fridge: mean = 13 min 2 s, SD = 2 min 58 s, range 7min 25 s-20 min). In an attempt to standardize the hydration state of elephants, only elephants that had been observed drinking at the river <1 h prior to urinating were chosen as donors of urine. No urine samples were taken from elephants identified to be in musth. In all cases of sample collection there was no evidence that another elephant had recently urinated at the same site, i.e. no dung boli were present (elephants mostly defecate when they urinate) or hardened flattened substrate indicative of previous urination.

Urine-soaked sand was collected using disposable latex gloves, and stored in sterile disposable storage containers in volumes of 2 litres. An abundance of substrate was always available, but collection focused on the most heavily saturated region of sand around where the penis rested just above the ground. For water control samples, we poured water from the river over sand and waited under 20 min before storage (mean = 11 min 38 s, SD= 3 min 26 s, range 7 min 3 s – 19 min). River water was used as a control as opposed to distilled water, which was unavailable in the field. Previous research on elephants' olfactory abilities have used vanilla extract as a positive control (Hollister-Smith et al., 2008; Schulte et al., 2007). However, for the current study, this approach was deemed inappropriate since the field site is a protected area and we were not permitted to introduce foreign material to the environment. Elephants were observed urinating on both the bank slope and the sand by the river edge. Because the two sand types differed in initial colour, consistency and water saturation level, we collected water control samples from the two sand types at random (number of samples of urine: bank slope= 22, river edge = 26; number of water control samples: bank slope = 11, river edge = 12). All samples were immediately stored at 4 °C in a car fridge, to slow microbial metabolic processes involving the compounds found in urine (Goodwin et al., 2012). In 50% of trials, samples were stored overnight and laid on pathways at dawn the next day, and in 50% of trials collected samples were presented the same day before sunset. This allowed us to expose both elephants travelling at night and during the day to the 'freshest' samples. When laid on the pathway, the sample was approximately 20 cm in length and 25 cm in width.

Because the likelihood of a male exhibiting a focused olfactory response to a sample was not predicted by different treatments of the samples prior to presentation (sand type, time spent in fridge, average temperature recording in fridge; Table 5.2), we could be confident that variation in sample treatment did not affect our results.

Table 5.2: Output of GLMM: likelihood of elephants exhibiting a focused olfactory response to a sample, predicted by the sample's treatment prior to presentation on pathways. Elephant ID and pathway number are included as random effects.

Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-0.073	0.929 (0.514–1.680)	0.808
Sand type	Bank sand	*Ref*	*Ref*	
	River edge	-0.143	0.867 (0.607–1.238)	0.432
Time in fridge		-0.0002	1 (0.999 – 1)	0.340

Average temperature at which sample kept	-0.045	0.956 (0.889–1.029)	0.228

Removal of Samples Between Trials

Trials were run for 48 h from the initial deposit of samples (or the first activation of camera traps when no sample was presented). At the end of trials, samples were carefully removed with a shovel from the presentation zone, collected in a disposable bag and removed from the experimental area. A thin, fresh layer of uncontaminated sand from the area around the pathway was then thrown lightly over the presentation zone, again using a shovel to be sure that no human contact was made with the substrate.

Some elephant pathway routes are thought to persist for decades (Haynes, 2006), and some of the pathways used in this study appear not to have moved since satellite imagery began in the area in 2004 (Personal observation; GoogleEarth, n.d.). It is therefore likely that the stretches of pathway sampled have historically had dung or urine deposited on them by elephants, giving the potential for odour residue. Indeed, a key hypothesis of our study is that trail maintenance and repeated travel on pathways is in part due to such historical chemical deposits (Blake & Inkamba-Nkulu, 2004; Mutinda et al., 2011). For the current study, however, we only chose stretches of pathway for our experimental set-up that were free of signs of fresh urine, or fresh, intact dung boli (Hedges et al., 2012). Successive trials were run on the same stretch of pathway (i.e. the number of samples previously presented and removed within the presentation zone varied between trials, to a maximum of nine samples) making it possible that elephants could increase responsiveness due to detection of urine cues from multiple individuals at the same location. However, olfactory responses from elephants were not predicted by the number of previous samples presented at a camera trap set-up, nor by a binary effect of whether a sample had or had not previously been laid and removed (Table 5.3). This suggests that the methods used for removing samples between trials was effective, and olfactory stimuli were not carrying over significantly between trials.

Table 5.3: Output of GLMMs: likelihood of elephants exhibiting olfactory responses to pathway, predicted by factors relating to number of samples previously presented at the camera trap set-up. Elephant ID and pathway location are included as random effects.

GLMM dependent variable	**Predictor**		**Coefficient**	**aOR (+95% CI)**	**P**
General olfactory response paid to pathway	Intercept		0.936	2.550 (1.197-5.435)	**0.015**
	Number of previous samples laid at camera trap set up		0.084	1.087 (0.957-1.235)	0.197
	Sample has been presented previous (binary)	No	*Ref*	*Ref*	
		Yes	-0.227	0.797 (0.332-1.910)	0.611
Elephant pauses to smell areas other than presentation zone	Intercept		-2.833	0.059 (0.018-0.188)	**<0.001**
	Number of previous samples laid at camera trap set up		0.097	1.102 (0.902-1.347)	0.342
	Sample has been presented previous (binary)	No	*Ref*	*Ref*	
		Yes	-0.180	0.835 (0.161-4.331)	0.830

Statistical analysis

Responses were scored in line with the ethogram (Table 5.1) in a blind procedure, meaning the identity of the sample was unknown to the scoring researcher. Behaviours were scored by one researcher (C.A.) to standardize scoring of behaviours. We ran generalized logistic mixed-effects models (GLMMs) where olfactory response was the dependent variable, with elephant ID and pathway location included as random effects in all models. The level of olfactory responsiveness was scored as elephants passed the presentation zone, with a binary score of 1/0 assigned to each behaviour performed (Table 5.1). Binary scores were assigned to behaviours (rather than, for example, duration of sniffs or number of vomeronasal system responses performed) due to a considerable right-skew in the distribution of the data set. If an individual elephant passed the same sample multiple times in the 48 h trial window, only the first response was considered. If an elephant was observed urinating or defecating in the camera frame, the trial was abandoned and the camera trap set-up relocated due to the potential influence of these fresher deposits on future passing elephants.

While it is theoretically possible that elephants detect chemical information with the trunk held in a variety of seemingly discrete postures (Poole & Granli, 2011), we focused scoring of responses on fixed behaviours and postures known to be indicative of an elephant using the olfactory sense (Table 5.1). ‘General olfactory response’ behaviours refer to an olfactory responsiveness to the pathway substrate, with no focus on a particular fixed point of interest. We first explored the extent to which male elephants showed general olfactory responses to the pathway substrate when no samples were presented, and whether age, grouping and position within groups affected these responses. For these GLMMs, the dependent variable was a binary 1/0 score whereby 1 represented a general olfactory response (‘Tracking’ and ‘J-sniff’ behaviours, Table 5.1) to a randomly preassigned point within the presentation zone (occupying the same volume as a sample, an approximately 0.2 m stretch of pathway), and 0 represented a non-olfactory response to this point (Table 5.1). We ran two GLMMs, (1) with age of receiver (adult/adolescent) and grouping condition (lone traveller/ in all male group) as the fixed effects and (2) with age of receiver (adult/adolescent) and position within the travelling group (leader/ middle/rear of groups) as the fixed effects. If an effect was identified as a significant predictor in either model, models were rerun to investigate any interaction between age class and grouping factors.

Second, we explored how the responses of elephants to the urine of different-aged male elephants changed over time since the deposit was laid, owing to the potency of cues fading, receivers losing interest or even new cues emerging due to microbially mediated processes (Goodwin et al., 2012). For these GLMMs, the dependent variable was a binary 1/0 score whereby 1 represented a focused olfactory response to the sample (i.e. the sample was the focus of the olfactory response in a manner that was distinct from the general olfactory monitoring of the pathway substrate, Table 5.1), and 0 represented either non-olfactory behaviour or a non-focused (general) olfactory response as the elephant passed over the sample (Table 5.1). Fixed effects in this model included sample type (adult urine, adolescent urine, water control), time since the sample was laid and the interaction between these two variables. In this model we switched the reference class of sample type, so that the effect of time could be explored in the three sample types separately, and pairwise comparisons could be made between sample types to explore the differential effect of time between sample types. Trampling on samples by previous passing elephants as well as other passing species may also affect the likelihood of response, and both were recorded and combined into a measure of trample rate. Trample rate also included physical contact made due to the accessory trunk behaviour 'Blow' and physical contact with the sample due to vomeronasal system responses (Table 5.1). Trample rate was found to have a weak positive correlation with time since a sample was laid (Spearman rank correlation: $r_S = 0.190$, $N = 454$, $P < 0.001$). Because time since a sample was laid had more relevance to temporal changes in olfactory cues, and therefore our question of interest, we included this variable instead of trampling rate in our model.

Lastly, we investigated whether vomeronasal system responses to urine deposits were influenced by age class interactions. For these GLMMs, the dependent variable was a binary 1/0 score whereby 1 represented vomeronasal system responses to the sample (pre-flehmen and flehmen behaviours, Table 5.1). Activation of the vomeronasal system is indicative of a heightened olfactory response to the sample, as opposed to a more general olfactory investigation (Rasmussen et al., 1982; Schulte et al., 2005). A score of 0 represented all other behaviours in the ethogram performed to the sample (Table 5.1). Fixed effects in these models included (a) age of the receiver (adult/ adolescent) and (b) sample type (adult urine, adolescent urine, water control), where again reference categories were switched to allow for pairwise comparisons between sample types.

5.4 Results

Lone travellers were more likely to pay general olfactory responses to pathways

With no samples presented on pathways, male elephants were still generally responsive to the pathway substrate, with 61.24% (*N* = 128/209) of passing elephants exhibiting general olfactory responses to the randomly assigned point on the pathway. Focused sniffs were only performed by 1.44% of passing elephants (3/209), accessory trunk behaviours by 0.5% (1/209), and no elephants were observed to perform pre-flehmen or flehmen behaviours when no sample was present. The likelihood of performing a general olfactory response to the pathway substrate was not predicted by season, temperature, wind level, whether the elephant was traveling in the day or night, or whether a musth male or female had walked on the pathway ahead of the subject elephant in the trial (Table 5.4).

Table 5.4: Output of GLMM: likelihood of elephants exhibiting general olfactory response to pathway predicted by various environmental factors. Elephant ID and pathway location are included as random effects.

Predictor		**Coefficient**	**aOR (+95% CI)**	***P***
Intercept		1.076	2.934 (0.390-22.074)	0.296
Temperature		-0.033	0.967 (0.904-1.035)	0.339
Season	Dry	*Ref*	*Ref*	
	Wet	0.277	1.320 (0.625-2.787)	0.467
Wind	No wind	*Ref*	*Ref*	
	Windy	0.131	1.140 (0.380-3.423)	0.815
Time of travel	Day	*Ref*	*Ref*	
	Night	-0.104	0.901 (0.323-2.517)	0.842
Musth male has passed in trial	No	*Ref*	*Ref*	
	Yes	-0.557	0.573 (0.152-2.154)	0.410
Female has passed in trial	No	*Ref*	*Ref*	
	Yes	0.679	1.971 (0.746-5.210)	0.171

There was no significant effect of subject age on the likelihood of an elephant exhibiting a general olfactory response to the pathway substrate (Age class adjusted odds ratio (aOR) adolescent compared to adult= 0.724, *P* =0.295; Table 5.5). There was, however, a significant effect of whether the individual was solitary or in a group, with greater probabilities of response in lone travellers compared to elephants traveling in all-male groups (Grouping aOR lone travel compared to all-male group travel= 5.039, *P* = 0.002; Table 5.5). Rerunning models to include interaction terms revealed that there was no interaction between grouping status and age, that is the effect of increased olfactory response when alone compared to when travelling in all-male groups was the same for both age classes. Whilst the effect of lone travel increasing the odds of paying a general olfactory response to a pathway was greater for adolescents (aOR lone travel compared to all-male group travel; adolescent as reference class=8.363, adult as reference class= 4.136), this difference in strength of effect was not significant (Table 5.5 for output of GLMMs; Figure 5.2).

Table 5.5: Output of GLMMs: effect of age and social grouping on the likelihood of elephants exhibiting a general olfactory response to pathway substrate.

Predictor		**Coefficient**	**aOR (+95% CI)**	***P***
Main effects model				
Intercept		0.492	1.636 (0.822-3.256)	0.161
Age class	Adult	*Ref*	*Ref*	
	Adolescent	-0.322	0.724 (0.396-1.324)	0.295
Grouping	Group travel	*Ref*	*Ref*	

	Lone travel	1.617	5.039 (1.808-14.046)	**0.002**
Interaction terms: adult as reference class				
Intercept		0.520	1.682 (0.853-3.316)	0.133
Age class	Adult	*Ref*	*Ref*	
	Adolescent	-0.379	0.685 (0.363-1.291)	0.242
Grouping	Group travel	*Ref*	*Ref*	
	Lone travel	1.420	4.136 (1.258-13.593)	**0.019**
Age class * Grouping	Adolescent *Lone travel	0.704	2.022 (0.177-23.065)	0.571
Interaction terms: adolescent as reference class				
Intercept		0.142	1.152 (0.598-2.221)	0.673
Age class	Adult	0.379	1.460 (0.775-2.751)	0.242
	Adolescent	*Ref*	*Ref*	
Grouping	Group travel	*Ref*	*Ref*	
	Lone travel	2.124	8.363 (1.00-69.982)	**0.050**
Age class * Grouping	Adult*Lone travel	-0.704	0.494 (0.043-5.640)	0.571

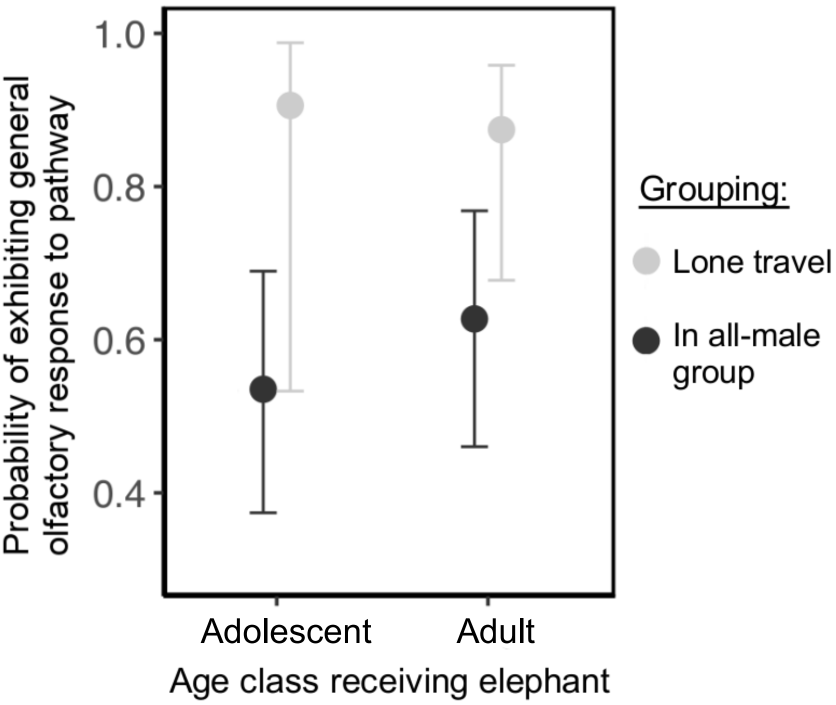


Figure 5.2: Probability of elephants of different age class and social grouping exhibiting general olfactory responses to pathway substrate when no sample was presented, with 95% confidence intervals indicated.

For elephants travelling in all-male groups, position within the group did not predict the likelihood of exhibiting a general olfactory response to the pathway substrate (Table 5.6).

Table 5.6: Output of GLMM: effect of age and position within group on the likelihood of elephants exhibiting a general olfactory response to pathway substrate. Elephant ID and pathway location are included as random effects.

Predictor		**Coefficient**	**aOR (+95% CI)**	***P***
Intercept		0.684	1.981 (0.823-4.771)	0.127
Age class	Adult	*Ref*	*Ref*	
	Adolescent	-0.360	0.698 (0.362-1.344)	0.282
	Leader	*Ref*	*Ref*	

Position in group	Middle	0.107	1.113 (0.513-2.416)	0.786
	Rear	-0.228	0.797 (0.343-1.850)	0.597

Elephants responded to experimental urine samples of urine and water differently over time

With time held constant at 0, adult urine had a greater probability of eliciting a focused olfactory response than adolescent urine (aOR adolescent urine compared to adult urine = 0.224, *P* = 0.003, Table 5.7), but not than the water control (aOR water control compared to adult urine= 1.363, *P* = 0.477, Table 5.7). Adolescent urine had the lowest probability of eliciting a focused olfactory response, significantly lower than both adult urine (aOR adult urine compared to adolescent= 4.463, *P* = 0.003, Table 5.7) and the water control (aOR water control compared to adolescent urine = 6.083, *P* <0.001, Table 5.7).

Over time, the water control rapidly decreased in its probability of evoking focused olfactory responses in passing elephants, with a significant “time since laid” coefficient of -3.013, *P* < 0.001 (Table 5.7, Figure 5.3). Probability of responding to adult urine remained more constant throughout the 48-hour sample time, with a shallower negative coefficient of -0.806, *P* = 0.012 (Table 5.7, Figure 5.3). Time since deposit was laid had no effect on probability of elephants exhibiting a focused olfactory response to adolescent urine, coefficient = 0.473, *P* = 0.284 (Table 5.7, Figure 5.3). The interaction between sample type and time since the sample was laid was significant in all pairwise comparisons, meaning all sample types were affected differently by time in its influence in predicting focused olfactory responses being made by elephants (Table 5.7; Figure 5.3).

Table 5.7: Output of GLMM: likelihood of elephants exhibiting focused olfactory responses to samples, predicted by sample type and time since sample laid, and interaction between both factors. Elephant ID and pathway location are included as random effects. Reference class switched to retrieve effect of time on likelihood of focused olfactory response being made to each sample type separately, and for pairwise comparisons between sample types regarding the effect of time on likelihood of response.

Predictor		**Coefficient**	**aOR (+95% CI)**	***P***
Reference class: water control				
Intercept		0.701	2.016 (1.015-4.002)	**0.045**
Sample type	Water control	*Ref*	*Ref*	
	Adult urine	-0.310	0.734 (0.312-1.724)	0.477
	Adolescent urine	-1.806	0.164 (0.063-0.428)	**< 0.001**
Time since sample laid		-3.013	0.049 (0.011-0.217)	**< 0.001**
Sample type * Time since sample laid	Adolescent urine * Time since sample laid	3.486	32.644 (6.420-165.978)	**< 0.001**
	Adult urine * Time since sample laid	2.207	9.089 (1.929-42.830)	**0.005**
Reference class: adult urine				
Intercept		0.391	1.478 (0.737-2.969)	0.271
Sample type	Water control	0.310	1.363 (0.580-3.203)	0.477
	Adult urine	*Ref*	*Ref*	
	Adolescent urine	-1.496	0.224 (0.084-0.595)	**0.003**
Time since sample laid		-0.806	0.447 (0.238-0.836)	**0.012**

Sample type * Time since sample laid	Adolescent urine * Time since sample laid	1.279	3.592 (1.271-10.150)	**0.016**
	Water control * Time since sample laid	-2.207	0.110 (0.023-0.519)	**0.005**
Reference class: adolescent urine				
Intercept		-1.105	0.331 (0.139-0.788)	**0.012**
Sample type	Water control	1.806	6.083 (2.337-15.829)	**< 0.001**
	Adult urine	1.496	4.463 (1.681-11.848)	**0.003**
	Adolescent urine	*Ref*	*Ref*	
Time since sample laid		0.473	1.604 (0.676-3.806)	0.284
Sample type * Time since sample laid	Adult urine * Time since sample laid	-1.279	0.278 (0.099-0.156)	**0.016**
	Water control * Time since sample laid	-3.486	0.031 (0.006-0.787)	**< 0.001**

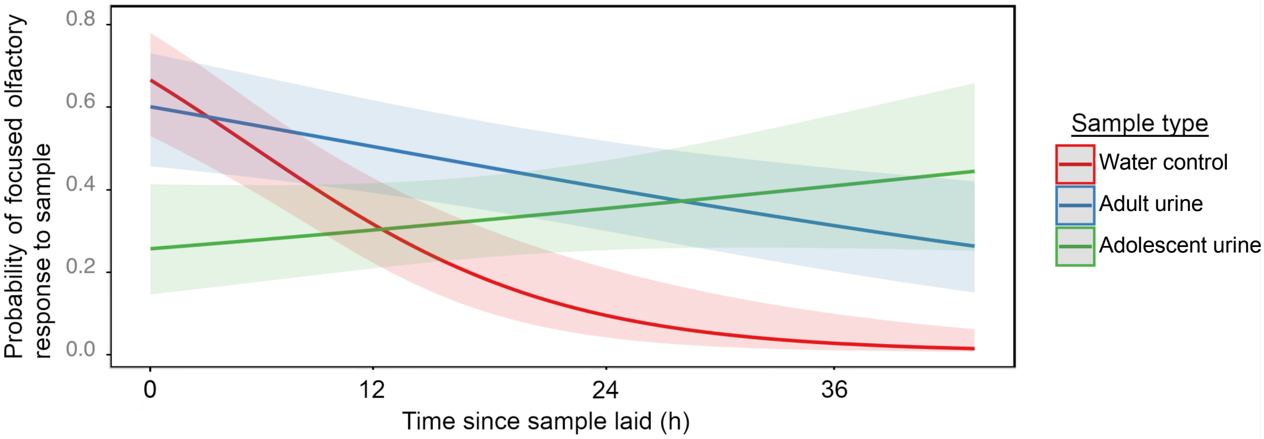


Figure 5.3: Probability of elephants exhibiting a focused olfactory response to each sample type over time since deposit was laid. Regression lines and 95% confidence intervals based on standard errors are indicated.

Adult urine was more likely to elicit heightened responses than adolescent urine

Owing to the high observed probabilities of response to water control samples soon after they were laid (Figure 5.3), we excluded all responses to all samples in the first 8 h in the following analyses testing for differences in vomeronasal system responses to samples by males of different age classes.

Age class of the receiving elephant did not predict likelihood of performing a vomeronasal system response to a sample. While overall adults performed these pre-flehmen and flehmen behaviours at a lower probability than adolescents did, this difference was not significant (aOR adolescent compared to adult = 2.488, *P* = 0.717, Table 5.8; Figure 5.4).

Table 5.8: Output of GLMM: likelihood of elephants exhibiting vomeronasal system responses to samples (pre-flehmen and flehmen behaviours) predicted by age class of receiving elephant. Elephant ID and pathway location are included as random effects.

Predictor		**% Response**	**Coefficient**	**aOR (+95% CI)**	***P***
Intercept			-13.540	1.317^{e-06} (1.102^{e-08} – 1.575^{e-04})	**<0.001**
Age class of receiving elephant	Adult	3.167	*Ref*	*Ref*	
	Adolescent	7.614	0.912	2.488 (1.814^{e-02} – 3.413^{e02})	0.717

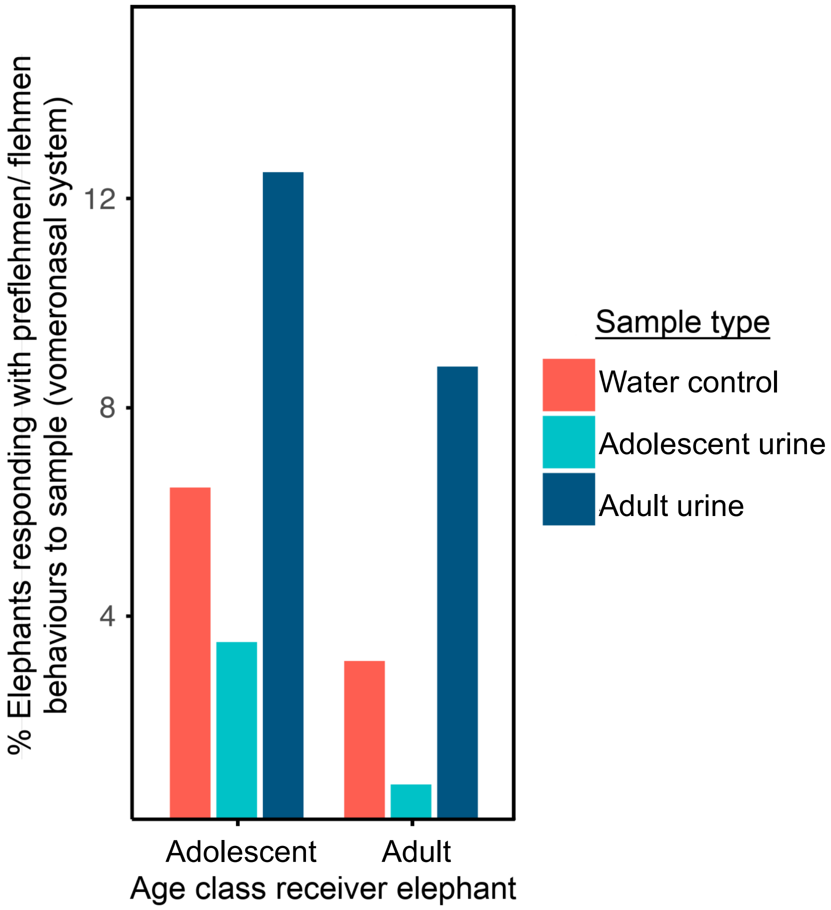


Figure 5.4: Percentage of adolescent and adult elephants exhibiting vomeronasal system responses to different sample types, indicative of heightened response to stimuli.

Adult urine elicited pre-flehmen and flehmen behaviours at greater probability than adolescent urine (aOR adolescent compared to adult urine = 1.986^{-6} , P = 0.010; Table 5.9; Figure 5.4). The water-based control did not elicit pre-flehmen and flehmen behaviours at a different probability than that from either urine sample type (Table 5.9; Figure 5.4).

Table 5.9: Output of GLMM: likelihood of elephants exhibiting vomeronasal system responses to samples (pre-flehmen and flehmen behaviours) predicted by sample type. Elephant ID and pathway location are included as random effects.

Predictor		**Coefficient**	**aOR (+95% CI)**	***P***
Reference class: water control				
Intercept		-14.110	7.451 $^{e-07}$ (2.620 $^{e-10}$ – 2.119 $^{e-03}$)	**<0.001**
Sample type	Water control	*Ref*	*Ref*	
	Adult	1.085	2.960 (1.466 $^{e-03}$–5.974 ^{e03})	0.780
	Adolescent	-12.044	5.877 $^{e-06}$ (1.854 $^{e-11}$– 1.863)	0.062
Reference class: adult urine				
Intercept		-13.025	2.205 $^{e-06}$ (3.849 $^{e-09}$– 1.264 $^{e-03}$)	**<0.001**
Sample type	Water control	-1.085	3.379 $^{e-01}$(1.667 $^{e-04}$ – 6.848 ^{e02})	0.780
	Adult	*Ref*	*Ref*	
	Adolescent	-13.130	1.986 $^{e-06}$ (8.784^{e-11} – 4.488^{e-02})	**0.010**

Since all vomeronasal system responses involved the cessation of movement of the subject elephant moving on the pathway, there is a possibility that responses of elephants to samples could be influenced by their group members’ responses. However, the tendency of an elephant to perform a vomeronasal system response to a sample showed no correlation with the presence of elephants either ahead of or behind him performing a vomeronasal system response to the sample (phi coefficient = 0.0816 and 0.160, respectively).

Further exploration of the high probability of response to the water control (Figure 5.4) led us to an additional analysis of the observation that in some cases elephants would throw the sample on themselves after physical contact and pinching (recorded as a vomeronasal system response, Table 5.1). Of the 18 occasions where this behaviour was observed, 13 involved a water control (72.22% of cases). A GLMM modelling the probability of throwing the sample on oneself following a vomeronasal system response by sample type revealed that the water control significantly predicted this response, with greater probability of response compared to both urine sample types (Table 5.10).

Table 5.10: Output of GLMM: likelihood of elephants throwing sample on themselves predicted by sample type. Elephant ID and pathway location are included as random effects.

Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Reference class: water control				
Intercept		-2.432	0.088 (0.050-0.155)	**<0.001**
Sample type	Water control	*Ref*	*Ref*	
	Adult	-1.329	0.265 (0.085-0.829)	**0.023**
	Adolescent	-2.338	0.096 (0.012-0.748)	**0.025**

Reference class: adult urine				
Intercept		-3.761	0.023 (0.009-0.063)	**<0.001**
Sample type	Water control	1.329	3.777 (1.206-11.833)	**0.023**
	Adult	*Ref*	*Ref*	
	Adolescent	-1.010	0.364 (0.040-3.302)	0.369

5.5 Discussion

Elephant pathways are used by African elephants to improve efficiency when moving between habitats and predictable resources such as waterholes and feeding areas separated in the landscape (Von Gerhardt et al., 2014; Shannon et al., 2009; Mutinda et al., 2011). We provide evidence that substrate-borne olfactory cues inherent to the elephant pathway (e.g. accumulations of dung and urine scents from previous travellers) are a key stimulus for elephants travelling on pathways, with the majority of elephants observed exhibiting general olfactory responses to the pathway substrate during travel when no samples were presented. While it has been shown that elephants travel in the core of their range using a 'Euclidean-cognitive map', relying on a mental representation of their spatial environment, in the periphery of their range they switch to habitual routes for movement, that is, pathways (Presotto et al., 2019). The MPNP stands at the fringes of the African elephants' range in Botswana (Thouless et al., 2016), and bulls are transitory in the area, staying on average for just 47 days (Pitfield, 2017). Many individuals on the pathways are therefore likely to be unfamiliar with the environment and may depend on the pathway as an indicator of movements of other African elephants in the area. In African forest elephants, *Loxodonta cyclotis*, following permanent trails as a search strategy may assist naïve elephants in finding resources connected by trails (Blake & Inkamba-Nkulu, 2004; Fishlock et al., 2016). This hypothesis is further supported by our finding that lone travellers were significantly more responsive to the pathway substrate than those travelling in all-male groups, potentially because those travelling in groups had more opportunity to rely on conspecifics rather than environmental olfactory cues for keeping on the scent trail of the pathway (Pettit et al., 2015).

While the pathway is probably also a visual stimulus (Figure 1.4), the high probability of elephants exhibiting a general olfactory response to it (61.24% of elephants at a 0.2 m randomly assigned stretch of pathway) supports the suggestion that the pathway acts as a public information scent trail (Mutinda et al., 2011; Fishlock et al., 2016). Across the animal kingdom, species follow the scent trails of conspecifics for the location of mates, prey, home and forage, as well as for mass migration (snakes, *Thamnophis sirtalis*, Costanzo, 1989; social insects, Edelstein-Keshet, 1994; rats, *Rattus norvegicus domestica*, Khan et al., 2012; wood mice, *Apodemus sylvaticus*. Jamon, 1994), and the olfactory sense is considered a widely utilised modality for spatial orientation and navigation (Lavenex & Schenk, 1998; Buehlmann et al., 2015; Etienne, 2003). We did not find any evidence that age class predicted tendency to exhibit a general olfactory response to the pathway substrate, suggesting olfactory attentiveness to pathways is important to all ages of independent (dispersed from natal herd) male African elephants. We also reject our hypothesis that those leading groups would be more responsive to odours on pathways, as position held within groups did not predict likelihood of response. This suggests olfactory elements of the pathway that are relevant for purposes other than navigation may be of interest to all travelling elephants (such as assessment of conspecifics, see below), or alternatively that during travel, memory acquisition and active learning of the route (relevant to both leaders and followers) is reinforced and/or encoded by olfactory cues as key informing modalities (Svensson et al., 2014; Piqueret et al., 2019; Lavenex & Schenk, 1998), that is, there is olfactory mapping of the environment (Tomlinson & Johnston, 1991).

The tendency of the water control to elicit focused olfactory responses declined rapidly with time since it was deposited. This differed significantly from the effect of time on adult and adolescent urine, suggesting elephants do monitor and can detect the urine deposits of conspecifics on pathways, as opposed to simply novel sand cues, for at least 48 h after they were deposited. The persistence of olfactory responses to urine samples over time is indicative that (i) the odours are still potent enough to be detected by conspecifics, and potentially (ii) that the odours are still of interest to passing conspecifics (Schulte & Rasmussen 1999). Greater overall probability of response to adult than to adolescent urine cues with time held constant at 0 could be due to the different chemical composition of adult and adolescent urine (Rasmussen & Wittemyer, 2002), again potentially affecting the potency of odours or their relevance to the receiver. The continued focused olfactory response to urine samples over time may be the result of microbial action on the compounds in urine transforming its chemical composition (Goodwin et al., 2012). This delayed release of compounds and change in chemical composition over time has been proposed to provide information about the age of a deposit, and hence an indication to the receiver of the proximity of the depositor (Rasmussen & Schulte, 1999; Goodwin et al., 2012). This would be highly adaptive for male elephants monitoring urine deposits on pathways used for travel, as an indication of the age and proximity of same-sex conspecifics.

We found no evidence that the age class of receiving elephants predicted the likelihood of vomeronasal system responses to urine cues, despite higher observed probabilities of adolescents performing these preflehmen and flehmen behaviours. Past research found wild male African elephants peak in their rate of performing olfactory investigatory behaviours to urine cues at waterholes in adolescence, but the decline in adulthood is compensated by a pattern of more refined behaviour, that is, adult elephants only respond to relevant urine cues, such as those that indicate a potential threat (Schulte et al., 2012). The age class of the depositor of urine did, however, predict the likelihood of response, with adult urine eliciting vomeronasal system responses at a greater probability than adolescent urine. A urine deposit from an adult male is likely to be of greater relevance than that of an adolescent to males of all ages. For adults the presence of another adult may indicate a potential threat or competitor to mating opportunities, or conversely a potential affiliate for acquisition of knowledge or a sparring partner (Chiyo et al., 2011a; Lee & Moss, 2014), whereas adolescent males in the environment would be of lesser threat or interest, as the dominance hierarchy of males is strictly related to age and musth state (Lee et al., 2011; Hollister-Smith et al., 2007). Both adults and adolescents may also respond more to adult urine in an attempt to discern musth state (Hollister-Smith et al., 2008; Rasmussen & Wittemyer, 2002), as an encounter with a musth bull could lead to dangerous physical confrontation for elephants of all ages (Lee et al., 2011; Poole, 1989a). While none of the urine samples in the study were from individuals identified to be in musth at the time of sampling, it is possible that urine may carry compounds indicating proximity in time to a transition to musth state, which requires more information to discern than an obvious and potent musth signal.

Indeed, studies supporting that African elephants can determine the musth state of remote signallers have found that elephants perform more flehmen behaviours to non-musth urine than musth urine (Hollister-Smith et al., 2007).

Notably, we did not find a significant difference between the probabilities of focused olfactory responses to adult urine and the water control (when time was held constant at 0), or for either age class of urine in eliciting a vomeronasal system response compared to the water control (even after eliminating the first 8 h since the sample was deposited). We suggest the high probability of responses to the water control may be due to different ecological reasons from that of the responses to urine samples. Elephants were more likely to throw samples of water controls over themselves (subsequent to a physical contact recorded as a vomeronasal response) than urine samples of either age class. This, along with the fact that focused olfactory responses were higher to water controls soon after the sample was deposited (Figure 5.3) than to other sample types, suggests that elephants are in general extremely sensitive to olfactory cues on pathways, and the presentation of the water sample may have elicited a ‘violation of expectation’ type response, as an unexpected stimulus to encounter on the pathway (Bates et al., 2008). Indeed, elephants, especially those in arid regions such as the MPNP are highly sensitive to the odour of water (Ramey et al., 2013; Ndlovu et al., 2018; Wood et al., 2021). We hypothesise that while the low vomeronasal system responses to adolescent urine may be due to a lack of importance of these cues to passing elephants in relation to adult urine (but no violation of expectation in being an odour cue encountered on a pathway), the high probability of response to the water control may be due to the expectations of elephants being violated in encountering this stimulus on the pathway.

Subsequent to physical contact using the trunk, elephants in some cases continued to throw the water control sample on themselves, as is common with mud wallowing and dusting behaviours performed by elephants (Mole et al., 2016). Future research conducted in this area is likely to face similar problems in finding an appropriate urine control due to wild elephants' high sensitivity to water (Ramey et al., 2013; Ndlovu et al., 2018) and novel objects and substances (Poole & Granli, 2011).

Our study highlights the olfactory responsiveness of wild African elephants to elephant pathways during travel. Our results support the hypothesis not only that male African elephants extensively use their olfactory sense during travel on pathways, but also that they may monitor urine deposits of conspecifics on pathways, potentially discerning an indication of the ages of males they can expect to encounter. We provide support for the hypothesis that a positive feedback loop establishes in the long-term maintenance of elephant pathways, whereby in utilising public information in following the olfactory trails of other elephants, travellers themselves deposit urine and dung cues that enhance pathway persistence (see pheromone trail deposits in foraging ants; Wendt et al., 2020; von Thienen et al., 2015; Frizzi et al., 2018).

5.6 Conclusion

In this chapter I explored the olfactory responsiveness of male African elephants on elephant pathways, as an example of male monitoring of same-sex conspecifics through remote cues in the environment. Whilst **Chapters 2-4** focused on how male elephants in each other's' immediate presence interact and are influenced by one another regarding impacting and guiding behaviour; in this chapter I explored how male elephants potentially use remote public social information left behind by conspecifics to guide behaviour and monitor each other.

Males were highly responsive to olfactory cues, particularly more so lone travellers, suggesting males without social companions are more dependent on, or interested in, the remote cues left by conspecifics in the environment. Males, particularly lone travellers, may be using olfactory cues on pathways as indicators for appropriate routes in which to travel to access critical resources connected by pathways.

In none of our experiments did adolescent and adult males interact with olfactory cues at divergent probabilities, suggesting monitoring of olfactory cues on pathways maintains an important behavioural adaptation from adolescence onwards.

Male urine cues attracted focused olfactory responses from same-sex conspecifics for at least 48 hours since they were deposited. Adolescent and adult urine were differentially affected by time in their probability of eliciting focused olfactory responses from passing elephants, and adult urine was more likely to elicit heightened responses (vomeronasal system responses) from receivers compared to adolescent urine. This suggests that males may be able to determine characteristics such as age of depositor from remote urine cues, which is likely to be adaptive when assessing the potential for same-sex conspecific encounters in the environment.

Exploiting a species' olfactory sense to achieve a desired behavioural outcome has remained relatively untapped as a tool in wildlife conservation and management (Campbell-Palmer & Rosell, 2011). However, regarding elephants, wildlife managers, conservationists and farmers have long exploited the elephant's olfactory sense regarding the use of "chemical repellents" to try and keep elephants out of certain areas, with varying success and degree of habituation to the aversive stimuli used (predator odours (Valenta et al., 2020), chilli pepper (Hedges & Gunaryadi, 2010), temporal gland secretions (Gorman, 1986), bee pheromones (Wright et al., 2018)). Indeed, the majority of elephant conflict mitigation techniques have foundations in fear conditioning (Mumby & Plotnik, 2018). However, elephants can learn just as effectively by positive reinforcement as they can by negative punishment (Fagen et al., 2014). I suggest instead to experiment with using olfactory cues to promote and encourage new or alternate movements for elephants. If elephants naturally experience a positive reinforcement to following scent trails (i.e., water or feeding resources, shaded tree spots, protected areas) (Mutinda et al., 2011; Von Gerhardt et al., 2014; Fishlock et al., 2016), then manipulating the placement of and direction that elephant pathways take to desired areas (that do provide a "reward" to elephants) may provide a great benefit to elephant management and conservation concerning more controlled elephant movements.

Understanding elephant pathway use is essential for land use planning and reducing wildlife conflict (Songhurst et al., 2016). In Botswana, elephant crop-foraging events are significantly more likely in fields closer to pathways (Von Gerhardt et al., 2014; Songhurst & Coulson, 2014). Pathways can persist for decades in the environment, their persistent location may be owing to elephants' excellent long term spatial memory (Presotto et al., 2019; Polansky et al., 2015), or alternatively as our study may suggest, their persistent and recurring use by elephants may build a strong, deeply engrained scent stimulus that future elephants can follow (Mutinda et al., 2011; Pittiglio et al., 2012; Haynes, 2006). Exploring whether elephant crop foraging events could be avoided by manipulating the pathway route away from human settlements (i.e., by removing existing pathway scents and redirecting to an alternative route with artificially placed urine and dung cues), whilst perhaps providing a buffer zone of undesirable habitat/ unpalatable crops between the artificial path and human settlements (Songhurst & Coulson, 2014; Osbourn & Parker, 2003a), is one suggestion for how our results could be extended to assist in elephant management.

In addition, because pathways are known to connect predictable, critical resources as well as act as dispersal routes (Shannon et al., 2009; Mutinda et al., 2011; Moss & Croze, 2011; Von Gerhardt et al., 2014), elephant mangers could experiment with using olfactory cues, elephant urine and dung deposits, to enhance desired corridor routes connecting protected areas (Osborn & Parker, 2003b; Baldus et al., 2007; Naidoo et al., 2018; Adams et al., 2016; Lindenmayer & Nix, 1993; Douglas-Hamilton et al., 2005), again potentially with buffer zones to reduce contact with humans (Songhurst & Coulson, 2014; Osbourn & Parker, 2003a). As a particularly wide-ranging species, providing elephants with safe transit between protected areas is a key priority for the conservation of elephant species (Croze & Moss, 2011; Pittiglio et al., 2012). This proposal would be of particular interest to the Kavango-Zambezi Transfrontier Conservation Area, which aims to link the elephant populations (encompassing an estimated 200 000+ elephants) across 36 protected areas over five countries in southern Africa through secure wildlife corridors, while avoiding negative impact on rural communities (Munthali et al., 2018; Metcalfe & Kepe, 2008).

Chapter 6: Discussion and Directions for Future Work

6.1 Foreword

This thesis set out to build upon our understanding of the behaviours of males in non-reproductive all-male groupings. I aimed to explore potential benefits males reap from associating with each other, the interactions that occur between males of similar or divergent age, and whether the age structure of males within all-male groupings influences the behaviours of its members. Notably, I drew particular attention to the influence of older males in all-male groupings, and their potential social role as reservoirs of knowledge regarding sex specific behaviour, location of critical resources, or effective assessors of risk. In this final chapter, I discuss the extent to which this study on male African elephant social behaviour in a bull area can contribute to these research aims. I discuss the importance of my findings within the wider literature on male sociality as well as male elephant sociality specifically, considering the species' high conservation concern and male elephants' involvement in various unresolved negative human-wildlife interactions. I also discuss potential directions for future research in the domains of behavioural ecology as well as conservation and management.

6.2 Age dependent benefits to male sociality in African elephants

6.2.1 Fission-fusion dynamics, a grouping strategy that allows males to flexibly exploit the benefits to being social

Non-reproductive all-male groups, including those of male African elephants, often have a high degree of fission-fusion dynamics, with individual males flexible in their membership in highly spatio-temporally dynamic groups (Lehmann et al., 2006; Chiyo et al., 2011a). By adopting this strategy, males can balance the current benefits that come with having social contacts and living in groups, against the costs of sociality such as resource competition and disease risk (Aureli et al., 2008; Fortin et al., 2009; Chiyo et al., 2011a; Lee et al., 2011; Goldenberg et al., 2014; Murphy et al., 2019). In this thesis I presented supporting evidence that the benefits to living or traveling with other males are likely to vary with age in male African elephants. In **Chapter 2** I showed how adolescents were more likely to travel in all-male groups than expected by chance, whereas mature adult males were more likely to travel alone. Increased male lone travel with greater age supports existing research on male elephants in Kenya (Lee et al., 2011). In this Kenya based study, adolescent male elephants (around 10-19 years in this study) spent between 70-80% of their time in association with females, and only around 17-26% of their time in association with other males in all-male groups (Lee et al., 2011). In the current study adolescents made up the majority of elephant sightings on pathways in this bull area (Figure 1.3). It is possible that in this bull area adolescents that have undergone dispersal from their natal herd, or are in the process of dispersing, may spend most of their time travelling in social groups with males, who would preferably be in association with family groups in areas with greater female presence (Lee et al., 2011). In **Chapter 4** I found adolescents performed more trunk-to-mouth “greeting” behaviours than adults did. These close contact behaviours may facilitate further positive interactions with social partners (Poole & Granli, 2021), whilst potentially simultaneously providing olfactory information on aspects of the target elephants phenotype (Rasmussen & Riddle, 2004; Poole & Granli, 2011, 2021; Lee & Moss, 1999). Adolescents may perform these behaviours at a higher rate, as they are more recently dispersed from the natal herd and may have a greater need to establish new contacts, and their hierarchal position in the highly fluid bull society (Lee et al., 2011; Murphy et al., 2019). Alternatively, as there may be more benefits to all-male grouping for adolescent male elephants compared to adults (reviewed below) these trunk-to-mouth contacts may assist young males in making a first contact with potential associates, that might facilitate further behavioural interactions between partners. Future research should therefore explore how the behaviours and grouping associations between particular males change following such "greeting" exchanges.

In **Chapter 5** I provided evidence that elephant pathways may be important sites for wide ranging male elephants to remotely monitor conspecifics sharing their environment over time and space (Mutinda et al., 2011). Males made focused responses to the urine cues of other males for up to 48 hours since their deposition. Previous research found adolescent male elephants were more exploratory of olfactory cues at water holes, whilst adults were more discriminate and only paid attention to relevant cues (Schulte et al., 2012). I did not however find any differences between adult and adolescent males concerning either their general responsiveness to pathways, or their responses to urine deposits of conspecifics artificially placed on the pathway. This suggests monitoring of same-sex conspecifics on elephant pathways is equally important for all males, regardless of age. However, the urine cues of adult males were more likely to evoke flehmen and pre-flehmen responses from other males, compared to the urine cues of adolescent males. I suggested this is due to adult cues being of greater interest to males of all ages. For example, for males to discern the likelihood of encountering a potentially dangerous musth bull (Hollister-Smith et al., 2007). Remote monitoring of same-sex conspecifics is likely an important mode of communication for species with high fission-fusion dynamics – as a mechanism to monitor the location of potential affiliates, threats and competitors they can expect to encounter in the environment.

The social associations observed between individuals in all-male groups may be random and simply serve to provide the immediate benefits of being in a group (e.g. antipredator benefits (Joubert, 2006)) (Couzin & Krause, 2003). Alternatively, males may have preferred long-term stable associates, and share social bonds despite a high turnover of group membership (Jack & Riley, 2014; Ostner & Schülke, 2014; Whitehead & Connor, 2005; Lee et al., 2011; Murphy et al., 2019). In long-lived species such as elephants, who also have an exceptional long-term memory regarding individual recognition (Rasmussen, 1995), such preferred associates could theoretically span decades (Murphy et al., 2019; Lee et al., 2011). Past research suggests older male African elephants do have preferred companions similar in age, whilst younger males associate with other males at random (Chiyo et al., 2011a). Similarly, a 30-year study in Kenya found males over 20 years of age have distinctive top associates that tend to be similar in age (Lee et al., 2011). The long-term persistence of these associations, or "friendships", however, is uncertain (e.g. a 16-year data set with 4 x 4 year sampling periods found males had stable relationships with top 3 associates across some sample periods but not others (Murphy et al., 2019)).

The presence of long-term bonds in male African elephants, and tenure of membership in fission-fusion groups was not a focus on this thesis, but is nevertheless a critical component to consider when exploring male elephant sociality. Male elephant social associations have been hard to study owing to the high turnover in group membership, and males' tendency to roam wide and varied distances (Roux and Bernard 2009; Ngene et al., 2009; Murphy et al., 2021). Attempts to conduct social-network analyses can be particularly problematic in open, unfenced systems such as the MPNP study area where repeat sightings of individuals can be rare (Pitfield, 2017). Elephants in the MPNP bull area stay on average 47 days in the study area (Figure 1.1), and then 238 days out of the study area (Pitfield, 2017). A dataset spanning 9 years is available regarding sightings of male elephants alone and in all-male groups away from the Boteti river in the wider MPNP (where unlike at the river hotspots, feeding dominates male behaviour) (Evans, Personal communication). An analysis of tenure of male associations and turnover of group membership in such a defined bull area, with males so distinctly separated from females would be interesting, as would a comparison of if these relationships persist between years upon males re-entry into the bull area.

Particular points on the Boteti River accumulated large aggregations of male elephants during the study period (Figure 1.1; Figure 1.6). Whilst the river as a water source was likely the primary motive for males visiting, elephants stayed far longer than was required for drinking, and were observed engaging in various social interactions. I therefore referred to these sites as “social hotspots” and suggest they are likely highly important sites for males to meet new social contacts, exchange information, engage in beneficial social interactions such as sparring, and perhaps change fission-fusion groupings (Fishlock & Lee, 2013). It is hypothesised that in cognitively advanced species with high fission-fusion dynamics, that unambiguous signals, “greetings”, may evolve that enable individuals to communicate affiliative intent, reduce tension, and update relationships at reunion events (Aureli & Schaffner, 2007; Aureli et al., 2008; Smith et al., 2011). In **Chapter 4** I found no evidence that males use trunk-mediated “greeting” behaviours to serve this purpose. Elephants arrived in coordinated all-male groups at the river, but were exposed to various new potential interactors from the wider male society at the social hotspot aggregations, trunk-mediated greeting behaviours were not preferentially directed to these new, less familiar elephants. Rather than a reunion signal, these trunk contacts likely better serve functions similar to other greeting behaviours discussed in the literature, such as testing relationships, assessing phenotype features, and facilitating further contact with individuals that are generally sharing the same ecological space (Dal Pesco et al., 2018; De Marco et al., 2014). It could be argued that it is not possible to discern the actual familiarity elephants at aggregations have with one another, as associations were not tracked between days in the study. It could be that all the elephants at aggregations were aware and familiar with one another despite on that day not arriving in a group together, since elephants stay in the study area on average for 47 days. However, without long-term tracking of individuals and their associations over time, this measure of grouping history (arrived in a group with the focal or not) was the best measure of relative familiarity I could work with considering the resources available. On occasion, I observed elephants that were fully white in colour, presumably new in the study area having travelled from salt pans in the east or Nxai pan in the north of the study area (Figure 1.1) (dusting with the salt pan substrate gives elephants a white colouration, whereas once elephants have mud wallowed and dustbathed in MPNP they become a darker brown or grey, even when dry). It could be possible to concentrate future study on the “greeting” behaviours of these white coloured males, since they are more likely to be completely new into the study area, and more likely to be experiencing first contact with males at the aggregations, or at least more certain to have been temporally separated from the elephants present for a more prolonged period.

The introduction (**1.6.5**) summarised how focal males changed groups between arrival and departure. All ages left in larger groups on average than those they arrived in (Table 1.3), and only 14.39% of males departed the social hotspot in the same group composition that they arrived in. After arrival, there was considerable mixing of males and the original all-male groups in which elephants arrived in most often broke up and became un-distinguishable from the larger male aggregation at the social hotspot. If social hotspots are important shareable ecological resources where males can exchange information (Western & Lindsay, 1984), engage in important social interactions (Fishlock & Lee, 2013), or change associates and form new all-male groups, future study should investigate the extent to which all-male groups change between arrival and departure in more depth. It should be considered however, following departure from hotspots, these groups could theoretically quickly break down, or merge with other groups, and such a study may therefore have to extend to tracking groups away from the river. Furthermore, exploring how a male’s social experience at the river affects his choice of who to leave with would also improve our understanding of the factors that influence group size, tenure of membership in all-male groups, as well as the value individuals place on particular associates in their environment. For example, concerning the trunk-mediated contacts examined in **Chapter 4**, whether the individuals contacted with these behaviours become social contacts that the focal leaves the river with may further support the proposal that these behaviours are important for facilitating social associations.

Finally, I observed that individuals leaving the social hotspots would on occasion stand on the bank “waiting” with the body orientated in the direction of intended travel (Poole & Granli, 2011, 2021). I also suspected that vocalisations, potentially “lets-go-rumbles” (Poole & Granli, 2021) were sometimes made by these individuals. Future study could explore which ages attempt to actively recruit group members to depart the hotspot with, as well as which ages are most effective at acquiring males to follow them in initiating departures from social hotspots (Meunier et al., 2007). In **Chapter 2** I discussed how the leadership role of older male African elephants is likely a passive role (King, 2010), with followers placing value on individuals with greater age and hence experience (Lee & Moss, 2012), and older males tolerating the attention they attract (Bercovitch & Berry, 2014). Future study could investigate whether older males conduct “lets-go-rumbles” and attempt to purposefully recruit followers when leaving social hotspots. Alternatively, older males may simply leave and be followed by other males without any waiting or recruitment behaviours. Such analysis of departure groups may further our understanding as to whether older males have benefits to being social and want to obtain a following, or whether they are merely tolerant to the social associations they attract.

6.2.2 Benefits of male-male associations: (i) competitor assessment and access to sparring partners

Competitor assessment (Goldenberg et al., 2014) and access to sparring partners (Evans & Harris, 2008; Chiyo et al., 2011a) are argued to be key “pull” factors to grouping in male African elephants, as well as in mammalian all-male groups more widely (Bon & Campan, 1996; MacFarlane & Coulson, 2009; Pérez-Barbería & Yearsley, 2010). Whilst male elephants of all age engage in sparring and play activity (Lee & Moss, 2014), adolescent elephants engage in more sparring activity than adults (Evans & Harris, 2008). This may be because they have greater need to develop the motor skills and strength acquired through sparring, and to establish their social position in the hierarchy, which sparring may facilitate (Evans & Harris, 2008; Lee & Moss, 2014). Furthermore, males prefer similar aged sparring partners, perhaps to maximise effectiveness of improving and maintaining competitive skills (Chiyo et al., 2011a; Sigmund, 1993). In line with these previous studies, in **Chapter 4** I found male elephants preferentially targeted age-matched males with trunk-mediated “greeting” behaviours. By preferentially targeting age-mates, these trunk behaviours as tactile signals may be used to facilitate further interaction with males of similar age (which could then progress to being a beneficial sparring partner), and as olfactory assessments may enable males to safely assess phenotype features relating to competitor assessment and dominance (e.g. levels of androgens like testosterone (Ganswindt et al., 2002; Rasmussen & Wittemyer, 2002)) in otherwise similar aged, hence similarly sized and strength matched partners. Previous research has shown younger male elephants have overall random associations with elephants of different age, which may be due to an attraction to age mates for competitor assessment and sparring benefits, and attraction to older males for knowledge acquisition (Chiyo et al., 2011a,b), whereas older males only benefit from age-mates for such benefits. Such an interest in a range of ages of social partners may also explain why 16-20 year olds overall directed trunk-mediated greetings to age-mates at random, as these older adolescents attempt to obtain information on, and initiate association with a more diverse range of beneficial social partners. Whilst theoretically younger adolescents (10-15 years) could therefore also benefit from a wider range of social partners, at this young age males may be less bold in initiating such close contact behaviours with older elephants owing to drastic size differences between them and older males (Lee & Moss, 1995; Laviola et al., 2003; Peper & Dahl, 2013).

6.2.3 Benefits of male-male associations: (ii) buffering of predator and anthropogenic risks

I provided evidence that grouping with other males in this study area may buffer adolescent elephants from predators and/or anthropogenic risks. In **Chapter 3** I found that adolescents performed more fear and aggression behaviours to non-elephant targets when socially isolated compared to when in the company of other males, indicative of a heightened state of risk perception when alone. Adult risk perception, however, appeared less affected by social isolation, and they performed these behaviours at an equal rate when alone and when in the company of other males. Overall, adolescents performed fear and aggression behaviours to non-elephant targets at a greater rate than adults. The social hotspots studied in this thesis have a moderate tourist presence (Zyl, 2019), and mark the boundary of the park with community owned land to the west of the

Boteti river (Figure 1.1). Adult males may be more habituated to tourist presence and not perceive tourists as a threat, compared to less experienced adolescents. Furthermore, males tend to develop preferences for the bull areas they utilise with age (Lee et al., 2011), and despite a human dominated landscape being in such close proximity to the site of data collection (Figure 1.1), adult bulls may have acquired the experience to know that they are not at risk of attack from humans in this particular location (the actual social hotspot). I.e. the behaviour of adults may have been different if sampled in the more human-dominated landscape of the community land to the west of the river (Figure 1.1; Douglas-Hamilton et al., 2005; Graham et al. 2009a; Chiyo et al. 2014). In contrast, adolescents may not have this site-specific knowledge yet, and through scent and auditory cues may sense close presence of humans and be uncertain about their safety (Bates et al., 2007; Kangwana, 2011; McComb et al., 2014). In addition, adolescent males are still of the age vulnerable to lion predation (Joubert, 2006), with lions sighted regularly at these social hotspots (Personal observation). Due to substantial body growth with age (Lee & Moss, 1995), a healthy adult male elephant is not at risk from predation from lions. An individual adolescent male is less at risk from predation when in a group (Roberts, 1996; Waterman, 1997; Averbeck et al., 2010), and hence may experience a lowered risk perception when grouped with other males (and consequently perform less fear and aggression behaviours to non-elephant targets).

Importantly, trophy hunting was not practiced in Botswana for the tenure of the study (September 2015-2018) (Mbaiwa, 2017), and whilst there is evidence that poaching may have been on the rise in parts of the country, elephant poaching was not a serve threat in the study area (Chase et al., 2016; Schlossberg et al., 2019). However, in 2020 trophy hunting was reintroduced in the unprotected land to the west of the study area (Figure 1.1; MENT, 2020; Evans, Personal communication). Trophy hunting introduces a new threat to adult male elephants, as the oldest males are often the preferred targets of hunts (Barnett & Patterson, 2005; Boddington, 2013; Selier et al., 2014; Muposhi et al., 2016). Future work may wish to compare rates of fear and aggression behaviours to non-elephant targets now that trophy hunting is practiced again in this area. Elephants form larger groups under high anthropogenic risk (Chiyo et al., 2014), and being alone may present a new threat to adult males now that they are at risk from trophy hunting, who may now perceive humans as a greater threat to their survival. Consequently, the anti-predator responses of adult males to non-elephant targets such as vehicles, may increase under such conditions.

Owing to permit restrictions, my study of risk related behaviours was only possible during daylight hours, and it is possible that behaviours of elephants could differ at night. It is likely that elephants also utilised the social hotspots at night, since groups traveling towards the river continued to be observed on camera traps through the night (Figure 6.1b). Elephants transverse areas with greater human presence and engage in more risk taking behaviours at night, where contact with humans is less likely (Douglas-Hamilton et al., 2005; Stevens, 2018). Conversely, lion predation risk is likely greater at night (Joubert, 2006). The few sightings of females and associated juveniles and calves in the study area primarily occurred at night (Figure 6.1a). Since female elephants are more sensitive to risk than males (Chiyo et al., 2014), this finding may indicate utilising hotspots at night is a less risky strategy. It is possible therefore that particularly risk sensitive individuals may be using the hotspot habitat at night, and it should be considered that our sample from daylight hours may represent a biased sample of less risk sensitive individuals.

Notably, the behaviour of male elephants moving on pathways captured on camera traps for **Chapters 2 and 5** appeared to differ from that described elsewhere in the literature. Such direct and purposeful elephant movements across the landscape are often associated with movement through high-risk areas, with elephants adopting a fast pace, and more commonly moving at night (Thouless, 1995; Berger, 2004; Douglas-Hamilton et al., 2005). Since camera traps were set to record video, we were able to observe that in this study however, elephants appeared in a relaxed state as they moved on pathways through this protected area (**Supplementary Information 4**, Note S4.1), including those that were moving at night. Elephants in the MPNP likely use pathways as paths of least resistance between critical ecological landscape features (Mutinda et al., 2011; Von Gerhardt et al., 2014), rather than as a means to effectively transverse high-risk habitats (Douglas-Hamilton et al., 2005).

A key benefit afforded to using camera traps to capture elephant movements and behaviours for **Chapters 2 and 5** was the non-invasive nature of data collection, and the fact that data could be collected 24 hours a day (Figure 6.1). This contrasts with methods such as video focal sampling (**Chapters 3 & 4**) that were restricted to daylight hours and ran risk of elephant behaviours being influenced by human presence (Supplementary Note S2.1). However, camera trap methods were not without their limitations and drawbacks. Elephants on occasion pulled down the camera traps and destroyed or carried them off further along pathways, with both data and equipment often unrecoverable, giving a considerable financial drawback to this method of data collection. Elephants are highly perceptive to novel items in their environment (Poole & Granli, 2011), and across Africa, many camera trap studies suffer camera loss and damage to elephants (Apps & McNutt, 2018). Past research also reports problems with trigger responses as a drawback to camera trap studies, for example non-uniformity of trigger response across different trap locations (Meek et al., 2015). However, one of the main reasons I suffered camera trap losses was because I was careful to ensure a uniform camera trap placement across all camera trap set ups, so as to improve reliability of trigger response (**1.6.4**). I attached cameras to uniformly placed poles with an unobscured view of the central point on the pathway (**1.6.4**) rather than attempt to hide cameras amongst existing vegetation (which could not provide an identical approach of elephants on pathways and view of the site of sample presentation across different pathway sites). Where possible I attempted to place poles amongst existing large trees to try and make the poles less obvious to passing elephants (I.e., camouflage the pole and camera's silhouette), but this was not always feasible. However, studies that suggest problems with camera trap trigger response reliability find this is mainly a problem for smaller species such as the African civet (*Civettictis civetta*) and genet spp. (*Genetta*) (Pirie et al., 2016). As our target species is the world's largest land mammal, it is less likely that they fail to trigger camera traps significantly. Furthermore, having two camera traps per station, as in our study, has been shown to be 29% more effective at capturing animals (Negrões et al., 2012). Finally, with data collected by video and not photographs from camera traps I found the battery of camera traps drained quicker, which may also affect trigger response and quality of infrared video (Apps & McNutt, 2018). Rechargeable batteries were used for financial reasons, and it is worth noting in field conditions with limited access to power as in the current study, being able to regularly change and recharge camera batteries is an important consideration for studies wishing to use camera trap methods.

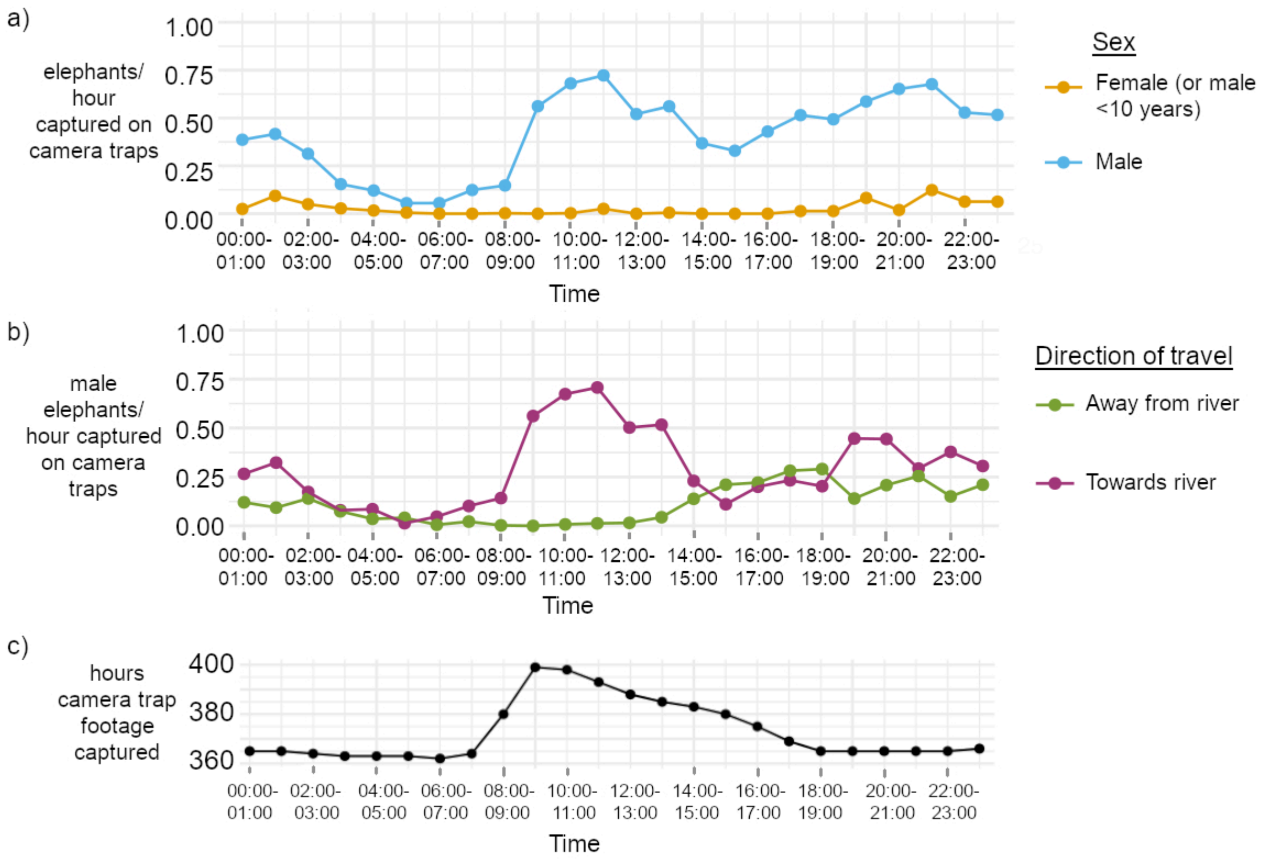


Figure 6.1: Time of elephant sightings captured on camera traps along elephant pathways, controlled for by number of hours camera traps active for in that time period. (a) Elephants did not primarily utilise pathways at night, and very low numbers of elephants travelled on pathways from 02:00 through to dawn hours. The few sightings of females and associated calves and juveniles were primarily at night. (b) Comparison of direction of travel of male elephants sighted on camera traps traveling on elephant pathways. (c) Methodology aimed to have an equal distribution of time that camera traps were active for over a 24-hour period, however a greater number of active camera trap hours captured between 09:00-16:00 is likely owing to camera traps being pulled down by passing elephants at

times where there were high volumes of elephants. (a) and (b) are controlled for by differences in time cameras active for over the 24-hour period.

6.2.4 Benefits of male-male associations: (iii) improved access to knowledgeable and experienced individuals

I provided evidence that an improved access to knowledgeable and experienced individuals may be a key benefit afforded to males by associating in all-male groups. Notably I found support for the hypothesis that older males are important sources of knowledge for younger males. In **Chapter 2** I demonstrated that older males are followed by adolescent males in elephant processions along pathways connecting critical resources. Additionally, in **Chapter 3** I showed how male elephants of all ages perform less aggressive behaviours to non-elephant targets with increased older male presence in their immediate environment, suggesting older males may be perceived by other males as particularly effective assessors of the environmental risk level. In contrast, in **Chapter 4** I found no evidence that trunk-mediated “greeting” behaviours are used by male elephants to preferentially acquire information from or initiate contact with older males in their environment. I concluded it is likely that the mechanism by which younger males learn from older males involves less intrusive and more eavesdropping type methods such as watching or listening (Bonnie & Earley, 2007; Evans & Harris, 2008). These findings are reviewed in more detail below in **6.3**.

For males using social information to improve their access to critical resources, an important discussion point raised by this thesis is the relative importance for males of (i) other males in their immediate environment, and (ii) other males that can be monitored through remote cues left in the environment. Whilst **Chapter 2** provided evidence that younger males may benefit from following older males for locating critical resources in the environment, **Chapter 5** provided parallel evidence that males of all age may use public social information (i.e., scent cues of the elephant pathway), as an indicator of other elephants' movements, which may guide and inform the subject to locate predictable critical resources in the environment (Blake & Inkamba-Nkulu, 2004; Fishlock et al., 2016). It may be that once on a pathway, males can use olfactory cues alone to navigate the existing route, evidenced by lone travellers having an increased responsiveness to pathways (**Chapter 5**). However, older males occupying lead positions in travel groups may represent younger males' dependence on these individuals for more specialist knowledge (Brent et al., 2015). For example, whilst Figure 1.1 illustrates the main channel of the elephant pathway towards the Boteti River, in reality, pathways are a network of paths with occasional branching events (Figure 6.2). Older males may provide advanced knowledge of how to navigate such branching events, or the direction of travel to take at particular times, both of which may be decisions that uninformed males may not be able to make from olfactory and visual cues from the pathway alone (Mutinda et al., 2011). Future research may wish to identify key branching points on pathways (Figure 6.2), and explore the olfactory behaviours, decisions regarding direction of travel, and age related leader-follower dynamics of elephants at these particular points. Older males may make better choices regarding paths of least resistance to critical resources, or for locating seasonally variable patches of food abundance. Alternatively, elephants may choose to travel on paths that olfactory cues indicate the most recent previous travellers have also utilised. Such a choice-based observational study would improve our understanding of how male elephants depend on same sex conspecifics for navigating the landscape and locating critical resources.

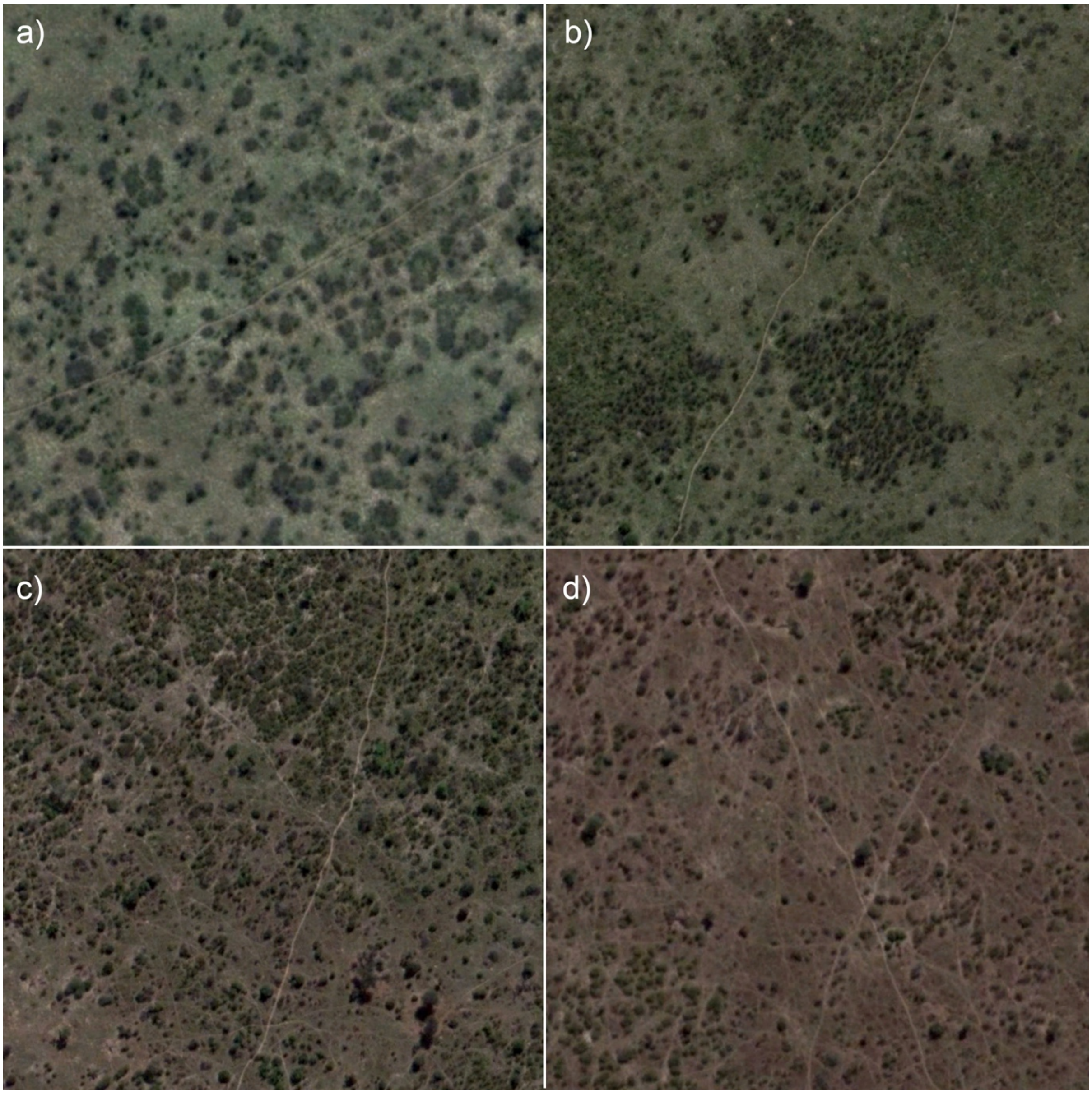


Figure 6.2: Satellite imagery of elephant pathways in the study area (Map data © 2021 Google, Maxar Technologies). Whilst for long stretches elephant pathways are distinct in the landscape for several kilometres (a & b), at other points there are branching points and minor trails coming off the main channel (c & d). These minor trails may also represent trails of other non-elephant species.

6.3 Evidence for important social roles of older males in non-reproductive all-male groupings

In **Chapter 3** I found males were more aggressive to non-elephant targets with a lower older male presence in their immediate environment. I discussed how this could be due to males experiencing uncertainty about their safety and a heightened risk perception when fewer older males are around (Kikusui et al., 2006), or alternatively that older males may police these behaviours that are potentially negative to group cohesion and safety (Flack et al., 2005a).

Older males may be perceived by other males in all-male societies as particularly effective assessors of risk. In male elephants, an age-related placement of value regarding knowledge may be carried over from growing up in family groups, where older matriarchs make more effective and appropriate assessments relating to risks (McComb et al., 2011a). The aggression observed in this study was sometimes towards targets that were obviously of no immediate threat to elephants (such as birds and bushes), so this aggression may be displacement aggression and a stress reducing outlet for males (Kazem & Aureli, 2005; Virgin & Sapolsky, 1997; Levine et al., 1989), and may be an indication that elephants experience a heightened stress level when experiencing a heightened sense of risk (Gobush et al., 2008; Jachowski et al., 2012; Hunninck et al., 2018). I recommend expanding on these findings and taking existing studies that explore elephants perception and response to risks in family groups, and replicating them on males in all-male groups. For example, playback experiments of predator threats (McComb et al., 2011a) and human voice stimuli (McComb et al., 2014) have measured the consequent bunching behaviour of group members around the matriarch. I recommend conducting similar experiments in the current study area on all-male groups of elephants. Such a study may be best conducted on male foraging groups in the wider MPNP away from the river (east of the Boteti River, Figure 1.1), owing to safety concerns regarding tourist presence at the river, and the potential that provoked elephants could retreat into the bordering community land if such experiments were conducted at the social hotspots. The responses of males in all-male groups to audio playbacks of human and predatory threats could be analysed for the prevalence of bunching behaviour with age, the extent of bunching centred around older males, and whether older males are followed by younger males in their direction of retreat. If, as the current study suggests, older males are relied upon as assessors of environmental risk, they may be the focal point of bunching activity, or groups with older males present may return to a relaxed state faster, or retreat shorter distances upon exposure to less severe threats.

Alternatively, the reduced aggression observed with increased older male presence may indicate that older males police other males aggression towards non-elephant targets (Flack et al., 2005a). In horses, a greater ratio of adult to young animals in groups reduces the rate of aggression in young horses (Bourjade et al., 2009), and mature male elephants appear to inhibit younger males from entering the aggressive state of musth (Slotow et al., 2000; Slotow & van Dyk, 2001). Interestingly, contrary to my hypothesis, I found no increases in aggression to conspecifics with reduced older male presence. This may be due to the males in this study not being as permanently removed from mature males as in other study systems where disruptions to linear dominance hierarchies leads to increases in conspecific aggression, or a pre-mature musth state in young males (O’Connell-Rodwell et al., 2011; Slotow et al., 2000; Slotow & van Dyk, 2001). If older males police other males’ aggression to non-elephant targets, there may theoretically be a benefit for older males in maintaining all-male group cohesion. This could stand in contradiction to a key general argument of this thesis that older males are largely passive in tolerating associations with other males in all-male groups (Bercovitch & Berry, 2014). Policing of other male's aggression levels to non-elephant targets, could be one mechanism by which older males regulate sexual status of males in their proximity, by potentially preventing physiological changes that may lead to musth (Slotow et al., 2000; Slotow & van Dyk, 2001; Ganswindt et al., 2005; Honess & Marin, 2006; Rasmussen et al., 2008; Peper & Dahl, 2013). Such a point is purely speculative but would be an interesting direction for future research. Alternatively, again in line with older males being largely indifferent to male associates, it may be that the policing influence of older males is itself a passive process. With elephants "behaving better" when older males are around (Semple et al., 2009), rather than older males actively inflicting a punishment as in policing by dominants in primate societies (de Waal, 1989; Flack et al., 2005a,b). In support of this, I found no increases in conspecific directed aggression with the increased presence of any age cohort. I observed that older males sometimes evoked submissive responses from other males from a simple approach without any aggressive signalling or dominance assertion behaviours (although aggressive vocalisations may theoretically have been made by the older male). In other words, older males being present, with their obvious size dominance and potential to be in aggressive musth state (Poole, 1987,1989a; Lee & Moss, 1995) may regulate the aggressive behaviours in other males without ongoing active policing.

In **Chapter 2** I showed that older males may be targeted by younger males for their heightened ecological knowledge, as they occupied lead positions in travelling groups on elephant pathways. I discussed how this is more likely a passive leadership role on the part of the leader, with older males being recognised as high value, knowledgeable individuals by less informed younger males, and hence followed in the environment (King, 2010). This contrasts with the leadership roles of matriarchs in elephant family groups who actively maintain group cohesion and guide their groups (King et al., 2009; Mutinda et al., 2011). Individuals should be selective of who they follow or copy, and tendency to follow or copy conspecifics can also vary with the state of the subject individual, such as their relative lack of experience (Galef & Laland, 2005; Kendal et al., 2018). Following older males would represent an attribute-based strategy, with older more experienced individuals in societies often emerging as leaders of group movements (Mueller et al., 2013; Brent et al., 2015; Tokuyama & Furuichi, 2017).

It could be argued a limitation to the current study was that I did not have access to information regarding how the all-male groups observed on elephant pathways formed. Hypothetically, the all-male groups captured on camera traps may have been foraging together at a distance from the river before a successful initiator recruited the group (with or without active signalling of intent to recruit a following) to move on the pathway towards an end point connected by the path (Lee & Teichroeb, 2016; Tokuyama & Furuichi, 2017). In another scenario, the group may have accumulated in size over time as the group crossed the landscape, as elephants in the environment observe the collective group and recruit into it (visibility for elephants across the MPNP landscape is likely very good for elephants past 2-5 km from the river, where open *Acacia* savannah-type vegetation dominates the landscape (Brooks, 2005)). Lacking this information limits our understanding of the true motivation for individual males' in following in a group, despite the observed age structuring of the lead position. Some young males for example, following a simple strategy of “if uninformed, follow”, may join collective movements regardless of the age of the leader, and may be more influenced by factors such as size of the group, or simply wanting to maintain group cohesion with the majority (Couzin & Krause, 2003). Furthermore, follow relationships may be influenced by “chain” effects, whereby an individual’s following behaviour is influenced by the need to maintain proximity with the animal directly ahead of them, rather than the overall group leader (King et al., 2008). In this way, it may be difficult to say for certain once a male elephant procession reaches a certain size who is really following (or maintaining proximity with) who within the procession, how aware individuals towards the back of a procession are with who is leading the group, and to what extent elephants recruiting into the procession are using a “follow an informed leader”, or “follow the majority” strategy (Kendal et al., 2018). Crucially however, previous research suggests that leadership by a minority of informed individuals can be self-sorting without the entire uninformed majority being aware of who is informed (Dyer et al., 2008; Reebs, 2000). Whilst individuals within the group may be following local heuristic rules such as avoidance of isolation (Couzin et al., 2005), overall the informed older male guiding movements at the front of groups is still of critical importance to the collective movement of the group reaching the desired location (Dyer et al., 2008; Reebs, 2000). That is, leader-follower dynamics can also be passive from the perspective of the followers (King et al., 2009), and followers’ knowledge of who is leading is not a necessary a pre-requisite for informed leaders to successfully lead groups to their desired locations (Couzin & Krause, 2003; Couzin et al., 2005; Reebs, 2000). Further study would be highly beneficial in this area, to confirm if older males are actively identified and targeted as valuable individuals to follow, or whether alternatively, younger adolescents are following simple localised decision rules to avoid isolation, that scale up to complex self-organised groups and age-structured leadership (Conradt & List, 2009; Smith et al., 2015). Expansion of this research may include monitoring changes to group composition over a transect length of one pathway, or as discussed above, to analyse which ages of elephants conduct waiting and recruitment behaviours when departing the Boteti River social hotspots (Poole & Granli, 2021), and how effective they are at recruiting followers.

Importantly, whilst the leader-follower dynamics observed in **Chapter 2** demonstrates a potential mechanism by which knowledge transfer about location of ecological resources and effective navigation of pathways could occur, the current study is observational, and is not able to provide any causal evidence that social learning is occurring between older and younger males. Furthermore, **Chapter 3** suggested older males may act as indicators of environmental risk levels to other males, yet I was unable to conclude whether males can learn about appropriate risk assessment from older males. The strategies animals adopt regarding who to follow, may similarly also apply to social learning and the partners from whom it is appropriate to learn from. Existing studies find animals adopt social learning strategies that are state dependent (e.g. learners can be subjects that are uncertain, young, dissatisfied), model dependent (e.g. learners can copy those that are familiar, knowledgeable, old, successful), and/or frequency dependent (e.g. learners can copy the majority) (reviewed in Kendal et al., 2018). Rather than engaging in time consuming or costly asocial, trial-and-error based learning, younger animals often observe and copy adult conspecifics when it comes to what food to eat (Galef & Clark, 1971), how to locate and access resources (Coelho et al., 2015; Foley et al., 2008), and what to avoid and fear (Cook & Mineka, 1989). The studies outlined in this thesis open discussion to further explore the potential of social learning of all these behavioural themes between males living in all-male societies.

Whilst most social learning in many mammal species may be primarily limited to the mother-offspring dyad (Galef & Clark, 1971; Mazur & Seher, 2008), from a very early age elephants learn from non-mothers in their wider family unit (Lee & Moss, 1999; 2011). Males also begin to show an interest in novel males outside the family unit for sparring behaviour in juvenescence, and in general are far more exploratory of non-family elephants compared to their female counterparts (Lee & Moss, 2011; Merte et al., 2009). Following departure from their female dominated natal herd, young males may recognise older males as high value partners from which they can learn sex specific behaviours (Evans & Harris, 2008; Chiyo et al., 2012). Elephants have an exceptional social, as well as spatial-temporal memory (Rasmussen, 1995; McComb et al., 2000; Bates et al, 2008; Presotto et al., 2019), and learning from social partners, group mates and individuals in the wider society through complex systems of communication (Langbauer, 2000) is likely a critical component to the species' success in navigating a complex and highly variable environment (Lee & Moss, 1999).

In other species, leader-follower behaviour can result in the transfer of information from informed to naïve individuals (Helfman & Schultz, 1984; Laland & Williams, 1997; Chernetsov et al., 2004; Berdahl et al., 2018). Manipulation studies in fish that involve demonstrators traveling with naive animals to a food source and subsequently being removed for future travel, results in successful navigation of routes in the “learner” fish (Laland & Williams, 1997; 1998; Reebs, 2000), with trained fish maintaining the learnt route even when it is less effective and more energetically costly than alternate routes available (Laland & Williams, 1998). Although in bird species with habitual migratory routes, there is evidence that more exploratory, uninformed individuals in groups may also play an important contrasting role in the discovery of alternate more efficient routes (Pettit et al., 2013; Valentini et al., 2021). In African elephants, matriarchs old enough to have been alive in historical droughts appear to have specialist knowledge in how to access critical resources in future droughts. Younger matriarchs that did not experience the historical drought, and did not have specialist knowledge of alternate resources suffered a greater calf mortality in their groups. This suggests past utilisation of routes led to solidification of the route and resources in the older matriarchs’ memory (Foley et al., 2008). This may suggest that elephants navigating pathways in the current study, either following older informed individuals (**Chapter 2**), or following scent cues of conspecifics (**Chapter 5**) may also be able to learn from the process and memorise the route for future travel and navigation.

Social learning experiments can be difficult to conduct in the wild (Hoppitt & Laland, 2013), and where social learning may be present, it can be difficult to refute alternate explanations such as genetic proclivities, or the animals own individual learning and innate response to resources (Laland et al., 2009). Experiments would be particularly difficult on wild large mammals such as male elephants that are wide ranging and have a frequent turnover of associates from whom they could learn behaviours (Chiyo et al., 2011a, 2012). Existing research on social learning in wild populations of elephants is often descriptive, observational, or correlative (Lee & Moss, 1999; Bradshaw & Schore, 2007; Pinter-Wollman et al, 2008). Future research may wish to expand to more experimental studies, perhaps with semi-wild individuals and observer-demonstrator paradigms, whereby uninformed observers can watch an informed conspecific perform a novel task (Greco et al., 2012), and effectiveness of learning according to social features of the demonstrator and observer such as age, familiarity and relative kinship could be explored ((Duffy et al. 2009; Krueger et al., 2013). Social learning would be particularly interesting to explore in all-male societies and non-reproductive all male groups, where recently dispersed males may have substantial amounts of behaviour to learn, and social maturity to undergo within all-male groups before they are fully mature (Evans, 2006). In **Chapter 4** I found that at all-male aggregations of African elephants, older males were not preferentially targeted by any age class younger than their own for trunk-mediated “greeting” behaviours, behaviours that simultaneously provide subject males with a close olfactory assessment of the target male. Older males may be valuable social contacts, demonstrated by them being the preferred nearest neighbours of males of all age (Evans & Harris, 2008), but younger males may avoid intimate and physical contact behaviours with older males because of their greater size, dominance and perhaps an element of fear on the younger elephant’s part. I suggest future research should focus on young elephants observing or listening to older male demonstrators as the likely sensory modality for social learning (Heyes, 1994; Lee & Moss, 1999; McComb et al., 2000; Zentall, 2004; Greco et al., 2012; Fishlock et al., 2016).

6.4 Conservation and management implications

In each chapter of this thesis, I drew attention to potential practical implications of my research findings. In many mammals, males spend a substantial portion of their lives in non-reproductive all-male groups (Ruckstuhl & Neuhaus, 2002; Estes, 2004; Chiyo et al., 2011a). It is therefore imperative to understand the social needs and dynamics between males in all male groupings to better inform animal management and conservation initiatives (Angeloni et al., 2008; Mumby & Plotnik, 2018). This is particularly important in species that have the potential to inflict harm on people and their livelihoods, species where males are more likely than females to be involved in negative interactions with people, and species of conservation concern, all of which apply to the African elephant (Chiyo et al., 2012; Stevens, 2018; IUCN, 2020).

Chapters 2 and **3** drew attention to the potential important social roles of older males to other males in all-male groupings. Firstly, **Chapter 2** found older males were more likely to lead the collective movements of all-male groups. Regardless of whether this involves passive leadership and followship processes (King et al., 2009; King, 2010), informed and knowledgeable older males appear to be important figures in the all-male society for guiding collective movements. As trophy hunting and poaching activity often favourably remove older males from populations (Barnett & Patterson, 2005; Archie et al., 2008; Boddington, 2013; Selier et al., 2014; Muposhi et al., 2016), such activities may cause disruptions to the successful movement of recently dispersed naïve males between critical resources, or to the transfer of knowledge from older males to younger males (Foley et al., 2008). My findings therefore may suggest that older males, who are already often rare in elephant populations (Moss, 2001; Whyte, 2001; Wittemyer et al., 2013; Jones et al., 2018), may be inappropriate targets of trophy hunting activity. It should also be noted that older males are more likely to engage in disruptive crop foraging activity (Stevens, 2018) and crop foraging appears to be one behaviour that can be socially learnt from older males (Chiyo et al., 2012). However, selective removal of the old males who may be sharing undesired behaviours may also be ineffective, as it is argued that removed problem elephants and habitual crop foragers will always be replaced by new crop foragers (Osborn, 1998; Hoare, 2001). Attempts to modify the behaviour of elephants and guide them away from disruptive activities such as crop foraging may wish to focus on first modifying the behaviour of older, highly influential individuals in the society, such as depriving them of opportunities to forage on crops (e.g. by creating buffer zones of unpalatable crops between areas with elephants and human-dominated landscapes (Songhurst & Coulson, 2014; Osborn & Parker, 2003a)).

Chapter 3 showed that increased older male presence in the environment reduces the aggressive behaviours of elephants to non-elephant targets. This demonstrates how a disturbed social environment has the potential to disrupt the social behaviour of males (Slotow et al., 2000; Slotow & van Dyk, 2001; Bradshaw & Schore, 2007). Male aggression to non-elephant targets may also be exacerbated by the biased removal of older males through trophy hunting or poaching activity. **Chapter 3** also found that isolated adolescents were more likely to act aggressively to non-elephant targets when alone. Aggressive encounters with elephants can lead to human mortality and damage to property (Dunham et al., 2010; DeMotts & Hoon, 2012) and my results are of great importance for understanding how to improve the welfare of human populations that live alongside elephants. For example, a common technique to drive away elephants, particularly in poorer communities, is to attempt to chase and scare away elephant whilst making substantial noise (Osborn & Parker, 2003a). My results suggest people should avoid approaching or confronting male elephants when there are less mature males around, as well as adolescent males when they are socially isolated. Furthermore, in support of previous research (Slotow et al., 2000; Slotow & van Dyk, 2001), my results suggest translocation and reintroduction schemes should assure mature males are present in populations in order to reduce aggressive behaviours of males towards non-elephant species and vehicles.

Finally, **Chapter 5** provided support for the notion that olfactory features on elephant pathways are utilised by travelling elephants for monitoring of conspecifics, as well as used to guide movements in locating critical and predictable features in the landscape (Mutinda et al., 2011; Von Gerhardt et al., 2014; Fishlock et al., 2016). Elephant pathways have been identified as key features influencing likelihood of elephant crop foraging events (Von Gerhardt et al., 2014; Songhurst & Coulson, 2014). I discussed how future research should experiment with manipulation of olfactory cues (scents of dung and urine) that characterise elephant pathways as a means to attempt to manipulate elephant movements. Such a technique may be of interest for diverting elephants away from areas with human-settlements and agricultural activity, as well as to assist in connecting areas of refuge for elephants (Douglas-Hamilton et al., 2005; Von Gerhardt et al., 2014).

6.5 Concluding remarks

This thesis contributes to a growing understanding of the complexity and importance of male social interactions in non-reproductive all-male groupings. All-male groupings are often high in fission-fusion dynamics, making individual males' membership in groups flexible. I concluded that the benefits to all-male grouping likely vary over the life course of males, with younger, adolescent males travelling in all-male groups more than predicted by chance, and older males travelling alone more than predicted by chance in this study. However, remote monitoring of other males appeared important to males of all age in this highly fission-fusion system, with adults and adolescents equally likely to respond to olfactory urine cues of conspecifics on publicly utilised travel pathways.

Younger males may benefit from a diverse range of ages of male social partners, for example age mates for developing competitive skills, and older males for acquisition of knowledge regarding sex specific behaviour, ecological resources, and environmental risks. However aside from the sparring, competitor assessment and knowledge benefits that can be acquired from age-mates, older males may not benefit from association with males younger than themselves, and tolerance of younger males may be adaptive for older males where the costs of constantly driving away same-sex conspecifics is high. However, the role of older male association in repressing sexual state in younger males is a topic that warrants further research.

I provided evidence that the age structure of other males present in all-male groupings can influence male behaviours such as aggression. Older males may have important roles in all-male groupings as either policers of aggression, or assessors and indicators to other males regarding the current level of environmental risk. Older males also appeared to have important social roles regarding leading all-male groups to critical resources in the landscape.

The African savannah elephant is both of high conservation concern, as well as a problem animal in terms of their involvement in several negative human-wildlife interactions across Africa. This makes understanding the social needs of male African elephants, and the social influences different ages of males have on one another, all the more imperative to understand. My findings highlight the need to further investigate the social role of mature individuals within all-male groups and provide new insights on the importance of older individuals from a wildlife management perspective.

Supplementary Information 1

Table S1.1: Likelihood ratio test of permutation-based GLMM: male elephant lone travel predicted by age class, elephant ID included as random effect, 1-minute cut-off to group membership.

Df	AIC	LRT	Pr (Chi)	Randomised P
3	1553.458	42.903	2.580^{e-09}	**<0.001**

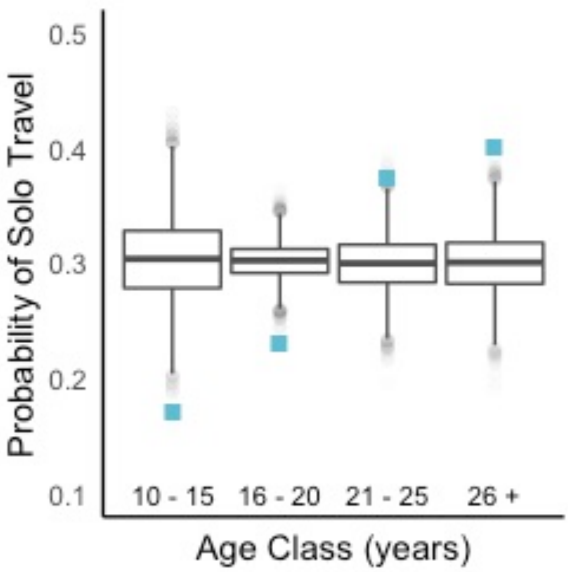


Figure S1.1: Probability of lone travel in different age classes with 1-minute cut-off applied to group membership. Adolescent males were less likely to travel alone than expected by chance, and adults more likely. Observed probabilities of lone travel for the different age classes of male elephants (blue squares), plotted against randomly permuted probabilities of lone travel (boxplots with median, interquartile range, minimum and maximum values). Observed probability for ages: 10-15 years = 0.177, 95% CI random = (0.235-0.373), p < 0.001; 16-20 years= 0.236, 95% CI random = (0.272-0.332), p < 0.001; 21-25 years= 0.379, 95% CI random = (0.253-0.347), p = 0.001; 26+ years= 0.406, 95% CI random = (0.252-0.350), p < 0.001.

Table S1.2: Likelihood ratio test of permutation-based GLMM: male elephant leadership of all-male groups predicted by age class, elephant ID included as random effect, 1-minute cut-off to group membership.

Df	AIC	LRT	Pr (Chi)	Randomised P
3	651.669	40.241	9.473 $^{e-09}$	**<0.001**

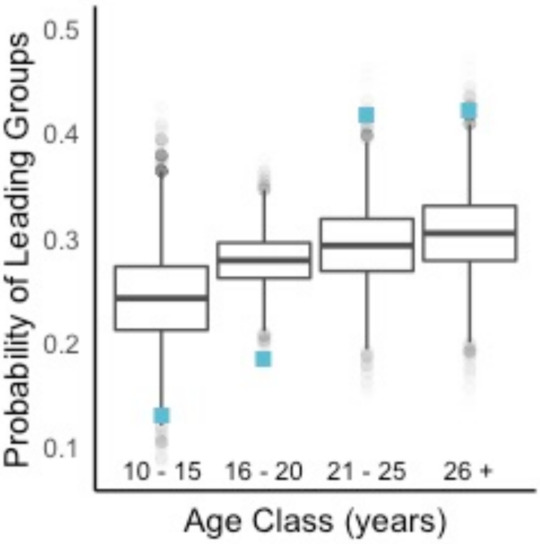


Figure S1.2: Probability of occupying lead position in all-male groups for different age classes with 1-minute cut-off applied to group membership. Adolescent males were less likely to lead groups than expected by chance, and adults more likely, with highest probabilities in the oldest age class. Observed probabilities of leadership for the different age classes of male elephants (blue squares), plotted against permuted probabilities of leadership (boxplots with median, interquartile range, minimum and maximum values). Observed probability for ages: 10-15 years = 0.136, 95% CI random = (0.152-0.344), p = 0.024; 16-20 years = 0.190, 95% CI random = (0.229-0.326), p = 0.001; 21-25 years = 0.423, 95% CI random = (0.220-0.372), p = 0.001; 26+ years = 0.426, 95% CI random = (0.226-0.383), p = 0.004.

Table S1.3: Likelihood ratio test of permutation-based GLMM: male elephant middle travel in all-male groups predicted by age class, elephant ID included as random effect, 1-minute cut-off to group membership.

Df	AIC	LRT	Pr (Chi)	Randomised P
3	597.761	30.673	9.963 $^{e-07}$	**<0.001**

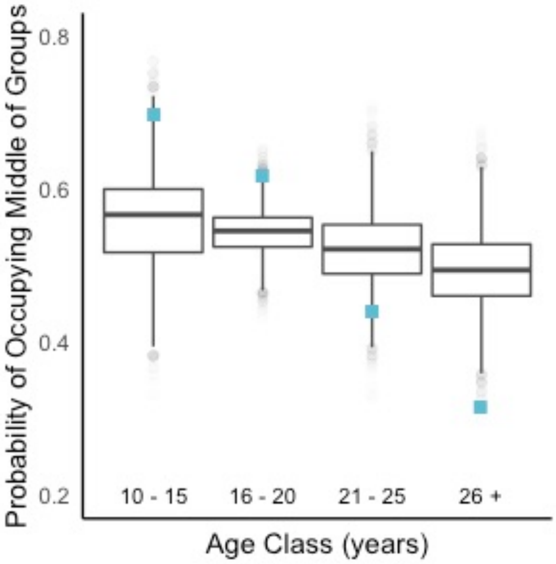


Figure S1.3: Probability of occupying middle position in all-male groups for different age classes with 1-minute cut-off applied to group membership. Adolescent males were more likely to occupy the middle of groups than expected by chance, and mature males aged 26+ years less likely. Observed probabilities of occupying the middle of groups for the different age classes of male elephants (blue squares), plotted against permuted probabilities (boxplots with median, interquartile range, minimum and maximum values). Observed probability for ages: 10-15 years = 0.704, 95% CI random = (0.450-0.669), p = 0.010; 16-20 years = 0.623, 95% CI random = (0.492-0.600), p = 0.004; 21-25 years = 0.446, 95% CI random = (0.436-0.617), p = 0.075; 26+ years = 0.322, 95% CI random = (0.404-0.584), p < 0.001.

Table S1.4: Likelihood ratio test of permutation-based GLMM: male elephant rear travel in all-male groups predicted by age class, elephant ID included as random effect, 1-minute cut-off to group membership.

Df	AIC	LRT	Pr (Chi)	Randomised P
3	654.607	4.479	0.214	0.378

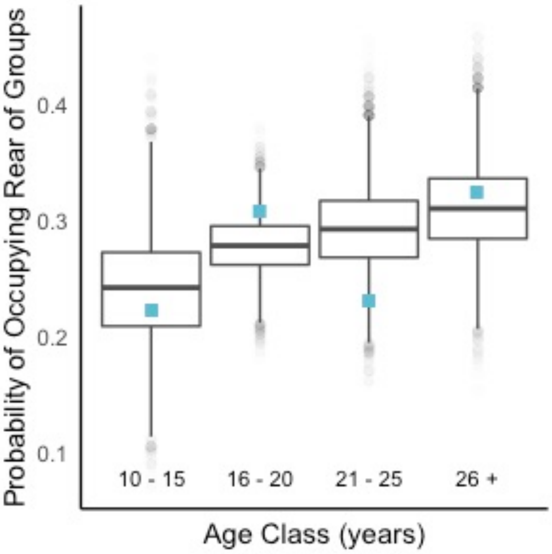


Figure S1.4: Probability of occupying rear position in all-male groups for different age classes with 1-minute cut-off applied to group membership. No age class of males were more or less likely compared to chance to occupy the rear of traveling groups. All observed probabilities (blue squares) fell within range of randomly permuted probabilities of occupying the rear of groups (boxplots). Observed probability for ages: 10-15 years = 0.227, 95% CI random = (0.149-0.333), p = 0.825; 16-20 years = 0.312, 95% CI random = (0.231-0.329), p = 0.193; 21-25 years = 0.236, 95% CI random = (0.220-0.369), p = 0.118; 26+ years = 0.328, 95% CI random = (0.237-0.388), p = 0.671.

Table S1.5: Likelihood ratio test of permutation-based GLMM: probability of male elephant lone travel predicted by age class, pathway location included as random effect instead of elephant ID.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3	1295.103	30.625	1.019 $^{e-06}$	**<0.001**

Table S1.6: Output of permutation-based GLMM: probability of male elephant lone travel predicted by age class, pathway location included as random effect instead of elephant ID. Observed probabilities of lone travel by age class given, and permutation-based significances.

Age class (years)	**Probability of lone travel**	**Coefficient**	**Std. Error**	**Pr(>|z|)**	**Randomised P**
10-15	0.102	-2.177	0.273	1.710 $^{e-15}$	**<0.001**
16-20	0.174	-1.557	0.134	2.036 $^{e-31}$	**0.008**
21-25	0.261	-1.043	0.150	3.420 $^{e-12}$	**0.009**
26+	0.289	-0.903	0.153	3.915 $^{e-09}$	**0.001**

Table S1.7: Likelihood ratio test of permutation-based GLMM: probability of leading all-male groups predicted by age class, pathway location included as random effect instead of elephant ID.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3	800.454	31.829	5.686 $^{e-07}$	**<0.001**

Table S1.8: Output of permutation-based GLMM: probability of leading all-male groups predicted by age class, pathway location included as random effect instead of elephant ID. Observed probabilities of leading an all-male group for each age class given, and permutation based significances.

Age class (years)	**Probability of leading all-male groups**	**Coefficient**	**Std. Error**	**Pr(>|z|)**	**Randomised P**
10-15	0.107	-2.122	0.338	3.390 $^{e-10}$	**0.002**
16-20	0.179	-1.520	0.154	5.707 $^{e-23}$	**0.003**
21-25	0.324	-0.734	0.169	1.380 $^{e-05}$	**0.034**
26+	0.344	-0.644	0.174	2.117 $^{e-04}$	**0.003**

Table S1.9: Likelihood ratio test of permutation-based GLMM: male elephant lone travel predicted by age class, elephant ID included as random effect, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3	1246.989	23.335	3.438 $^{e-05}$	**0.001**

Table S1.10: Output of permutation-based GLMM: probability of male elephant lone travel predicted by age class, elephant ID included as random effect, musth male excluded data set. Observed probabilities of lone travel by age class given, and permutation-based significances.

Age class (years)	**Probability of lone travel**	**Coefficient**	**Std. Error**	**Pr(>|z|)**	**Randomised P**
10-15	0.092	-2.290	0.327	2.669 $^{e-12}$	**0.009**
16-20	0.159	-1.662	0.203	2.979 $^{e-16}$	**0.030**
21-25	0.239	-1.156	0.189	9.176 $^{e-10}$	0.109

26+	0.246	-1.122	0.182	6.412 $^{e-10}$	**0.029**

Table S1.11: Likelihood ratio test of permutation-based GLMM: probability of leading all-male groups predicted by age class, elephant ID included as random effect, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3	782.603	29.833	1.496 $^{e-06}$	**<0.001**

Table S1.12: Output of permutation-based GLMM: probability of leading all-male groups predicted by age class, elephant ID included as random effect, musth male excluded data set. Observed probabilities of lone travel by age class given, and permutation-based significances.

Age class (years)	**Probability of leading all-male groups**	**Coefficient**	**Std. Error**	**Pr(>|z|)**	**Randomised P**
10-15	0.103	-2.163	0.383	1.627 $^{e-08}$	**0.006**
16-20	0.171	-1.582	0.213	1.024 $^{e-13}$	**0.006**
21-25	0.314	-0.780	0.195	6.251 $^{e-05}$	**0.046**
26+	0.338	-0.670	0.197	6.547 $^{e-04}$	**0.002**

Table S1.13: Likelihood ratio test of permutation-based GLMM: probability of male middle travel in all-male groups predicted by age class, elephant ID included as random effect, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3	828.093	45.922	5.894 $^{e-10}$	**<0.001**

Table S1.14: Output of permutation-based GLMM: probability of male middle travel in all-male groups predicted by age class, elephant ID included as random effect, musth male excluded data set. Observed probabilities of lone travel by age class given, and permutation-based significances.

Age class (years)	**Probability of male middle travel**	**Coefficient**	**Std. Error**	**Pr(>|z|)**	**Randomised P**
10-15	0.748	1.088	0.266	4.313 $^{e-05}$	**0.020**
16-20	0.716	0.923	0.153	1.529 $^{e-09}$	**<0.001**
21-25	0.507	0.029	0.172	8.667 $^{e-01}$	**0.030**
26+	0.405	-0.385	0.186	3.886 $^{e-02}$	**<0.001**

Table S1.15: Likelihood ratio test of permutation-based GLMM: probability of male rear travel in all-male groups predicted by age class, elephant ID included as random effect, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3	778.069	6.407	0.093	0.176

Table S1.16: Output of permutation-based GLMM: probability of male rear travel in all-male groups predicted by age class, elephant ID included as random effect, musth male excluded data set. Observed probabilities of lone travel by age class given, and permutation-based significances.

Age class (years)	**Probability of male rear travel**	**Coefficient**	**Std. Error**	**Pr(>|z|)**	**Randomised P**
10-15	0.200	-1.386	0.264	1.437 $^{e-07}$	0.881
16-20	0.203	-1.366	0.143	1.736 $^{e-21}$	0.289
21-25	0.250	-1.099	0.178	7.007 $^{e-10}$	0.811

26+	0.305	-0.825	0.177	3.045^{e-06}	0.087

Table S1.17: Likelihood ratio test of permutation-based GLMM: probability of leading all male groups, predicted by interaction of camera trap setup distance from river and male age class, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3 (Distance*AgeClass)	760.737	2.050	0.562	0.559

Table S1.18: Likelihood ratio test of permutation-based GLMM: probability of occupying middle of all male groups, predicted by interaction of camera trap setup distance from river and male age class, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3 (Distance*AgeClass)	789.868	2.381	0.497	0.479

Table S1.19: Likelihood ratio test of permutation-based GLMM: probability of occupying rear of all male groups, predicted by interaction of camera trap setup distance from river and male age class, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3 (Distance*AgeClass)	778.941	2.623	0.453	0.407

Table S1.20: Likelihood ratio test of permutation-based GLMM: probability of lone travel, predicted by interaction of season and male age class, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3 (Season*AgeClass)	1224.294	2.688	0.442	0.445

Table S1.21: Likelihood ratio test of permutation-based GLMM: probability of leading all male groups, predicted by interaction of season and male age class, musth male excluded data set.

Df	**AIC**	**LRT**	**Pr (Chi)**	**Randomised P**
3 (Season*AgeClass)	753.381	0.124	0.989	0.991

Supplementary Information 2

Note S2.1: Addressing tourist vehicle presence in the study.

The MPNP has a low tourist presence compared to other national parks in Botswana (Zyl, 2019), however tourist activity tended to focus on routes along the Boteti River for best wildlife viewing, which was also the site of data collection. Previous research in Madikwe Game Reserve, South Africa, found that elephants increased conspecific aggression as tourist pressure increased (Szott et al., 2019). Whilst importantly, the authors in this study noted that these elephants were founded from a population of cull and poaching survivors, who are highly sensitive to human presence (unlike the population of the MPNP who appear relaxed around appropriately distanced vehicles (50m+) with the engine off (personal observation)), it is recognised from various other studies that tourist presence can have large influences on animals' stress, aggression, vigilance and fear behaviours (Ranaweerage et al., 2015; Zanette & Clinchy, 2020). We therefore conducted supplementary analyses to confirm that tourist vehicle presence did not correlate with key social context factors, to be sure this factor was not likely to explain the significant effects in our models.

A tourist vehicle entering within 50m of a focal elephant's proximity showed no correlation with the age category of focal elephants, nor with a focal elephants' social isolation condition (phi coefficient = 0.060 for both factors). Wilcoxon rank sum tests were used to determine if focal samples with more elephants present dominated situations where a tourist vehicle did or did not enter within 50m of the focal follow. There were no differences in number of elephants present between focal follows where a tourist vehicle did or did not enter within 50m of focals (Wilcoxon rank sum test with continuity correction: W=158850, p=0.4513, mean N elephants present with focal in 10-minute follow when vehicle entered within 50m focal= 9.65, vehicle did not enter within 50m focal= 10.50 (excludes lone male focals)).

Table S2.1: Output of GLMMs: likelihood of focal elephants a) directing aggression to conspecific, b) directing aggression to non-elephant target and c) directing fear behaviours to non-elephant targets during a 10-minute focal follow, predicted by presence of females at hotspot with focal. Focal elephant ID included as random effects in all models.

a) Dependent Variable: Aggression directed by focal to conspecific target				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P**
Intercept		-1.884	0.152 (0.122-0.189)	**<0.001**
Females	Absent	*Ref*	*Ref*	
	Present	1.179	3.250 (0.792-13.335)	0.102
b) Dependent Variable: Aggression directed by focal to non-elephant target				
Intercept		-0.884	0.413 (0.348-0.490)	**<0.001**
Females	Absent	*Ref*	*Ref*	
	Present	-0.801	0.449 (0.080-2.510)	0.362
c) Dependent Variable: Fear directed by focal to non-elephant target				
Intercept		- 2.290	0.104 (0.082-0.133)	**<0.001**
Females	Absent	*Ref*	*Ref*	
	Present	1.096	2.993 (0.666-13.452)	0.153

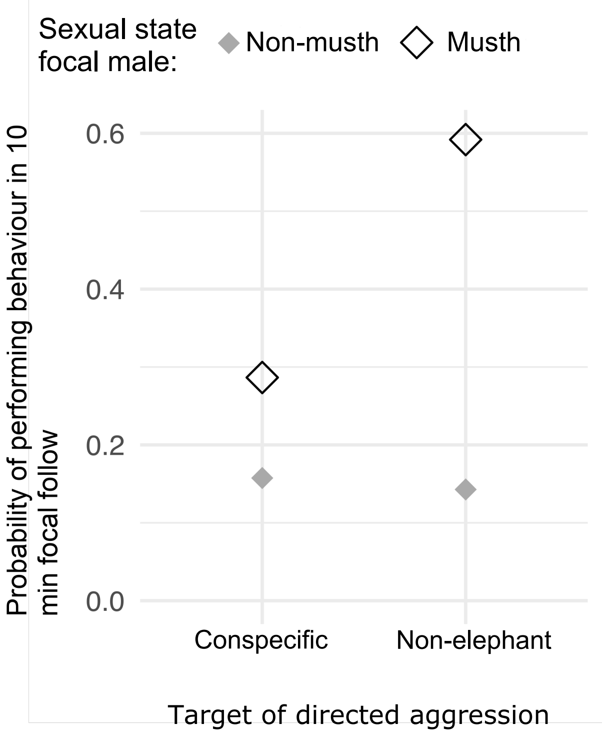


Figure S2.1: Comparison of probabilities of directing aggression to conspecific and non-elephant targets during a 10-minute focal follow between focal elephants aged 26+ years that were and weren't identified as being in musth at the time of sampling. 52 10-minute focal follows were made of elephants identified to be in musth, and were subsequently removed from further analysis.

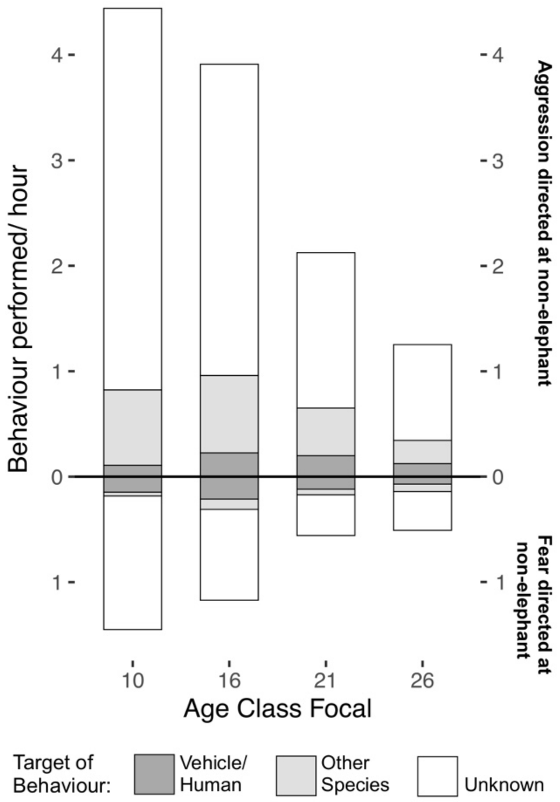


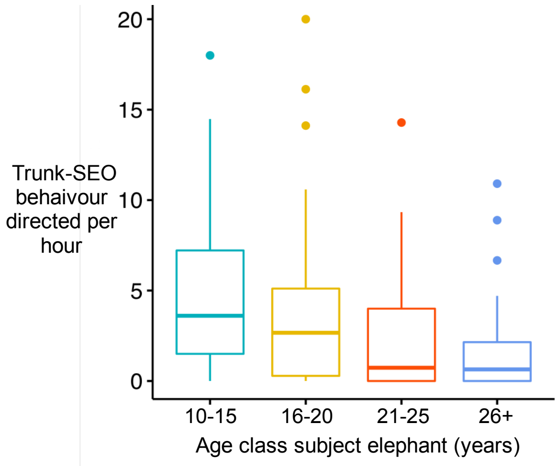
Figure S2.2: Distribution of targets of aggression and fear behaviours to non-elephant targets by age class (10= 10-15 years, 16= 16-20 years, 21= 21-25 years, 26 = 26+ years). Accumulated total number of all observed instances of behaviours, from all focal follows, controlled for by sample time collected for each age class.

Note S2.2: Addressing temporal autocorrelation in the study.

Lack of temporal independence between 10-minute follows may impact expression of behaviours through autocorrelation, activity fatigue or state-behaviour feedback effects (Sih et al., 2015; Mitchell et al., 2019). To be conservative, for all our models exploring performance of behaviours of interest, we included a fixed effect of whether this aggression behaviour had been performed in the preceding 10-minute follow to control for the influence of temporal autocorrelation.

Supplementary Information 3

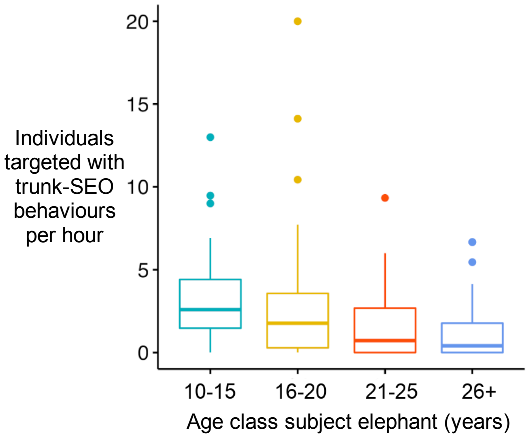
Table S3.1: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of trunk-to-SEO behaviours performed per hour.

Figure	**Pairwise comparisons between age classes (Age class (years))**			
		*10-15*	*16-20*	*21-25*
	16-20	0.210	-	-
	21-25	**0.001**	**0.020**	-
	26+	**<0.001**	**0.001**	0.210

P value adjustment method: BH

Both adolescent age classes performed more trunk-to-SEO behaviours of conspecifics per hour than both adult age classes

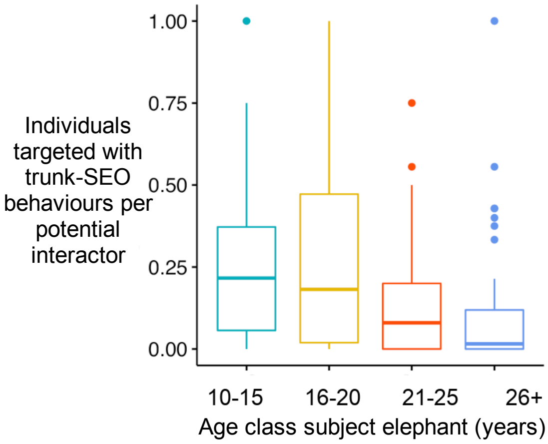
Table S3.2: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of individuals targeted with trunk-to-SEO behaviours per hour.

<table>
<tr><th>Figure</th><th colspan="4">Pairwise comparisons between age classes (Age class (years))</th></tr>
<tr><td rowspan="4">
</td><td></td><td>*10-15*</td><td>*16-20*</td><td>*21-25*</td></tr>
<tr><td>*16-20*</td><td>0.127</td><td>-</td><td>-</td></tr>
<tr><td>*21-25*</td><td>**0.001**</td><td>**0.047**</td><td>-</td></tr>
<tr><td>*26+*</td><td>**<0.001**</td><td>**0.001**</td><td>0.167</td></tr>
</table>

P value adjustment method: BH

Both adolescent age classes targeted more individuals with trunk-to-SEO behaviours per hour than both adult age classes

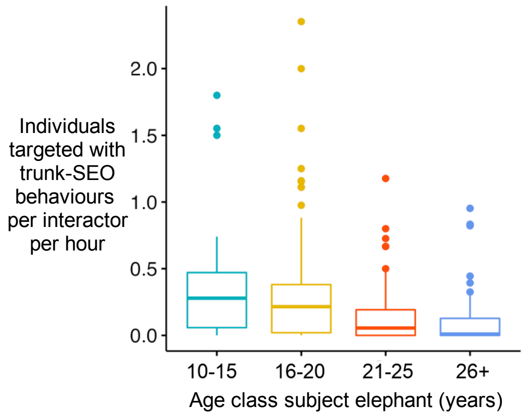
Table S3.3: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of individuals targeted with trunk-to-SEO behaviours per potential interactor exposed to during visit to social hotspot.

Figure	**Pairwise comparisons between age classes (Age class (years))**			
		*10-15*	*16-20*	*21-25*
	16-20	0.933	-	-
	21-25	**0.001**	**0.002**	-
	26+	**<0.001**	**<0.001**	0.250

P value adjustment method: BH

Both adolescent age classes targeted more individuals with trunk-to-SEO behaviours per potential interactor than both adult age classes

Table S3.4: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of individuals targeted with trunk-to-SEO behaviours per potential interactor per hour.

<table>
<tr><th>Figure</th><th>Pairwise comparisons between age classes (Age class (years))</th></tr>
<tr><td>
</td><td><table>
<tr><th></th><th><i>10-15</i></th><th><i>16-20</i></th><th><i>21-25</i></th></tr>
<tr><td><i>16-20</i></td><td>0.607</td><td>-</td><td>-</td></tr>
<tr><td><i>21-25</i></td><td>0.002</td><td>0.008</td><td>-</td></tr>
<tr><td><i>26+</i></td><td><0.001</td><td><0.001</td><td>0.192</td></tr>
</table></td></tr>
</table>

P value adjustment method: BH

Both adolescent age classes targeted more individuals with trunk-to-SEO behaviours per potential interactor per hour than both adult age classes

Table S3.5: Pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of trunk-to-mouth behaviours performed per hour.

Pairwise comparisons between age classes (Age class (years))			
	10-15	*16-20*	*21-25*
16-20	0.255	-	-
21-25	**0.001**	**0.017**	-
26+	**<0.001**	**<0.001**	0.156

P value adjustment method: BH

Both adolescent age classes directed more trunk-to-mouth behaviours to conspecifics per hour than both adult age classes

Table S3.6: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of individuals targeted with trunk-to-mouth behaviours per hour.

Pairwise comparisons between age classes (Age class (years))			
	10-15	*16-20*	*21-25*
16-20	0.173	-	-
21-25	**0.001**	**0.264**	-
26+	**<0.001**	**<0.001**	0.173

P value adjustment method: BH

Both adolescent age classes targeted more individuals with trunk-to-mouth behaviours per hour than both adult age classes

Table S3.7: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of individuals targeted with trunk-to-mouth behaviours per potential interactor exposed to during visit to social hotspot.

Pairwise comparisons between age classes (Age class (years))			
	10-15	*16-20*	*21-25*
16-20	0.734	-	-
21-25	**0.002**	**0.003**	-
26+	**<0.001**	**<0.001**	0.245

P value adjustment method: BH

Both adolescent age classes targeted more individuals with trunk-to-mouth behaviours per potential interactor than both adult age classes

Table S3.8: Post hoc pairwise comparisons using Wilcoxon rank sum test with continuity correction, showing differences between the 4 age classes concerning number of individuals targeted with trunk-to-mouth behaviours per potential interactor per hour.

Pairwise comparisons between age classes (Age class (years))			
	10-15	*16-20*	*21-25*
16-20	0.578	-	-
21-25	**0.002**	**0.008**	-
26+	**<0.001**	**<0.001**	0.213

P value adjustment method: BH

Both adolescent age classes targeted more individuals with trunk-to-mouth behaviours per potential interactor per hour than both adult age classes

Table S3.9: Observed adjusted odds ratios and permutation-based significances of elephants of different age class targeting an age-matched relative to non-age-matched individual with trunk-to-SEO behaviours of different target organs.

Behaviour directed to conspecific	**Age class (years)**	**Observed odds ratio of directing behaviour to age-matched relative to non-age-matched individual**	**95% CI randomised odds ratios**	**Randomised P**
Trunk-to-SEO behaviour (all organs combined)	10-15	3.268	0.818-1.775	**< 0.001**
	16-20	1.454	0.700-1.508	0.085
	21-25	2.056	0.445-1.730	**0.014**
	26+	2.185	0.232-1.912	**0.048**
Trunk-to-mouth	10-15	3.389	0.991-2.208	**< 0.001**
	16-20	1.532	0.691-1.607	0.077
	21-25	1.905	0.366-2.190	0.134
	26+	2.228	0.375-2.242	0.061
Trunk-to-temporal-gland	10-15	0.340	0.243^{e-06}-5.342	0.233
	16-20	1.729	0.486-2.564	0.317
	21-25	1.671	0.110^{e-06}-2.373	0.400
	26+	2.217	0.191^{e-06}-3.756	0.581
Trunk-to-genitals	10-15	4.042	0.499-4.058	0.069
	16-20	1.102	0.237-2.271	0.789
	21-25	4.078	0.551^{e-07}-2.717	**0.026**
	26+	0.758	0.965^{e-07}-3.945	0.713

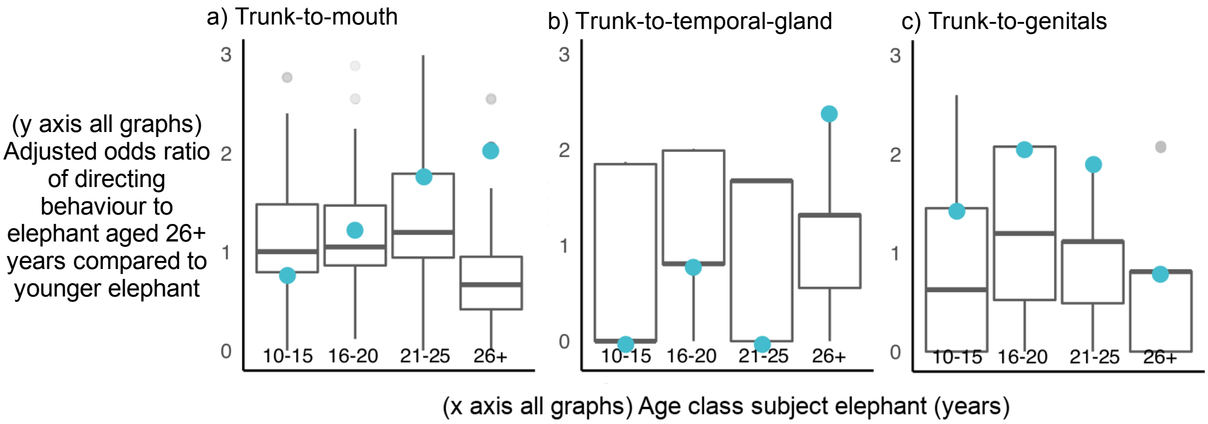


Figure S3.1: Observed adjusted odds ratios of elephants directing trunk-to-SEO behaviours to an elephant aged 26+ years relative to a younger elephant (blue circles), plotted against randomly permuted adjusted odds ratios of directing trunk-to-SEO behaviour to elephant aged 26+ years relative to a younger elephant (boxplots with median, interquartile range, minimum and maximum values). All age classes directed trunk behaviours to the mouth, temporal glands and genitals of elephants aged 26+ years as expected by random chance (Supplementary Table S4.10 for observed adjusted odds ratios, 95% confidence intervals and p values for each age class and target organ).

Table S3.10: Observed adjusted odds ratios and permutation based significances of elephants of different age classes targeting a male aged 26+ years relative to younger male with trunk-to-SEO behaviours of different target organs.

Behaviour directed to conspecific	**Age Class (years)**	**Observed adjusted odds ratio of directing behaviour to 26+ year old relative to younger elephant**	**95% CI Randomised odds ratios**	**Randomised P**
Trunk-to-SEO behaviour (all organs combined)	10-15	0.816	0.416-1.926	0.574
	16-20	1.081	0.503-2.045	0.839
	21-25	1.668	0.459-2.425	0.455
	26+	2.077	0.251-2.074	**0.042**
Trunk-to-mouth	10-15	0.794	0.275-2.394	0.487
	16-20	1.250	0.382-2.244	0.814
	21-25	1.788	0.506-2.985	0.572
	26+	2.052	0.196-2.053	0.052
Trunk-to-temporal-gland	10-15	0.941^{e-07}	0.926^{e-07}-5.784	0.171
	16-20	0.804	0.456^{e-07}-7.01	0.478
	21-25	0.123^{e-06}	0.122^{e-06}-15.640	0.223
	26+	2.405	0.702^{e-07}-4.070	0.583
Trunk-to-genitals	10-15	1.448	0.102^{e-06}-2.584	0.675
	16-20	2.076	0.231^{e-06}-4.868	0.512
	21-25	1.928	0.443^{e-07}-3.011	0.340
	26+	0.810	0.944^{e-07}-4.234	0.921

Only 10-minute focal follows where at least one elephant of each age category (26+ years and younger than 26 years) was present as a potential interactor were included in models. In the case of trunk-to-temporal-gland behaviours, despite a total of 456 10-minute follows being included in these models, only 23 trunk-to-temporal-gland behaviours were observed in these follows, including 0 trunk-to-temporal-gland behaviours towards 26+ year olds from elephants aged 10-15 years and 21-25 years, and only 1 trunk-to-temporal-gland behaviour of a 26+ year old by 16-20 year olds. Similarly the trunk-to-genital model was generated from only 40 observed trunk-to-genital behaviours, 9 of which were to elephants aged 26+ years. The small number of trunk behaviours in both these models may explain the wide randomised confidence intervals, and a larger data set may be warranted (despite 456 follows equivaling 76 study hours of elephant behaviour) to explore the observed trends for lower odds of elephants younger than 26+ years directing trunk-to-temporal-gland behaviours to mature males over 26 years relative to younger male potential interactors, and higher odds of elephants younger than 26+ years directing trunk-to-genital behaviours to elephants over 26 years relative to younger male potential interactors.

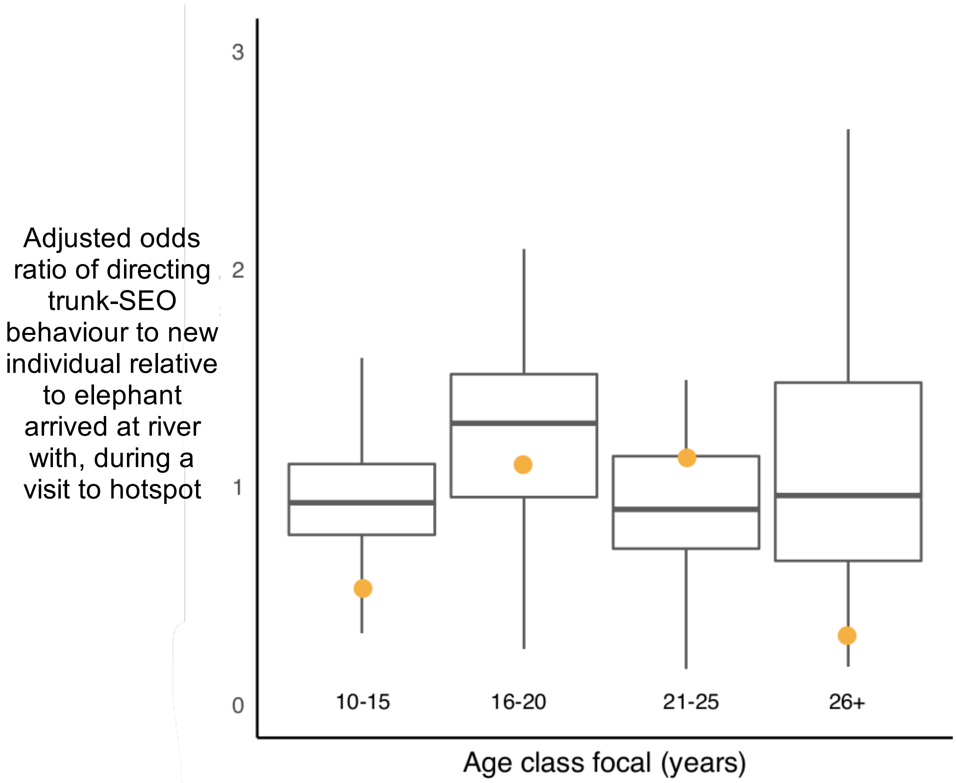


Figure S3.2: Observed adjusted odds ratios of subjects directing trunk-to-SEO behaviours to an individual met new at the hotspot relative to an elephant he arrived at the river with (orange circles), plotted against randomly permuted adjusted odds ratios of directing trunk-to-SEO behaviours to new elephants relative to elephants arrived with at hotspots (boxplots with median, interquartile range, minimum and maximum values). All age classes of focal directed trunk-to-SEO behaviours to new individuals within the range expected by random assignment of behaviours to all elephants present (observed odds ratios for ages: 10-15 years = 0.560, 95% CI random = (0.472-1.939), p = 0.175; 16-20 years = 1.110, 95% CI random = (0.600-2.472), p = 0.727; 21-25 years = 1.138, 95% CI random = (0.384-2.676), p = 0.625; 26+ years = 0.340, 95% CI random = (0.339-2.580), p = 0.059).

Supplementary Information 4

Note S4.1: A supplementary video is available online demonstrating examples of focal olfactory responses to pathways and samples, and can be found at: https://www.youtube.com/watch?v=hFRmUVEiERQ

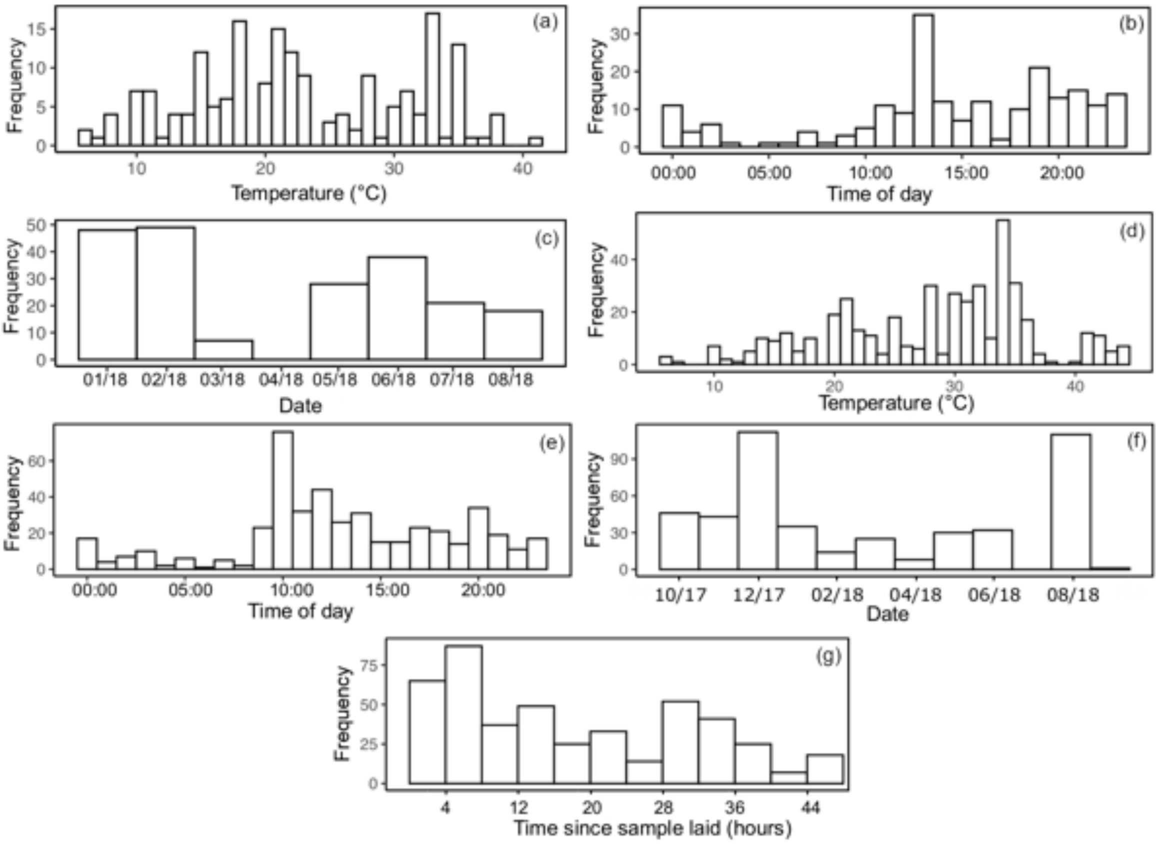


Figure S4.1: Distributions of responses caught on camera in different trial types under various time and climate conditions. (a) Temperature at the time of the response, no sample presented. (b) Time of day of the response, no sample presented. (c) Date of the response, no sample presented. (d) Temperature at the time of the response, sample presented. (e) Time of day of the response, sample presented. (f) Date of the response, sample presented. (g) Time since sample laid when response was caught, sample presented. The decrease in responses of passing elephants over time since the sample was laid was largely due to camera traps capturing responses being pulled down by passing elephants.

Table S4.1: Summary table of sample sizes of responses caught for different trial types in the study. Distributions and sample sizes of responses caught for ages of receiving elephants, sample types and climatic conditions given for both “No sample presented: models on general olfactory responses to pathways” and “Samples presented: models on focused olfactory response and vomeronasal system responses to samples”

Trial type	**Variable**			**Sample size / distribution**
No sample presented on pathways	Age class receiver (total)	Adolescent		99
		Adult		110
	Grouping (total)	Lone traveller		37
		Group traveller		172
	Position (total)	Leader		47
		Middle		73
		Rear		46
	Age Class* Grouping	Adolescent	Lone traveller	10
			Group traveller	89
		Adult	Lone traveller	27
			Group traveller	83
	Age Class* Position	Adolescent	Leader	20
			Middle	45
			Rear	20
		Adult	Leader	27
			Middle	28
			Rear	26
	Temperature			See Figure S4.1
	Time of travel (24-hour clock)			See Figure S4.1
	Month of year			See Figure S4.1
	Day/ night travel (infrared footage)	Day		102
		Night		107

	Season	Wet	103
		Dry	106
	Wind	No wind	185
		Windy	24
	Direction of travel	Toward river	159
		Away from river	50
Sample presented on pathway	Age class receiver	Adolescent	248
		Adult	208
	Day/ night travel (infrared footage)	Day	298
		Night	158
	Season	Wet	82
		Dry	374
	Wind	No wind	346
		Windy	110
	Direction of travel	Toward river	373
		Away from river	83
	Sample type	Water control	161
		Adolescent urine	119
		Adult urine	176
	Sand type sample deposited on	River edge	274
		Bank slope	182
	Temperature		See Figure S4.1
	Time of travel (24-hour clock)		See Figure S4.1
	Month of year		See Figure S4.1
	Time since deposit laid		See Figure S4.1

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