ASSOCIATIONS, DOMINANCE INTERACTIONS, AND MUSTH IN MALE ASIAN ELEPHANTS IN NAGARAHOLE AND BANDIPUR NATIONAL PARKS, SOUTHERN INDIA

A thesis submitted for the degree of

Doctor of Philosophy

by

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CERTIFICATE

This is to certify that the work presented in this thesis titled "**Associations, Dominance Interactions, and Musth in Male Asian Elephants in Nagarahole and Bandipur National Parks, Southern Indi**a" has been carried out by Ms. Keerthipriya P. under my supervision at the Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru, India, and that the results in this thesis have not previously formed the basis for the award of any other degree, diploma, or fellowship.

Date: Prof. T.N.C. Vidya

DECLARATION

I declare that the matter presented in my thesis titled "**Associations, Dominance Interactions, and Musth in Male Asian Elephants in Nagarahole and Bandipur National Parks, Southern India**" is the result of studies carried out by me at the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, India, under the supervision of Prof. T.N.C. Vidya, and that this work has not been submitted elsewhere for any other degree.

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made wherever the work described has been based on the findings of other investigators. Any omission, which might have occurred by oversight, is regretted.

Place: Bengaluru Keerthipriya P.

Date:

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My father retired as a well-regarded Professor of English literature with a distinguished career and he had a teacher who told him when he was young that there was no chance he would ever be proficient in the language. However many things we may disagree upon, I seem to have inherited his tendency to not ‘know my place’ at the right times. He made an effort to get to know me as a person and not just his daughter and if I have any self esteem at all, I owe it to that effort. My mother is the most generous person I have met in my life and I am indebted to her for financially (and not just financially) supporting me this last year. Thanks to you I had to worry about far fewer things than I otherwise would have. I remembered how hard she worked, working on her thesis when she was almost 50 years old and during her subsequent career as an Associate Professor, whenever I felt intimidated by my work.

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THESIS ABSTRACT

This thesis examines the associations and dominance interactions of adult and subadult male Asian elephants and explores how female presence and musth affect these associations and interactions. In polygynous species, the number of sexually mature males is usually greater than the available reproductive opportunities at any point in time and, hence, males are expected to compete with each other for acquiring access to receptive females (Emlen and Oring 1977). Male societies and individual relationships are, therefore, expected to be shaped strongly by their effects on the males' current or future prospects of reproductive success. Asian elephants have a polygynous mating system and show female philopatry and male dispersal (Sukumar 1989, Desai and Johnsingh 1995, Vidya and Sukumar 2005). Female elephants are rarely receptive because of their long gestation period and offspring dependency after birth. Given their long lifespan, the possibly long gap between sexual maturity and reproductive competitiveness of males, strong competition for matings because of the unavailability of females, and the phenomenon of musth, Asian elephants provide an interesting system to study male association and competition and how they change with age. I examined male associations and dominance in the Kabini population of Asian elephants (ranging in Nagarahole and Bandipur National Parks; see Vidya *et al*. 2014), in which we have identified a large number of individuals and monitored them over a long term. I carried out field work during February 2011-July 2014 and carried out analyses additionally on field data collected by others. Thus, this thesis is based on data collected for over five years (from March 2009 till July 2014) on 96 identified adult males and 105 identified subadult males. In Chapters 4 and 5, in which I examined musth and compared some aspects of it in the Kabini population to other populations of Asian elephants, I used data collected from March 2009 till August 2016 (with 157 identified males older than 10 years).

A general introduction to male affiliation and competition in mammalian species and a brief introduction to the study species and the study population are provided in ***Chapter 1***. In ***Chapter 2***, I examine the associations between adult male elephants and how these associations were affected by the presence or absence of female groups in the vicinity of males and by male age. I classified adult males, who were presumed to have completed dispersal from their natal herds, into two broad age-classes: 15-30 years of age (young

adults) and 30 years of age and older (old adults). I found that associations among adult males in all-male groups were rare and that they spent the majority of their time solitarily. In the time that they spent in all-male groups, males spent more time than expected with other males from the same age-class and less time with males from the other age-class. Older males were not more central or connected in association networks of all-male groups than younger males. This was different from male associations in the phylogenetically related African savannah elephants, in which males spent a much higher proportion of their time in all-male groups, and older adult males had more associates and were more central in the association networks (Chiyo *et al*. 2011). Therefore, males in the Kabini population seemed to form all-male groups primarily to spend time with age-peers, possibly to test strength against each other, rather than for social learning from older males. The differences between species could possibly be due to the differences in the distribution of food resources in the habitats that the two species occupy. When I compared the associations adult males made in the presence and absence of female groups, I found that male-male association networks were denser and more connected in female absence. Old males seemed to avoid one another in female presence, probably viewing each other as competitors, while old and young males met each other at random in female presence. I also found that, while associations were not stable across years, there seem to be some preferred associations among adult male elephants. Thus, male associations were complex and not necessarily always competitive.

In ***Chapter 3***, I describe the associations of subadult males (5-15 years old) and compare the patterns of their associations with those of adult males. Subadult males are expected to start spending some time away from female groups but are still in the process of dispersing from their natal groups. Subadult males were classified into two age-classes: 5-10 years of age (young subadults) and 10-15 years of age (old subadults). I found that subadult males spent most of their time in mixed-sex groups (in the presence of females) but spent most of their time in female absence solitarily. Thus, the networks of subadult male associations were denser in female presence than in female absence, with subadults of all three age-class combinations meeting more numbers of each other and spending a greater proportion of their time associating with other subadults in female presence than in female absence. This was in contrast to adult male associations, which were more extensive and common in female absence than in female presence. Subadult male associations were also stable across years in female presence but not in female absence. Given the greater sociality of subadult males in female presence than in female absence, forming associations with age/sex peers is not likely to be the primary proximate cause for male dispersal. However, in the small time that subadult males spent with one another in all-male groups, they spent more time with age-peers than with the other age-class. Therefore, it is possible that subadults, like adults, also use their time in all-male groups to test strength against closely matched age-peers.

In ***Chapter 4***, I examine some aspects of musth (a rut-like phenomenon that is characterised by temporal gland secretion and elevated plasma testosterone levels in Asian elephant males; Jainudeen *et al*. 1972a,b) and how musth affects the associations of adult males. Older males were more likely to be sighted in musth than younger males. A greater proportion of new males in musth than nonmusth males were sighted across years, suggesting that musth is a roving strategy adopted by males to find more reproductive opportunities. Old adult musth males spent a slightly greater proportion of their time with female groups when compared to old adult nonmusth males, and associated with larger female groups than nonmusth males did. Young adult males, on the other hand, spent a smaller proportion of their musth time with female groups when compared to their nonmusth time, and associated with similarly sized female groups. Further, while old adult musth males seemed to tolerate young adult nonmusth males in the presence of females, young adult musth males were never sighted with old nonmusth males in the presence of females. Therefore, across these broad age-classes in the Kabini population, musth seems to be primarily a strategy for old males to rove rather than a means for young males to gain a temporary reproductive advantage over old males (see Hall-Martin 1987). Moreover, the distribution of number of musth males across days was not different from that expected at random and I found no evidence for large-scale spatiotemporal separation of musth males in the study population.

Chapter 5 is a small chapter that compares the age-structure, frequency of musth males, and seasonality of musth in the Kabini population with data from two previously studied populations of Asian elephants – in Mudumalai Wildlife Sanctuary (data from Daniel *et al*. 1987, Desai 1987) and Kaziranga National Park (data from Chelliah and Sukumar 2015). I found that the sex ratios in Kabini and Mudumalai at the time of the two studies were similar, but the sex ratio in Kaziranga was less skewed than that in Kabini. However, the age-structure of adult males was not different between Kabini and Kaziranga but was different between Mudumalai and Kabini, with a greater proportion of very old males in

Mudumalai. The proportion of sightings of musth males in Kabini was much lower than those in both Kaziranga and Mudumalai. Thus, the number of competitor males in the area may possibly influence the occurrence of musth. There were no seasonal differences in the frequency or ages of musth male in Kabini, unlike in Mudumalai, wherein a higher frequency of musth males was found during the wet season than in the dry season. Ecological differences between the two parks may explain these differences.

I describe agonistic interactions of adult and subadult males in ***Chapter 6*** and examine the role of some factors that might affect the outcome of such dominance interactions. Based on field observations that I carried out between February 2011 and July 2014 and subsequent scoring of videos, I observed 456 independent dominance bouts, each of which could consist of more than one agonistic interaction. Analysing dominance between nonmusth males, I found a greater proportion of resolved dominance bouts among adult males than subadult males. Subadults showed greater physical contact and initiation of agonism by the eventual loser of the bout, and also interacted with greater numbers of opponents and new opponents than adults. Although linear dominance hierarchies were not found because of the small proportion of dyads that interacted, the dominance in all age-classes were unidirectional and a greater proportion of transitive triads were found than expected by chance. Older males tended to win over younger males among adults and among subadults. Age and body condition had a significant effect on the outcome of dominance bouts between nonmusth adult males, while tusk length did not. Musth males were rarely observed engaging in dominance, but, when they did, almost always won over nonmusth males. Thus, there were some differences between the dominance styles of adult and subadult males but both showed some orderliness of dominance relationships.

In the conclusions chapter, ***Chapter 7***, I summarise and discuss the main results of the previous chapters. This thesis includes the first study examining adult and subadult male Asian elephant societies in detail, the first long-term dataset to examine musth in free-ranging Asian elephants, and only the second study that examined dominance interactions between male Asian elephants. The findings in this thesis show that the associations and agonism between male elephants were modulated by their age, immediate presence of female groups and musth status in complex ways.

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CHAPTER 1

General Introduction

Introduction

Polygyny is the common mating system among mammalian species (Orians 1969, Kleimann 1977) and is expected in populations with a biased operational sex ratio, with the number of sexually receptive females being smaller than the number of sexually active males at a given point in time (Emlen and Oring 1977). It is thus generally expected that adult male mammals in such species would compete with one another to obtain matings (van Hooff and van Schaik 1994). The strength of this intrasexual competition for mates is thought to affect differences in morphology (Mitani *et al*. 1996) and lifestyles between the sexes. The latter may include male-biased dispersal from natal groups (Dobson 1982), males forming relatively stable associations with different groups of females after dispersal (for example, in hamadryad baboons - Kummer 1968, rhesus macaques - Boelkins and Wilson 1972, and olive baboons - Packer 1979), or males roving between different social groups (for example, sperm whales - Whitehead and Arnbom 1987). Thus, in polygynous species, competition among males is expected to be intense and to shape male society.

Male competition is often reflected as intrasexual agonism, with males who are high-ranking in the dominance hierarchy being more successful at acquiring matings than low-ranking males (Dewsbury 1982, Cowlishaw and Dunbar 1991, Ellis 1995). However, alternative reproductive tactics also exist, and coalitions with other males to defend females (Packer and Pusey 1982, Parsons *et al*. 2003), extension of support to dominant males to obtain reproductive concessions (Duffy *et al*. 2007, Snyder-Mackler *et al*. 2012), special associations with females (Silk 2002), and sneak matings (Berard *et al*. 1994, Soltis *et al*. 2001) may allow males to obtain some reproductive success beyond that expected from a strict hierarchy. Although competition between males is expected, affiliations between males may also be beneficial by facilitating social learning from older males or providing opportunities for age-mates to test their strengths against each other (Chiyo *et al.* 2011, 2012). Thus, I wanted to examine male associations and agonism in this thesis.

The study species: Asian elephant (Elephas maximus)

The Asian elephant is an endangered species that now occupies about 3.5% of its historic range (Baskaran *et al*. 2011). There are an estimated 41,400-52,300 elephants across the world (Sukumar 2003), of which the majority are found in India (26,000-28,000 individuals; Baskaran *et al*. 2011). Southern India harbours the largest population of elephants in India and, within it, the Nilgiris-Eastern Ghats landscape hosts the largest population of ~8,800 elephants (Baskaran *et al*. 2011). Only male Asian elephants carry tusks (although not all males do) and males have been subject to poaching for ivory in various populations. Thus, adult sex ratios are often skewed (Menon *et al*. 1997, Ramakrishnan *et al*. 1998), and the effective population size of the species is probably much smaller than census sizes. It was thought that there were no more than 1,500 adult males in India in 1997 (Menon and Kumar 1998).

Asian elephants live in a range of habitats, from dry thorn forests to dry and moist deciduous forests to evergreen and riparian forests (Sukumar 2003). They are thought to be generalist feeders (Sukumar 1989, Baskaran *et al*. 2010) and, being megaherbivores, require large quantities of food. Asian elephants are estimated to spend ~50%-~75% of their time feeding (McKay 1973, Sukumar 2003, Baskaran *et al*. 2010). Wild Asian elephant adult males may weigh up to 4000 kg (Sukumar 2003) and consume 1.5-2.0% of their weight as dry forage mass in a day (McKay 1973, Sukumar 2003, Baskaran *et al*. 2010). Therefore, foraging itself may influence male associations and interactions in the species, apart from competition for reproduction. Male and female Asian elephants experience very different societies as the species shows female philopatry and male dispersal (Sukumar 1989, Desai and Johnsingh 1995, Vidya and Sukumar 2005). Female society is organised into clans that are the most inclusive social unit of organisation and some clans have further social sub-structuring (Nandini *et al*. 2018). Female Asian elephants in the Nagarahole-Bandipur population did not show significant seasonal changes in social structure and appeared to have constraints on group size (Nandini *et al*. 2017). Fission-fusion dynamics allowed for changing group compositions within clans (Nandini *et al*. 2017) and interactions between clans were generally aggressive (Shetty 2016). While female Asian elephants, being philopatric, form associations with related females (Vidya and Sukumar 2005, Shetty 2016), males disperse away from their natal herds to different locations (Vidya and Sukumar 2005, Vidya *et al*. 2005, Ahlering *et al*. 2011) through an extended process of dispersal (Desai and Johnsingh 1995). Thereafter, males form temporary associations with other males and female groups (McKay 1973, Daniel *et al*. 1987, Desai and Johnsingh 1995).

Asian elephants are polygynous (Sukumar 1989) and possibly show scramble competition polygyny because they have to search widely for access to fertile females. Female elephants are rarely receptive because of their long gestation period and offspring dependency after birth and come into oestrous for only a few days (Eisenberg *et al*. 1971, Hess *et al*. 1983) during their long inter-birth interval of several years (de Silva *et al*. 2013). Adult male Asian elephants show the phenomenon of musth, which is similar to rut in deer. Musth males have high plasma testosterone levels and show more aggression than nonmusth males (Jainudeen *et al*. 1972a,b). A study of adult male dominance in an Asian elephant population with equal proportions of tusked and tuskless males showed that, musth overrode body size, which in turn overrode tusk length in deciding the winner of dominance interactions (Chelliah and Sukumar 2013). In the same population, female elephants were shown to prefer larger/older males as mates (Chelliah and Sukumar 2015). There have been no detailed studies on adult male societies or on subadult male societies and agonism in this species.

The Kabini Elephant Project

The Kabini Elephant Project is an ongoing long-term project on Asian elephants that was started in 2009 in the Nagarahole and Bandipur National Parks and Tiger Reserves (Nagarahole: 11.85304°-12.26089° N,76.00075°-76.27996° E, 644 km^2; Bandipur: 11.59234°-11.94884° N, 76.20850°-76.86904° E, 872 km^2). These parks form part of the Nilgiris-Eastern Ghats landscape (which, as mentioned above, holds the single largest population of Asian elephants; Baskaran et al. 2011). These national parks have a high density of elephants (~1-2 elephants/ km^2; AERCC 2006) and the dominant habitats are dry and moist deciduous forests. The study area receives ~950mm of annual rainfall from the southwest and northeast monsoons. The two National Parks are separated by the backwaters of the dammed Kabini river. During the dry season, the backwaters recede, providing abundant fresh grass and water for herbivores including elephants. The area also provides good visibility for behavioural observation. The field study was carried out on the Nagarahole and Bandipur elephant population centred around the Kabini reservoir (called the Kabini population). Sampling included the forests of both National Parks and the area around the backwaters. However, due to better visibility, a large part of the behavioural data come from the backwaters area. As part of the long-term project, which I contributed to building up, hundreds of individual elephants have been identified by natural physical characteristics (see Vidya *et al*. 2014). Thus, data on identified males could be collected for this thesis.

This study

In this thesis, I describe the first long-term, detailed study of male sociality and musth on free-ranging Asian elephants, and only the second on adult male dominance in the species. As mentioned above, adult male associations in Asian elephants have not been studied in detail before. Although the species is polygynous, there might be benefits to male associations as mentioned above in the form of social learning or testing strengths. Affiliations between adult males are observed in a number of polygynous mammalian species (Packer and Pusey 1982, Connor *et al.* 2001, Chiyo *et al*. 2011) and male affiliations have been shown, in some cases, to be stable over time (Mitani 2009, Lee *et al*. 2011) and quite complex (Wiszniewski *et al*. 2012). Therefore, one of my objectives was to examine how frequently adult and subadult males associated amongst themselves and with each other and whether and how their associations differed based on their age and the presence or absence of females in the vicinity. I expected that female presence would affect older and younger males differently, depending on whether they were competitively mate-searching.

Males of long-lived species, in which females range over areas that are too large to defend, are expected to rove between different female groups in search of mating opportunities (Whitehead 1990, 1994). Males of such species (like African savannah and Asian elephants) show striking size dimorphism and often grow throughout their lifetime (Roth 1984, Haynes 1991, Lindeque and van Jaarsveld 1993). There may be a considerable delay between when males are sexually mature and physiologically capable of mating, and when males actually compete with other males for access to mates. In such cases, the younger males might opportunistically obtain some mating success but are expected to refrain from risky, competitive strategies (like musth - Poole and Moss 1981, Jainudeen *et al*. 1972b) in favour of increased growth or survival (Whitehead 1994). Thus, younger, non-competitive males are expected to modulate their associations and aggressive interactions based on how they will affect their future reproductive success, whereas the older, competitive males are expected to make those decisions based on how they affect their current chances of obtaining matings. Therefore, another objective of this study was to examine how musth might affect male associations and how that might be affected by male age. I also wanted to examine the spatiotemporal distribution of musth males and see if there was any avoidance between musth and nonmusth males, at scales larger than immediate associations. I compared the age-structure and proportion of musth male sightings of the Kabini population with two other Asian elephant populations.

Finally, as competitive interactions are expected to be important in polygynous species and might change with age as explained above, another objective of this study was to analyse and compare dominance interactions of adult and subadult males, life stages at which males are expected to have different motivations. I expected agonism between adult males to be different in nature from those between subadult males, with subadult males' dominance possibly serving as practice for future fights.

This work was based on six to eight years of data on associations, agonism, and musth status, collected on individually identified male elephants. I collected field data from February 2011-July 2014 and additionally analysed data collected by others.

Outline of the thesis

This thesis is written in manuscript format; each chapter is structured as a separate manuscript, some of which have already been submitted. In the second chapter, I describe adult male associations, and the effect of age and female presence on these associations. I examined two potential reasons for all-male group formation among adult males and compared the results from Kabini to what was observed in African savannah elephants. I then describe subadult associations in all-male and mixed-sex groups in the third chapter and examine whether associating with age-sex peers could be a proximate reason for male dispersal. I analyse the age-specific effect of musth on male-male and male-female associations and examine the spatiotemporal distribution of musth males in the fourth chapter. I also check whether our observed results support the hypothesis that musth is primarily a means for younger males to temporarily gain advantage over older males (Hall-Martin 1987). In the fifth chapter, I compare the age-structure and proportion of musth male sightings in the Kabini population with those from two previously studied Asian elephant populations. The sixth chapter investigates agonistic interactions among adult males and among subadult males, examining how resolved and asymmetric the relationships are and whether they show a linear hierarchy. I also analyse the effects of some factors in predicting the outcome of adult male dominance interactions. The seventh and last chapter is a short summary and discussion of the results.

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CHAPTER 2

Effects of Male Age and Female Presence on Male Associations in a Large, Polygynous Mammal in Southern India

Title: Effects of male age and female presence on male associations in a large, polygynous mammal in southern India

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Author contributions

P. Keerthipriya and T.N.C. Vidya conceived this work. PK collected field data during February 2011-July 2014 and carried out the analyses. S. Nandini helped with field data collection during January 2011-May 2013 and TNCV helped with initial field data collection in 2009-2010. PK primarily and TNCV wrote the manuscript and all the authors read and finalised the manuscript.

Abstract

We present here, the first detailed study of immediate adult male associations in an Asian elephant population, using six years of data collected on identified males. As expected in a large, polygynous species, adult males spent greater proportions of their time solitarily or in mixed-sex groups than in all-male groups. However, the adult male associations seen were complex, with different patterns of male associations based on their age and on the presence or absence of females. Both old and young males spent more time associating with their age-peers, and less time associating across age classes than expected at random in the absence of females. Young males did not spend a greater proportion of their time with old males, relative to the proportion they spent with other young males. Young males did not initiate associations with old males to a greater extent than old males approaching young males. Moreover, male age was not correlated with centrality measures in association networks and was negatively correlated with the number of unique associates per time in the absence of females. All of these suggest that male associations in female absence are primarily a means for males to spend time with age-peers, possibly to test their strength against each other, rather than an opportunity for social learning from old males. Male associations in female presence were rarer than in female absence, and old, reproductively competitive, males avoided each other in female presence, resulting in different male association network properties. Although male associations were generally weak and not stable across years, there were some significant associations. Overall, there was a smaller proportion of time spent in all-male groups, smaller group sizes, and a limited role of older males in the association network in the Kabini Asian elephant population compared to the phylogenetically closely related African savannah elephant. These differences may be related to differences in resource distributions in the two habitats.

Keywords

Asian elephant, male associations, association networks, Kabini, Kabini Elephant Project, testing-strengths hypothesis, social learning hypothesis, female presence/absence, male age.

Introduction

Adult males and females of many large mammals exhibit sexual dimorphism and strikingly different lifestyles, with female philopatry and male dispersal (see Greenwood 1980 and Ruckstuhl and Neuhaus 2000, Fitzpatrick *et al*. 2012). Adult male associations with females are of different types, expected to be shaped by the spatiotemporal distribution and monopolisability of mating opportunities (Emlen and Oring 1977). Adult males in some species that show male dispersal form relatively stable bonds with female groups after dispersing from their natal herd and spending some time either alone or in all-male groups (for example, seen by Hrdy 1977 in Hanuman langurs, van Noordwijk and van Schaik 1985 in longtailed macaques, Packer and Pusey 1987 in lions, Smale *et al*. 1997 in spotted hyaenas, Sprague *et al*. 1998 in Japanese macaques, Alberts and Altmann 1995 in baboons). In some species, which have distinct breeding seasons, males form mixed-species groups during the breeding season and all-male groups outside of the breeding season (for example, Clutton-Brock *et al*. 1987 in red deer, Villaret and Bon 1995 in Alpine ibex, Mooring *et al*. 2003 in desert bighorn sheep). In a few species, males rove between different female groups and form only temporary associations with female groups throughout the year (for example, Best 1979 in sperm whales, Poole 1982 in African savannah elephants, Derocher and Sterling 1990 in polar bears, Desai and Johnsingh 1995 in Asian elephants, Baird and Whitehead 2000 in killer whales). The interactions between males themselves in polygynous species with these different kinds of lifestyles are expected to be competitive rather than affiliative, with males competing with one another for access to receptive females (van Hooff and van Schaik 1994). Therefore, strong associations are not expected between males in species with female-philopatry and may occur primarily only in the context of coalitions to defend or contest access to females (for example, Saayman 1971 in baboons, Bygott *et al*. 1979 in lions, Caro and Collins 1987 in cheetahs, Connor *et al*. 1992, Moller *et al*. 2001 in bottlenose dolphins, Hill and van Hooff 1994, van Hooff and van Schaik 1994 in non-human primates, Wagner *et al*. 2008 in hyaenas). However, male-male interactions in all-male groups may be less competitive or aggressive than those within mixed-sex groups (Pusey and Packer 1987 in primates, Robbins 1996 in mountain gorillas). All-male groups may provide an opportunity to test strength against and assess competitors in a more relaxed setting (Latour 1981 in polar bears, Bon *et al*. 1993 in mouflon sheep, Chiyo *et al*. 2011 in African savannah elephants). Male associations in all-male groups may also be motivated by the opportunities available for social learning from older, more experienced males (Evans and Harris 2008, Chiyo *et al*. 2011, 2012 in African savannah elephants possibly African). Increased efficiency in obtaining food resources (river otters, Blundell *et al*. 2002) and improved defense against predators (Cape ground squirrels, Waterman 1997, sperm whales, Cure *et al*. 2013) are also possible benefits from associating with other males, despite the intrasexual competition possible. There has been little study on male association patterns in mammals overall, especially on those species that rove between female groups and do not form multimale multifemale groups or large multimale groups in the non-breeding season. We, therefore, wanted to examine the extent and nature of male associations in such a roving species that is large, polygynous, and faces potentially high male-male competition and potential group size restriction, but is also phylogenetically related to a species with complex male association patterns.

Asian elephants (*Elephas maximus*) are polygynous, with males and females exhibiting different morphologies and adult lifestyles. Female society in this species is organised into clans that show fission-fusion dynamics (Sukumar 1989, Nandini *et al*. 2017, 2018), while pubertal males disperse from their natal groups and only temporarily associate with other males and with female groups thereafter (McKay 1973, Desai and Johnsingh 1995). Males are not known to form coalitions to defend females. They can also breed throughout the year and are not spatially segregated by sex for foraging during a non-breeding season. Moreover, female elephants are sexually receptive only for a few days (Eisenberg *et al*. 1971) every four to five years, making receptive females a rare resource, for which males are expected to compete intensely. Male-male dominance interactions have been observed in this species (McKay 1973, Daniel *et al*. 1987, Chelliah and Sukumar 2013), implying that there is contest competition between the males. When males enter musth (a rut like phenomenon in male elephants that is associated with increased levels of serum testosterone and aggression; Jainudeen *et al*. 1972 a,b), their home ranges are much larger than their non-musth home ranges (Fernando *et al*. 2008), suggesting that there is also some scramble competition to find rare, receptive females. Therefore, male-male affiliative associations in the species are expected to be very weak. However, males in the closely related African savannah elephants have been shown to have complex relationships, with males preferring to associate with age-mates (Chiyo *et al*. 2011, Goldenberg *et al*. 2014 – in the case of sexually inactive males) and related males (Chiyo *et al*. 2011, although the effects of age and relatedness in this study were small), and older males being preferred associates or being more central to male society than young males (Evans and Harris 2008, Chiyo *et al*.

2011). Male associations were also shown to facilitate social learning: bulls who had an older crop raider as a top associate were more likely to raid themselves (Chiyo *et al*. 2012). Thus, temporary all-male groups seem to provide an opportunity to spar and test strength and also possibly for younger males to learn from knowledgeable, older males in African savannah elephants.

While Asian and African elephants were previously assumed to have similar societies, female Asian elephant society is now known to be different from that of the African savannah elephant (de Silva and Wittemyer 2012, Nandini *et al*. 2018), probably because of female group sizes being constrained due to ecology in the Asian elephant (Nandini *et al*. 2017, 2018). Since males, being larger and continuing to grow in size as they age (Sukumar *et al*. 1988), are likely to require more food than females, such a constraint might also exist in male Asian elephants and lead to differences in male societies across species, despite their phylogenetic closeness. Moreover, male African savannah elephants were known to return to the same bull areas (areas frequented by males and not by many female groups) when sexually inactive (Poole 1982), providing an opportunity for repeated associations with specific individuals. An absence of separate bull areas in Asian elephant populations might lower male sociality in this species. We, therefore, wanted to examine associations among adult male Asian elephants in order to find out whether ecological differences possibly correlate with a different male social structure than that in the African savannah elephant, despite the phylogenetic similarity between species.

We aimed to find out how prevalent, stable, and strong male associations were in the Asian elephant and what factors might affect such associations. We hypothesized that male associations in all-male groups might primarily be based on opportunities available for a) social learning from older individuals and/or b) testing strengths, while those in mixed-sex groups might, in addition, be affected by the competition for mating opportunities. These hypotheses are not mutually exclusive and may both play a role in male associations. Increased efficiency in obtaining food resources was not likely to be a factor for adult male groupings in elephants because individuals require large amounts of food and grouping is likely to create food competition instead. Defense against predators was also not likely to be important because adult male elephants inside protected areas do not have any natural predators. We did not examine genetic relatedness as a reason for associations in this paper.

We set out to address the following questions:

1) *What is the proportion of time that males spend in all-male groups and how is this related to male age?* Based on high competition amongst males in polygynous species and the possibility that female Asian elephants prefer older males (Chelliah and Sukumar 2015), we expected that older males would spend less time associating with other males in all-male groups and more time in mixed-sex groups than younger males. Although older males were seen more often than younger males in all male groups of the African savannah elephant (see Chiyo *et al*. 2011, Goldenberg *et al*. 2014), that pattern would possibly be reversed if there was a constraint on group size.

2) *How does male age and the presence or absence of females in the vicinity affect patterns of associations between males?* We expected different patterns of male associations based on male age depending on whether associations were based on social learning or testing strengths. If male associations were primarily based on social learning from older individuals (a), younger males would seek out older males more often than expected by chance alone. If there was social learning, but older males were restricted in the amount of time they spent with other males (possibly due to group size constraints), we expected that we would find older males to spend less time in all-male groups (as mentioned in point 1 above), but the proportion of young males' time that was spent with older males to be higher than that spent with young males. We also expected that older males would have more associates than young males and, hence, be more central in networks of all-male associations. If the primary purpose of male associations was to test strengths (b), males would be expected to preferentially associate (relative to population age-structure) with age-mates than with much younger or older individuals, whose relative strengths are easily assessed by size differences. Older males might know their strengths better through their experience, and need to assess strength with other old males less often than younger males who are still learning. Therefore, we expected that, among common males, old males would meet each other at random while younger males would spend more time with each other than expected. However, this might not be true when more uncommon males were included and both old and young males might associate more with males from the same age-class than of the other age class if associations were primarily to test strengths. Older males might also be expected to spend less time in all-male groups or form smaller all-male groups than younger males because of increasing food competition due to larger body size.

Since competition for females could play a major role in how males associated, we examined male associations in the immediate presence and absence of females. Unlike in the African savannah elephants, there were no separate bull areas in our study area and there were no clear indicators of active and inactive sexual states outside of musth (the proportion of time males spent with female groups was also not different between musth and nonmusth males, Keerthipriya *et al*. 2018). We expected the amount of time spent in male associations to be lower overall in female presence compared to female absence because of potential competition. We also expected the competition in mixed-sex groups to be more intense for older, reproductively competitive males. If associations were based on testing strength (b), males (of similar ages) were expected to spend a greater proportion of their time in female absence than in female presence associating with other males. Further, if the absolute time spent by males was greater in female absence than presence, males might also meet a greater number of other males in female absence, resulting in the male association network in female absence being denser and better connected than that in female presence. If associations were based on social learning (a), males might associate with older males to a smaller extent in female presence if the learning was only related to resources, to a larger extent if the learning was related to reproduction, or to the same extent if both played an equal role. The network would be better connected in female absence than presence, with older males being more central and having more connections in the network if the learning was related to resources, and better connected in female presence than absence, with older males being more central and having more connections if the learning was related to reproduction.

3) *Are there preferential associations between males and, if so, are they were stable over time?* We did not have any *a priori* expectation about whether preferred, stable associations should be present or not, but if they occurred, we expected them to be less frequent than that in the African savannah elephant due to possible group size constraints.

Methods

Field data collection

The field study was carried out in Nagarahole and Bandipur National Parks and Tiger

Reserves (Nagarahole: 11.85304°-12.26089° N,76.00075°-76.27996° E, 644 km^2; Bandipur: 11.59234°-11.94884° N, 76.20850°-76.86904° E, 872 km^2) in southern India from March 2009 to July 2014. Nagarahole and Bandipur are part of the larger Nilgiris-Eastern Ghats landscape (see Nandini *et al*. 2017) and support a high density of elephants (~1-2 elephants/km^2,AERCC 2006, Baskaran *et al*. 2011). We refer to the elephants in these two parks as the Kabini population. Nagarahole and Bandipur National Parks are separated by the Kabini reservoir, which is a perennial source of water in the dry season. Because of the higher density of elephants around the reservoir and better visibility for behavioural observations, our sampling was centred around the reservoir, and extended to the forests in either direction with lower frequency of sampling (see Nandini *et al*. 2017). Elephants in the area are accustomed to tourist vehicles. We sampled pre-selected forest routes(see Nandini *et al*. 2017 for details) in the study area from early morning to late evening (~6:30 AM to 6:00-6:45 PM depending on field permits and light conditions).

We tried to sex, age, and identify all the elephants sighted. Asian elephants are sexually dimorphic, with males being taller and bulkier than females (Sukumar *et al*. 1988) apart from differences in genitalia. Females do not possess tusks, although some males (called makhnas) are also tuskless. We estimated age based on shoulder height, body length, skull size, and skin folds (see Vidya *et al*. 2014), with semi-captive elephants in the same area serving as a reference for ageing older animals. We placed males into the following age categories: calves (<1year), juveniles (1-<5 years), sub-adults (5-<15 years), young adults (15-<30 years), and old adults (>=30 years). Subadult males would be starting to disperse away from their natal groups or still be in the process of dispersing. Young adult males were likely to have completely dispersed from their natal herds but were possibly less reproductively competitive than old adult males, based on studies of African savannah elephants (Poole 1982, Poole *et al*. 2011). The ages used for classifying males into these categories were those calculated at the mid-point of the study period (November 2012). We identified individuals based on a combination of ear, back, tail, tusk, and body characteristics (detailed in Vidya *et al*. 2014). We recorded details of group size, GPS location, and time of sighting, and also whether adult males were in female presence or absence. Females were classified as adults when they were 10 years old (see Nandini *et al*. 2018). Adult males were said to associate with a female group (one or more adult females and their young that were in close proximity and showed coordinated movement; see Nandini *et al*. 2018) if they fed within 10m (easy physical reach) of a group member or interacted with any group member. When two males associated with the same female group at the same time, they were said to be associating with each other in female presence. Occasionally (only three different sightings totaling 23 minutes), males were seen to associate with subadult females (5-10 years old) in the absence of an adult female and this was also considered to be association in female presence. Males were said to associate with each other in female absence if they fed within about 30-50 m of each other and there were no females in the vicinity. At this distance, the males would be able to display or react to visual signals, apart from sensing one another through sound or smell. These were also distances that were relevant to physical interactions. Elephants are capable of communicating over longer distances through auditory and olfactory signals. However, there would be no way for us to identify coordinated movement between two elephants separated by, say 2 km, in the forest in the absence of radiocollaring. Moreover, we were interested in immediate associations. Beyond about 50 m or so, we did not find males in the area to show any clear signs of interest in each other. Males that associated with one another based on this definition could indulge in sparring during their associations. However, if males, upon encountering each other, displayed only aggressive interactions and moved away, they were not said to be associating. We are taking distances that are relevant to physical interactions, although elephants are capable of communicating through auditory and olfactory signals over longer distances. Male associations were sampled at every minute as they were found to change very quickly (see Supplementary material 1). Analyses were also carried out considering only the first sighting of the day for each male, as has been done in African savannah elephants, but this did not capture the time males spent with various female groups properly (Supplementary material 1).

Data Analysis

Data analysis was carried out using only those sightings in which all adult males were aged and identified and female group compositions (if applicable) were known. Of the 878 days of field work between 2009 and 2014, elephants were sighted on 853 days and identified adult males were sighted on 718 days. In many of the analyses mentioned below, only males who were sighted on at least 5 different days in that particular category (such as group composition type or female presence) were used, as associations of males seen rarely are unlikely to represent their actual association patterns and may bias the results. Similarly, if there was a comparison between different categories (such as associations in female presence and absence), common males seen on at least 5 different days in each of the categories were used. ANCOVAs and non-parametric tests (Mann-Whitney *U* tests, Wilcoxon's matched-pairs test and Spearman's rank order correlations) were performed using Statistica 7 (StatSoft, Inc. 2004) and randomisations were carried out using MATLAB (MATLAB R2011a, MathWorks, Inc, 1984-2011, www.mathworks.com) unless specified otherwise.

Proportions of their time that males spent in all-male and mixed sex groups and their relationship with male age

We calculated the number of minutes individual males (that were seen on at least 5 different days) were seen in the following group types and calculated the proportions of each individual's time spent in such groups: 1) solitary, 2) all male groups with only one adult male (but including subadult or juvenile males and, therefore, not solitary), 3) all male groups with more than one adult male, and 4) mixed-sex groups. An ANCOVA was carried out on the logit transformed proportions of their time individual males spent in different group types, using group type as the independent categorical variable and age of the male as a continuous covariate, in order to examine whether the proportions of time spent in different group types were significantly different and whether they were based on male age. Since the four proportions add up to one and are, therefore, not independent, and the number of males seen in group type 2 was small, we performed the ANCOVA on two of the four categories: all male groups with more than one adult male, and mixed-sex groups.

Effect of male age and the presence or absence of females on male association patterns

We looked at the initiation of associations and the pattern of associations between males to understand whether social learning might be a possible reason for associations. In order to find out whether younger males sought out older males more often than expected by chance alone, we examined all the instances (dyadic combinations) of a male (or males) approaching another male (or males) to associate in the presence or absence of females. Of the dyads that included one old (30+ years old) and one young (15-30 years old) male, we calculated the number of times the old male approached the young male and vice versa. Given two males of different ages in close proximity, it was theoretically possible that either of them could approach the other. We tested for a significantly higher number of older males or younger males being approached by using a *z* test approximation of the binomial test. For this analysis, we used data from the years 2011-2014 (during which detailed behavioural observations were available). We also carried out the test using the relative ages of the two males instead of placing them in two age-classes. Younger males would approach older males more often than expected if social learning were the primary reason for associations.

We examined male associations with respect to age to find out whether associations were largely between age-mates (expected in the testing-strengths hypothesis) or between old and young males (expected in the social learning hypothesis). In order to find out whether males preferentially associated with age-mates more often than expected by chance, we used the procedure for randomising associations found in Whitehead (2008, pg. 124, following the method of Bejder *et al*. 1998). We permuted associations between all identified adult males, by switching individual males across sightings (where each sighting represented one minute of association) while keeping the group size and the time seen for each male constant. In one set of randomisations (referred to as *males permuted*), we permuted males separately for the dataset of males in female presence and in female absence. In a second set of randomisations (referred to as *males and female presence permuted*) we used the entire dataset combining female presence and absence, and permuted individual males and also randomly assigned the sightings as being in female presence or absence (conserving the total number of sightings in both categories). For each set of randomisations, we used 5000 permutations, with the number of flips performed in each permutation being five times the number of sightings in that dataset. We calculated the time old (>=30 years) and young (15-30 years) males spent in groups with other males of the same or different age class in the observed dataset and compared these observed values to the values from the permuted datasets. We calculated the probability of the observed value being significantly higher or lower than that expected at random using the number of randomisations in which the randomised value was higher or lower than observed ($P<0.025$ for statistical significance as we had no prior expectation about whether the observed values would be lower or higher than the random values). We repeated the "*males permuted*" randomisations with the common males alone (seen on five days or more both in female presence and absence) to verify whether the results remained unchanged.

Using the common males, we also calculated the age difference (rather than using the old-young classification above) between all unique pairs of males who associated together and tested for differences in age when the association was in female presence and in female absence, using a Mann-Whitney *U* test. We further weighted these age differences by the number of minutes the males associated with each other and compared the distributions of age difference between associates in female presence and absence using a Kolmogorov-Smirnov two sample test (Sokal and Rohlf, 1981, pp. 440-445).

The proportion of time (out of total time the male was seen) that males spent associating with other males in female presence and absence was compared using an ANCOVA with female presence as a categorical factor and age of the male as a covariate. In order to find out whether young males spent more time associating amongst themselves in female absence than old males (who might know their strengths better) did amongst themselves in female absence, we compared the proportions of their time young males spent associating with other young males with the proportions of their time old males spent associating with other old males in female absence using a Mann-Whitney *U* test (individual males used as the replicate). We also compared the proportion of their time young males spent with other young males to the proportion of their time young males spent with old males using the Wilcoxon’s matched-pairs test. This was done separately for time spent in female presence and absence. We had expected that if there was social learning, but older males were restricted in the amount of time they spent with other males, the proportion of young males’ time that was spent with older males would still be higher than that they spent with other young males.

In order to find out whether old males experienced smaller group sizes than young males, we examined the effects of age-class and female presence on the number of males present within groups (including solitary males of group size 1). We compared the average group sizes experienced by males seen for five days or more, both in female presence and absence, using an ANOVA with age-class and female presence as factors.

Since we had wanted to examine how females affect male associations, we also compared male association networks in female presence and absence. In order to do this, we first calculated association indices (AI) between pairs of males as the duration of time two males spent together (N_{AB}), divided by the total duration of time the two males were seen ($N_A+N_B-N_{AB}$). We found male associations to change quickly (unlike female associations, where the associates were stable for longer periods of time): therefore, every minute of association was used to calculate the association index between pairs of males, making it a proportion of time rather than the more conventionally used proportion of sightings when two animals were seen together. Using AIs, we constructed association networks of adult males seen on at least 5 different days in both female presence and female absence (for instance, $\mathrm{AI}_{\mathrm{AB(F\_abs)}}=N_{\mathrm{AB(F\_abs)}}/(N_{\mathrm{A(F\_abs)}}+N_{\mathrm{B(F\_abs)}}-N_{\mathrm{AB(F\_abs)}}$, where F_abs refers to female absence). The networks were visualized and network statistics (see below) calculated using Gephi 0.8.2 (Bastian *et al*. 2009). The network comprised males (*nodes* or *vertices* in the network) connected to one another depending on their associations (connections being *edges* in the network). The *degree* of a node (male) is the number of edges (associates of the focal male) arising from the node. We compared the degree distributions of association networks in female presence and absence to their Poisson expectation (expected for an Erdös-Rényi random network; Erdös and Rényi 1960) using Statistica 7 (StatSoft, Inc. 2004) to test whether associations were random.

We then compared the following network statistics between male association networks in female presence and absence: average degree, average *clustering coefficient*, average *path length*, and *network density* (Latapy 2008; see Wasserman and Faust 1994). We calculated the average degree of old and young males with other old and young males (all four combinations) separately. Clustering coefficient of a male is the proportion of the total possible connections between his associates that exist. The average clustering coefficient was calculated by averaging across all males who had at least two associates (i.e. degree>=2). The path length between two nodes (males) is the number of edges that lie on the shortest path between them. Path lengths were averaged for all pairs of nodes that were connected in the network to obtain average path length. Shorter path lengths indicate closer connections. Density is the proportion of all possible edges that exist in the network and is also a measure of the connectedness the network. In order to examine how male age and female presence or absence might affect the strength of male associations, we also calculated the average non-zero AI between pairs of old males, young males, and old and young males. As AI values are properties of dyads (unlike degree which is a node-level property and hence, averaged over the number of males in the focal males' age-class) and symmetric (that is $\mathrm{AI}_{\mathrm{AB}}=\mathrm{AI}_{\mathrm{BA}}$) the average non-zero AI of old-young dyads is the same as the average value for young-old dyads (averaged over the number of old-young dyads which were observed associating). Thus, while there were four combinations when we compared degree, there were only three when we compared non-zero AI.

We compared these network statistics and AIs in female presence and absence using a sampled randomization test (Sokal and Rohlf 1981, pp. 791-794). In this test, we created 10,000 permuted datasets (permuted by randomly assigning rows of data to female presence or absence, while conserving the sample size for both the categories) and the observed differences in network statistics and AI between the original female presence and female absence datasets were compared to the differences between the permuted ‘female presence’ and ‘female absence’ datasets. The probability of a significant difference between the observed values was calculated as the proportion of randomisations that yielded a greater or equal difference in statistic based on the permuted datasets compared to the difference between the observed values.

We also compared the number of associates controlled by the time seen (*degree/time*) for the same male in female presence and absence using Wilcoxon’s matched-pairs test. While we had compared the time spent together by males of different age-classes in female presence and absence, that time could either be spent by forming weaker alliances with many males or stronger alliances with fewer males. Therefore, we examined degree/time as well as degree.

Since we had expected that older males would be more central to male social networks if social learning played an important role in male associations, we calculated three measures of network centrality – *closeness centrality*, *betweenness centrality* and *Eigenvector centrality* –for different individuals (see Bonacich 1972, Wasserman and Faust 1994).Closeness centrality is the inverse of the sum of path lengths from a focal node to all the other nodes, making it a measure of how close the focal node is to other nodes. Betweenness centrality is the proportion of all shortest paths between all other pairs of nodes that pass through the focal node. Therefore, a node with high betweenness centrality is important to the connectedness of the network. Eigenvector centrality is a measure of the influence of the node. Nodes are assigned relative scores and their connections to nodes are weighted by the centrality value of the associate nodes; connections to high scoring nodes contribute more to this centrality than connections to a low scoring node. Centrality measures and clustering coefficient were calculated using Gephi 0.8.2 (Bastian *et al*. 2009). We compared centrality values, as well as clustering coefficient and degree/time between males of different ages in female presence and in female absence in order to find out whether old males were more central, more connected, and had a higher rate of associations.

This was done by correlating these statistics with male age using Spearman's rank-order correlations.

Preferred male associations and stability of associations

We wanted to see if there were preferred associations or avoidance amongst identified males within sampling periods smaller than the entire dataset and, therefore, tested for this using SOCPROG 2.6 (Whitehead 2009). We used a sampling period of 14 days and 10,000 permutations with 10,000 flips for each permutation. We used the '*permute associations within samples*' method which tests for long-term (across sampling period) preferences and avoidances (Whitehead 2009). The presence of long-term preference/avoidance is indicated by significantly higher SD (standard deviation) and CV (coefficient of variation) of AI values from the real dataset when compared to the randomised datasets. We additionally determined a top associate (based on AI value) for all identified males who associated with more than one male (degree>=2) of a particular age category. We checked whether the AI values of males' top associates from the same age-class were significantly higher than the non-zero AI values of other associates in that age-class. This was done by comparing the list of all focal males' top associates' AI values with that of other non-zero AI values using a Mann-Whitney *U* test (paired values for each male would obviously give a significant difference).Similarly, the AI values with the top associates of the other age-class were also compared with the average non-zero AI values with males of the other age-class.

In order to determine whether adult male associations were stable across years, we compared AI matrices between consecutive years, using those males that were common to and seen for at least 30 minutes in both years, by performing Mantel tests of matrix correlation (Mantel 1967) with 5000 permutations, using MATLAB (MATLAB R2011a, MathWorks, Inc, 1984-2011, www.mathworks.com). Implementing a cutoff of males seen at least for 5 days in a year would reduce the sample size drastically; therefore, a 30 minute cutoff was used for this analysis. However, we found that the number of minutes and the number of days males were sighted were strongly correlated with each other (Supplementary material 2). Since the amount of data collected during 2009 and 2010 were small, only data from 2011-2014 were used for this analysis. Mantel tests were performed separately on male associations in female presence and in female absence.

Results

Proportion of their time that males spend in all-male groups and its relationship withmale age

Based on sightings in which all adult males were aged and identified, there were a total of 96 identified elephants (see Supplementary material 2, 3). Only 56 males were seen in the presence of females and 91 males were seen in the absence of females. When we examined the percentage of time we observed males in different group types, about 61% of our observation time comprised males that were solitary, about 29% comprised males as part of mixed-sex groups, and about 6% comprised males as part of all-male groups with more than one adult male. However, since this time could include males seen just once, we used the set of males seen on at least five different days and examined what proportion of their time was spent in groups of different types. The trend was the same, with males spending a greater proportion (average=50.7%) of their time solitarily, followed by that in mixed-sex groups (35%), and in adult all-male groups (10.6%) (Table 1). When the percentages of time males were observed in different group types were calculated using the first sightings of the day of males, the proportion of sightings of solitary males (number of adult males in the sighting=1) increased, the proportion of sightings of all-male groups remained similar, while the proportion of sightings of mixed-sex groups were much smaller (Supplementary material 1). Surprisingly, there was no effect of age on the proportion of their time spent in different group types (ANCOVA: male age as covariate: N=43 males seen on >=5 days, $F_{1,83}$=2.110, P=0.150) but the proportion of time spent in mixed sex groups was higher than that spent in all-male groups with other adult males (ANCOVA: group type as fixed factor: $F_{1,83}$=101.637, P<0.001; the results did not change when untransformed data were used, see Supplementary material 4).

Table 1. Observation time for all identified adult males and males seen on at least 5 days (in female presence or absence) in different group types, whether the group type represents the presence or absence of females in the vicinity, and the average percentage of their time spent by males in different group types. The percentage of hours of observation in different group types is simply based on the total hours of observation in different group types. The average percentage of time spent by males seen on at least 5 days in different group types is based on the percentages of their time each of those males spent in each of the group types.

Group type	Female presence / absence	Hours of observation in group type (*N*=96 males seen in all)	Percentage of hours of observation in different group types	Hours of observation (*N*=43 males seen on >=5 days)	Average percentage of their time spent by 43 males ± SD
Solitary	Female absence	732.18	60.56%	685.40	50.72 ± 22.405
All-male groups (1 adult male)	Female absence	50.30	4.16%	47.77	3.66 ± 4.349
All-male groups (>1 adult male)	Female absence	74.77	6.18%	157.20	10.56 ± 10.614
Mixed-sex groups	Female presence	351.78	29.10%	374.63	35.07 ± 23.108

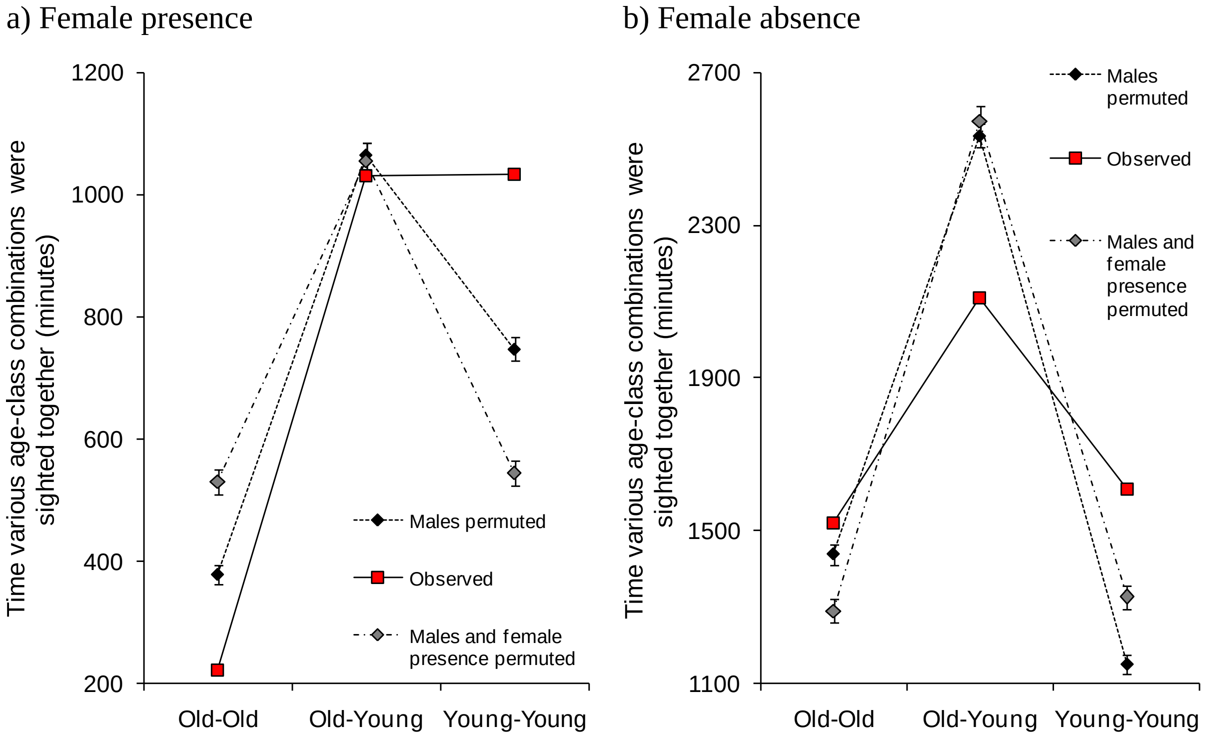
Effect of male age and the presence or absence of females on male association patterns

Frequency of males approaching older and younger males

In the presence of females, we observed 19 instances of old male (30+ years old)-young male (15-30 years old) dyads where one male approached the other (as opposed to dyads already present when we began the observation). The young male approached the old male on 8 (42.1%) occasions, which was not statistically significantly different from 50% (z=0.689, P=0.491). In female absence, we observed 27 old male-young male dyads and the young male approached the old male on 14 (51.9%) occasions, which was also not significantly different from 50% (z=0.187, P=0.852). When we used the relative ages of the two males approaching instead of placing them within the two age-classes, the younger male approached the older male in female presence 14 out of 28 times and the younger male approached the older male in female absence 19 out of 50 times. Neither of these was statistically different from 50% (female presence: z=0.000, P=1.000; female absence: z=1.697, P=0.090). Therefore, old and young males were equally likely to approach each other to associate. If at all there was a trend in the last test, it was in the direction of older males possibly approaching younger males to a greater extent than vice versa.

Associations between males of different age-classes/ages in female presence and absence

The total amount of time males were seen in female presence was 21,107 minutes (351.78 hours) and the total amount of time males were seen in female absence was 51,435 minutes (857.25 hours, Table 1). The observed amount of time males spent together was higher in female absence than female presence, for all three age-class combinations (Figure 1). As mentioned in the Methods, we compared the observed male associations in female presence and absence with those obtained by randomly permuting either males alone within the female presence or female absence datasets, or by permuting both males and female presence/absence status for the sighting across the entire dataset. We found that the time spent together by old adult males (>=30 years) in female presence (222 minutes) was significantly lower than that expected from both the randomly permuted datasets (males permuted: average ± SD: 377.6 ± 16.32, P<0.001;males and female presence permuted: average ± SD: 529.7 ± 21.38, P<0.001). However, the time spent together by young males (15-30 years) in female presence (1034 minutes) was significantly higher than that expected from the randomly permuted datasets (males permuted: average ± SD: 747.0 ± 19.61, P<0.001;males and female presence permuted: average ± SD: 544.1 ± 21.49, P<0.001; Figure 1).The observed time old and young males were seen together (1031 minutes) was not significantly different from random (males permuted: average ± SD: 1063.6 ± 121.02, P=0.055;males and female presence permuted: average ± SD: 1055.7 ± 29.22, P=0.397). On the other hand, when we examined the time spent together in female absence, both old males (1518 minutes) and young males (1608 minutes) spent a greater amount of time associating amongst themselves than expected at random (old males: males permuted: average ± SD: 1436.5 ± 28.73, P=0.002;males and female presence permuted: average ± SD: 1289.8 ± 30.02, P<0.001; young males: males permuted: average ± SD: 1149.2 ± 26.24, P<0.001;males and female presence permuted: average ± SD: 1325.9 ± 30.81, P<0.001; Figure 1).Thetime that old and young males spent together (2110 minutes) was significantly lower than random (males permuted: average ± SD: 2535.0 ± 32.61, *P*<0.001;males and female presence permuted: average ± SD: 2573.0 ± 38.44, *P*<0.001; Figure 1). When the '*males permuted*' randomisations were run using only the 33 common males (who were seen on five days or more both in female presence and absence), we found that old males met each other at random in female absence, while the other results remained similar (see Supplementary material 5). We also performed the '*males permuted*' randomizations using the first sightings of the day of males. In female absence, old males were sighted together more than expected by chance and old and young males were sighted together less often than expected by chance. Young males were sighted together more than expected by chance, but this trend was not significant, with a borderline *P* value (Supplementary material 5). Thus, the results remained the same based on the first sightings of the day as with minute-to-minute sightings. In female presence, when the first sightings of the day were considered, there were very few sightings in which males were sighted together and none of the male age-classes were sighted together more or less than expected by chance (Supplementary material 5). However, using the first sightings of the day are not appropriate for female presence sightings as explained in Supplementary material 1.



a) Female presence

b) Female absence

Figure 1. Permuted and observed values of time spent together by adult males of the same and different age-classes in a) female presence and b) female absence. Old males are >=30 years and young males are 15-30 years old. Please note that the Y axis is on different scales in the two panels.

The age differences between unique pairs of associating common males were not significantly different between female presence (average ± SD: 11.2 ± 7.54) and absence (average ± SD: 9.5 ± 6.61) (Mann-Whitney U test: $N_{\text{F\_presence}}$=33 pairs of males, $N_{\text{F\_absence}}$=68 pairs, U=971.000, Z_{adj}=1.093, P=0.277), but the distributions of age differences, taking into account, the amount of time spent together in associations, were significantly different between the two categories (Kolmogorov-Smirnov two sample test: D=0.331, P<0.001). Males with an age difference of less than five years spent the maximum percentage of time in female absence together, while such males spent among the least percentage of time in female presence together (Figure 2).

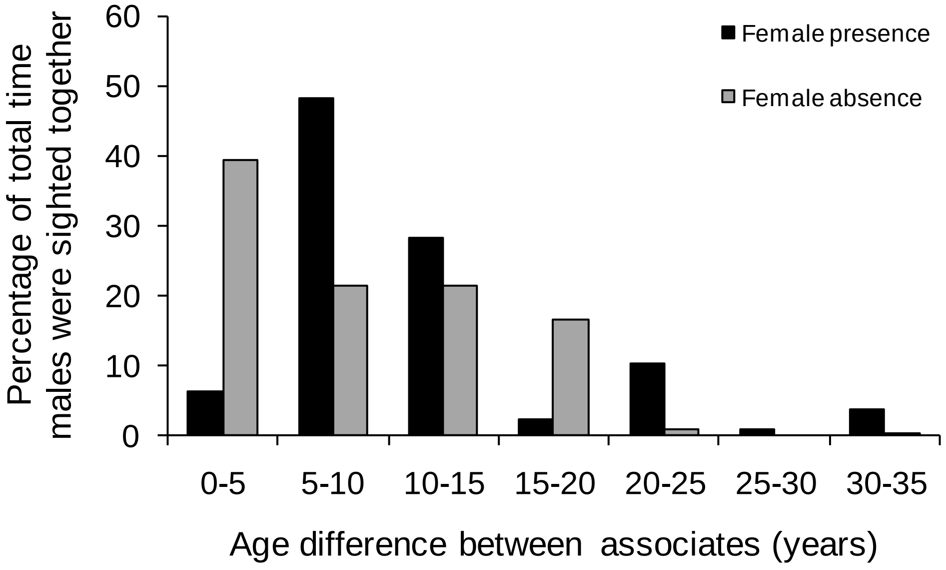


Figure 2. Percentage of total time in female presence and absence thatmales of various age differences spent together.

While there were interesting differences between the *amounts* of time males spent with others of the same or different age class in female presence and absence, the logit *proportion* of time that males (who were sighted on >=5 days and were seen both in female presence and absence during that time; N=42) spent associating with other males of any age-class was not affected by female presence or male age (ANCOVA: Female presence: $F_{1,81}$=1.788, P=0.185; Age: $F_{1,81}$=0.822, P=0.367; same results with untransformed data, see Supplementary material 6).Males spent (average ± SD) 0.232 ± 0.241 of their time in female presence and 0.157 ± 0.146 of their time in female absence with other males. Contrary to expectation, old males did not spend a significantly smaller proportion of their time in female absence associating with other old males (average ± SD = 0.110 ± 0.149) than the corresponding proportion of their time young males spent associating with other young males (average ± SD = 0.120 ± 0.088) (Mann-Whitney U test: N_{Young}=22, N_{Old}=18, males seen on >=5 days in female absence used, U=152.000, Z_{adj}=-1.254, P=0.219). We had also expected (in the case of social learning) that the proportion of young males' time that was spent with old males might be higher than that spent with young males. However, we found that the proportions of their time young males spent with other young males (average ± SD: female presence: 0.117 ± 0.104; female absence: 0.120 ± 0.088) were not significantly different from the proportions they spent with old males (average ± SD: female presence: 0.110 ± 0.117; female absence: 0.110 ± 0.136) both in female presence and absence (Wilcoxon's matched-pairs test: female presence: N=19 young males seen on >=5 days in female presence, T=68.000, Z=0.402, P=0.687; Female absence: N=22 young males seen on >=5 days in female absence, T=104.000, Z=0.400, P=0.689).

Effect of age and female presence/absence on male group size

The group size distributions of multi-male groups that we observed in female presence and absence were small in general with a mode of 2 (~85% of the observations, see Supplementary material 7). The modal experienced group size (counted as the number of adult males) was 1 (Supplementary material 7). The average of group sizes experienced by individual adult males (seen on >=5 days in female presence and absence, N_{Young}=18, N_{Old}=15) was calculated for males of different age-classes in female presence and absence. While there was a small tendency for the average group sizes experienced by old males (average ± SD: female presence: 1.195 ± 0.182; female absence: 1.175 ± 0.190) to be slightly smaller than those experienced by young males (average ± SD: female presence: 1.221 ± 0.161; female absence: 1.244 ± 0.177), they were not statistically different. The average experienced group size was not affected by female presence, age-class of the male, or their interaction (Factorial ANOVA: female presence: $F_{1,62}$=0.002, P=0.968; age-class: $F_{1,62}$=1.196, P=0.278; interaction: $F_{1,62}$=0.248, P=0.620; Figure 3).

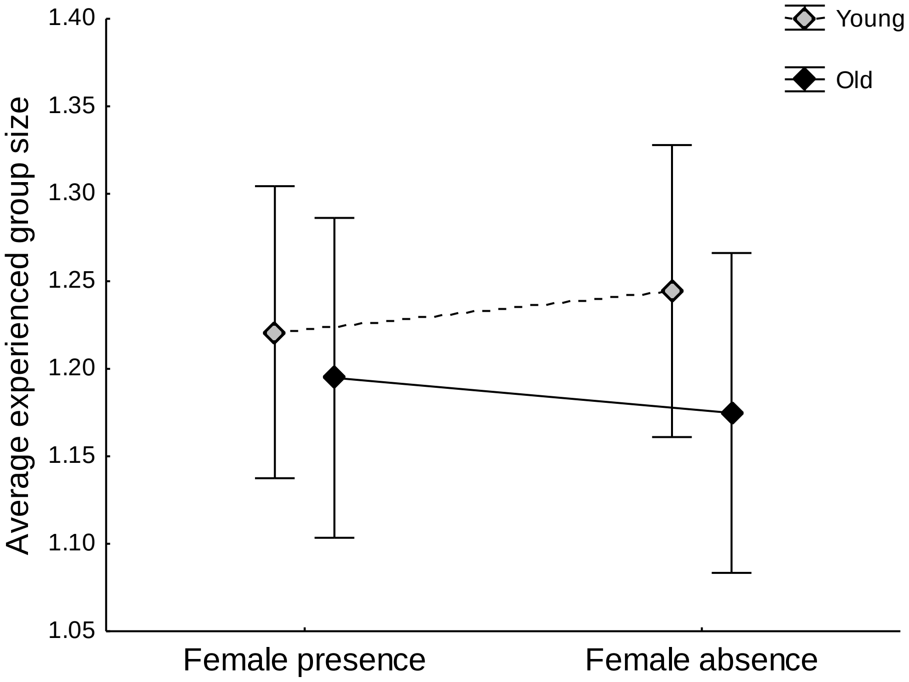


Figure 3. Average experienced group size (number of adult males) experienced by common males of both age-classes, in female presence and absence. Error bars are 95% CI.

Effect of male age and female presence or absence on social networks

We found that the association network of adult males in female presence was not significantly different from a random network (χ^2=0.965, P=0.326) but the network in female absence was significantly different from random (χ^2=26.552, P<0.001, Figure 4), with some males having a lower degree than expected and others having a greater degree than expected in female absence (Supplementary material 8). Based on the sampled randomisation test (using the same 33 common males seen in female presence (19,297 minutes) and absence (46,289 minutes)), the average clustering coefficient and density were higher in female absence than in female presence and the average path length was lower in female absence than in female presence (Table 2), suggesting a more highly connected male network in female absence than in female presence.

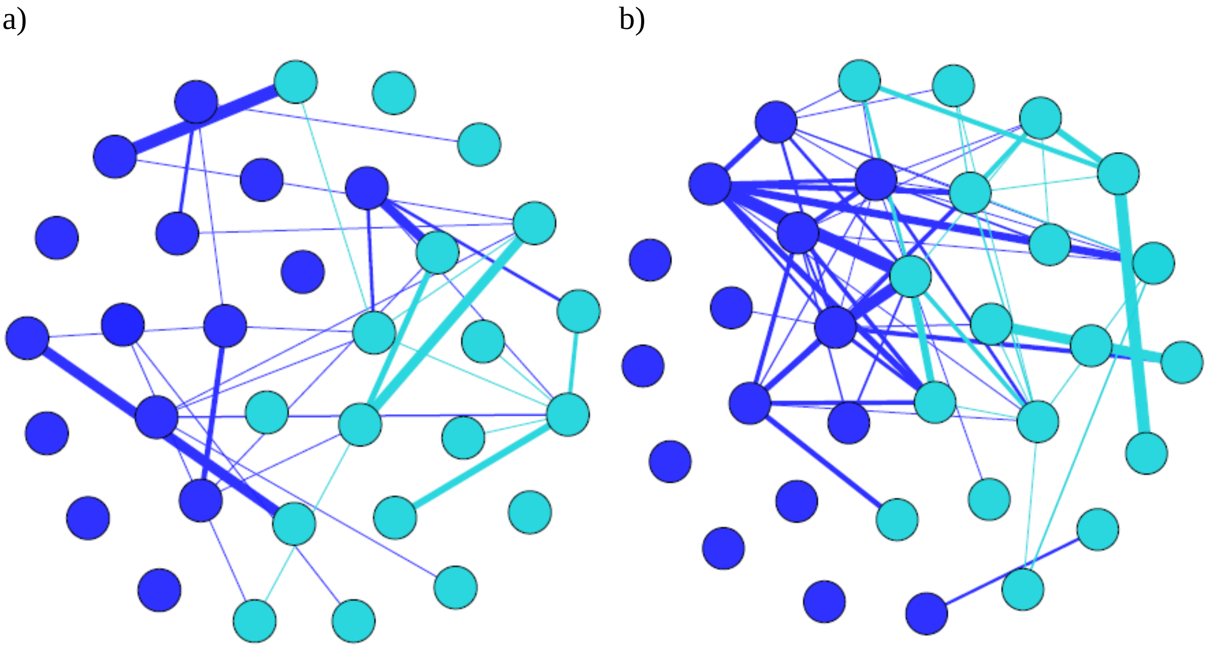


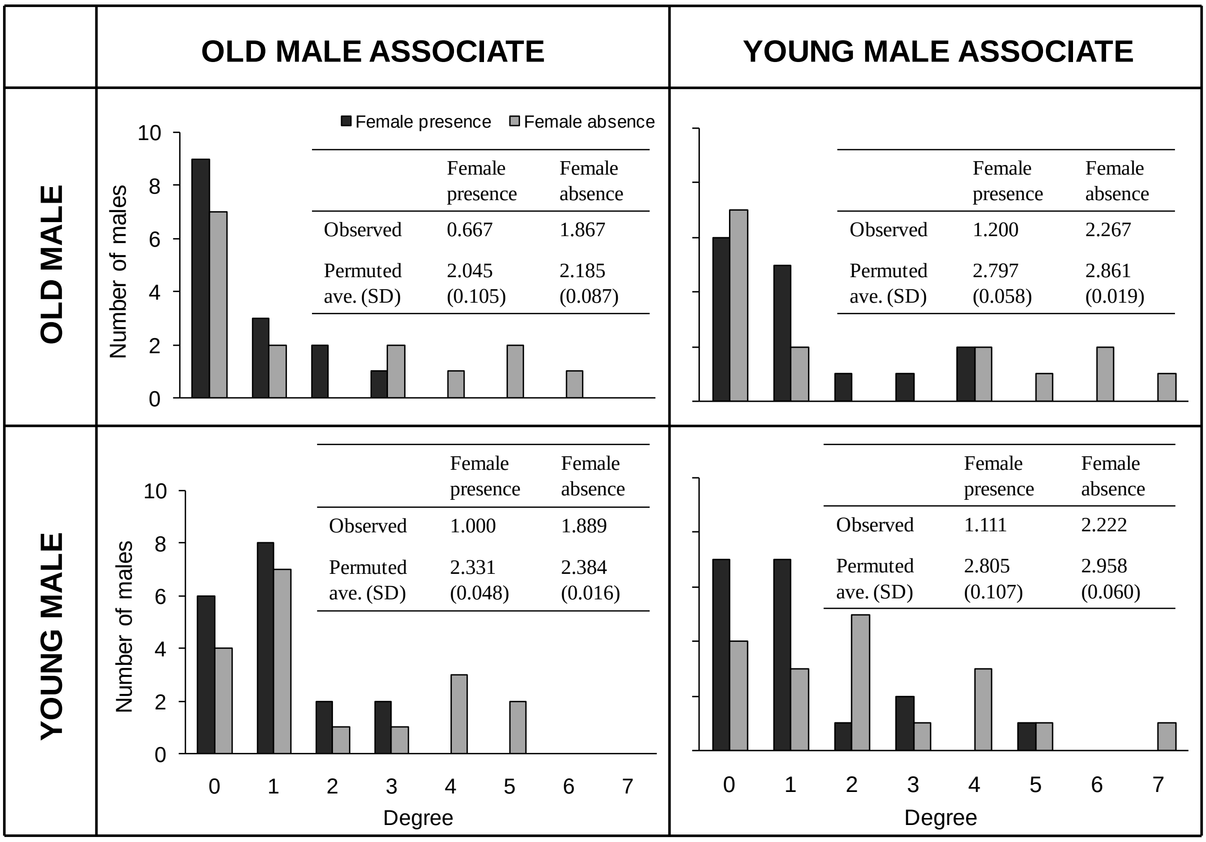
Figure 4. Undirected association networks of adult males (33 males seen on >=5 different days each in female presence and absence) in a) female presence and b) female absence. Nodes representing males >=30 years are coloured dark blue and those representing 15-30 year old males are coloured light blue. The thickness of the edge is proportional to the strength (AI value) of that connection.

Table 2. Network statistics based on observed and permuted male associations in female presence and female absence. *P*=(number of times difference$_{\text{random}}$≥ difference$_{\text{observed}}$) / number of randomisations (10,000). Significant *P* values are marked in bold.

Category	Ave. clustering coefficient	Ave. path length	Density
Female presence observed	0.234	2.967	0.063
Female absence observed	0.588	2.061	0.129
Female presence permuted ave. (SD)	0.626 (0.0250)	2.005 (0.0831)	0.156 (0.0030)
Female absence permuted ave. (SD)	0.644 (0.0168)	2.037 (0.0788)	0.163 (0.0017)
P value	**<0.0001**	**<0.0001**	**<0.0001**

Based on the sampled randomisation test, the average degree between old males, that between young males, and that between young and old males were all higher in female absence than in female presence (Figure 5). This was in keeping with the greater amount of time spent by males belonging to all these three combinations in female absence than in female presence (Figure 1 a,b). The degree/time, when compared for the same 33 common males, was not different between female presence and absence (Wilcoxon's matched-pairs test: *T*= 189.000, *z*=0.319, *P*=0.750). Thus, the greater number of associates in female absence ensued from the greater amount of time spent in female absence since the group size distributions were also not different between female presence and absence (Supplementary Material 7). Based on the sampled randomisation test, the AIs between old males were statistically significantly higher in female absence than in female presence while the AIs between young males and those between young and old males were statistically significantly higher in female presence than in female absence (Supplementary Material 9). However, the absolute differences in AI values were too small to draw biological inferences. AI values were low overall, being mostly close to zero, with only a few pairs of males that showed AI values greater than 0.05 (there were none above 0.07; see Supplementary

Material 9).



Old male – old male associate:

	Female presence	Female absence
Observed	0.667	1.867
Permuted ave. (SD)	2.045 (0.105)	2.185 (0.087)

Old male – young male associate:

	Female presence	Female absence
Observed	1.200	2.267
Permuted ave. (SD)	2.797 (0.058)	2.861 (0.019)

Young male – old male associate:

	Female presence	Female absence
Observed	1.000	1.889
Permuted ave. (SD)	2.331 (0.048)	2.384 (0.016)

Young male – young male associate:

	Female presence	Female absence
Observed	1.111	2.222
Permuted ave. (SD)	2.805 (0.107)	2.958 (0.060)

Figure 5. Degree distributions in female presence and absence of (clockwise from top left) old males with old males, old males with young males, young males with young males and young males with old males. The average degrees, based on the observed and permuted datasets, are shown inside each panel. The observed degrees were significantly greater in female absence than in female presence in all four categories ($P<0.001$).

The three measures of centrality that we calculated were significantly correlated amongst themselves (see Supplementary material 10). Therefore, we used just one measure – closeness centrality. We correlated closeness centrality, clustering coefficient, and degree/time seen with male age. Closeness centrality and clustering coefficient were not significantly correlated with male age in either female presence or absence. Degree/time was not significantly correlated with male age in female presence, but was negatively correlated with male age in female absence (see Table 3).

Table 3. Results of Spearman's rank-order correlations between closeness centrality, clustering coefficient, and degree/time with male age. The *P* value for significance is <0.008 (flat Bonferroni correction for six comparisons). Significant correlations are marked in bold.

Network statistic	Female presence (N=33)	Female absence (N=33)
Closeness centrality	R=-0.005, R^2<0.001, P>0.05	R=-0.086, R^2=0.007, P>0.05
Clustering coefficient	R=-0.041, R^2=0.002, P>0.05	R=-0.342, R^2=0.117, P>0.05
Degree/time	R=-0.030, R^2=0.001, P>0.05	**R=-0.461, R^2=0.212, P<0.007**

Preferred male associations and stability of associations

In keeping with the low AIs between males (see Supplementary Material 9), we found no evidence of preferred male associations across 14-day sampling periods in female presence. In female absence, the CV of all AI values and the SD of non-zero AI values of the real dataset were significantly higher than those of the randomised datasets, but the CV of non-zero AI values and SD of all AI values were not significantly different between the observed and randomised datasets (Supplementary material 11). When we used only the first sighting of the day for each male, we found no evidence for preferential association in female absence or in female presence (Supplementary material 11). AI values of top associates were significantly higher than those of other associates in all combinations of age-class and female presence and absence, except for old associates of old males in female presence, for which the sample size was very small (Table 4).

Mantel tests showed no significant correlation between association matrices across years, in all the three comparisons in female presence and in two out of the three comparisons in female absence (Supplementary material 12).

Table 4. Mann-Whitney *U* test results, comparing AI values with top associates to AI values with other associates, for all combinations of age-classes, in female presence and female absence. The median AI values of top associates and median AI values of other associates are shown for the different categories. *P* value for significance is 0.008 (flat Bonferroni correction for 8 tests). Significant values are marked in bold.

	Female presence				Female absence			
	N_{Top}, N_{Others}	U, Z_{adj}	MedianAI$_{\text{Top}}$, AI$_{\text{Others}}$	P	N_{Top}, N_{Others}	U, Z_{adj}	MedianAI$_{\text{Top}}$, AI$_{\text{Others}}$	P
Old associates of old males	3, 6	1.000, -2.092	0.062, 0.005	0.048	**9, 32**	**18.500, -3.953**	**0.039, 0.010**	**<0.001**
Young associates of old males	**11, 29**	**25.000, -4.074**	**0.046, 0.011**	**<0.001**	**8, 36**	**48.000, -2.921**	**0.029, 0.008**	**0.002**
Old associates of young males	**10, 25**	**33.000, -3.359**	**0.042, 0.008**	**<0.001**	**11, 33**	**76.500, -2.846**	**0.026, 0.009**	**0.003**
Young associates of young males	**9, 29**	**10.000, -4.140**	**0.047, 0.011**	**<0.001**	**16, 55**	**86.500, -4.865**	**0.024, 0.007**	**<0.001**

Discussion

This is the first detailed study of non-dominant immediate adult male associations (at spatial scales relevant to physical interactions) in Asian elephants in a relatively undisturbed natural habitat. In keeping with the strong competition expected amongst males, we found that adult males spent only ~11% of their time in all-male groups. As we had conjectured, the percentage of their time adult males spent in all-male groups in Kabini was much smaller than the percentage of time adult males spent in all-male groups in African savannah elephants (~63% in Amboseli; Chiyo *et al.* 2011). This is possibly because of the presence of distinct “bull areas” (Poole 1982), which ‘sexually inactive’ adult male elephants inhabit but females seldom do in the African savannah but are absent in Kabini. Adult males may be more likely to encounter one another in such bull areas, if present.

Again, possibly because of the absence of bull areas in Kabini, adult males in Kabini spent more time in mixed-sex groups (average=35%) than adult males in Amboseli (average=18%; see Table 5). The percentage of time spent alone (without females or another adult male) was greater in Kabini (~54%) than in Amboseli (~18%). In Sri Lanka, McKay (1973) also found that the percentages of female-absence sightings in which only one adult male was present were 80.80% in Gal Oya and 82.11% in Ruhuna, similar to that in Kabini (average ± SD: 84.53 ± 14.56%, *N*=43 males sighted on 5 days or more). This was only 60.58% in Lahugala, Sri Lanka, in which female herds were larger and male group size was also larger (average ± SD: 1.765 ± 0.354) than in Gal Oya (1.273 ± 0.441) and Yala (1.203 ± 0.227) (McKay 1973). Thus, the percentage of time spent in all-male groups, while somewhat variable across different Asian elephant populations, were all much lower than that observed in the Amboseli African savannah elephant population (Chiyo *et al*. 2011).

Not only was the percentage of time spent in all-male groups lower in Kabini than in African savannah elephants, but the group size experienced in all-male groups was also lower in Kabini (average ± SD group size of all-male groups with more than one male: Kabini: 2.100 ± 0.328, Amboseli: 3.325 ± 1.995; Supplementary material 13). The average group size of adult males (including solitary males) was, similar to our study, only 1.1 in Mudumalai Wildlife Sanctuary, southern India, also (Daniel *et al*. 1987), although Mudumalai has greater grass biomass (Sivaganesan 1991, Baskaran *et al*. 2010) than our study area (Gautam *et al*. 2017). The maximum all-male group size was 2 in Mudumalai (Daniel *et al*. 1987), 6 in Kabini (although observed only for 65 minutes; 0.13% of the total female absence time), and 5 in Gal Oya in Sri Lanka (McKay 1973). In contrast, the maximum group size in Amboseli was 18 (Chiyo *et al*. 2011). Female group sizes have been found to be constrained in the Kabini population (Nandini *et al*. 2017) compared to an African savannah elephant population (Nandini *et al*. 2018), while following the same definition of association, and it is possible that the adult males, being larger, experience an even greater restriction on their group sizes (including solitary males, the average group size of adult males was 1.1 in Kabini). Thus, ecological differences rather than phylogenetic similarity may have shaped these male association patterns. It is unlikely that the difference in male sociality between Kabini and Amboseli is due to the differences in the definitions of associations; in Amboseli males within a 100 m radius were said to be associating with each other. We did not find a large number of instances of males within a 100-m radius but outside a 50-m radius. Moreover, the spatial scales of habitats in Asia and Africa are very different, with large, open spaces not being present in Asia. Additionally, due to the difference in female sociality between Asian and African savannah elephants, with the same definition of association, and the large difference in the proportion of time spent in all-male groups between multiple Asian elephant populations and Amboseli, we think it is unlikely that the differences observed in male sociality (between Kabini and Amboseli) is due to the discrepancy in definition of association, although we cannot rule out a small contribution to the difference. In African savannah elephants, it was shown that male sociality may be underestimated by not controlling for behavioural state (Goldenberg *et al*. 2014). The lack of bull areas in our study area, however, does not allow for males to be classified as being in a sexually active/inactive state just based on associations. Moreover, using associations of males based on the first sighting per day led to a decrease in the proportion of sightings in all-male groups, thereby decreasing sociality, not increasing it. The relative extents to which the presence/absence of bull areas and differences in feeding competition in non-bull areas explain differences in group size and association time between adult males in the African savannah and Kabini would be interesting to examine.

Differences in the nature of male associations between phylogenetically related species have been observed in primates and other taxa: chimpanzees and bonobos show different levels of agonism (Furoichi and Ihobe 1994), macaque populations/species differ in the frequencies of male affiliations depending on group sizes and group sex ratios (Hill 1994), male lions differ in the time spent with, and the extent they scavenged from, female prides, depending on the type of habitat the population occupied (Funston *et al*. 1998), differences in food resource availability were accompanied by differences in male sociality during the breeding season in different populations of mouflon sheep (Bon *et al*. 1992). However, while differences between related species in overall social organisation (Grevy's zebra and onager: Sundaresan *et al*. 2007, Rubenstein *et al*. 2015, dolphin species: Parra *et al*. 2011) or female social organisation (African savannah and Asian elephants: Nandini *et al*. 2018, squirrel monkey species: Mitchell *et al*. 1991, colobine species: Korstjens *et al*. 2002) that are consistent with resource distributions are known, there is little information on food resource distributions differently affecting male social organisation in related species of large mammals. Studies on the foraging ecology of male elephants are required in the future to further understand the differences in social organisation between species.

We had expected older males to spend more time with female groups to acquire mating opportunities and less time in all-male groups, but found that there was no effect of male age on the proportion of time spent in mixed-sex groups or all-male groups. The greater nutritional requirement of larger, older males may lead to greater costs to feeding in the presence of female groups, resulting in older males not being able to increase their time spent with female groups. We had expected older males to form smaller group sizes than younger males if there was a constraint on group size due to feeding costs, but the average experienced group sizes were close to 1.2, precluding much further reduction in group sizes. Intra-group feeding competition has been discussed as a constraint on group sizes in primates (Wrangham *et al*. 1993, Chapman *et al*. 1995, Chapman and Chapman 2000, Gillespie and Chapman 2001, Asensio *et al*. 2009), including in all-male groups (Rajpurohit 1995, Steenbeek *et al*. 2000). Future studies on foraging in male elephants are required to find out the extent to which foraging constraints exist and affect group sizes.

Table 5. A comparison of time spent in different group types by adult males in the study population with that in Amboseli National Park (data from Chiyo *et al*. 2011).

	Amboseli (ave. ± sd)	Kabini (ave. ± sd)
Percentage of time spent alone (1 adult male)	18.39 ± 11.61	54.38 ± 21.55
Percentage of time spent in all-male groups (>1 adult male)	63.24 ± 18.68	10.55 ± 10.61
Percentage of time spent in mixed-sex groups	18.36 ± 16.42	35.06 ± 23.11

Reasons for adult male associations

While adult males spent a smaller proportion of time with each other than they did with females or solitarily, the amount of time they spent with other males was not in keeping with random expectation, suggesting that these associations were biologically meaningful. We had hypothesised that all-male groups could provide an opportunity for younger males to learn from older males or for males to test strengths against each other (learning about their relative dominance status, instead of resources). The former, social learning hypothesis, was based on the expectation that the superior knowledge of experienced, older males might facilitate younger males to learn about the location of food resources in the absence of females, and about interactions with females in the presence of females. Based on our observations in Kabini, we did not find support for the former. Contrary to the expectations based on the social learning hypothesis, we found that young males did not spend a higher proportion of their time with old males than with other young males, in female presence and absence. We also found that males spent a greater absolute amount of time with their age-class peers and less time with males from the other age-class in female absence. Old and young males did not spend more time together than expected in female presence either. During the small amount of time that old and young males spent together, both age classes were equally likely to approach the other to associate, both in female presence and absence. Therefore, young males did not seek out old males. Moreover, the centrality, clustering coefficient and the number of associates of older males in the male social network were not higher than those of younger males, either in female absence or presence. In fact, in female absence, older males had fewer associates after controlling for the time they were sighted. This could be a consequence of old males possibly needing to clarify their dominance relationships with fewer males in their age class, due to a combination of previous experience and better knowledge of their strengths. We found that, in female absence, common older males, who might be familiar with one another, met each other at random while common younger males still preferentially associated with each other (Supplementary material 5). However, when rarer, possibly unfamiliar, males were included, both age-classes spent more time with their age-peers than expected as mentioned above.

Contrary to our finding that social learning from old males did not appear to be important in male associations, older males spent more time with other males in the Amboseli African savannah elephant population (Poole 1982, Chiyo *et al*. 2011). Older males also had a greater number of associates in all-male groups in the Amboseli population (Chiyo et al. 2011) and showed significant affiliation with a higher proportion of available dyads when they were sexually inactive in the Samburu population (Goldenberg et al. 2014), when compared to younger males. Old males had higher Eigenvector centrality in association networks based on all-male groups in Amboseli (Chiyo *et al*. 2011), although when males were classified based on their sexual state (sexually active and sexually inactive) in the Samburu population, there was no correlation between centrality and age in sexually inactive networks and a negative correlation between centrality and age in sexually active networks (Goldenberg *et al*. 2014). Male associations were also shown to facilitate social learning; males who had an older crop raider as a top associate were seen to be more likely to raid themselves (Chiyo *et al.* 2012). Older African savannah elephant males were preferred as associates by males of all ages in Okavango Delta, Botswana also (Evans and Harris 2008) and have been considered analogous to the knowledgeable matriarchs of female groups in the species (McComb *et al*. 2001, Evans and Harris 2008).Young, immature males of Hanuman langur have been found to follow older males in all-male groups, possibly due to the superior knowledge of older males about the distribution of food and water (Rajpurohit *et al*. 1995). In mixed-sex groups of baboons, young juvenile males approached unrelated older adult males more often than juvenile females, possibly to gain access to high-quality food or to learn sex-specific behaviours (Pereira 1988).

The greater social role of older males in the African savannah elephant compared to the Asian elephant in female absence may stem from differences in the habitats they occupy. Asian elephants occupy moister, more forested habitats, in which food is possibly more dispersed and unpredictable in space (but not time) on a local scale. This might make it difficult to obtain knowledge about resources and their distributions. In roving species, males are expected to delay their competitive breeding till they are older (Whitehead 1994), such that there is a considerable interval between when a male is physiologically capable of mating and when the male starts competing for matings (Best 1979 in sperm whales, Ramsay and Stirling 1986 in polar bears, Poole 1989a in African savannah elephants, Keerthipriya *et al*. 2018 in Asian elephants). In the model proposed by Whitehead (1994), roving males were expected to invest in growth/survival instead of competitive breeding until there were 2-4 competitive males competing for access to each receptive female. While the distribution of food resources may explain the lack of social learning from older males in the context of food resources, young males primarily focusing on growth and not reproduction may explain a lack of social learning from older males in the context of reproductive behaviours. In our study population, matriarchs of female clans have also not been found to be the most central individuals (Shetty 2016), which has also been suggested in Uda Walawe in Sri Lanka (de Silva *et al*. 2011). However, while group size constraints were found to result in clans being split among small groups (Nandini *et al*. 2017), which may result in the matriarch not being central to the clan, group size constraint alone may not lead to the pattern we see amongst males.

When males associated in small group sizes, they preferred their age-class peer to older age-class males, and young males did not preferentially approach old males when associations did occur. Therefore, it appears that social learning was not the main reason for adult male associations, even accounting for possible limitations on group size. Instead, with young and old males spending more time than expected with their age-class peers in female absence, and young males spending more time than expected with their age-class peers in female presence also, it appears that male associations may allow for bonding within the age-class and settling of close dominance ranks while (in the case of young males) avoiding potentially costly interactions with the larger, older males. Associations between adult males were stronger when the age differences between them were smaller in Amboseli also, though the relationship was weak (Chiyo *et al.* 2011). Males also picked sparring partners who were closer to their own age. In Samburu, the males who associated when sexually inactive were closer in age than the males who associated when sexually active (Goldenberg *et al.* 2014). This indicates that competitor assessment through spending time with age-peers is also a component of all-male groups / sexually inactive associations of African savannah elephant males. All-male groups were found to facilitate an increase in male-male interactions without increasing aggression levels in Thomas's langurs (Steenbeek *et al.* 2000) also, while in mountain gorillas, the frequency of aggression and affiliation were both higher in all-male groups, but aggression between males in mixed-sex groups were more intense and resulted in wounds (Robbins 1996). Thus, even in species in which males stay for relatively long time with female groups, all-male groups, rather than mixed-sex groups, seem to facilitate male-male interactions in a more relaxed setting. The social preference hypothesis (Bon and Campan 1996, Ruckstuhl and Neuhaus 2000), posited first in the context of ungulates, suggested that individuals with similar social motivations are behaviourally compatible with each other and hence remain in the same groups while individuals that are behaviourally incompatible become segregated socially, leading to i) sexual segregation between males and females and ii) age/size-based segregation among males. Thus, similar-aged males, who share social motivations (which may not necessarily only be testing strength against each other), are expected to form all-male groups. Similar-aged males have been shown to preferentially associate with each other and test strengths in all-male groups of other species (Villaret and Bon 1995 - Alpine ibex, Cransac *et al.* 1998 -

mouflon sheep, Bon *et al*. 2001 - Alpine ibex).It would be interesting to examine the identities of sparring partners amongst males and the establishment of a dominance hierarchy, if any, in the Kabini population.

Effect of female presence on adult male associations

We found that the association network of males was non-random in female absence but random in female presence. The former association network showed higher density and average clustering coefficient than the latter. This was similar to the finding in African savannah elephants in Samburu, of association networks of sexually inactive males being denser and more clustered than those of sexually active males (Goldenberg *et al*. 2014). In our study, males were said to be associating in female presence when they visited the same female group at the same time. Therefore, it is possible that the associations we observe here are a combination of active association/avoidance and males visiting female groups independent of each other and happening to associate with random males at female groups, leading to the random male association network in female presence. Males in multi-male mixed-sex groups have also been found to invest in affiliations with females rather than with each other, like in mountain gorillas (Watts 1992, Sicotte 1994). Similar to the lower age differences between associates in female absence when compared to female presence in Kabini, age differences between significant associates in the sexually inactive state were smaller than those in the sexually active state in Samburu (Goldenberg *et al*. 2014). We found that neither the group size (of males) that males experienced, nor the proportion of time spent associating with other adult males was different between female presence and absence. However, the number of associates, time spent together and the strength of associations were strikingly different between female presence and absence when examined based on the age-classes of males. Old males (>=30 years old) who were reproductively competitive preferred spending time with age-peers in female absence while avoiding spending time with each other in female presence, and met more numbers of other old males in female absence than in female presence. Thus, associations among this age-class conformed to our expectations of the effect of female presence on adult associations, with males viewing each other as competition and avoiding each other while in the presence of the resource they are competing over. Young males (15-30 years old), however, spent more time with age-peers than expected by chance both in female presence and absence and met more numbers of each other in female absence. This suggests that young males may not view each other as competition, even in female presence. This age-class specific effect of female presence is also in agreement with the expected delay in competitive breeding in roving males (Whitehead 1994). The two age-classes avoided each other in female absence while the time males of different age-classes spent together was not different from random in female presence. Avoidance between old males but not between an old and young male in female presence suggests that old males do not consider young males a threat and, hence, tolerate the presence of younger males in female presence. As young adults are sexually mature and capable of mating, this tolerance may provide an opportunity for young males to attain sneak matings (seen in Amboseli by Poole 1989, Kaziranga by Chelliah and Sukumar 2015, Kabini Elephant Project, unpublished data). Males modulating their affiliations towards other males in multi-male mixed sex groups based on their own and their associate's age has been observed in other species, such as the Ursine colobus (Teichroeb *et al*. 2013). We would expect male-male tolerance in elephants (when males associate very temporarily with female groups) to be affected by the dominance relationships between the males and female choice. If females resist mounting attempts by younger males (see Chelliah and Sukumar 2015), and larger, older males are dominant over smaller, younger males (see Chelliah and Sukumar 2013) a young male associating with the same female group would be inexpensive to tolerate for an old male, whereas the young male might still have a non-zero probability of attaining a sneak mating.

Stability and non-randomness of associations

We did not find high correlations between associations across years, both in female presence and absence. When we tested for preferred associations/avoidances across 14-day sampling periods, we obtained some, but not unequivocal, evidence for preferred associations in female absence but not in female presence. There was also some evidence that, with the exception of old male-old male associations in female presence, males of both age-classes had one significant associate of the same and the other age-class, both in female presence and absence. Adult all-male groups of African savannah elephants in Serengeti and Amboseli National Parks were also found to change in composition (Croze 1974, Poole 1982) and less than 10% of the AI values were greater than 0.1 and were not predicted under a model of random associations in Amboseli (Chiyo *et al*. 2011). The compositions of all-male groups in polar bears and sperm whales, in which males rove between different social units, have also been found to change over time (Derocher and Stirling 1990, Lettevall *et al*. 2002). We also found AI values between males to be very small. Older (>20 years old) adult males in Amboseli were also found to have at least one significant top associate, who was usually close in age to the focal male (Lee *et al*. 2011), similar to what we found in Kabini. Thus, in African savannah elephants, there is evidence for associations based on social learning from older males, and some (weak) support for testing strength against age-peers and kinship in all-male groups. The smaller time spent by Kabini males in all-male groups, in comparison to the African savannah elephant (see Table 1) may result from a combination of no bull-areas, possible constraints on group size, and fewer reasons to associate (social learning does not seem to be a primary reason). Stable and significant affiliation among adult males have been observed in many species (Packer and Pusey 1982 - lions, Connor *et al*. 2001 - bottlenose dolphins, de Villiers *et al*. 2003 - African wild dogs, Mitani 2009 - chimpanzees, Berghänel *et al*. 2011 - barbary macaques) but these relationships are usually thought to be a means to form coalitions to defend females. Adult male coalitions have not been observed in Asian elephants and are unlikely, given the low probability of finding a receptive female and the small sizes of female groups (Nandini *et al*. 2017). It will be interesting to explore other possible reasons for the significant affiliations we find amongst males. It is possible that these males are related (see Vidya and Sukumar 2005) but familiarity could also influence male associations. While our study was carried out within Protected Areas, some of our elephants move outside the park limits and raid crops. Crop raiding is risky and male groups may be formed when they raid crops in risky situations (see Srinivasaiah *et al*. 2012). Our results apply to situations with little anthropogenic interference.

Thus, we show that associations among adult male Asian elephants are not always competitive and were affected by their age and immediate presence of females. Social learning from older males did not seem to have a large effect on these associations and associations with age-peers likely allow for testing strengths. The role of kinship in male associations remains to be explored. When we compared our results to those observed in African savannah elephants, we found that Kabini males spent a much smaller proportion of their time in all-male groups of smaller sizes, making their associations weaker, and that older males had a more limited role in male association networks. We posit that the difference in the role of older males is due to the difference in the dispersion of food resources in habitats they occupy, making accumulated knowledge of resources, that older males possess, less valuable in Asian elephants. Thus, ecological differences possibly result in the differences in male social structure between the two species, despite phylogenetic similarity.

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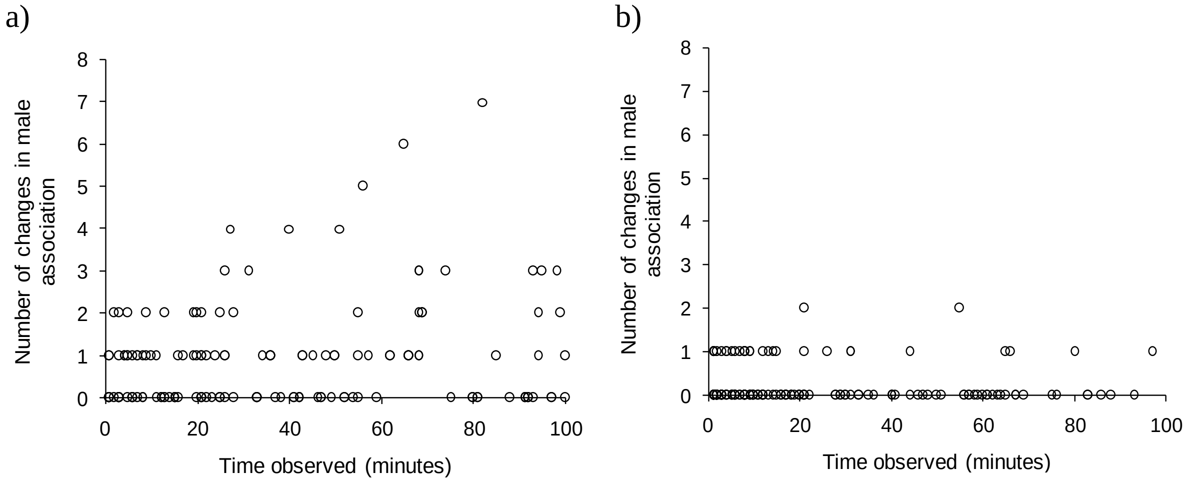
Supplementary Material

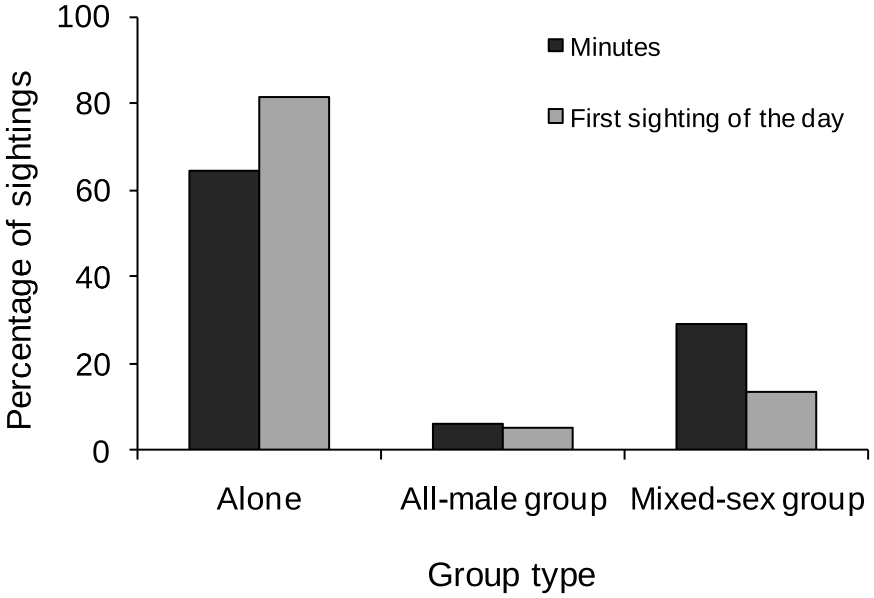
Supplementary Material 1. The number of changes of male association and proportion of sightings in different group types when only the first sightings of the day were used for each male.

We found that male associations change many times within a day. A change in the identities of adult males in the group or a switch from female presence to absence or vice versa, were considered as changes. Using data for the year 2009, up to 7 changes were observed within 82 minutes of observation for one male (Figure 1). Changes were observed in male associations even within one minute of observation (Figure 1). When males were alone, the associations were more stable with time (Figure 1b). Desai and Johnsingh (1995) have suggested that male Asian elephants spend a lot of their time on their own and only temporarily associate with other males and female groups. Our observations also suggest the same.



Supplementary material 1, Figure 1. The number of changes in male associations during different durations of observation (in minutes) when males were in a) all-male or mixed-sex groups or b) alone, shown upto 100 minutes of uninterrupted observation.

When we considered only the first sighting of a male in a day, for every identified male (regardless of the group he was sighted in), we had 2244 sightings in total. In this case a male can either be sighted in female presence or female absence in a day (depending on the group composition when he was sighted), and not in both. This included 118 sightings of all-male groups, 295 sightings of adult males in mixed-sex groups and 1831 sightings of solitary adult males. This led to a slight decrease in the proportion of sightings in all-male groups and a larger decrease in the proportion of mixed-sex group sightings, when compared to the values calculated using every minute of observation (Figure 2). There was a great increase in the proportion of sightings seen alone, probably due to the relative temporal stability of male associations when sighted in female absence (see Figure 1). Using the first sighting of the day would also increase the proportion of solitary sightings because more numbers of females were sighted in the backwaters area in the evening time (Hansraj Gautam, unpublished data) and, therefore, using only the first sighting of the day would exclude associations with females.



Supplementary material 1, Figure 2. The percentage of sightings of different group types when a) the sighting was for every minute and b) the first sighting of the male in the day was used.

The group sizes of adult males in female absence were not different when only using the first sighting of the day or using sightings based on every minute (1.1066 using the first sighting, 1.106 using minutes). The group sizes of adult males in female presence were also not very different based on using either sighting criterion (1.139 using the first sighting, 1.108 using minutes).

When we compared the number of associates, using 33 males who were sighted on 5 different days in female presence and in female absence in the original dataset (sightings for 1 minute), we found the number of associates were lower when using only the first sighting in female presence (number of associates using every minute: ave. ± SE: 2.0 ± 0.66; number of associates using the first sighting of the day: ave. ± SE: 1.0 ± 0.40; Wilcoxon's matched-pairs test: T=0.000, z=3.621, P<0.001), and female absence (number of associates using every minute: ave. ± SE: 4.1 ± 1.38; number of associates using the first sighting of the day: ave. ± SE: 3.4 ± 1.17; Wilcoxon's matched-pairs test: T=0.000, z=2.803, P=0.005). Thus, taking the first sighting of the day for male associations in Kabini resulted in missing out many dyadic associations between common males and also led to a significant reduction in the proportion of time spent in mixed-sex groups.

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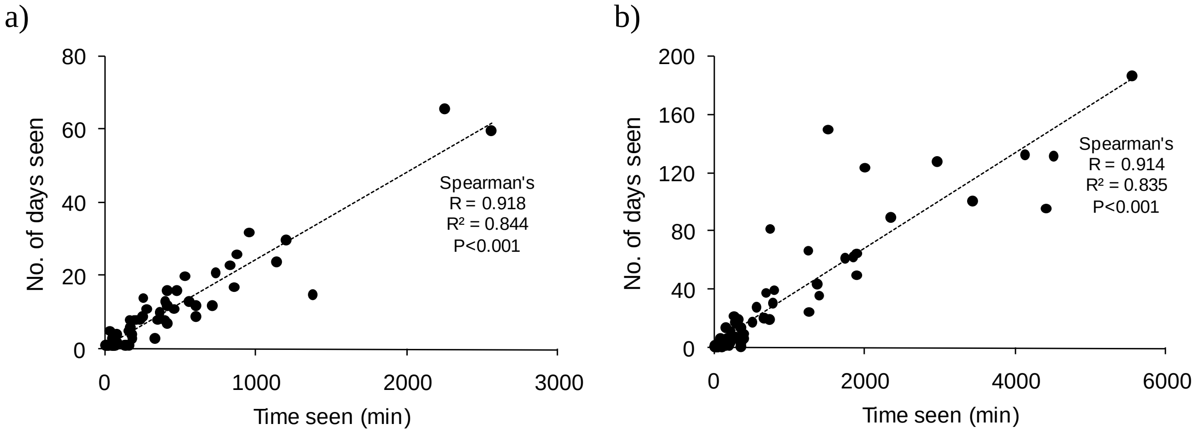
Supplementary Material 2. Plots of number of minutes a male was seen versus the number of days he was sighted.



Supplementary Material 2, Figure 1. The number of days a male was sighted and the number of minutes he was totally sighted, in a) female presence (*N*=56) and b) female absence (*N*=91). The values are strongly correlated in both cases.

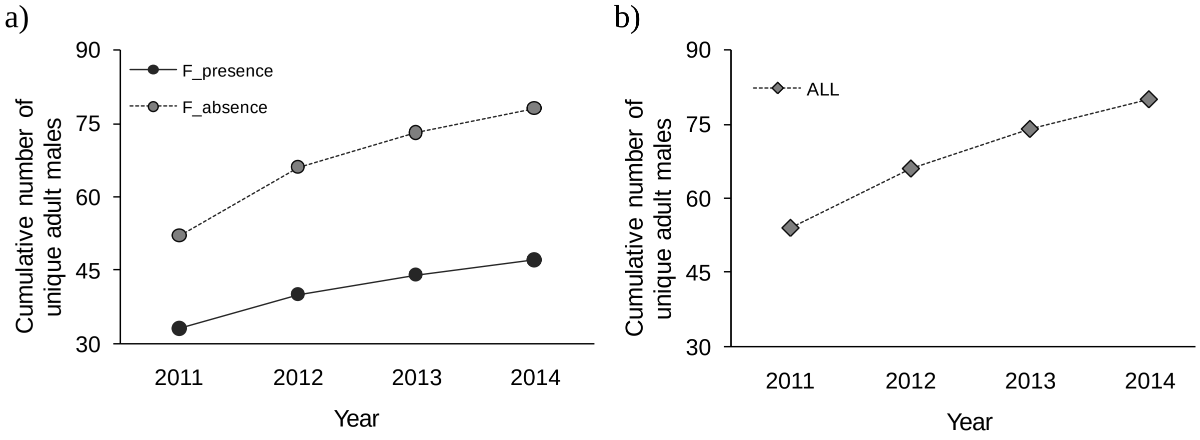
Supplementary Material 2, Table 1. The number of minutes and the number of days (in female presence and female absence) that 33 common males (seen on5 days or more both in female presence and absence).

	Female presence		Female absence	
Male	Time seen (minutes)	Days sighted	Time seen (minutes)	Days sighted
Kanishka	364	10	683	38
Ghatotgaja	713	12	212	12
Sanjaya	1379	15	385	10
Veerpratap	167	8	262	22
Aidan	353	8	376	10
Longcross	832	23	5547	187
Bheeshma	212	8	352	14
Horace	2251	66	4122	133
Airavata	607	12	555	28
Ekalavya	531	20	3423	101
Hercules	34	5	1389	36
Kshitij	737	21	4399	96

Suhel	168	6	1838	63
Marcus	415	16	1883	50
Ahobala	255	14	2338	90
Morris	1142	24	4502	132
Shravan	415	12	296	17
Howard	876	26	1990	124
Columbus	401	13	1244	67
Sudarshan	959	32	1734	62
Shimanta	277	11	1255	25
Manco	2562	60	2959	128
Pan	236	8	1500	150
Tushar	160	5	732	20
Pruthvi	1203	30	1356	44
Vayuputra	606	9	171	7
Bryan	861	17	1891	65
Krishna	200	8	272	18
Karna	252	9	737	82
Siddhartha	463	11	774	31
Pesto	398	8	339	14
Sudama	481	16	221	6
Christopher	562	13	790	40

Supplementary Material 3. Cumulative number of males identified.

Based on sightings in which all adult males were aged and identified, there were a total of 96 identified elephants. While it is natural for new elephants to arrive in the area due to dispersal, the cumulative number of identified adult males did not increase drastically during the last two years of the study period (Figure 1).



Supplementary material 3, Figure 1. Cumulative numbers of identified adult males sighted across years and (plotted separately based on female presence or absence (a), and also totally (b)) that were sighted during 2011-2014. During the last year of sampling, we sighted only 3 new males in female presence (6.5% of the 47 adults sighted from 2011-2014) and 5 new males in female absence (6.4% of the 78 adults sighted in female absence during this period).

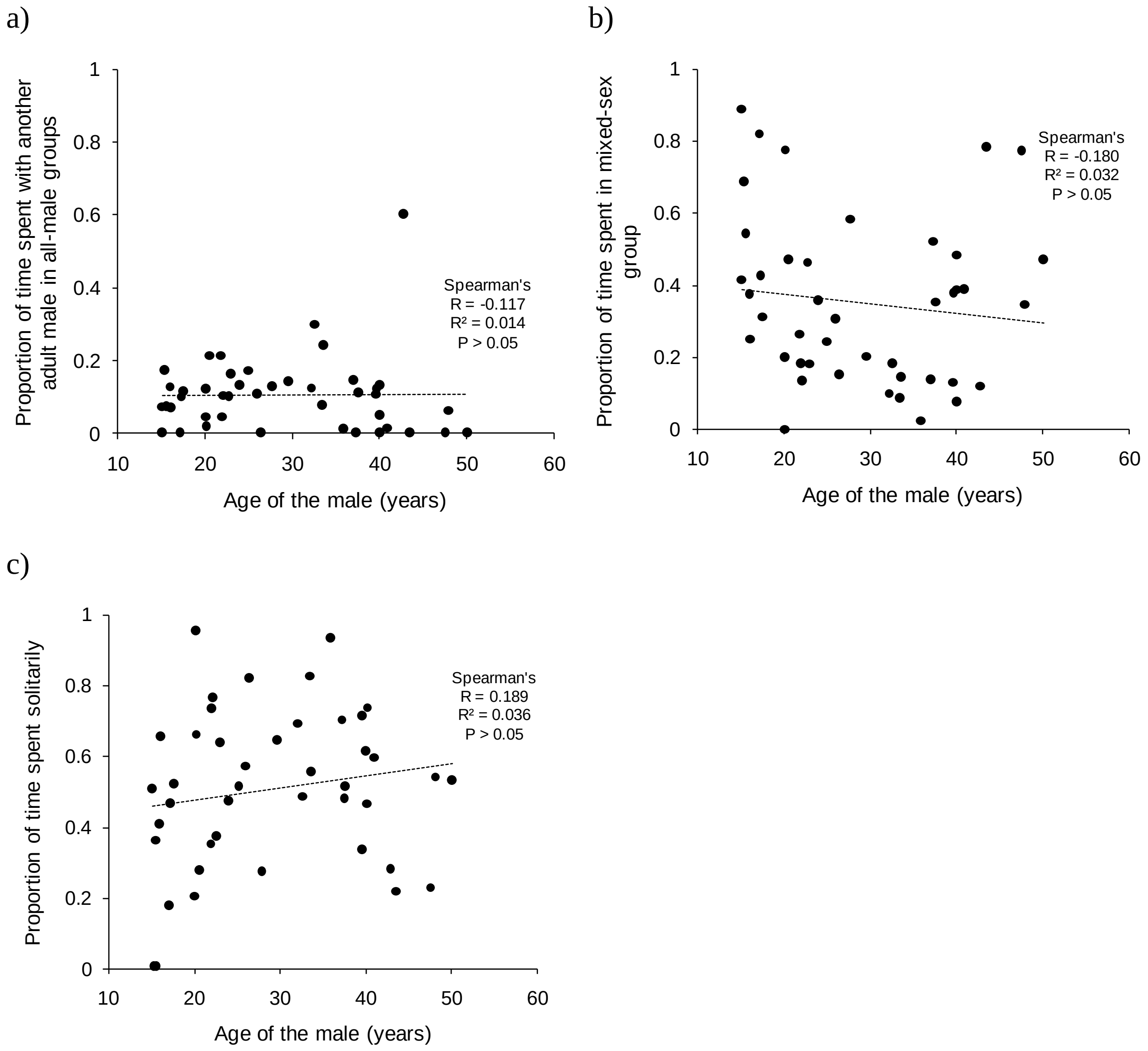
Supplementary Material 4. ANCOVA results with actual proportion values and Spearman's rank-order correlations between male age and proportion of time spent in groups of different types.

Supplementary material 4, Table 1. ANCOVA on proportion of time a male spent in different group types with group type (all-male groups and mixed-sex groups) as a categorical factor and male age as the covariate. Group type, but not age, had a significant effect. Significant results are marked in bold.

	SS	*Degree of freedom*	*MS*	*F*	*P*
Age (years)	0.015	1	0.015	0.474	0.493
Group type	**1.292**	**1**	**1.292**	**39.699**	**<0.001**
Error	2.701	83	0.032	-	-

A Spearman's rank-order correlation was carried out between individual male ages and the proportions of time spent by those males in all-male groups. A similar correlation was also carried out between age and the proportion of time spent in mixed-sex groups and the proportion of time spent solitarily. We used those males who were seen on five different days or more during the study period (N=43 for all three correlations) for these correlations.

We compared the proportion of time spent by a male in all-male groups with other adults (AM>1) with his age and we found that there was no significant correlation (Spearman's rank-order correlation, R=-0.117, R^2=0.014, P>0.05). Similarly, we also found that the age of the male did not affect the proportion of time he spent in mixed-sex groups (Spearman's rank-order correlation, R=-0.180, R^2=0.032, P>0.05) or the proportion of time he spent solitarily (Spearman's rank-order correlation, R=0.189, R^2=0.036, P>0.05) These values are plotted, along with the correlation results, in Figures 1 a,b and c.

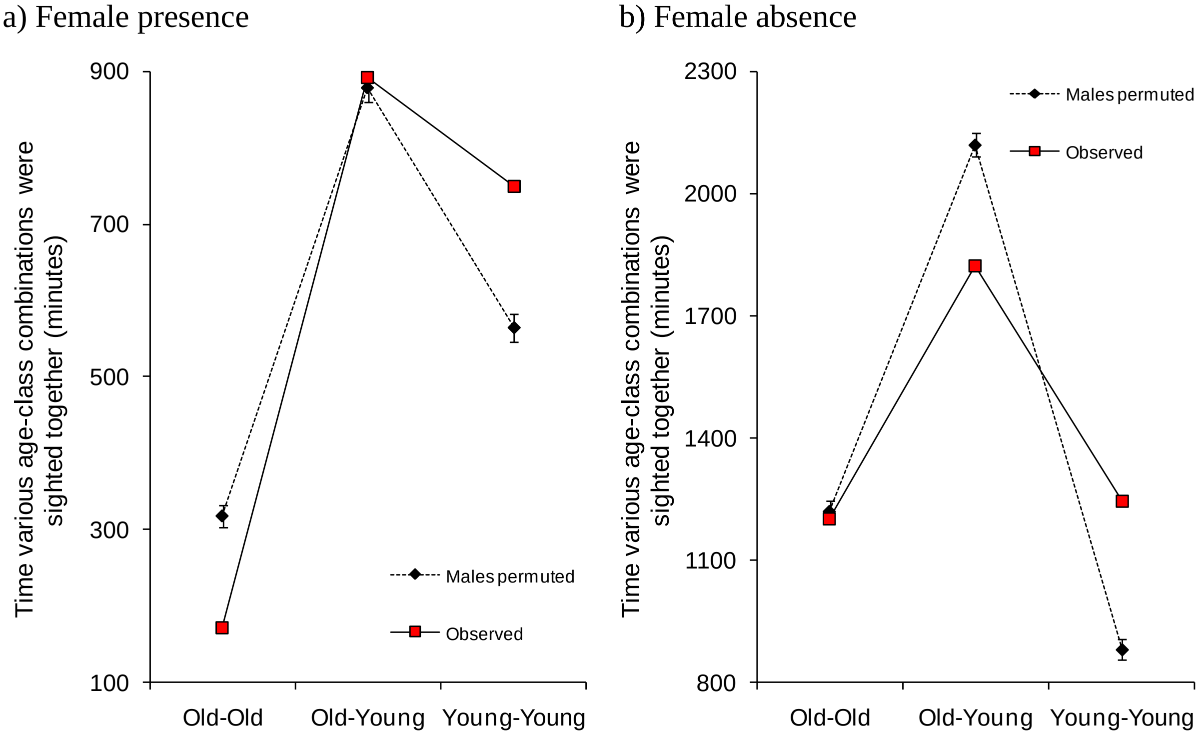


Supplementary material 4, Figure 1. Proportion of total time spent in a) all-male groups with multiple adult males, b) mixed-sex groups, plotted against male age and c) solitarily.

We calculated the interquartile range (the difference between the upper (75%) quartile value and the lower (25%) quartile value) for each set of proportion values and assigned those values which lay outside the inner fences of the dataset (calculated as 1.5*interquartile range + upper quartile to 1.5*interquartile range - lower quartile) as outliers. By this definition, we detected only one outlier in the proportion of time spent in all-male groups with other adult males and after removing it, the result of the correlation between age and the proportion remained the same (Spearman's rank-order correlation, N=42, R=-0.176, R^2=0.031, P>0.05).

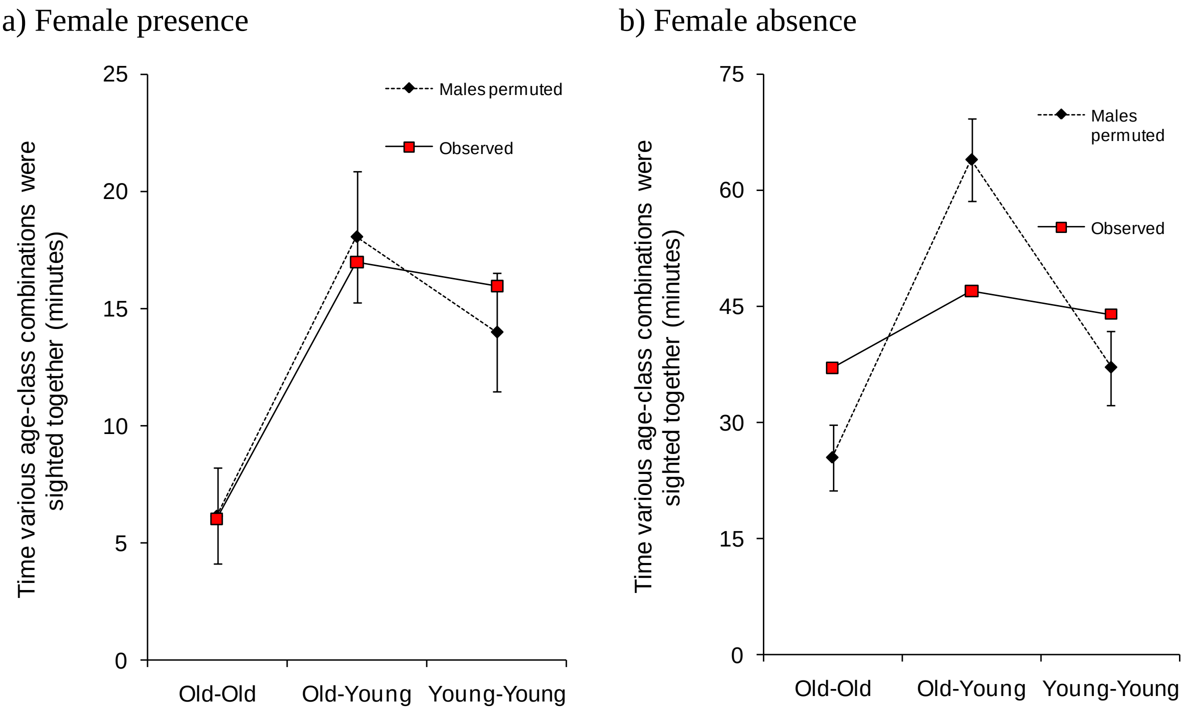
Supplementary material 5. Time spent together by the commonly seen adult males of the same and different age-classes.

As mentioned in the Methods and in the main Results, we compared the observed male associations in female presence and absence with those obtained by randomly permuting either males alone within the female presence or female absence datasets, or by permuting both males and female presence/absence status for the sighting across the entire dataset. While results based on sightings of all males are shown in the Results, we also carried out this analysis on the dataset of only the 33 common males that were sighted for 5 days or more, both in female presence and in female absence. When we randomised these sightings by switching males between sightings in female presence, we found that old males spent less time with each other than expected by chance (Observed: 170 minutes; Randomised: average ± SD: 317.7 ± 15.09, $P<0.001$), the time that old and young males spent with each other (891 minutes) was not different from what was expected by chance (average ± SD: 878.9 ± 19.51, $P=0.130$), and the time that young males spent with each other (750 minutes) was greater than expected by chance (average ± SD: 563.8 ± 17.76, $P<0.001$; Figure 1). In female absence, the time that old males spent together (1201 minutes) was not different from what was expected by chance (average ± SD: 1218.1 ± 26.44, $P=0.365$), the time that old and young males spent together (1822 minutes) was less than expected (average ± SD: 2120.1 ± 30.51, $P<0.001$), and the time that young males spent together (1243 minutes) was greater than expected by chance (average ± SD: 880.4 ± 23.72, $P<0.001$; Figure 1). Thus, the only difference between the results obtained based on only the common males as opposed to all 96 identified adult males was that, in female absence, the commonly seen old males spent time with each other as expected by chance, whereas old males in general (when all 96 were included) spent more time with each other than expected by chance. If male associations were primarily a means for testing strengths, such a pattern is expected as males that are common in an area may be familiar with one another’s strengths, not necessitating extended associations.



Supplementary material 5, Figure 1. Permuted and observed values of time spent together by 33 common adult males of the same and different age-classes in a) female presence and b) female absence. Please note that the Y axis scales differ across the two panels.

We also performed the randomizations using the first sighting of the day for each identified male (not the common males alone). In female absence, the patterns observed were the same as before. Old males were sighted together more than expected by chance (observed number of sightings: 37, random expectation (ave. ± SD): 25.4 ± 4.22, *P*=0.003) and old and young males were sighted together less than expected by chance (observed number of sightings: 47, random expectation (ave. ± SD): 63.9 ± 5.32, *P*=0.001). Young males were sighted together more than expected at random, but this trend was not significant with a borderline *P* value (observed number of sightings: 44, random expectation (ave. ± SD): 37.0 ± 4.76, *P*=0.056; Figure 2b). In female presence, however, there were very few sightings in which males were sighted together and none of the male age-classes were sighted together more or less than expected by chance (old-old: observed number of sightings: 6, random expectation (ave. ± SD): 6.2 ± 2.02, *P*=0.419, old-young: observed number of sightings: 17, random expectation (ave. ± SD): 18.0 ± 2.80, *P*=0.572, young-young: observed number of sightings: 16, random expectation (ave. ± SD): 14.0 ± 2.54, *P*=0.170; Figure 2a).



Supplementary material 5, Figure 2. Permuted and observed number of times adult males of the same and different age-classes were sighted together in a) female presence and b) female absence. This randomisation was performed using the first sighting of the day for each identified male. Please note that the Y axis scales differ across the two panels.

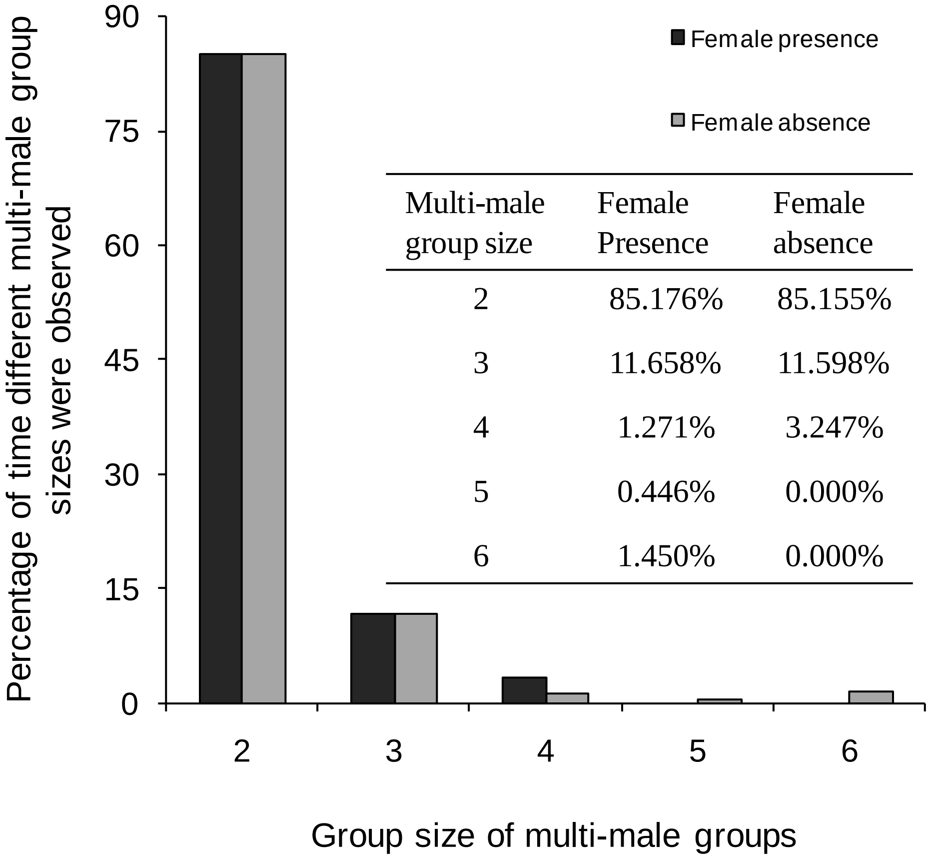
Supplementary Material 6. ANCOVA results on proportion of time a male spent with other males, in female presence and absence, using the actual proportion values.

Supplementary material 6, Table 1. ANCOVA on the proportion of time a male spent with other males in female presence and absence, with female presence as a categorical factor and male age as the covariate. Neither female presence nor age had a significant effect. Significant results are marked in bold.

	SS	*Degree of freedom*	*MS*	*F*	*P*
Age (years)	<0.001	1	<0.001	0.007	0.933
Female presence	0.117	1	0.117	2.901	0.092
Error	3.260	81	0.040	-	-

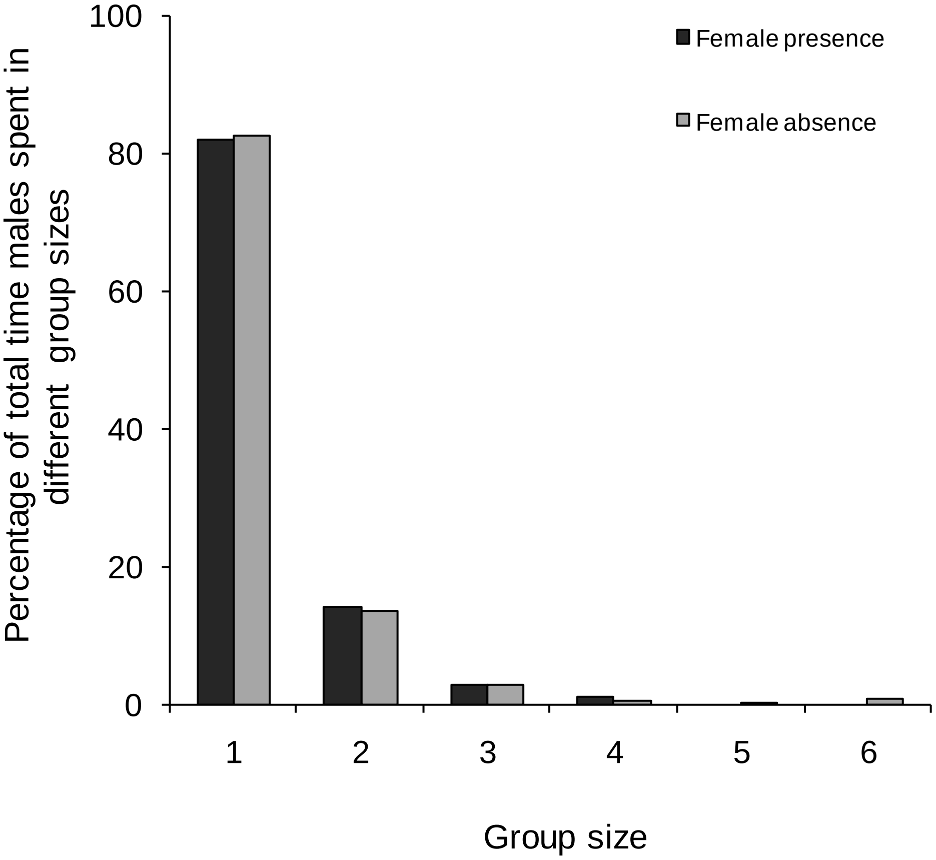
Supplementary material 7. Group size distributions of multi-male groups and experienced group sizes of males in female presence and absence.

As mentioned in the main text, the group size distributions of multi-male groups that we observed in female presence and absence were small, with a mode of 2 (Figure 1 below). The group sizes (counted as the number of adult males) experienced by adult males were small, with a mode of 1 (Figure 2 below), in female presence and in female absence.



Multi-male group size	Female Presence	Female absence
2	85.176%	85.155%
3	11.658%	11.598%
4	1.271%	3.247%
5	0.446%	0.000%
6	1.450%	0.000%

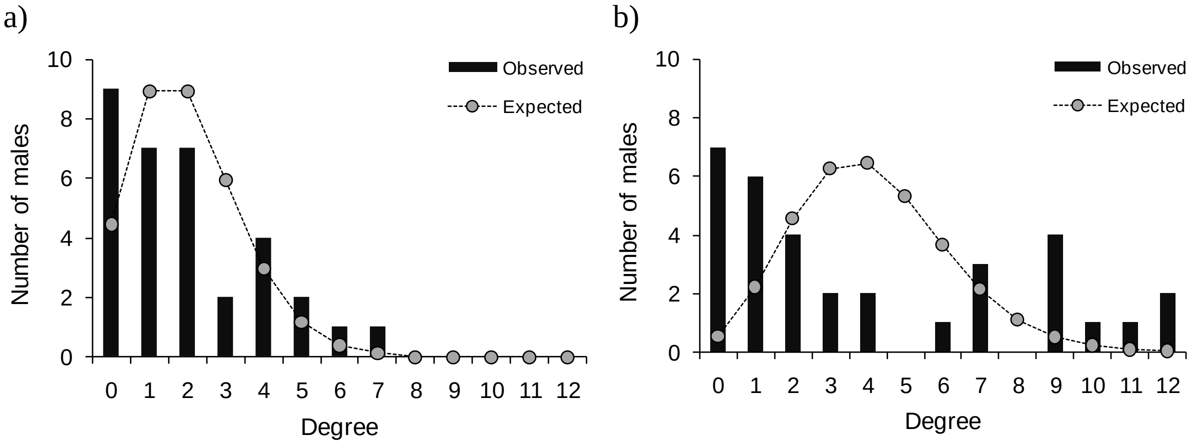
Supplementary material 7, Figure 1. Percentage of observation time of multi-male groups of different sizes (number of adult males) in female presence and absence.



Supplementary material 7, Figure 2. Percentage of the male’s total time spent in groups of different sizes (different numbers of adult males) in female presence and absence. Groups in female absence include solitary males and all-male groups, while groups in female presence include mixed-sex groups.

Supplementary Material 8. Degree distributions of association networks in female presence and female absence.

We compared the degree distribution of our observed networks to Poisson distributions (expected for an Erdös-Rényi random network; Erdös and Rényi 1960). We found that the observed distribution in female presence was not significantly different from Poisson (χ^2=0.965, *P*=0.326) while the one in female absence was significantly different (χ^2=26.552, *P*<0.001). The distributions are plotted below.



Supplementary Material 8, Figure 1. Observed (bars) and expected (lines) degree distributions of male association networks in a) female presence and b) female absence.

References

1. Erdös P and Rényi A (1960). On the evolution of random graphs. *Publications of the Mathematical Institute of the Hungarian Academy of Sciences* 5: 17–61.

Supplementary Material 9. Results of the sampled randomisation test based on AI between males in female presence and female absence and AI distributions.

Based on the sampled randomisation test, the non-zero AIs between old males were significantly higher in female absence than in female presence (Table 1 below). As mentioned in the main text, the time spent by old males together had also been higher in female absence than in female presence (Figure 1 a,b in the main text). However, while the absolute amounts of time young males were seen together had been higher in female absence than in female presence (Figure 1 a,b in the main text), the non-zero AIs between young males were significantly higher in female presence than in female absence (Table 1 below), indicating a higher strength of associations in female presence despite the smaller time spent. Similarly, while the absolute amounts of time young and old males were seen together had been higher in female absence than in female presence (Figure 1 a,b in the main text), the non-zero AIs between young and old males were also significantly higher in female presence than in female absence (Table 1 below). However, the magnitudes of differences in AI values are too small to make far-reaching inferences.

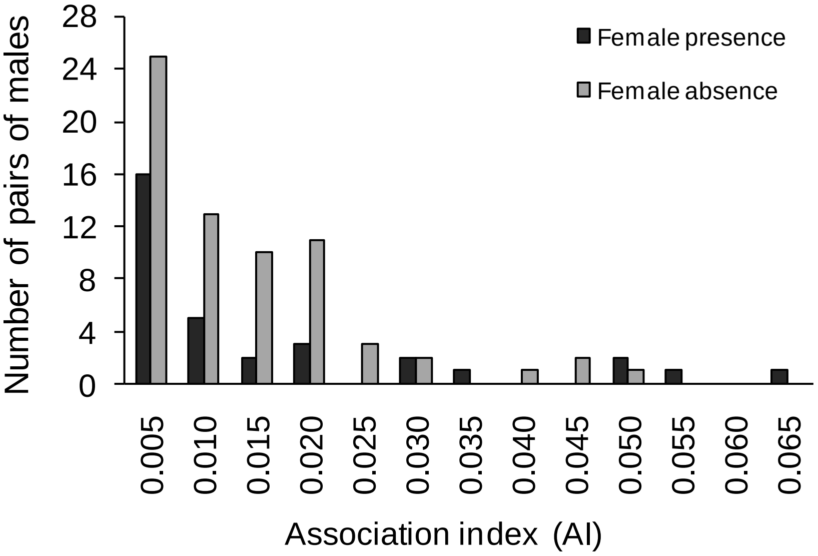
When we included the zero AI values and calculated an average AI for the same set of males, the average AI values for all three age classes of males were higher in female absence than in female presence (Table 2 below) because the degrees for all combinations of age-classes were higher in female absence (see main text). The AI distributions are shown in Figures 1-3 below.

Supplementary material 9, Table 1. AI between associates, within and between age-classes, in observed and permuted female presence and female absence datasets. *P*=(number of times $\text{difference}_{\text{random}} \geq \text{difference}_{\text{observed}}$) / number of randomisations (10,000). Significant *P* values are marked in bold.

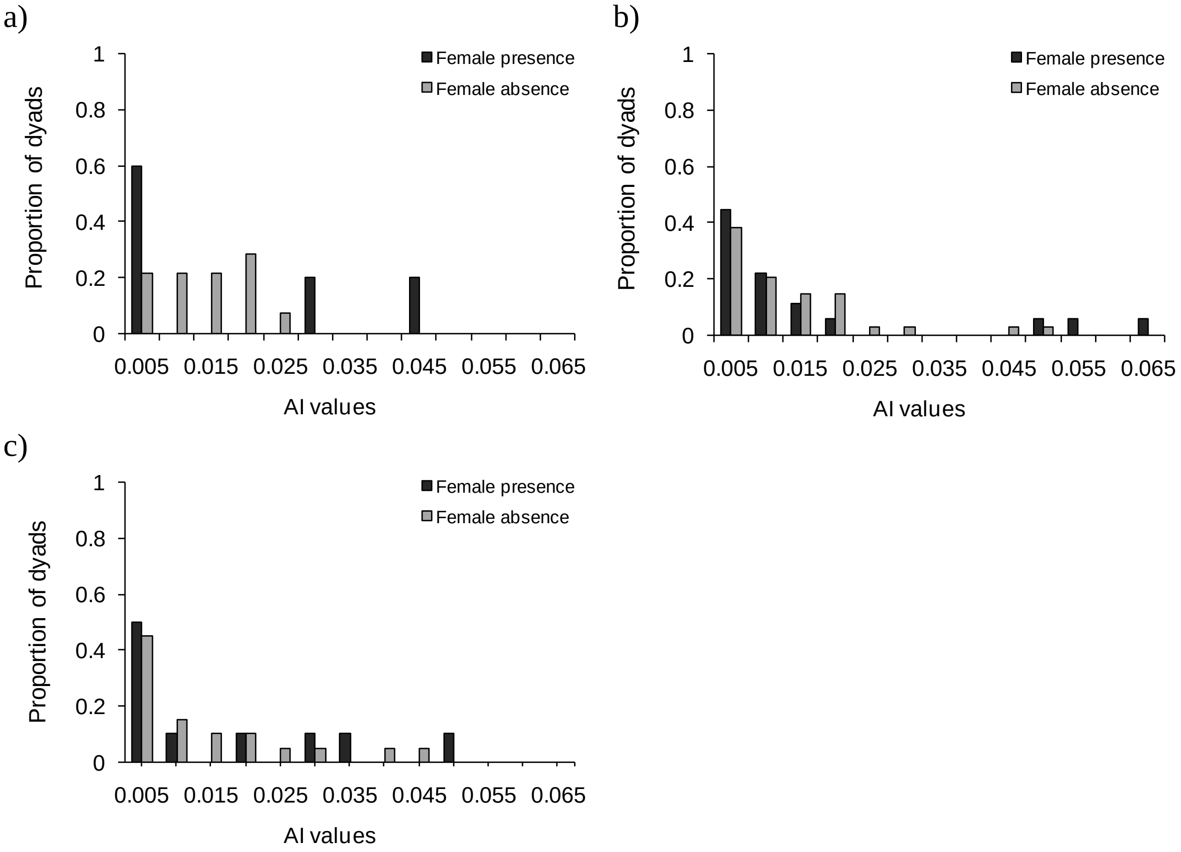
Category	Ave. non-zero AI between two 30+	Ave. non-zero AI between 30+ and 15-30	Ave. non-zero AI between two 15-30
Female presence observed	0.0096	0.0140	0.0152
Female absence observed	0.0112	0.0107	0.0117
Female presence permuted ave. (SD)	0.0089 (0.0007)	0.0087 (0.0005)	0.0073 (0.0002)
Female absence permuted ave. (SD)	0.0084 (0.0004)	0.0085 (0.0002)	0.0077 (0.0005)
P value	**0.0197**	**<0.0001**	**<0.0001**

Supplementary material 9, Table 2. Average AI (including zero values) between males, within and between age-classes, in observed and permuted female presence and female absence datasets. *P*=(number of times $\text{difference}_{\text{random}} \geq \text{difference}_{\text{observed}}$) / number of randomisations (10,000). Significant *P* values are marked in bold.

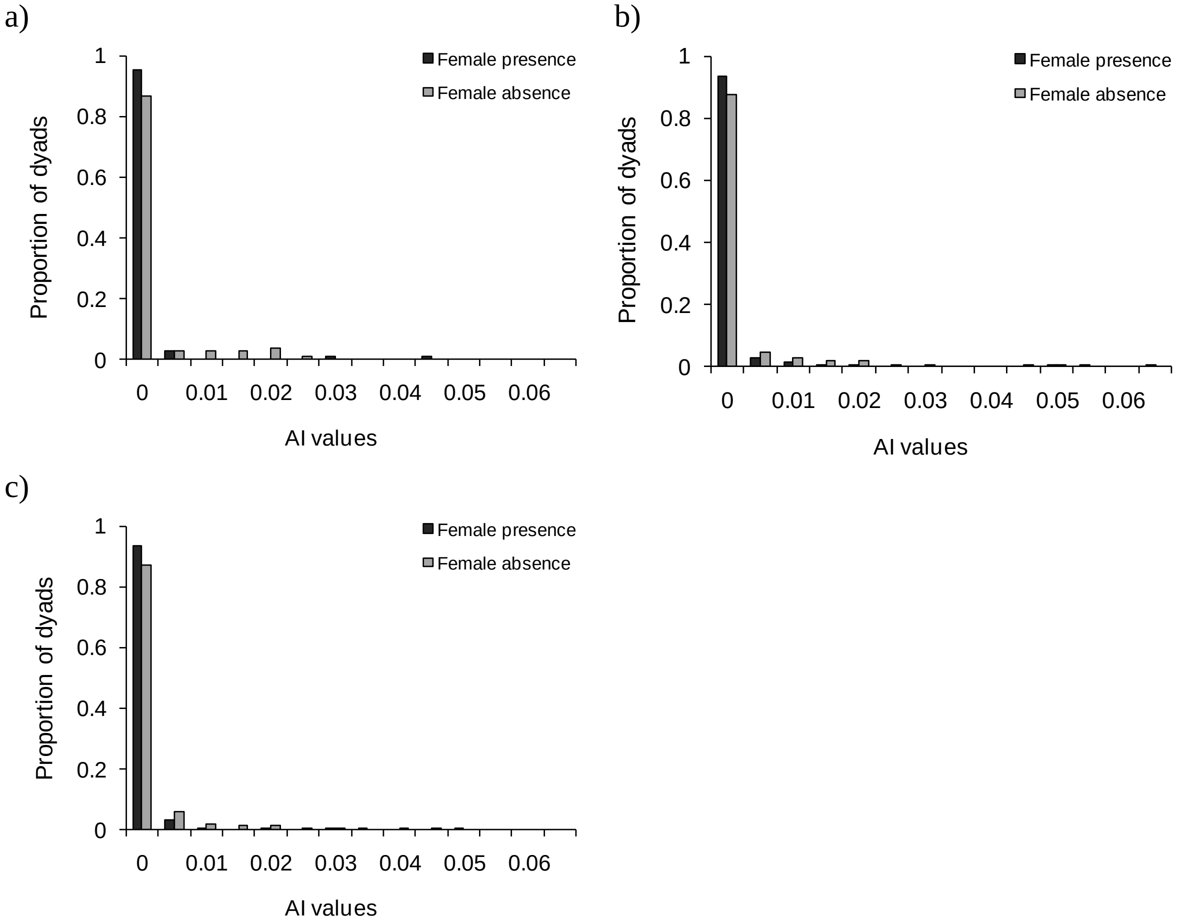
Category	Ave. AI between two 30+	Ave. AI between 30+ and 15-30	Ave. AI between two 15-30
Female presence observed	0.0004	0.0009	0.0009
Female absence observed	0.0014	0.0013	0.0014
Female presence permuted ave. (SD)	0.0012 (0.0001)	0.0013 (0.0001)	0.0012 (0.0001)
Female absence permuted ave. (SD)	0.0012 (<0.0001)	0.0013 (<0.0001)	0.0012 (<0.0001)
P value	**<0.0001**	**<0.0001**	**<0.0001**



Supplementary material 9, Figure 1. Distribution of non-zero AI values between males (seen on >=5 days each in female presence and absence, *N*=33) in female presence and absence.



Supplementary material 9, Figure 2. Frequency distributions of non-zero AI values between a) pairs of 30+ year old males, b) 30+ year old males and 15-30 year old males, c) pairs of 15-30 year old males, in female presence and absence.



Supplementary material 9, Figure 3. Frequency distributions of average AI values of a) pairs of 30+ year old males, b) 30+ year old males with 15-30 year old males, and c) pairs of 15-30 year old males, in female presence and absence.

Supplementary material 10. Correlations between different centrality measures

We found that all the three centrality measures we had measured in the male association networks were strongly correlated with each other. Therefore, we chose only one of them (closeness centrality) to correlate with male age. Results of the correlations are provided in the table below.

Supplementary material 10, Table 1. Correlation test results between different centrality measures. All comparisons were significant and are, hence, marked in bold.

Network statistics	Female presence (N=33)	Female absence (N=33)
Closeness centrality and Betweenness centrality	**Spearman's R=0.896, R^2=0.803, P<0.001**	**Spearman's R=0.704, R^2=0.496, P<0.001**
Closeness centrality and Eigenvector centrality	**Spearman's R=0.963, R^2=0.927, P<0.001**	**Spearman's R=0.782, R^2=0.611, P<0.001**
Betweenness centrality and Eigenvector centrality	**Spearman's R=0.798, R^2=0.637, P<0.001**	**Spearman's R=0.859, R^2=0.738, P<0.001**

Supplementary Material 11. Permutation tests to test for preferential associations.

We used SOCPROG 2.6 to perform permutations tests to check for preferred associations across 14-day sampling intervals (*permute associations within samples*). This method accounts for differences in gregariousness. We used 10,000 permutations with 10,000 flips per permutation for this test. We performed these tests on the dataset where every minute of observation is used (Results in Table 1) and on the dataset where only the first sighting of the day for each male was used (Results in Table 2).

Supplementary Material 11, Table 1. Observed and random values of statistics and *P* values from the permutation test for preferred associations in female presence and in female absence, using 10,000 permutations and 10,000 flips per permutation. These randomizations were performed on the dataset where every minute of observation was used. The number of identified males in each category are shown. Statistically significant values (P<0.05) are marked in bold. The significance of mean AI is not meaningful in this test.

Category	Statistic	Observed value	Ave. random value using 10000 flips	*P* (1-sided) (10000 flips)
Adult males in female presence; *N*=56	Mean AI	0.0021	0.0021	-
	SD of AI	0.0106	0.0106	0.5765
	CV of AI	5.1244	5.0830	0.2109
	Mean non-zero AI	0.0385	0.0387	0.5709
	SD of non-zero AI	0.0265	0.0259	0.3857
	CV of non-zero AI	0.6867	0.6683	0.2750
Adult males in female absence; *N*=91	Mean AI	0.0005	0.0005	-
	SD of AI	0.0043	0.0042	0.0962
	CV of AI	**8.4534**	**8.3012**	**0.0097**
	Mean non-zero AI	0.0176	0.0172	0.0958
	SD of non-zero AI	**0.0183**	**0.0177**	**0.0189**
	CV of non-zero AI	1.0366	1.0343	0.4431

Supplementary Material 11, Table 2. Observed and random values of statistics and *P* values from the permutation test for preferred associations in female presence and in female absence, using 10,000 permutations and 10,000 flips per permutation. These randomizations were performed using the first sighting of the day for each identified male. The number of identified males in each category are shown (might not match with the values in Table 1 as some males who were sighted both in female presence and absence in the same day will only be represented in one category in this dataset). Statistically significant values (P<0.05) are marked in bold. The significance of mean AI is not meaningful in this test.

Category	Statistic	Observed value	Ave. random value using 10000 flips	*P* (1-sided) (10000 flips)
Adult males in female presence; *N*=51	Mean AI	0.0031	0.0032	-
	SD of AI	0.0317	0.0320	0.9452
	CV of AI	10.1547	10.0597	0.0573
	Mean non-zero AI	0.0866	0.0874	0.6453
	SD of non-zero AI	0.1445	0.1447	0.5754
	CV of non-zero AI	1.6689	1.6560	0.3187
Adult males in female absence; *N*=91	Mean AI	0.0006	0.0006	-
	SD of AI	0.0054	0.0054	0.2774
	CV of AI	8.3923	8.2506	0.1577
	Mean non-zero AI	0.0220	0.0282	0.1154
	SD of non-zero AI	0.0223	0.0219	0.2388
	CV of non-zero AI	0.7569	0.7744	0.4688

References

1. Whitehead H (2009). SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology* 63: 765-778.

Supplementary material 12. Mantel test results of correlations between association index matrices of consecutive years in female presence and absence.

Results of Mantel tests of matrix correlations between AI matrices of consecutive years, using common males (males seen for 30 minutes or more in the years being compared). None of the comparisons, except for one in female absence, yielded a significant correlation (Table 1 below).

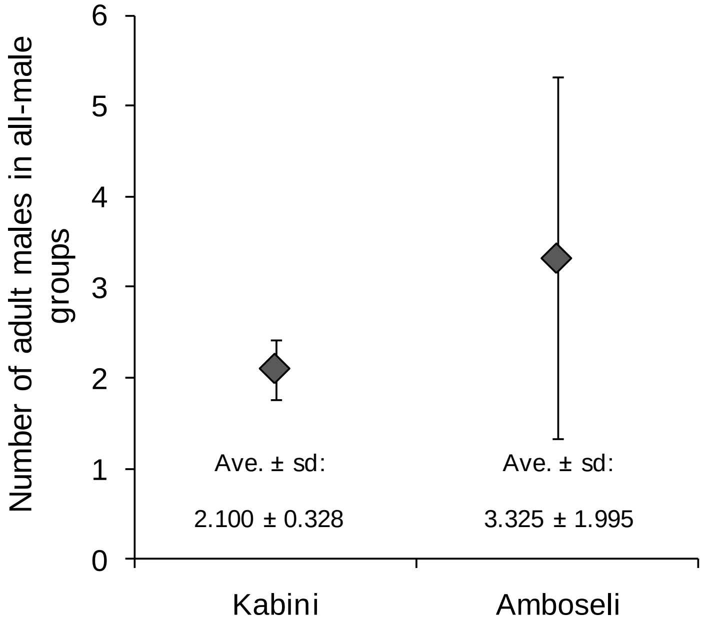
Supplementary material 12, Table 1. Mantel test results with 5000 permutations for comparisons between AI matrices of common males in consecutive years in female presence and female absence.

	Female presence			Female absence		
	N	*R*	*P*	*N*	*R*	*P*
2011-2012	17	-0.062	1.000	28	-0.012	0.429
2012-2013	15	-0.037	0.463	24	0.005	0.328
2013-2014	9	-0.061	1.000	**21**	**0.238**	**0.008**

Supplementary Material 13. Adult male group sizes in all-male groups in Kabini and Amboseli.

We examined the adult male group sizes in all-male groups in Kabini and Amboseli. The average group size of groups of adult males in all-male groups in the Amboseli population was (average ± SD) 3.325 ± 1.995 (*N*=939 groups; Chiyo *et al*. 2011). As groups were sampled once a day in Chiyo *et al*.'s (2011) study (while we had looked at changes in group composition minute by minute), we also sampled from our data similarly to compare the group sizes. Thus, an all-male group would only be sampled if at least one of the adult males in it was being sighted for the first time that day in female absence. After sampling in this manner, we obtained 120 sightings of all-male groups. We compared the average all-male group sizes in Kabini (average ± SD: 2.100 ± 0.328, *N*=120) to the all-male group sizes in Amboseli using Welch's two sample test (Welch 1937, see Fagerland and Sandvik 2009). We found that the group sizes were significantly different, with the adult male groups in Amboseli being larger than those in Kabini (Welch's two sample test: *U*=17.095, *fu*=1017.865, *P*<0.001; Figure 1, Table 1).

Thus, males in the Kabini population not only spent much less time in all-male groups than in the Amboseli African savannah elephant population, but, when they formed all-male groups, their group sizes were also smaller than in Amboseli.



Supplementary material 13, Figure 1. Group sizes of adult males in all-male groups in

Amboseli and Kabini, when each male was sampled once a day.

Supplementary material 13, Table 1. The average, standard deviation, mode, median, maximum and minimum of group sizes of all-male groups in Kabini and Amboseli.

Group sizes in all-male groups	Amboseli	Kabini
Average±SD	3.325 ± 1.995	2.100± 0.328
Median	2	2
Mode	2	2
Minimum	2	2
Maximum	18	4

References

1. Chiyo PI, Archie EA, Hollister-Smith JA, Lee PC, Poole JH, Moss CJ and Alberts SC (2011). Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. *Animal Behaviour* 81: 1093-1099.
2. Fagerland MW and Sandvik L (2009). Performance of five two-sample location tests for skewed distributions with unequal variances. *Contemporary Clinical Trials* 30: 490-496.
3. Welch BL (1937). On the *z*-test in randomized blocks and Latin squares. *Biometrika* 29: 21-5.

CHAPTER 3

Associations of Subadult Males in All-Male and Mixed-Sex Groups and a Comparison with Adult Male Associations in Asian Elephants in Nagarahole-Bandipur, Southern India

Title: Associations of subadult males in all-male and mixed-sex groups and a comparison with adult male associations in Asian elephants in Nagarahole-Bandipur, southern India

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Manuscript in preparation.

Author contributions

This work was conceived by PK and TNCV. PK collected field data during February 2011-July 2014 and carried out the analyses. SN helped with field data collection during January 2011-May 2013 and TNCV helped with initial field data collection in 2009-2010. PK primarily wrote the manuscript.

Abstract

We studied the immediate associations formed by subadult male Asian elephants, who are in the process of dispersing away from their natal herds, and compared them to those formed by adult males. Associations between individuals of the different age-classes of males were mostly distinct from each other. Older subadult males spent a greater proportion of their time with other subadult males in all-male groups, than younger subadult males. Subadult males spent a vast majority of their time in mixed-sex groups and there seemed to be a gradual decrease in the time spent in mixed-sex groups as males grew older. Unlike adult males who associated more among each other in female absence, the association networks of subadult males were denser and more cohesive in female presence than absence. Further, subadults of both age-classes met more numbers of each other, spent a greater proportion of their time associating with other subadults and, in the time they spent with other subadults, formed larger groups in female presence than female absence. Since male-male sociality among subadult males was higher in female presence than in female absence, associating with age/sex peers does not seem to be a motivation for male dispersal. Subadult males spent a similar proportion of their time in female presence and absence associating with adult males. In the time they did associate with each other in all-male groups, subadults spent more time with their age-class peers than expected and less time with the other age-class. This is similar to what was seen in adult male associations in female absence and subadult males may also be using these associations to test strength against age-peers. However, given that both young and old sub adults spent more time than expected with old subadults in female presence, social learning may play a role in subadult male associations in female presence. Associations of subadult males seemed to be stable across years in female presence but not in female absence.

Keywords

Asian elephant, subadult males, associations, networks, male dispersal.

Introduction

In polygynous mammals that exhibit female philopatry and male dispersal (male biased dispersal is common among males; see Greenwood 1980), the social lives of males undergo dramatic changes as they grow older. While in many species, males move away from their natal herd and form stable associations with another female group (for example, rhesus macaques - Boelkins and Wilson 1972, olive baboons - Packer 1979), in some species (such as the sperm whale - Whitehead and Arnbom 1987), post-dispersal males rove between different social units and spend a lot of time alone. Asian elephants are an example of the latter type of social system, with the females remaining in their natal clans with related females (Vidya and Sukumar 2005, Shetty 2016) and the males dispersing away after puberty (Sukumar 1989, Desai and Johnsingh 1995). Male elephants begin their lives being apparently similar to their female counterparts, associating and interacting with their mothers, allomothers (Gadgil and Nair 1984,Vidya 2014, Revathe T, unpublished data) and other group members, but by the time they are adults, they have dispersed from their natal herd (Desai and Johnsingh 1995) to a different location (Vidya and Sukumar 2005) and spend a majority of their time on their own (McKay 1973, Desai and Johnsingh 1995, Keerthipriya *et al*. 2018a). In the phylogenetically related African savannah elephants, differences in behaviour between the sexes have been reported very early in life, with males from the age of three years onwards being more explorative and showing a greater tendency to interact with unfamiliar peers than females (Lee and Moss 1999, Lee and Moss 2014). Though their behaviours might similarly diverge from the females sooner, male Asian elephants start spending time away from their natal herd regularly only after 4-5 years of age (Daniel *et al*. 1987, Desai and Johnsingh 1995). Thus, subadult male elephants (5-15 years of age) have just begun to form associations independent of their mothers and spend time both in female presence and absence. It is interesting to examine the associations formed by such subadult males’ as they occur during the transition between the almost exclusively mixed-sex societies of juvenile males and the largely solitary lives of adult males.

Male dispersal is expected to play a big role in subadult male associations. Two modes of male dispersal have been described: locational mode of dispersal, which involves the male leaving not only the natal group, but also the natal home range, and the social mode of dispersal, where the male leaves the natal group but not the natal home range (Isbell and van

Vuren 1996). Asian elephant males have been found to show locational dispersal in three different landscapes (Vidya and Sukumar 2005, Vidya *et al*. 2005, Ahlering *et al*. 2011), with some evidence, based on small sample sizes, for non-random locational dispersal in the Nilgiris-Eastern Ghats landscape in southern India (Vidya and Sukumar 2005). Male dispersal may occur gradually, with males spending less and less time with their natal group over many years (Desai and Johnsingh 1995) or may occur more abruptly over a short time span. The social preference hypothesis (Bon and Campan 1996, Ruckstuhl and Neuhas 2000) posits that young males are expected to preferentially associate with same age/sex peers and these differences in social motivations (between males and females) are responsible for sexual segregation. Finally, while adult males Asian elephants in the Kabini population seemed to associate primarily with age-peers in female absence and showed no evidence of social learning from older males, the younger, less experienced subadult males, who had just started spending time away from familiar individuals might show social learning from older, more experienced subadult males.

In the current study, we wanted to examine some aspects of subadult male associations in the Kabini elephant population and compare them with what was earlier seen among adult males. Our main objectives were as follows:

1) *Examine whether associations of various age-classes of adult and subadult males are distinct from one another:* We wanted to examine whether young and old subadult males (based on the stage of dispersal; see Methods) and young and old adults (based on reproductive maturity/competitiveness, Keerthipriya *et al*. 2018a) showed different patterns of associations. As the motivation of an old adult male is assumed to be very different from a young male who has begun dispersing, and because even within adults we found differences in the associations of different age-classes, we expected the associations made by subadult and adult males to be distinct from one another.

2) *Examine the time spent by subadult males in mixed sex groups:* Adult males spent 35% of their time in mixed-sex groups and most of their time alone. We expected the subadults to spend much more of their time associating with female groups. We wanted to see whether the expected reduction in time spent in social groups occurred suddenly or gradually across years.

4) *Compare the effect of female presence on subadult associations with that on adult associations:* Adult males associated among themselves more commonly and extensively in all-male groups than in mixed-sex groups (Keerthipriya *et al*. 2018a). We wanted to see whether subadults associations were similarly more extensive in female absence than in female presence. We expected subadults to spend more time in female presence due to their affiliation with their natal clans. Hence, overall, we expected their associations to be higher in female presence but had no *apriori* expectation for the comparison between female presence and absence after controlling for the amount of time spent with females.

4) *Examine the social preference hypothesis as the mechanism for male dispersal:* We wanted to find out whether subadult males dispersed away from their groups in order to associate with fellow subadult males or with more experienced males. If this were the case, we would expect some measure of subadult male-male sociality to be higher in female absence than in female presence. They might spend more time with other males, meet more numbers of them or meet novel associates in female absence than female presence.

5) *Examine reasons for subadult male associations in all-male groups:* We tested two, non mutually exclusive, possible reasons for subadult male associations in all-male groups: social learning from older males and testing strengths against age-peers. If social learning from older males was important in subadult male associations in all-male groups, we expected older subadults to be more central in the association network and spend more time in all-male groups than younger males. We also expected old and young subadult males to spend more time with each other than expected by chance. If the associations in female absence were formed to test strengths, we would not expect age and network statistics to be correlated and we would expect males to spend more time with closely matched age-peers and less time with the other age-class.

Methods

Field data collection

The study was conducted in Nagarahole and Bandipur National Parks (644km^2 and 874 km^2; Kabini population) from March 2009 to July 2014. The Kabini reservoir separates these two

National Parks. The study area has a high elephant density (~1-2 elephants / km^2; AERCC 2006).We drove along pre-selected forest roads from ~06:30 AM till ~06:30-07:00 PM in the evening, depending on sampling permits. When an elephant or a group of elephants were sighted, all individuals were sexed, aged, and identified. Males were aged based on the first sightings of the male, using his shoulder height, body length, head size, the presence of wrinkles, and the presence of semi-captive elephants of known ages in the area (see Vidya *et al*. 2014). Age-classes of some males were also available from TNCV's prior fieldwork in the study area, from 2000-2005. Males were placed in 5 or 10 year age intervals and the median date in that interval was assigned as their date of birth. Some analyses use male ages and that is calculated as the difference between the estimated date of birth and the midpoint of the study period. Therefore, if an elephant was, for instance, aged as approximately 40 years old in the year 2000, it would be aged approximately 56 in the year 2016. Thus, the age was not a precise age but an approximate estimate with intervals on both sides of the estimate. Many subadults had been sighted from a very young age and ages could be estimated more accurately. Subadult males who were sighted for the first time when they were older were compared to males born to identified females (sighted when they were calves/juveniles) whose ages were more accurately known. Apart from the estimated ages, we also classified the males into the following age-classes: calves (<1year), juveniles (1-<5 years), young sub-adults (5-<10 years), old sub-adults (10-<15 years), young adults (15-<30 years), and old adults (30 years and above). The associations made by juveniles and calves are highly dependent on their mother's association and, thus, they were not used in these analyses. The four age-classes that were used (based on the age of identified males at the midpoint of the study period- November 2012) were young sub-adults, old sub-adults, young adults, and old adults. The males were classified as such because young subadult males are just starting to disperse away from their groups, still spending large amount of times with female herds, while old subadults were found more often in female absence but were still in the process of dispersing. Young adults were likely to have dispersed from natal herds and were found spending most of their time alone or with other males. They had the potential to attain matings but were rarely sighted in musth. Old adult males were reproductively competitive males. Identification of individual males was based on a combination of ear, back, tail, and tusk characteristics, along with presence of warts/wounds etc. (detailed in Vidya *et al*. 2014). Male associations were said to occur in female presence if the two males fed within 10m of a female group or interacted with members of the same female group at the same time and they were said to be associating in female absence if they fed within 30-50m of each other and there were no female groups nearby (detailed in Keerthipriya *et al*. 2018a). These are a male's immediate associations, relevant to physical interactions and detection of visual cues. Associations were also observed at every minute as male associations were found to change many times within the same day as mentioned in the previous chapter. We only used sightings wherein all subadult males were identified for most analyses. When we compared associations between adult and subadult males, we used the dataset with sightings in which all adult and subadult males were identified (a subset of the previous dataset).

Data Analysis

Since data on associations between males during the wet seasons and during 2009 and 2010 were much less than in the dry seasons and other years, respectively, we used only data from 2011-2014 for the analyses that compared associations across individual years. We only used subadults seen on 5 days or more in that category for analyses where the measure was taken on individual males and, when we used individual years' data, we used males seen for 30 minutes in that year (as the number of days a male was seen was strongly correlated with the time he was seen, both in female presence and absence; see Supplementary material 1).

A time-based association index (AI) (explained in detail in Keerthipriya *et al*. 2018a) was calculated as the amount of time two males spend together (N_{AB}), scaled by the amount of time the two males were seen in total ($N_A+N_B-N_{AB}$), for unique pairs of males. AI was calculated separately for the same pair of males in female presence and female absence. We compared the association indices of individual males of the four age-classes (young subadults, old subadult, young adults, and old adults) by testing for structural equivalence using Euclidean distances (see Wasserman and Faust 1994). The Euclidean distance between male i and male j was calculated as $d_{ij} = \sqrt{\sum}(AI_{ik} - AI_{jk})^2$, summed over all k where $k \neq i,j$. AI_{ik} refers to the association index between males i and k. If two males had the exact same association indices with all other males, their Euclidean distance would be zero. If males of two age-classes were similar in the associations they formed with other males, the Euclidean distances between males within each of the age-classes would be similar to those between males between the two age-classes. The dataset of sightings of all identified adult and subadult males was used to calculate Euclidean distances, using a MATLAB code

(MATLAB R2011a). The cumulative numbers of unique, identified, subadult males sighted across the years from 2011-2014 are shown in Supplementary material 2).

We calculated the proportion of time subadult males spent in different group-types to compare it with the time adults spent in different group types. We performed Spearman rank-order correlations between male age and the proportion of time the male spent in all-male groups with other subadult males or in mixed-sex groups. To examine whether the change in the time spent in mixed-sex groups was a sudden or a gradual one, the proportion of time spent in mixed-sex groups by adult and subadult males who were seen for 30 minutes in each of the four years (2011-2014) were calculated and, after logit transforming the values, compared using a repeated measures ANOVA (with year as the repeated measure, individual male as the replicate and age-class as a categorical factor). For this analysis, we used data from sightings wherein all adults and subadults were identified.

In order to see whether subadults spent time with age-class peers or the other age-class, we permuted the associations of all identified subadult males separately in female presence and absence, using the procedure explained by Whitehead (2008, pg. 124), by switching individual males across sightings while keeping the group sizes (of subadult males) and the time seen for each male constant. Each sighting was of one-minute duration; if a male was sighted for 5 minutes, there would be 5 sightings. We performed 5000 permutations and, in each permutation, performed (5*number of sightings) number of flips. The observed time that subadult males of different age-classes spent together were compared to the 5000 randomised values and, as we had no expectation of whether the observed values should be greater or less than the randomised values, used alpha=0.025 (for two tailed test) as the threshold for significance.

We wanted to examine whether subadults spent more of their time associating with sex peers in female absence. Therefore, we also calculated the proportion of their time that subadults spent associating with other subadults and with adult males in female presence and compared them to the corresponding values in female absence, using Wilcoxon’s matched-pairs tests. We also compared the group size (counted as the number of identified subadult males) distribution of sightings with multiple subadult males in them, in female presence and absence, using the Kolmogorov-Smirnov two sample test.

To compare the effect of female presence on subadult associations with the effect it had on adult male associations, we used association index values between subadult males seen on 5 days or more, both in female presence and absence, and constructed association networks in female presence and absence (visualized using Gephi 0.8.2 (Bastian *et al*. 2009). We compared the degree distributions of the two networks to a Poisson distribution (expected for an Erdös-Rényi random network; Erdös and Rényi 1960) using distribution fitting in Statistica 7 (StatSoft, Inc. 2004). We compared some networks statistics- *average degree, average clustering coefficient, average path length* and *density* (see Keerthipriya *et al*. 2018a) - between the subadult male association networks in female presence and in female absence. We calculated the degree for each combination of subadult age-classes. We compared all these network statistics of the female presence and female absence datasets using the sampled randomisation test with 10,000 randomisations (Sokal and Rohlf 1981, pp. 791-794, test is explained in detail Keerthipriya *et al*. 2018a) and compared the observed differences between the two datasets to the differences between the permuted datasets. The observed difference was considered significant if it was greater than the differences in more than 95% of the permuted datasets.

To examine the role of older males in association networks, we calculated three measures of centrality (*closeness centrality, betweenness centrality, Eigenvector centrality*; Bonacich 1972, Wasserman and Faust 1994), clustering coefficient and degree for individual males in both networks using Gephi 0.8.2. We then correlated the centrality measures, clustering coefficient and degree/time seen with the age of the male using Spearman's rank-order correlations. We also compared the AI matrices in female presence and absence using a Mantel test of matrix correlation (Mantel 1967) with 5000 permutations using a MATLAB code (MATLAB R2011a; The MathWorks, Inc, 1984-2011, www.mathworks.com).

We tested for stability of associations and preferred associations among subadults in female presence and absence. AI matrices were constructed for sightings of males, in female presence and in female absence separately, for each year from 2011-2014. We used males seen for 30 minutes or more in both the years being compared, and compared association matrices across consecutive years (2011-2014) using Mantel tests (Mantel 1967), with 5000 permutations using a MATLAB code. We also tested for preferred associations across sampling periods among subadult males using SOCPROG 2.6 (Whitehead 2009) with

10000 permutations and 10000 flips for each permutation, using the *permute associations within sample* method.

All Wilcoxon's matched-pairs tests, ANOVAs and Spearman's rank order correlations were performed using Statistica 7 (StatSoft, Inc. 2004). Other analyses and data manipulation were carried out in MATLAB unless specified otherwise.

Results

We identified 105 unique subadults (101 in sightings which were used for the association analyses) between March 2009-July 2014. Out of these, 93 different subadults were sighted in female presence and 75 were sighted in female absence.

Proportion of time spent in different group types

We found that subadult males spent most of their time (~76%) in mixed-sex groups. Out of the time they spent in female absence (~24%), they spent a vast majority of their time solitarily (~72% of the female absence time) (Table 1). Among the 64 subadult males seen on five days or more, male age was positively correlated with the proportion of time these males spent in all-male groups with other subadult males (Spearman's rank-order correlation: R=0.490, R^2=0.240, P<0.001; see Figure 2a), while it was negatively correlated with the proportion of time they spent in mixed-sex groups (Spearman's rank-order correlation: R=-0.640, R^2=0.410, P<0.001; see Figure 2b).

Table 1. Observation time for all identified subadult males and subadults seen on 5 days or more, in different group types (three of which are in female absence and one in female presence) and the average percentage of their time that they spent in those group types. The percentage of time spent in different group types for all subadult males is calculated using the total hours of observation in different group types, while for the subadults seen on five days or more, the percentage values is summed across the males and the average percentage is averaged across the males.

Group type	Female presence / absence	Hours of observation in group type (*N*=101 subadult males seen in all)	Percentage of hours of observation in different group types	Hours of observation (*N*=64 subadult males seen on >=5 days)	Average percentage of time spent by 64 subadult males ± SD
Solitary	Female absence	217.82	17.14%	209.60	13.95 ± 18.979
All-male groups (1 adult male)	Female absence	48.25	3.80%	47.22	2.35 ± 3.996
All-male groups (>1 adult male)	Female absence	34.68	2.73%	68.52	3.54 ± 6.320
Mixed-sex groups	Female presence	970.05	76.33%	1380.82	80.16 ± 22.857

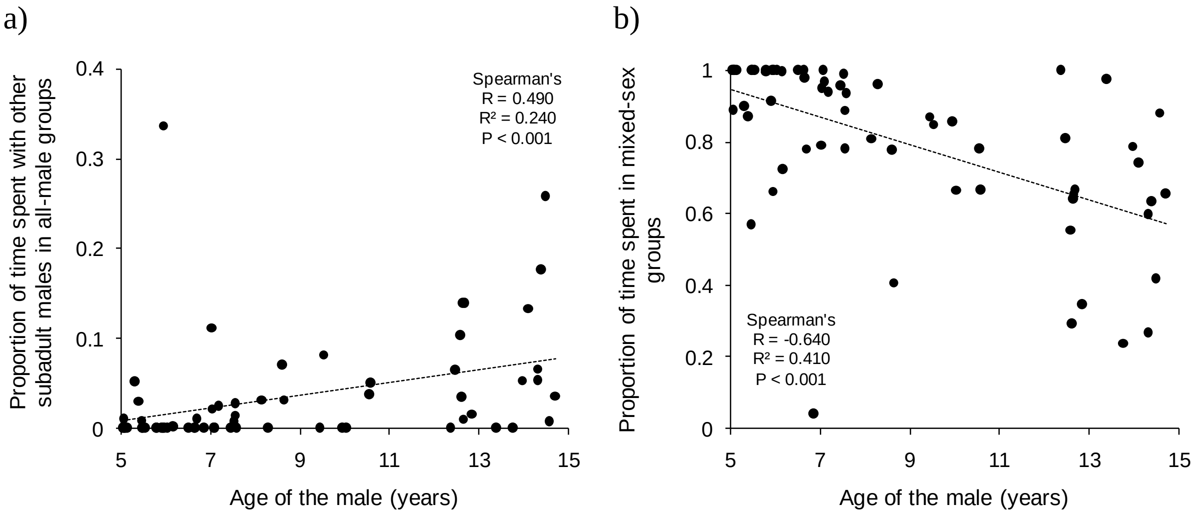


Figure 2. The proportion of time spent in a) all-male groups with other subadult males and b) in mixed-sex groups by subadult males of different ages.

The proportions of time spent in mixed-sex groups by different adults and subadults were logit transformed and used in a repeated measures ANOVA with age-class of the male as a factor and year as the repeated measure. Forty males who were seen every year from 2011-2014 for 30 minutes or more were used for this analysis. The age-class of the male (F=12.9461, df=3, P<0.0001) and the year (F=4.0320, df=3, P=0.0092) both exhibited a significant main effect. Some of the pairwise comparisons using Tukey's HSD tests were significant (after applying a flat Bonferroni correction for six comparisons), with the values for the year 2014 being significantly lower than the values for 2011 (*P*=0.009) and the values for the 5-10 years old age-class being significantly higher than those for the 15-30 years old (*P*<0.001) and the 30+ years old (*P*<0.001) age-classes (see Figure 3). However, there was no significant interaction effect (*F*=1.255, *df*=9, *P*=0.270).

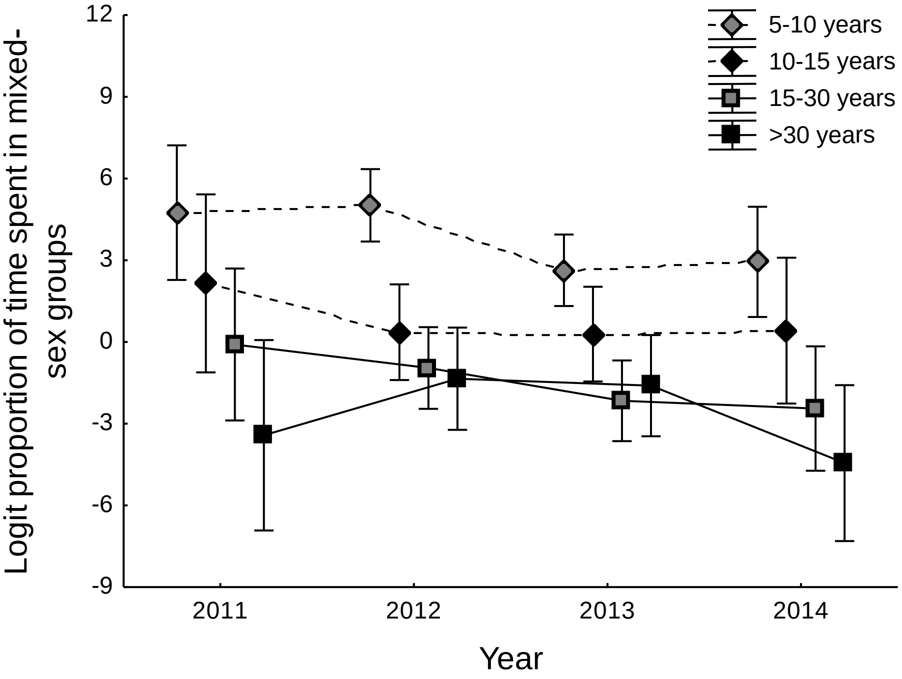


Figure 3. Proportions of time (logit transformed) spent in mixed-sex groups for males of different age classes across years.

Associations between subadult males of different age-classes

Subadult males were sighted for 58,203 minutes in female presence and 18,045 minutes in female absence. In female presence, the observed time that old (10-15 years) subadult males spent with each other (2,536 minutes) was higher than expected at random (average ± SD: 1650.7 ± 32.48, *P*<0.001), the time that old and young (5-10) subadults spent together (8637 minutes) was also higher than expected (average ± SD: 8282.0 ± 55.85, *P*<0.001), while the time that young subadults spent together (11,655 minutes) was less than expected from random associations (average ± SD: 13039.8 ± 48.69, *P*<0.001; Figure 4). On the other hand, in female absence, the time that old subadults spent together (938 minutes) and the time that young subadults spent together (434 minutes) were both higher than expected at random (Old subadults: average ± SD: 687.0 ± 19.56, *P*<0.001; Young subadults: average ± SD: 394.9 ± 16.51, *P*=0.010) but the time that old and young subadults spent together (789 minutes) was less than expected (average ± SD: 1107.5 ± 22.39, *P*<0.001; Figure 4). As expected, the total amount of time that subadult of all age-class combinations spent together was much higher in female presence than female absence.

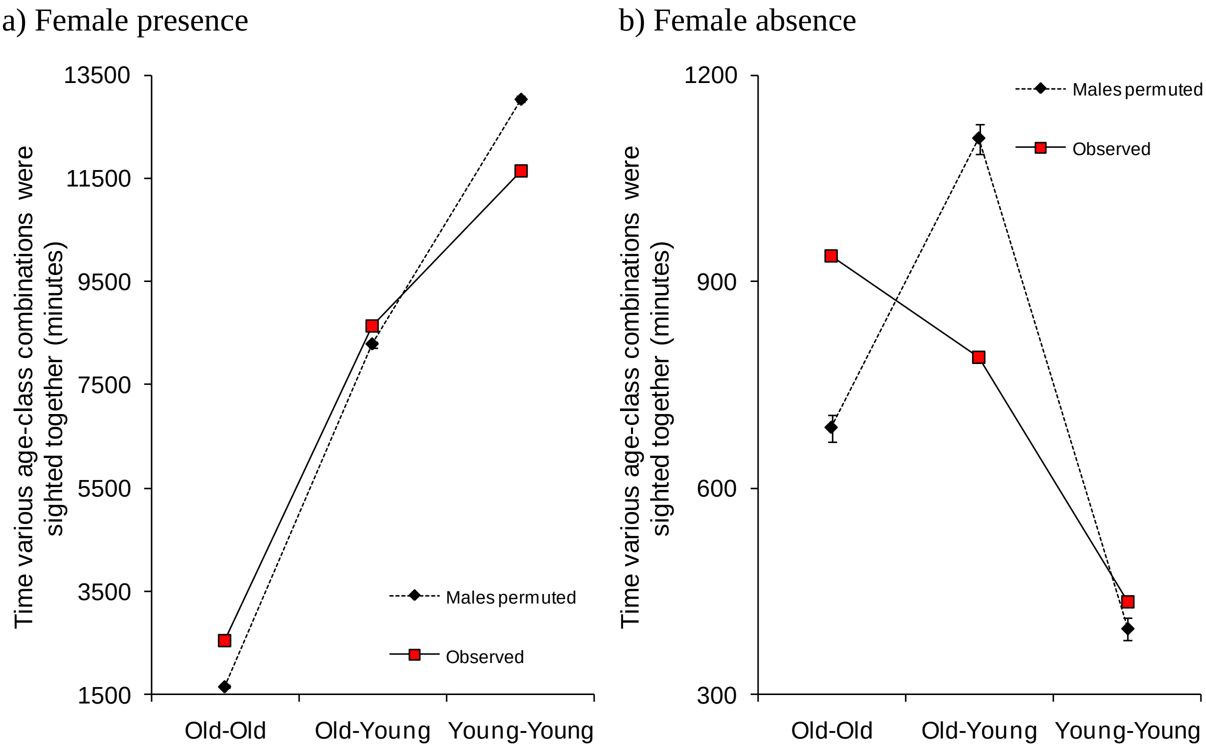


Figure 4. Permuted and observed values of time spent together by old (10-15) and young (5-10) subadult males with the same and the other age-class in a) female presence and b) female absence. Please note that the Y axis scales are very different in the two graphs.

The proportion of their time (out of the time they spent in that category) that 30 common subadults (seen on five days or more both in female presence and absence) spent with other subadult males was higher in female presence than in female absence (Wilcoxon's matched-pairs test: *T*=5.000, *z*=4.679, *P*<0.001). Using the same 30 males, we found that the proportion of time they spent associating with adult males was similar in female presence and absence (Wilcoxon's matched pairs test: *T*=221.000, *z*=0.236, *P*=0.813).

Group size distributions in female presence and absence

We calculated the number of minutes we sighted groups of various sizes (group size counted as the number of identified subadults) in female presence and in female absence. We found that, using sightings with multiple subadult males, the group size distributions of sightings in female presence (N=19041 minutes, average ± SD of group sizes: 2.446 ± 0.802) and absence (N=2081 minutes, average ± SD of group sizes: 2.068 ± 0.262) were significantly different from one another (Kolmogorov-Smirnov two sample test: D=0.242, P<0.001; see Figure 5).

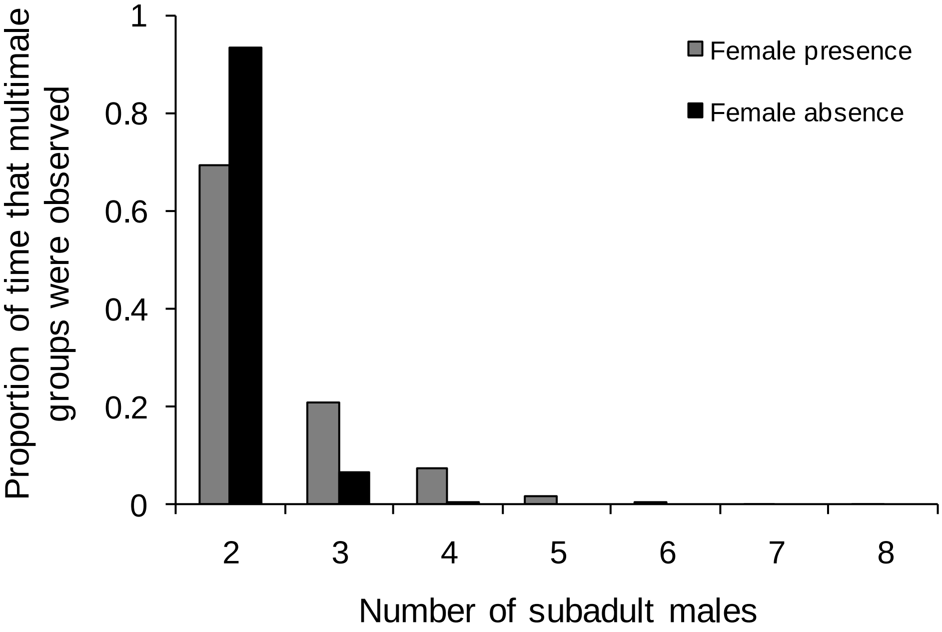


Figure 5. The proportion of observation time (of multi-subadult male sightings) that sightings with different number of subadult males were observed, in female presence and absence.

AI, Association networks and comparison of network statistics in female presence and absence

When we compared the Euclidean distances between dyads of different age-class combinations of adult and subadult males, we found that most comparisons were significantly different (see Supplementary material 3). Therefore, the associations made by the four age-classes were distinct from one another. The only case where both age-classes showed similar Euclidean distances within and between the two age-classes were old and young adult males in female presence.

We constructed undirected association networks using association indices between 30 common subadults (seen on 5 days or more both in female presence and absence) (Figure 6). We found that, both in female presence and in female absence, the distributions of degree (number of associates) of the 30 males were not significantly different from a Poisson distribution (see Supplementary material 4). When we compared network statistics using the sampled randomisation test, we found that the network in female presence had higher density and average clustering coefficient and lower average path lengths than the network in female absence (Table 2). The degree, between all combinations of subadult age-classes, was higher in female presence than female absence (Figure 7). The age of the male was not correlated with closeness centrality (see Supplementary material 5). We found that the AI matrices in female presence and absence were weakly but significantly positively correlated with each other (Mantel test: *R*=0.135, R^2=0.018, *P*=0.020).

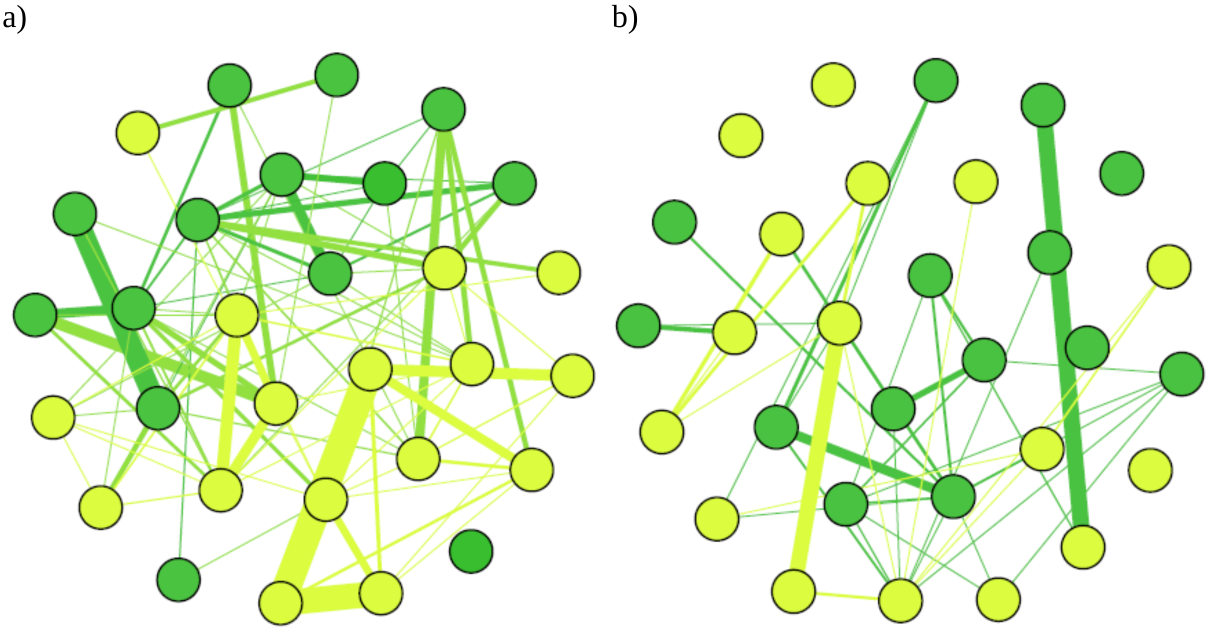
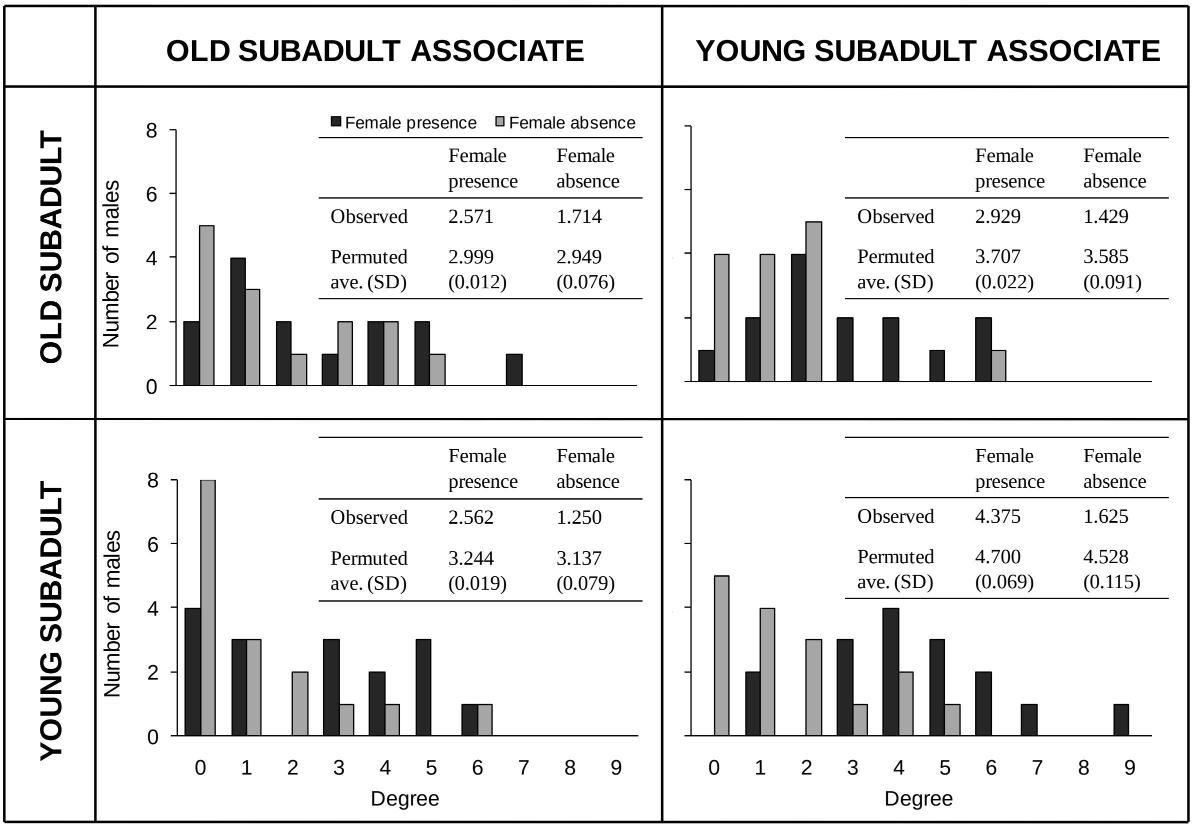


Figure 6. Undirected association networks of subadult males (30 subadult males seen on >=5 different days each in female presence and absence) in a) female presence and b)

female absence. Nodes coloured in the darker shade of green represent subadult males of the 10-15 years age-class and those coloured in the lighter shade of green represent subadult males of the 5-10 years age-class. The edge thickness is based on the AI between the two nodes being connected.

Table 2. Network statistics based on observed and permuted subadult male associations in female presence and female absence. *P*=(number of times difference$_{\text{random}}$≥ difference$_{\text{observed}}$) / number of randomisations (10,000). Significant *P* values are marked in bold.

Category	Average clustering coefficient	Average path length	Density
Female presence observed	0.465	2.044	0.216
Female absence observed	0.399	2.5	0.103
Female presence permuted ave. (SD)	0.568 (0.0078)	1.874 (0.0063)	0.254 (0.0015)
Female absence permuted ave. (SD)	0.558 (0.0270)	1.902 (0.0197)	0.246 (0.0038)
P value	**0.0419**	**<0.0001**	**<0.0001**



Old subadult with old subadult associate:

	Female presence	Female absence
Observed	2.571	1.714
Permuted ave. (SD)	2.999 (0.012)	2.949 (0.076)

Old subadult with young subadult associate:

	Female presence	Female absence
Observed	2.929	1.429
Permuted ave. (SD)	3.707 (0.022)	3.585 (0.091)

Young subadult with old subadult associate:

	Female presence	Female absence
Observed	2.562	1.250
Permuted ave. (SD)	3.244 (0.019)	3.137 (0.079)

Young subadult with young subadult associate:

	Female presence	Female absence
Observed	4.375	1.625
Permuted ave. (SD)	4.700 (0.069)	4.528 (0.115)

Figure 7. Degree distributions in female presence and absence of (clockwise from top left) old (10-15 years) subadult males with old subadult males, old subadult males with young (5-10) subadult males, young subadult males with young subadult males, and young subadult males with old subadult males. The average degree values of the observed and permuted datasets from the sampled randomisations test with 10,000 randomisations, are provided inside each panel. In all four cases, the average degree in female presence was significantly greater than the average degree in female absence (*P*<0.001).

Preferred male associations and stability of associations

We found no evidence of preferred subadult male associations across 14-day or 30-daysampling periods in female absence. However, in female presence, the SD and CV values of the real dataset were not different from the randomised datasets for the 14-day sampling period but they were both significantly higher in the real dataset when we used a 30-day sampling period (see Supplementary material 6). Mantel tests between AI matrices of consecutive years showed no significant correlation in female absence while in female presence, all the three comparisons showed significant positive correlations (Supplementary material 7).

Discussion

We examined the associations of subadult male Asian elephants in the presence and absence of female groups. Subadult males, who are likely still in the process of dispersing away from their natal clans, were seen to spend most (~76%) of their time with female groups. In the time they spend away from female groups, subadults spend ~72% solitarily. When we compared the associations of the four age-classes of adult and subadult males, we found that the associations of males of different age-classes were mostly distinct from the others. Given the likely differences in a male's motivations as he grows older, this result is not surprising and matches our expectation. As we had noted earlier, male Asian elephants move from living in social groups to leading largely solitary lives but the decrease in time spent in mixed-sex groups seems to be gradual across years. This could happen either because males gradually decreased their time spent with natal clans or, because they spend time with other clans after leaving their own. It would be interesting to look at associations with natal and other clans separately to see if associations with non-natal clans was indeed a buffer for the males, between philopatry and their largely solitary adult lives. In African savannah elephants, a lot of individual variability has been found in the age at which males began to spend time away from their natal group and the speed (the time from the first sighting of the male away from his natal clan till when he spent more than 80% of his time away from his natal family unit) of dispersal. Males who started dispersal at a later age tended to disperse faster while males who started dispersal young, gradually reduced the time spent with their family (Lee *et al*. 2011). In the future, with longitudinal data on the subadult males of the Kabini population, it would be interesting to similarly examine their patterns of dispersal.

Associations of subadult males in female presence and absence

The subadult association network in female presence was denser and more clustered than that in female absence. Subadults of both age-classes met more numbers of each other in female presence than absence (even after controlling for the time spent in female presence). Age of the subadult did not affect any of the network statistics that we compared, in either network. Subadults spent a greater proportion of their time associating with other subadult males in female presence than female absence and, out of the time they spent with other subadults, the group sizes were larger in female presence than female absence. In the absence of females, subadult males spent more time with subadults from the same age-class than with the other age-class, similar to what adult males did (Keerthipriya *et al*. 2018a). When they were in female presence, the old subadults spent more time with other old subadults and with young subadults than expected, while the time young subadults spent with other young subadults was less than expected by chance. The result for the youngest age class mirrors what we saw for the oldest age-class of adults (30+ age-class, see Keerthipriya *et al*. 2018a). In the case of the old adult males, the likely reason for the pattern of association was avoiding other old adults as competitors. In the case of the young subadults, the association pattern may be a result of still spending most of their time with their natal clan. Thus, even though young subadults are sighted commonly in female presence, the time spent with other young subadults is restricted if they are both from different clans. Older subadults, who move between different female groups more, would not face this restriction.

Subadults did not seem to show preferential associations across 14-day sampling periods in female presence, but when the sampling period was increased to 30 days, there was evidence for preferential associations. Further, associations seemed to be stable across years in female presence. On the other hand, in female absence, there was no evidence of preference or stability of associations. When we examined the degree distributions of networks, combining all five years of data, both in female presence and absence, the distribution was not different from the expectation for a random network. Therefore, in female absence, at all the temporal scales that we examined, there were no signs of non-random associations, while in female presence, there were preferential associations, but only at intermediate time intervals. When we compared the proportion of time that subadults spent with adult males, we found no difference between female presence and absence. Overall, associations of subadult males were more common, extensive and stable in female presence than in female absence.

This makes the associations of subadult males starkly different from those among adult males. We posit that affiliation with their natal clan members and not being reproductively mature contributes to the extensive associations of subadult males in female presence. As male elephants grow older and become capable of acquiring matings, their associations with female groups will be motivated increasingly by finding and mating with rare, receptive females and thus, associations with other older males are expected to become competitive.

Proximate reasons for male dispersal

Subadults spent a greater proportion of their time in female presence than female absence socializing with other subadults. The associations that subadults made in female presence was correlated with those made in female absence and hence, subadult males do not seem to associate with new associates in female absence. As none of the measures of subadult male sociality that we looked at (proportion of time spent, number of associates, presence of novel associates) was higher in female absence than presence, the main proximate reason for subadults moving away from natal clans is unlikely to be to associate with other males. The social preference hypothesis, therefore, seems inadequate to explain male dispersal in the Kabini population. Availability of age-peers did have an effect on the age and speed of dispersal in African savannah elephants in Amboseli (Lee *et al*. 2011). Males from small family units who did not have many age/sex peers to interact with seemed to disperse quicker from their natal units. Given the much smaller proportion of time spent in all-male groups and the limited role of older males in all-male group associations of adult males in Kabini when compared to Amboseli (Chiyo *et al*. 2011, Keerthipriya *et al*. 2018a), male-male association may not be as important a factor to consider for dispersing males in Kabini, relative to Amboseli. Ruckstuhl and Neuhaus (2000) also discuss how social preferences may increase cohesion within male or female groups but it is similarities in nutritional requirements or activity budgets which will hold a group together, and social preference on its own in unlikely to cause sexual segregation. In Amboseli also, availability of peers to interact with was one of many factors which had an effect on male dispersal (whether the mother was alive and whether the mother was the matriarch of the unit also affected when and how quickly the male dispersed; Lee *et al*. 2011).

Other possible, non-mutually exclusive reasons for male dispersal include feeding restrictions and increased intersexual aggression in the natal clan. Feeding restrictions on either the amount or type of food may be faced while feeding in a group, likely because of the marked sexual dimorphism seen in Asian elephants (Sukumar *et al*. 1988) and the group size restriction on female group sizes in the study population (Nandini *et al*. 2018). Sex differences in nutritional requirements and feeding behaviour were found and have been discussed as a possible reason for sexual segregation in the African savannah elephant

(Stokke and du Toit 2000, Shannon *et al*. 2006) and in ungulate species (for example, white tailed deer - Beier 1987, bighorn sheep - Ruckstuhl 1998, mule deer - Bowyer 1984). Increased intersexual aggression in the natal clan leading to eviction of natal males is another possible reason for male dispersal. This was not the case in African savannah elephants in Amboseli; females showed aggression towards dispersing non-natal males but natal males were tolerated (Lee *et al*. 2011). Sex differences in exploratory behavior may act as a mechanism to facilitate dispersal. From a very young age, male African savannah elephants spend more time away from their mother and natal group, and interact with non-family members more than their female counterparts (Lee and Moss 1999, Lee and Moss 2011, Lee and Moss 2014). It is possible that such differences in exploratory behaviour also exist in the Asian elephant. Data on feeding and dominance in males of different ages can be used in the future to better understand the proximate reasons for male dispersal in the Kabini population.

Reasons for subadult associations

During the time that subadult males spent associating with each other in female absence, they spent more time with age-peers and less time with males from the other age-class. Further, older subadult males were not more central or better connected in the association network than younger subadults. This is similar to the results we find in adults and hence, adult and subadult males of all ages spend their time in female absence with similarly aged males. Males segregating themselves based on their age and spending less time with males distant from themselves in age, has been observed in some species of ungulates (mouflon sheep - Bon *et al*. 1993 and Cransac *et al*. 1998, Alpine ibex - Bon *et al*. 2001). We had expected that adults used their time spent with age-peers to test strength against closely matched males and subadults might similarly be using their time spent in these groups to test strength against peers. Social learning from older males does not seem to be the primary reason for subadult male associations in female absence. However, in their associations in female presence, both younger and older subadult males spent more time than expected with older males. Therefore, it is possible that mixed-sex groups provide an opportunity for younger subadults to learn from older subadults.

In summary, we found that subadult male Asian elephants make associations distinct from those of adult males, their associations in female presence remain stable across years and the social network is better connected in female presence than female absence. Subadults spent most of the time in female absence solitarily and associating with fellow subadult or adult males does not seem to be a plausible cause for male dispersal. They associated with similarly aged subadult males in female absence and old subadult males in female presence, indicating that social learning from older males may have a bigger role to play, if at all, in their associations in female presence than in female absence.

Acknowledgments

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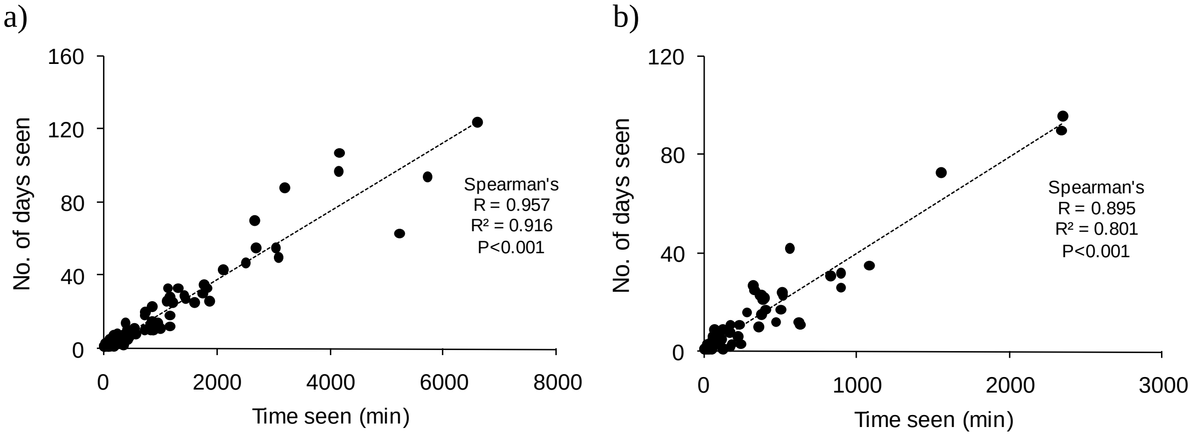
Supplementary Material

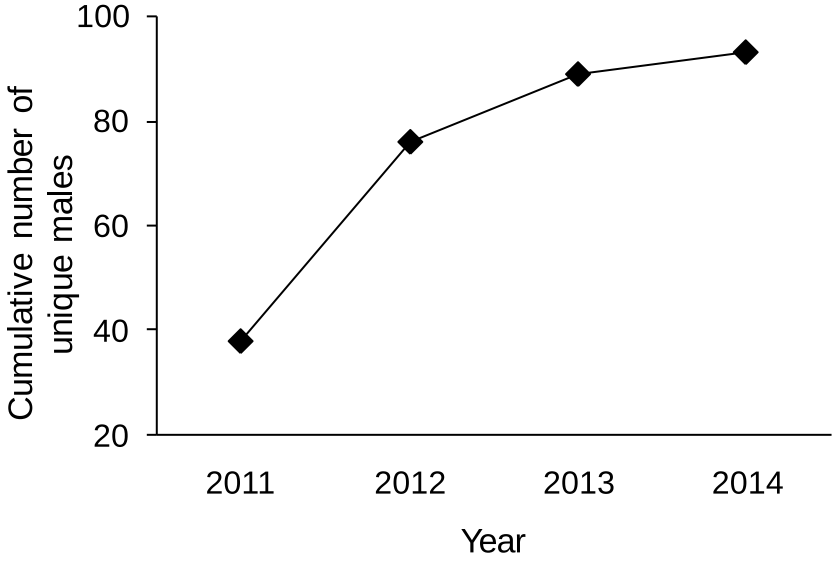
Supplementary Material 1. Plots of number of minutes a male was seen versus the number of days he was sighted.



Supplementary Material 1, Figure 1. The number of days a subadult male was sighted and the number of minutes he was totally sighted, in a) female presence (*N*=93) and b) female absence (*N*=75). The values are strongly correlated in both cases. Please note that the scales are different in the two figures.

Supplementary Material 2. Cumulative numbers of identified adult and subadult males sighted across years.

We calculated the cumulative numbers of identified subadult males sighted across years from 2011-2014 and we found that the curves showed little increase between the third and fourth year of sampling (only 4 new subadult males, out of the 93 sighted from 2011-2014, were sighted first in 2014, indicating that we have sampled most of the subadult males in the area during the study period.



Supplementary material 2, Figure 1. Cumulative numbers of identified subadult males sighted across years.

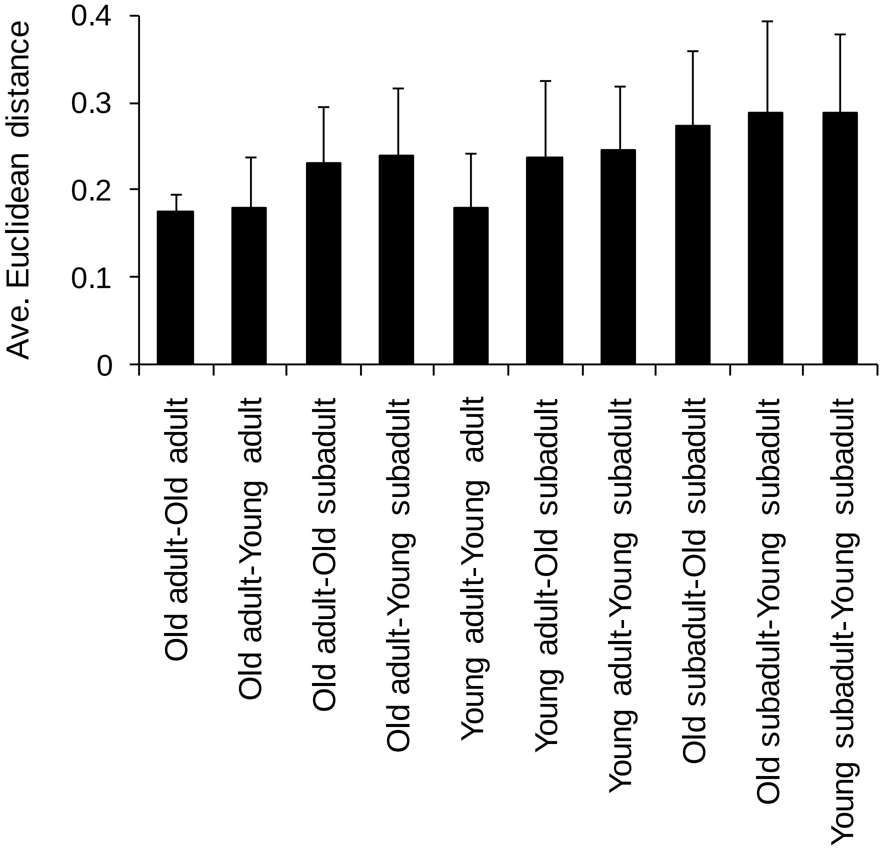
Supplementary Material 3. Euclidean distances within and across age-classes.

We compared the Euclidean distances between pairs of males of different age-class combinations and compared the distances of dyads belonging to the same age-class with those of dyads belonging to different age-classes using a code written in MATLAB (MATLAB R2011a). The lists of Euclidean distances of different age-class combinations were compared using Wilcoxon's rank sum test. A *h* value of 1 indicates that the null hypothesis (that distances in the two lists are similar) can be rejected at $P<0.05$ and h=0 means that the null hypothesis cannot be rejected ($P>0.05$).

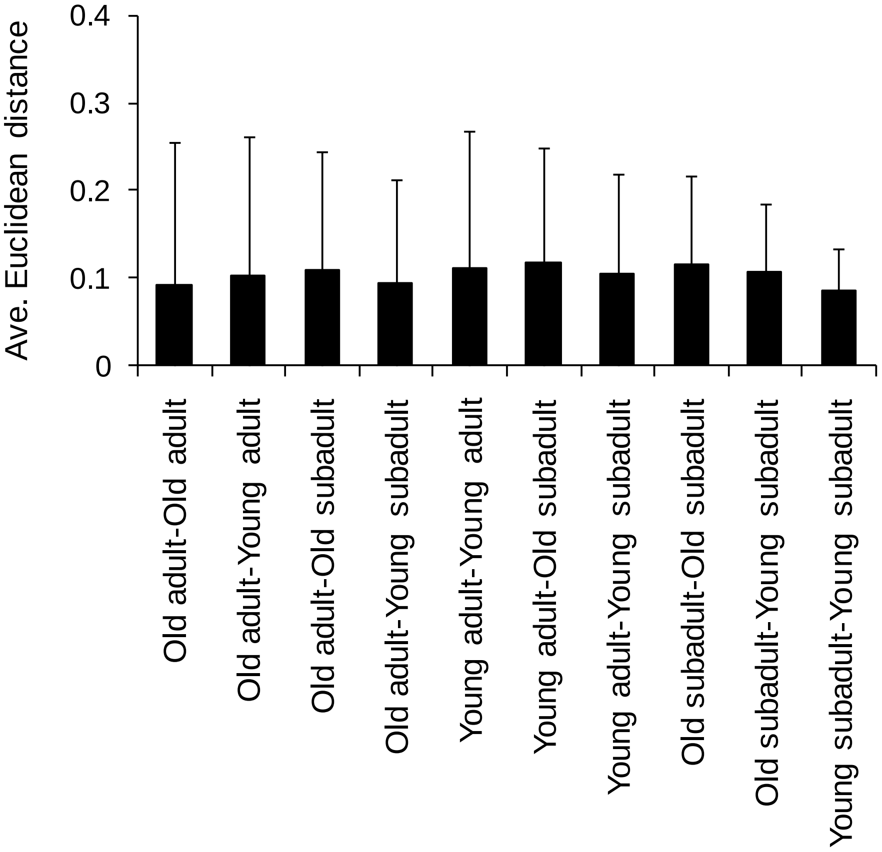
In female presence, old and young adults associated similarly with each other as they do with males from the same age class. The old subadults, unlike in female absence, associated differently with males of all other age classes compared to how they associated with peers. Young subadults associated similarly with old subadults in female presence. The reverse, however, was not true (see Table 1 for test results and Figure 1 for the distances).

When females were absent, the associations made by the different age classes were largely different from one another. However, the associations of old subadult males with other old subadult males were not significantly different from their associations with young subadults and with young adults. Also, associations of young subadults with old subadults were not significantly different from their associations with other young subadults. As young subadult males do not spend much time in female absence, the results involving them might have not been significant. However, old subadults seem to associate similarly with young adults as they do with their age-peers. The adults however associated differently with all the other classes compared to their peers (see Table 2 for test results and Figure 2 for the distances).

Thus, the four age classes of males formed distinct associations from each other, with the exception of old and young adults in female presence. Thus, we analysed the associations of the four age classes separately unless the sample sizes were low.



Supplementary material 3, Figure 1. Average Euclidean distances between males of different age-classes in female presence. Error bars are standard deviation.



Supplementary Material 3, Figure 2. Supplementary material 3, Figure 1. Average Euclidean distances between males of different age-classes in female absence. Error bars are standard deviation.

Supplementary Material 3, Table 1. Test results of comparison of Euclidean distances between different age-class combinations in female presence.

Comparison (Euclidean distances between A. compared with those between B.)		*h*	*P*
A	B		
Old adult-Old adult	Old adult-Young adult	0	0.9165
Old adult-Old adult	Old adult-Young subadult	1	**<0.001**
Old adult-Old adult	Old adult-Young subadult	1	**<0.001**
Young adult-Young adult	Young adult-Old subadult	1	**<0.001**
Young adult-Young adult	Young adult-Young subadult	1	**<0.001**
Young adult-Young adult	Old adult-Young adult	0	0.8472
Old subadult-Old subadult	Old subadult-Young subadult	1	**0.0011**
Old subadult-Old subadult	Young adult-Old subadult	1	**<0.001**
Old subadult-Old subadult	Old adult-Young subadult	1	**<0.001**
Young subadult-Young subadult	Old adult-Young subadult	1	**<0.001**
Young subadult-Young subadult	Young adult-Young subadult	1	**<0.001**
Young subadult-Young subadult	Old subadult-Young subadult	0	0.0699

Supplementary Material 3, Table 2. Test results of comparisons of Euclidean distances between different age-class combinations in female absence

Comparison (Euclidean distances between A. compared with those between B.)		*h*	*P*
A	B		
Old adult-Old adult	Old adult-Young adult	1	**0.033**
Old adult-Old adult	Old adult-Young subadult	1	**<0.001**
Old adult-Old adult	Old adult-Young subadult	1	**<0.001**
Young adult-Young adult	Young adult-Old subadult	1	**<0.001**
Young adult-Young adult	Young adult-Young subadult	1	**<0.001**
Young adult-Young adult	Old adult-Young adult	1	**0.0201**
Old subadult-Old subadult	Old subadult-Young subadult	0	0.8645
Old subadult-Old subadult	Young adult-Old subadult	0	0.1842
Old subadult-Old subadult	Old adult-Young subadult	1	**<0.001**
Young subadult-Young subadult	Old adult-Young subadult	1	**<0.001**
Young subadult-Young subadult	Young adult-Young subadult	0	0.1888
Young subadult-Young subadult	Old subadult-Young subadult	1	**0.0068**

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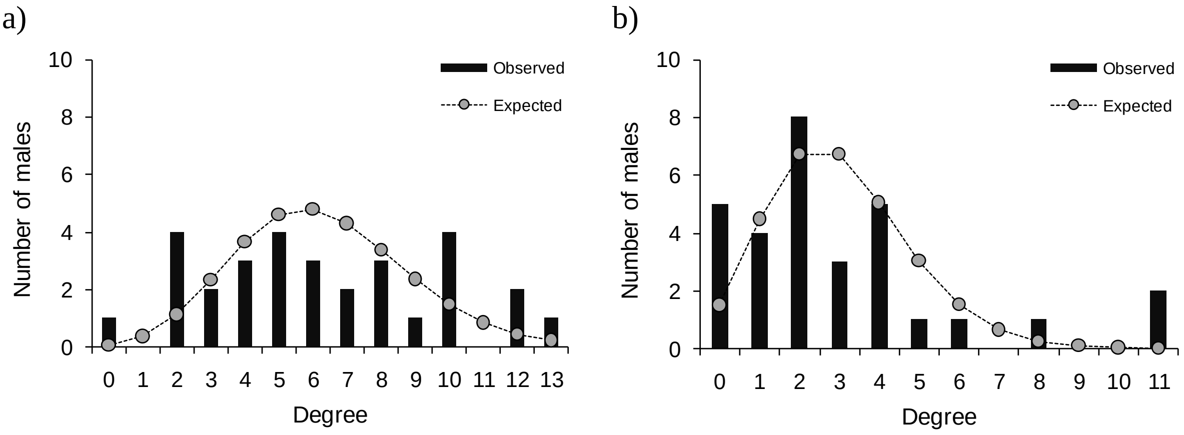
Supplementary Material 4. Degree distributions of association networks in female presence and female absence.

We compared the distribution of degree (number of associates) of 30 subadult males (who were seen on 5 days or more both in female presence and absence) with Poisson distributions (expected for an Erdös-Rényi random network; Erdös and Rényi 1960). We found that the observed degree distributions were not different from the random Poisson expectation in female presence (χ^2=3.531, P=0.171) or in female absence (χ^2=3.889, P=0.274; Figure 1 below).



Supplementary Material 4, Figure 1. Observed (bars) and expected (lines) degree distributions of subadult male association networks in a) female presence and b) female absence.

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Supplementary Material 5. Correlations between various centrality measures.

We found that all the three centrality measures that we measured in the subadult male association networks were strongly correlated with each other. We chose one of them (closeness centrality) to correlate with male age. Results of the Spearman's rank-order correlations between the measures in female presence and absence are shown in Table 1. When we correlated closeness centrality, clustering coefficient and degree/time seen of a male in the network with his age, we did not find any significant correlations; see Table 2.

Supplementary material 5, Table 1. Correlation test results between different centrality measures. All comparisons were significant and are, hence, marked in bold.

Network statistics	Female presence (*N*=30)	Female absence (*N*=30)
Closeness centrality and Betweenness centrality	**Spearman's** **R=0.815, R^2=0.665, P<0.001**	**Spearman's** **R=0.663, R^2=0.440, P<0.001**
Closeness centrality and Eigenvector centrality	**Spearman's** **R=0.947, R^2=0.927, P<0.001**	**Spearman's** **R=0.941, R^2=0.885, P<0.001**
Betweenness centrality and Eigenvector centrality	**Spearman's** **R=0.787, R^2=0.619, P<0.001**	**Spearman's** **R=0.652, R^2=0.425, P<0.001**

Supplementary material 5, Table 2. Results of Spearman's rank-order correlations between closeness centrality, clustering coefficient, and degree/time with subadult male's age. Significant correlations are marked in bold (*P* value for statistical significance, with a flat Bonferroni correction for six comparisons, is <0.008).

Network statistic	Female presence (N=30)	Female absence (N=30)
Closeness centrality	R=-0.063, R^2=0.004, P>0.05	R=0.190, R^2=0.036, P>0.05
Clustering coefficient	R=-0.141, R^2=0.020, P>0.05	R=-0.042, R^2=0.002, P>0.05
Degree/time	R=0.335, R^2=0.112, P>0.05	R=-0.014, R^2<0.001, P>0.05

Supplementary Material 6. Permutation tests to test for preferred associations.

We used SOCPROG 2.6 to perform permutations tests with 14-day and 30-day sampling periods; sightings within a sampling period would be grouped together and then permuted. We used the *permute associations within samples* method which checks for long-term (between sampling periods) preferences/avoidances in associations. Association data on identified subadult males were randomly permuted in order to find out whether there were preferred associations in that category. This method preserves the number of minutes the male was seen and the group size distribution while permuting. We used 10000 permutations with 10000 flips per permutation for this test. Only subadult associations in female presence using 30-day sampling periods showed signs of preferred associations, and the results of the permutation tests are tabulated below (Tables 1, 2).

Supplementary Material 6, Table 1. *P* values for the permutations carried out on subadult male associations in female presence and absence, with a 14-day sampling period, using 10,000 and 10,000 flips per permutation. Number of identified males in that category are also given in the table. Statistically significant values (*P*<0.05) are marked in bold.

Category	Statistic	Observed value	Ave. random value using 10000 flips	*P* (1-sided) (10000 flips)
Subadult males	Mean AI	0.0055	0.0055	-
in female presence	SD of AI	0.0250	0.0231	0.3018
N= 93	CV of AI	4.5046	4.1996	0.3232
	Mean non-zero AI	0.0614	0.0514	**<0.0001**
	SD of non-zero AI	0.0590	0.0509	0.2959
	CV of non-zero AI	0.9603	0.9874	0.4441
Subadult males	Mean AI	0.0013	0.0014	-
in female absence	SD of AI	0.0090	0.0133	0.6131
N= 75	CV of AI	6.8236	8.8549	0.5473
	Mean non-zero AI	0.0432	0.0461	0.5620
	SD of non-zero AI	0.0293	0.0570	0.6025
	CV of non-zero AI	0.6778	1.1683	0.6993

Supplementary Material 6, Table 2. *P* values for the permutations carried out on subadult male associations in female presence and absence, with a 30-day sampling period, using 10,000 and 10,000 flips per permutation. Number of identified males in that category are also given in the table. Statistically significant values (*P*<0.05) are marked in bold.

Category	Statistic	Observed value	Ave. random value using 10000 flips	*P* (1-sided) (10000 flips)
Subadult males	Mean AI	0.0078	0.0075	-
in female presence	SD of AI	0.0351	0.0297	**0.0232**
N= 93	CV of AI	4.4822	3.9350	**0.0176**
	Mean non-zero AI	0.0869	0.0718	**<0.0001**
	SD of non-zero AI	0.0826	0.0610	**0.0199**
	CV of non-zero AI	0.9507	0.8467	0.1764
Subadult males	Mean AI	0.0019	0.0021	-
in female absence	SD of AI	0.0122	0.0186	0.7640
N= 75	CV of AI	6.4966	8.6975	0.7817
	Mean non-zero AI	0.0611	0.0669	0.6874
	SD of non-zero AI	0.0348	0.0797	0.8109
	CV of non-zero AI	0.5702	1.1401	0.9015

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Supplementary Material 7. Mantel test results of AI matrices across consecutive years, in female presence and absence

We compared AI matrices of common males (seen for 30 minutes or more in both the years being compared) across consecutive years in female presence and absence. None of the comparisons in female absence yielded a significant correlation (the AI matrices in the 2011-2012 comparison had no non-zero AI values and hence could not be compared) while all matrices in female presence were significantly positively correlated. The results are shown in Table 1.

Supplementary material 7, Table 1. Mantel test results with 5000 permutations for comparisons between AI matrices of common subadult males in consecutive years in female presence and female absence.

	Female presence			Female absence		
	N	*R*	*P*	*N*	*R*	*P*
2011-2012	**25**	**0.413**	**0.002**	5	-	1.000
2012-2013	**23**	**0.242**	**0.005**	6	-0.156	1.000
2013-2014	**17**	**0.372**	**0.004**	7	-0.098	0.452

CHAPTER 4

Musth and its Effects on Male-Male and Male-Female Associations in Asian Elephants in Nagarahole-Bandipur, Southern India

Title: Musth and its effects on male-male and male-female associations in Asian elephants in Nagarahole-Bandipur, southern India

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Manuscript submitted, under review.

Author contributions

PK and TNCV conceived this work. All the authors helped to collect field data. PK collected most of the field data, from 2011-2014 and carried out all the analyses. PK primarily and TNCV wrote the manuscript and all the authors read and finalised the manuscript.

Abstract

We present one of the first studies on musth in free-ranging Asian elephants based on long-term data from the Kabini elephant population in Nagarahole and Bandipur, southern India. Older males were more likely to be sighted in musth as expected. There was a greater turnover of musth than nonmusth males in the study area although the age-classes of new males that entered the study area were similar to those of resident males. This suggests that musth is a roving strategy, enabling males to travel widely to gain access to females. We examined whether musth provided a temporary advantage to younger males by increasing their access to female groups. Surprisingly, young musth males spent a smaller proportion of their musth time than their nonmusth time associating with females and associated with similar sized female groups. Old males spent a slightly higher proportion of their musth than nonmusth time with females, but associated with larger female groups when in musth. Therefore, the payoff from musth, as a strategy to gain access to females, is age-specific. Old adult musth males also associated with young adult nonmusth males more often in female presence than in female absence, suggesting a tolerance of the latter by the former in female presence. However, young adult musth males were never sighted with old nonmusth males in the presence of females, and musth males almost never associated together. Therefore, musth seems to be primarily a strategy for old males to find and associate with females, and may be suppressed or not useful in young males. There was no spatial avoidance between musth and nonmusth males sighted within an hour of each other and the distribution of musth males across days was not different from random, suggesting no spatiotemporal separation of musth at scales larger than immediate associations.

Keywords

Asian elephant, musth, age, male-male associations, male-female associations, male spacing, roving behaviour, Nagarahole-Bandipur, Kabini Elephant Project.

Introduction

Many mammalian species exhibit polygynous mating systems (Orians 1969, Kleimann 1977), in which males compete for mating opportunities with rarer, sexually receptive females (Emlen and Oring 1977). Males in such species may employ different mating strategies depending upon the spatiotemporal distributions of receptive females (Emlen and Oring 1977, Clutton-Brock 1989). In species wherein females are unpredictably distributed and range over large areas, males may adopt a roving strategy, moving between different female social units and temporarily associating with females (for example, sperm whales- Best 1979, African savannah elephants- Poole 1982, polar bears- Derocher and Sterling 1990, Asian elephants- Desai and Johnsingh 1995, killer whales- Baird and Whitehead 2000, giraffes- Bercovitch et al. 2006). Individual males may invest differentially in competitive breeding at different stages in their life (older males invest more in competitive breeding in roving males; see Whitehead 1994), or at specific times of the year (rut in ungulates- de Vos et al. 1967, musth in individual elephants- Jainudeen et al. 1972a, Poole and Moss 1981), depending on their ability to compete with other males and the mating opportunities available (see Poole et al. 2011 for timing of musth in African savannah elephants). We wanted to study some aspects of an expensive mating strategy, musth, in the Asian elephant, a polygynous species in which males move between different female groups.

Male and female Asian elephants (*Elephas maximus*) live in different kinds of societies. Females are philopatric, remaining in their natal clan as part of a fission-fusion society (see Nandini *et al*. 2018), while males gradually disperse away from their natal groups after they attain puberty (Desai and Johnsingh 1995) and subsequently spend most of their adult life alone, only temporarily associating with other males and female groups (McKay 1973, Daniel *et al*. 1987, Keerthipriya *et al*. 2018). Females may reproduce from the age of about 10 years (Nandini *et al*. 2018) but are sexually receptive only for a few days (Eisenberg *et al*. 1971) every four to five years because of extended periods of gestation and nursing. Therefore, competition amongst adult males for access to females is expected to be intense.

Musth is a rut-like phenomenon seen in the males of Asian elephants (Eisenberg *et al*. 1971, Jainudeen *et al*. 1972a) and African savannah elephants (Poole and Moss 1981, Hall-Martin 1987).Musth in the Asian elephant is characterised by temporal gland secretion and, sometimes, urine dribbling, and is associated with an increase in the level of serum testosterone and aggression towards conspecifics (Jainudeen *et al*. 1972a,b). Musth occurs annually but individual males may exhibit musth at different times of the year and reproduction is not restricted to the musth period. The timing and duration of the musth period, and the ranging during the musth period is expected to be a balance between the competition the male faces (which will affect his future reproductive success, through risk of injury) and the number of mating opportunities currently available (Rasmussen 2005, Poole et al. 2011). As pointed out by Fernando *et al*. (2008), physiological and behavioural characteristics of musth are well known in Asian elephants (for example, Jainudeen *et al*. 1972 a,b, Rasmussen *et al*. 2002, Rasmussen and Greenwood 2003), largely from studies of captive elephants, but little data exist on musth in this species from the wild. It has been speculated that musth in Asian elephants may even be functionally different from that in African elephants (Fernando *et al*. 2008).Not surprisingly, given the ~7.6 million years of divergence between *Loxodonta* and *Elephas-Mammuthus* (Rohland *et al*. 2007), there are sex-based differences in testosterone concentrations from temporal gland secretions in the Asian but not African savannah elephants, and some biochemical compositional differences in temporal gland secretions between musth males in the two species (Rasmussen *et al*. 1996). African savannah elephant males have also been found to exhibit a distinct sexually active, nonmusth state (when they associate with female groups and have increased androgen levels), and a sexually inactive, nonmusth state, apart from the sexually active, musth state (characterised by urine dribbling, aggression, and increased androgen levels; Ganswindt *et al*. 2005, Rasmussen *et al*. 2008a). No such distinction in sexual activity during the nonmusth period has been shown in Asian elephants. Further, in Asian elephants, the physiological and behavioural correlates of musth among younger males have been found to be different from those of older musth males (Rasmussen *et al*. 2002, Rasmussen *et al*. 2005). Given these differences, we wanted to examine some aspects of musth in a free-ranging Asian elephant population.

Previous studies had suggested that Asian elephant males come into musth sporadically from around the age of ten years and more regularly after the age of 30 years (Jainudeen 1972a, Desai and Johnsingh 1995), and that older males were more likely to be sighted in musth (Daniel *et al*. 1987, Chelliah and Sukumar 2015). However, there is scant data overall on the age distribution of musth males based on identified elephants. Therefore, we first wanted to find out 1) *how male age affect musth status*.

When Asian elephants enter musth, they may adopt a roving strategy in order to search for oestrous females over large distances (see Fernando *et al*. 2008) and/or a conditional strategy where younger males obtain a temporary reproductive advantage over older males, both of which have been proposed in the African savannah elephant (Hall-Martin 1987). Male elephants in India are thought to show locational dispersal, in which males not only disperse from their natal clans but also from their natal home ranges to new locations (Vidya and Sukumar 2005, Vidya *et al*. 2005). However, once in a new location, males may further extend their ranging during musth in order to search for receptive females. If musth were a roving strategy, a greater proportion of (older age-class) new males that entered a monitored area would be expected to be in musth rather than not in musth. Subadult males entering the area as part of locational dispersal might, however, not tend to be in musth. Similarly, males previously seen in nonmusth status in the study area may often not be sighted in the study area during their musth periods. Therefore, we wanted to find out 2) *whether there was a difference in the turnover rates of musth and nonmusth males and whether new males that entered the study area were more likely to be sighted in or out of musth*. If musth were to provide a temporary advantage to younger males (as males can grow indefinitely, resulting in older males being larger and more capable of dominating younger males), being in musth would be expected to increase the access of younger males to female groups. Younger males would then be expected to spend a disproportionately greater proportion of their musth time than their nonmusth time in female presence, compared to older males.

Musth, like rut, is expected to increase male association with females, and musth males were observed to associate with female groups to a greater extent than nonmusth males in Mudumalai in southern India (Desai 1987) and in Kaziranga in northeastern India (Chelliah and Sukumar 2015). In our study population, we had found that the proportion of time adult males spent with females was not related to the male’s age (Keerthipriya *et al*. 2018). Therefore, we wanted to find out whether this was also true of musth males of different ages. It is possible that older males might secure more mating opportunities than younger males as expected (but not known in our population) either by virtue of them spending more time than younger males did with females when they were in musth (and spending less time than younger males did when not in musth) or by being more effective while spending the same amount of musth time with females as younger males. In order to examine this and whether younger males obtain a temporary advantage over older males in meeting females (see paragraph above), we wanted to find out 3) *whether musth affects male associations with female herds and, if so, whether this was dependent on male age*.

Musth in Asian and African savannah elephants is considered an honest signal of male condition and an intent to male conspecifics as it is expensive to maintain and can adversely affect body condition (Jainudeen *et al*. 1972a, Poole 1989a, Ganswindt *et al*. 2005). In the Amboseli population of African savannah elephants, older/larger males were expected (Poole 1989a, Wyse et al. 2017) and observed (Poole et al. 1989a) to enter musth when mating opportunites were maximum, while medium sized males temporally separated their musth form larger males, to avoid competition. High-ranking musth males were found to suppress musth amongst low-ranking males in the African savannah elephant, resulting in low-ranking males being found in musth significantly more frequently in the absence of higher ranking musth males (Poole 1989a). Older musth males avoided each other through spatiotemporal separation of musth (Poole 1989a). In the Asian elephant population around the Kabini reservoir in southern India (see Methods), it had been previously noted anecdotally that several males came into musth at the same time, with apparently no aggression between them (Vidya and Sukumar 2005). Therefore, we wanted to examine 4) *how musth status affected the time males spent in all-male groups and whether female presence affected musth male associations*. We also wanted to find out 5) *whether musth status and age affected the spatiotemporal distribution of males*.

Methods

Study area and field data collection

We carried out the study from March 2009-August 2016 (although we could not sample during a large part of 2010 due to permit issues) in Nagarahole (11.85304°-12.26089° N,76.00075°-76.27996° E, 644 km^2) and Bandipur (11.59234°-11.94884° N, 76.20850°-76.86904° E, 872 km^2) National Parks and Tiger Reserves, in southern India. The two parks primarily comprise dry and moist deciduous forests and harbour a high density of elephants (AERCC 2006). The backwaters of the Beechanahalli dam on the River Kabini separate the parks and form large, open areas with abundant grass and access to water during the dry season (see Nandini *et al*. 2017). We drove along pre-selected routes (see Nandini *et al*. 2017) from ~6:30 AM till ~5:45-6:45 PM, depending on field permits, and aged, sexed, and individually identified elephants that were encountered based on various natural physical characteristics (see Vidya *et al*. 2014). Individuals were classified based on age as calves (<1 year old), juveniles (1-<5 years old), subadults (5-<10 years old for females and 5-<15 years old for males), and adults (>=10 years old in the case of females and >=15 years old in the case of males). Adult males were grouped into age classes of 15-30 years(young males) and 30+ years (old males) as these age classes had been found to have distinct associations (Keerthipriya *et al*. 2018). We recorded the musth status of males over 10 years old. We classified males with temporal gland secretion and/or urine dribbling as musth males and those with no temporal gland swelling, temporal gland secretion or urine dribbling as nonmusth males (Supplementary material 1). Males that were too far away (>150-200 m) to evaluate properly and those that had slight temporal swelling but no secretion or urine dribbling were classified as being of unknown musth status (Supplementary material 1).A musth period refers to the duration that a male remained in musth during a year (as musth occurs annually). We also noted down associations between males and whether the associations occurred in the immediate presence or absence of females. Adult males were said to associate in female presence if they were both within 10m (easy physical reach) of the same female group. Males were considered to associate in female absence if they fed within about 50 m of each other and there were no females nearby (Keerthipriya *et al*. 2018).

Data analysis

1) Effect of age on musth

In order to examine how age affected the probability of a male being sighted in musth, we used a generalized linear mixed-effects model with musth status as a binomial dependent variable (0 if a male was not in musth and 1 if he was in musth; males of unknown musth status were excluded from the sighting data),age of the male on that day as a continuous predictor variable, and male identity as a random factor. We used all identified males who were ten years old or older for this analysis and each male’s musth status was written once a day (on the days he was sighted and his musth status determined). The analysis was carried out using the *fitglme* function in MATLAB R2011a, with a binomial distribution for the dependent variable, logit link function and Laplace estimation method, and the model was fit using maximum likelihood.

2) Turnover rates of musth and nonmusth males and comparison of ages and occurrence of musth among resident and new males

We compared the cumulative distributions of musth and nonmusth males seen across years from 2011-2016 using the Kolmogorov-Smirnov two sample test (Sokal and Rohlf, 1981, pp. 440-445). If musth were a roving strategy, we would expect the turnover rates of musth males to be higher than that of nonmusth males. We used males over 10 years old for this analysis. We also used the same dataset to compare the age-class composition of identified males sighted till the midpoint of the study period (01-Dec-2012), referred to as ‘resident males’, with that of males sighted and identified for the first time after the midpoint of the study (called ‘new males’). Males were divided into three age-classes, 10-15, 15-30, and 30+, and a 2x3 *G*-test of independence carried out to compare the age-class structures of resident and new males (see Sokal and Rohlf 1981). If the new males mostly included males who had recently dispersed, we expected a larger number of the youngest age-class males among the new males. Alternatively, if new males included both young males who had recently dispersed and old males searching for mating opportunities, we expected the age-class composition of new males to include young and old males, but also expected a higher proportion of (old) musth males among the new males when compared to the resident males. We compared the frequencies of males seen in musth and not in musth among resident and new males by performing a *G*-test (likelihood ratio test) of goodness of fit (Sokal and Rohlf 1981). The null hypothesis was that the same proportion of musth males would be found among the new males as in the resident males, and the alternate hypothesis was that a higher proportion of musth males would be found among the new males than among the resident males.

3) Effect of musth on associations with females

Adult males could spend their time in different group types – mixed-sex groups, all-male groups with adult males, and alone (without other adult males or female groups). In order to find out whether musth affected associations with females, we calculated the proportions of times (out of the total number of minutes they were seen in or out of musth) that individual adult musth and nonmusth males spent with female groups. The logit transformed proportions of time spent by individual males with female groups were compared between males of two age-classes (15-30 and 30+ years) and different musth statuses using a factorial ANOVA (with musth status and age-class as fixed factors). We used males seen on three days or more in that musth status for the ANOVA.

In order to find out whether musth enabled greater male association with females through the number of females that males had access to, we also compared the group sizes of female herds that musth and nonmusth adult males of the two age-classes visited (weighted by the number of minutes they spent with that group). Group size was measured as the number of adult females (above 10 years of age) and a factorial ANOVA with musth status and age-class as fixed factors was used to compare group sizes.

4) Effect of musth on the time spent in all-male groups and the effect of female presence on musth male associations

In order to find out how musth status affected adult male associations, we calculated the proportion of time (out of the total time that the male was sighted in that musth status) that individual musth and nonmusth males spent with other adult males in all-male groups. As before, males who were seen on three different days or more in that musth status were used. The logit transformed proportions of time spent in all-male groups were compared across male age-class and musth status using a factorial ANOVA in Statistica 7 (StatSoft, Inc. 2004).

We additionally examined the time adult musth and nonmusth males of different age-classes spent with one another in the immediate presence and absence of females. Thus, we measured, separately in female presence and absence, the number of minutes spent together by males of the four combinations of age-class (15-30 and 30+ years old) and musth status (in musth and not in musth). We used the sampled randomisation test (Sokal and Rohlf 1981, pp. 791-794) to compare the differences (in time spent together by the relevant categories of males) between female presence and absence, between the observed and randomised datasets. We ran 10,000 randomisations wherein the sightings (represented according to their duration in minutes) in which musth males were present (either in female presence or in female absence) were redistributed randomly to female presence or female absence, conserving the number of minutes the musth males were seen in the two categories. The number of minutes spent by young (15-30 years) and old (30+ years) musth males with young and old nonmusth males were compared between the observed and randomised datasets. As two musth males were sighted together only twice during the entire study period, they were not used in these analyses, and only musth-nonmusth male associations were analysed.

5) Effect of musth status and age on the spatiotemporal distribution of males

Apart from associations themselves, during which males were present within about 50 m of each other, we also wanted to investigate possible spatial avoidance between adult males based on their musth status and their relative ages. We used a subset of data from three forest ranges (D.B. Kuppe, Gundre and Antharasanthe) in the study area, which are adjacent to each other and are near the Kabini backwaters. We divided the field days sampled into one-hour time slots and calculated the pairwise distances between all pairs of adult males sighted in the same slot, using the GPS coordinates obtained during the sighting. There were some field days when sighting data were collected by two different groups of observers sampling in these ranges but taking different routes. On these days, we only used the sightings observed by one group of observers and chose the dataset that included the greater number of adult males. The distances between adult males were classified based on the identity of the two males and the combination of their musth statuses (musth-musth, nonmusth-nonmusth and musth-nonmusth). The musth-nonmusth pairs were further classified, depending on the relative ages of the two males, into older musth-younger nonmusth and younger musth-older nonmusth pairs. For each pair of identified males, an average distance was calculated for each combination of musth statuses in which they were sighted together. These distances were compared across musth status combinations (both males in musth, both males nonmusth, older male in musth-younger nonmusth, and younger musth-older nonmusth) using an ANOVA in Statistica 7 (StatSoft, Inc. 2004). The data used in this analysis was obtained from the sighting data (used for associations) and were not systematically collected for this purpose.

In order to examine the randomness of the temporal distribution of musth across the study period, we compared the frequency distribution of the number of musth males (of all ages and across the study area sampled) sighted per day with a Poisson distribution in which the parameter was the daily probability of being sighted in musth. The expected and observed counts of the number of musth males sighted per day were compared using a *G*-test of goodness of fit (Sokal and Rohlf 1981).

All analyses, unless otherwise mentioned, were carried out in MATLAB (MATLAB R2011a; The MathWorks, Inc, 1984-2011, www.mathworks.com).

Results

We identified 157 unique males over ten years old during March 2009-August 2016 and these males were sighted in the field on 1057 days. Out of these, 138 unique males were sighted on 1029 days while not in musth and 50 unique males were sighted on 267 days in musth (see Supplementary material 2 for additional details). The 50 unique musth males were sighted in a total of 75 musth periods, that is, some males were sighted during multiple years when they were in musth. Only 2 males were sighted at least during five different years and they showed similarity in the timing of their musth periods across years (Supplementary material 3).

1) Effect of age on musth

Musth males varied in age from 14 to 56 years old and the percentage of males of various age-classes sighted in musth showed an increasing trend with increasing age-class (Figure 1). We found that age had a significant effect on musth status, with older males being more likely to be sighted in musth (generalised linear mixed effects model, binomial distribution, logit link function: *Estimated coefficient*=0.166, t_{stat}=6.270, *df*=4124, $P<0.001$). The number of unique males of different age-classes and the age-specific probability of being in musth are shown in Figure 2.

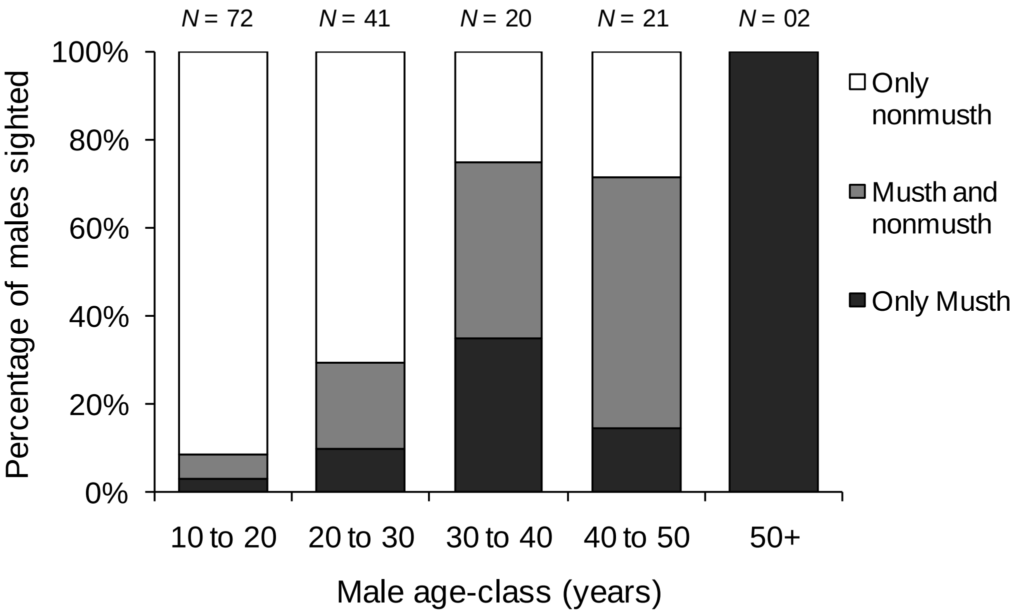


Figure 1. Percentage of unique identified males of different age-classes that were sighted only in musth, both in and out of musth, and only when not in musth. The numbers of unique males are shown above the bars. Each male is represented only once in this graph; therefore, the age-class to which he was assigned here was based on his age during the mid-point of the study. The total number of males here is 156 because one male that was sighted only once could not be unambiguously assessed for musth status.

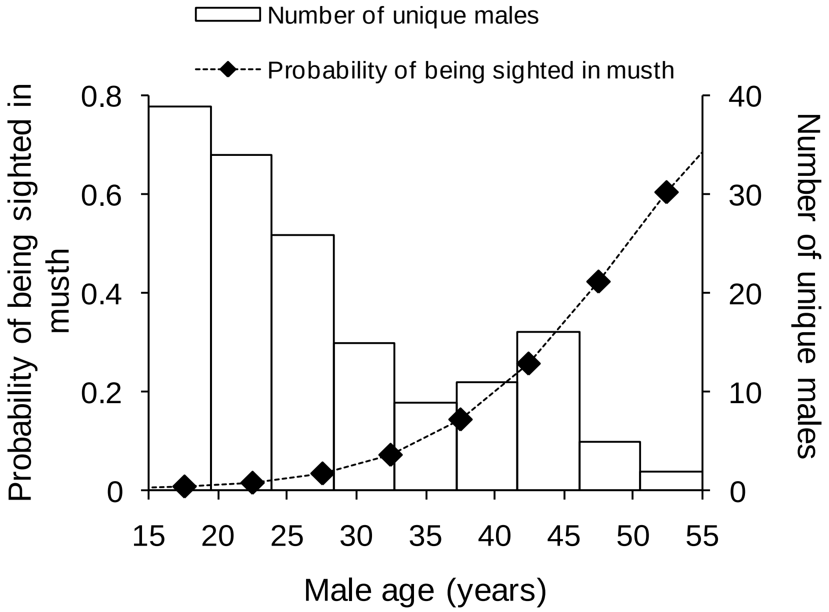


Figure 2. The number of unique identified males of different age-classes (shown as bars)

sighted in the study and the expected probability of being in musth in those age-classes (black markers). To obtain a single curve for the expected probability of being in musth, the logistic regression was repeated without male identity as a random factor. The probability of being seen in musth was represented by the equation $e^{(-7.3572+(0.1484)*age) / (1+exp(-7.3572+(0.1484)*age))}$.

2) Turnover rates of musth and nonmusth males and comparison of ages and occurrence of musth among resident and new males

The cumulative distributions of unique males in musth and not in musth were significantly different from each other (Kolmogorov-Smirnov two-sample test: D=0.321, P<0.005), with a higher turnover rate of musth males than nonmusth males (Figure 3). The age-class compositions of males were not dependent on whether they were resident or new males (2x3 G-test of independence: $G_{\text{corrected}}$=0.346, df=2, P=0.841, Figure 4). The percentage of males sighted in musth among the new males seemed to be higher than that among resident males, but the sample sizes were not large enough to obtain statistical significance (G-test of goodness of fit: G_{adj}=3.557, df=1, P=0.059). The percentages of males in musth were higher among the new males than among resident males in all three age-classes (see Figure 5). We also repeated the above analysis on different age-class compositions and percentages of males sighted in musth using four age-classes (10-15, 15-30, 30-40, and 40+) and did not find different results (see Supplementary material 4).

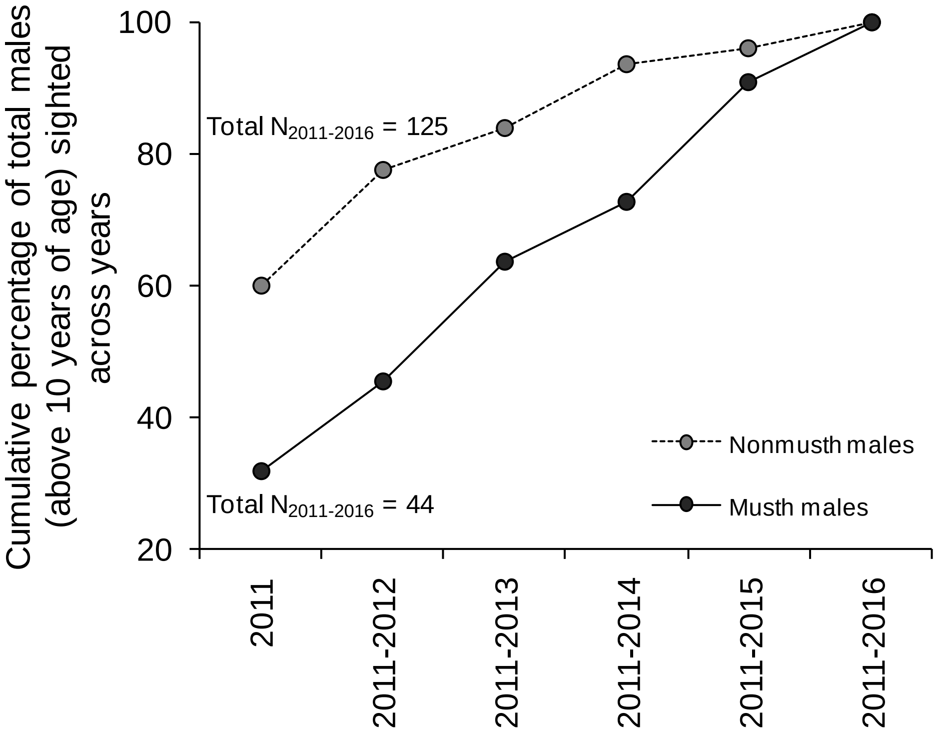


Figure 3. The cumulative percentage of musth and nonmusth males over ten years old (of the total numbers sighted from 2011 to 2016) across years.

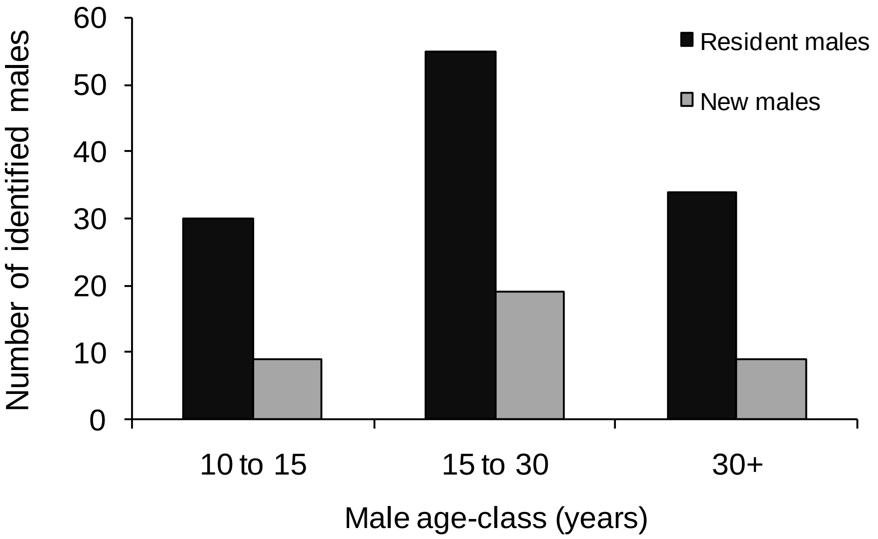


Figure 4. The number of unique resident (sighted before the midpoint of the study) and new (sighted first only after the midpoint of the study) males of different age-classes. The age-class compositions were not different across the two categories.

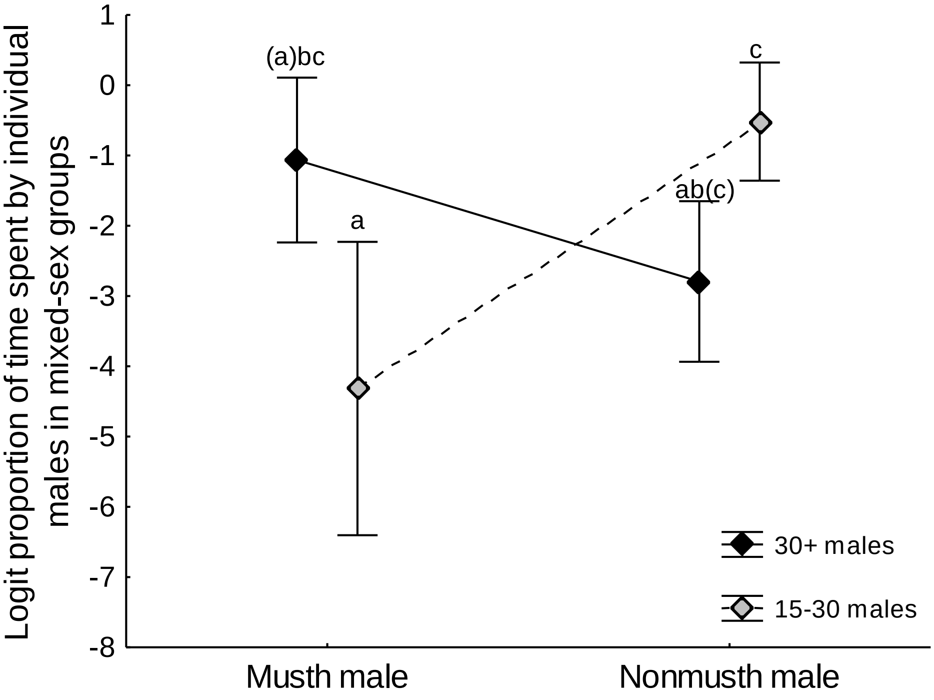
Figure 5. Percentages of unique resident and new males of different age-classes who were sighted in musth.

3) Effect of musth on associations with females

We found no significant main effect of age-class or musth status on the logit transformed proportions of time (out of the total time in that musth status) that individual males (seen on at least three days in that musth status) spent in association with female groups (Factorial ANOVA: age-class: $F_{1,78}$=0.488, P=0.487; musth status: $F_{1,78}$=2.193, P=0.143). However, there was a significant interaction between age-class and musth status ($F_{1,78}$=15.641, P<0.001). Pairwise Tukey's HSD tests showed that the proportion of time 15-30 year old males spent with females when in musth (average ± 1.96 SE: 0.118 ± 0.152) was significantly lower than that they spent with females when not in musth (average ± 1.96 SE: 0.440 ± 0.091) (P=0.007, Figure 6), while the proportion of time 30+ year old males spent with females when in musth (average ± 1.96 SE: 0.385 ± 0.129) was not significantly different from what they spent when not in musth (average ± 1.96 SE: 0.159 ± 0.080) (P=0.162, Figure 6). The proportion of time spent with females by musth 15-30 year old males was lower than that spent by musth 30+ year old males (P=0.041) and the proportion of time spent with females by nonmusth 15-30 year old males was higher than that spent by nonmusth 30+ year old males (P=0.011), but both these comparisons were not statistically significant after a flat Bonferroni correction (P<0.008 for 6 pairwise comparisons) was applied (Figure 6).

The results remained the same when we performed the ANOVA on the actual, non-transformed proportion values. Because of the unusual interaction effect observed, we repeated the ANOVA using another time cutoff and only the same males seen both in and out of musth and obtained similar results (Supplementary material 5). We also performed the analysis by further dividing the 30+ year old age-class into 30-40 and 40+ year old age-classes and found similar results (Supplementary material 5) but when only 30-40 and 40+ year old males were compared in the absence of the young males, there was a marginal effect of musth status also on the logit proportion of time spent in mixed-sex groups, with musth males spending a greater proportion of time in mixed-sex groups than non-musth males (40+ years old, in musth: average ± 1.96 SE proportion of time: 0.400 ± 0.170; 30-40 years old, in musth: average ± 1.96 SE: 0.367 ± 0.207; 40+ years old, nonmusth: average ± 1.96 SE: 0.145 ± 0.129; 30-40 years old, nonmusth: average ± 1.96 SE: 0.176 ± 0.091). Age-class did not have a significant main effect and there was no significant interaction between the two factors (Factorial ANOVA: age-class: $F_{1,35}$=2.534, P=0.120; musth status: $F_{1,35}$=4.252, P=0.047; age-class x musth status: $F_{1,35}$=0.455, P=0.504; Figure 6).

A.



B.

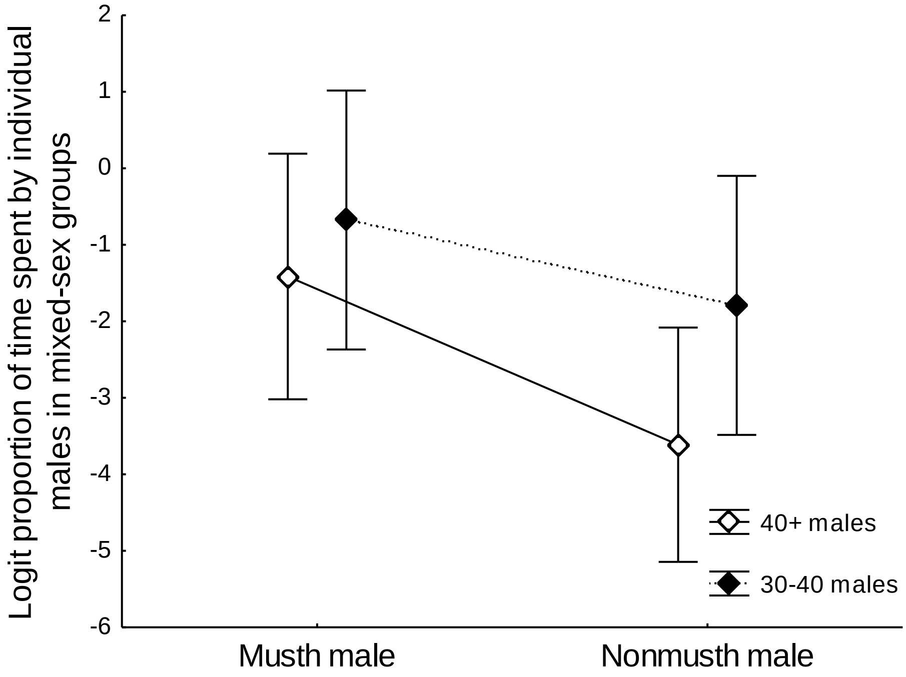


Figure 6. Logit transformed proportion of time (out of the time that male was sighted in that musth status) spent by individual adult males with female groups across age-classes and musth statuses. A) Two age classes, 15-30 and 30+ years, were used and $N_{30+\text{musth}}$=19, $N_{30+\text{non-musth}}$=20, $N_{15\text{-}30\text{musth}}$=6, $N_{15\text{-}30\text{non-musth}}$=37.Shared letters above the bars indicate no statistical significance in pairwise comparisons (a<b<c). Letters within parentheses include a flat Bonferroni correction of $P<0.008$ for six comparisons. B) The 30+ age class was further divided into 30-40 years and 40+ years. Error bars are 95% CI.

We found that musth status significantly affected the sizes of female groups with whom males associated (Factorial ANOVA: $F_{1,37634}$=74.597, $P<0.001$). There was no overall effect of male age-class ($F_{1,37634}$=0.056, P=0.814) but a significant effect of the interaction between age-class and musth status ($F_{1,37634}$=143.619, $P<0.001$) also on the sizes of female groups. The group sizes of female groups visited by 30+ year old males in musth (average ± SD female group size: 6.0 ± 4.35, N=7043 minutes) were significantly larger than those visited by 30+ year old males not in musth (average ± SD: 3.4 ± 2.49, N=6473 minutes) (Tukey’s HSD test: $P<0.001$, Figure 7). However, the sizes of female groups visited by 15-30 year old males in musth (average ± SD: 4.5 ± 1.69, N=261 minutes) were not significantly different from those visited by 15-30 year old males that were not in musth (average ± SD: 4.9 ± 4.05, *N*=23,861 minutes) (Tukey's HSD test: *P*=0.305, Figure 7). The sizes of female groups visited by 15-30 year old males when in musth or not in musth were higher than those visited by 30+ year old males when not in musth (*P*<0.001).

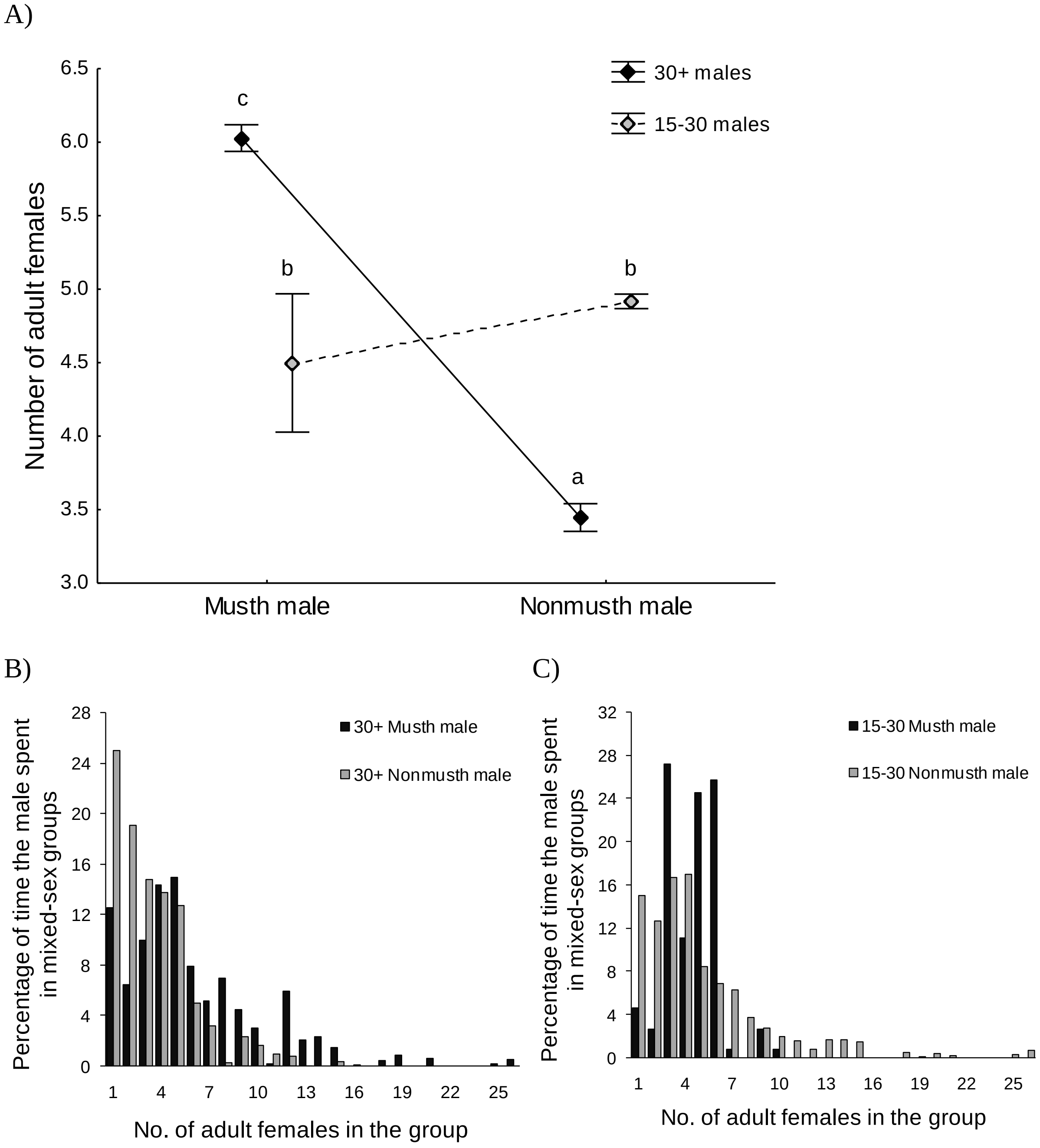


Figure 7. A) Group sizes (number of adult females) of female groups that musth and nonmusth males of different age classes associated with. Letters above the bars indicate statistical significance in pairwise comparisons (a<b<c). B and C) Percentages of time spent

by B) 30+ years old musth and nonmusth males and C) 15-30 years old musth and nonmusth males, in female groups of different sizes.

4. Effect of musth on the time spent in all-male groups and the effect of female presence on musth male associations

We found a significant effect of musth on the logit transformed proportions of time (out of the total time in that musth status) that individual males (seen on at least three days in that musth status) spent in all-male groups (Factorial ANOVA: $F_{1,78}$=22.373, P<0.001; Figure 8), with musth males spending a lower proportion of their time (average ± 1.96 SE: 0.026 ± 0.018) in all-male groups than nonmusth males (average ± 1.96 SE: 0.122 ± 0.044). Neither age-class nor the interaction between musth and age-class affected the proportion of time spent in all-male groups (Factorial ANOVA: age-class: $F_{1,78}$=1.862, P=0.176; interaction: $F_{1,78}$=0.020, P=0.889; Figure 8). The results remained the same when the ANOVA was performed on the non-transformed proportions and using another time cutoff (Supplementary material 5).

The sampled randomisation test to compare the time musth adult males of the two age-classes spent with nonmusth adult males of the two age-classes in female presence (total duration of musth male sightings in female presence=7304 minutes) and female absence (total duration of musth male sightings in female absence=9487 minutes) showed differences in male associations based on female presence/absence. We found that 30+ year old musth males spent more time with 30+ year old nonmusth males in female absence than in female presence but spent more time with 15-30 year old nonmusth males in female presence than in female absence. On the other hand, 15-30 year old musth males spent more time with 30+ year old nonmusth males in female absence than in female presence while they were never sighted associating with a nonmusth 15-30 year old male either in female presence or in female absence (Table 1). As mentioned earlier, two musth males were sighted together only twice during the entire study period.

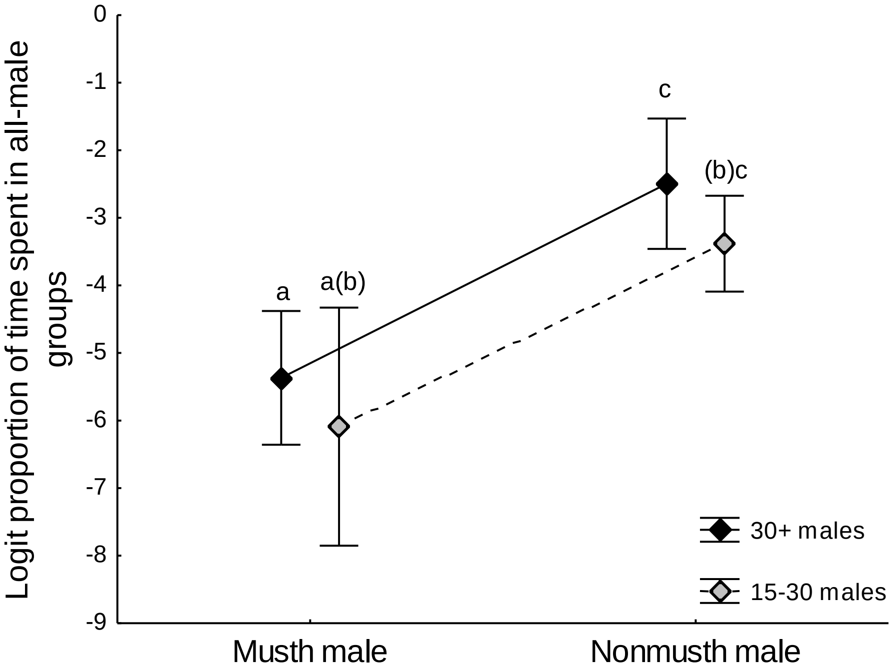


Figure 8. Logit transformed proportion of time (out of the time that male was sighted in that musth status) spent in all-male groups across age-classes and musth statuses. $N_{30+musth}=19$, $N_{30+nonmusth}=20$, $N_{15\text{-}30musth}=6$, $N_{15\text{-}30nonmusth}=37$. Error bars are 95% CI. Shared letters above the bars indicate no statistical significance in pairwise comparisons (a<b<c). Letters within parentheses include a flat Bonferroni correction of $P<0.008$ for six comparisons.

Table 1. Time spent together by identified musth males with identified nonmusth males. *P*= (no. of times difference$_{random}$≥difference$_{observed}$)/no. of randomisations (10,000). Significant *P* values are marked in bold.

Category	30+ year old musth male with 30+ year old nonmusth male (minutes)	30+ year old musth male with 15-30 year old nonmusth male (minutes)	15-30 year old musth male with 30+ year old nonmusth male (minutes)	15-30 year old musth male with 15-30 year old nonmusth male (minutes)
Female presence, observed data	12	678	0	0
Female absence, observed data	201	153	40	0
Female presence, permuted data, average (SD)	92.6 (7.22)	361.5 (13.93)	17.4 (3.14)	-
Female absence, permuted data, average (SD)	120.4 (7.22)	469.4 (13.93)	22.6 (3.14)	-
P value	**<0.001**	**<0.001**	**<0.001**	**-**

5) Effect of musth status and age on the spatiotemporal distribution of males

Within the subset of the study area examined, we found 17occasions (involving 12 unique pairs of adult males) when two adult musth males were sighted within a one-hour time slot, 54occasions (31 unique pairs) when a younger musth male and an older nonmusth male were sighted within the time slot, 477 occasions (204 unique pairs) when an older musth male and a younger nonmusth male were sighted within the time slot, and 2970 occasions (647 unique pairs) when two nonmusth males were sighted in the same time slot. We found no significant effect of musth status combinations on the average pairwise distance between males (one-way ANOVA: $F_{3,890}$=0.244, *P*=0.866; Figure 9). The same results were obtained when the analysis was repeated for two- and three-hour time slots also (*P*>0.05).

As mentioned above, we had sighted musth males on 267 days out of the 1057 days on which fieldwork was carried out (overall daily probability of sighting a musth male of 0.253). The maximum number of musth males sighted in a day was 3. The observed frequency distribution of the number of musth males seen per day was not different from Poisson expectation (*G*-test of goodness of fit: G_{adj}=5.926, *df*=3, *P*=0.115; Figure 10).

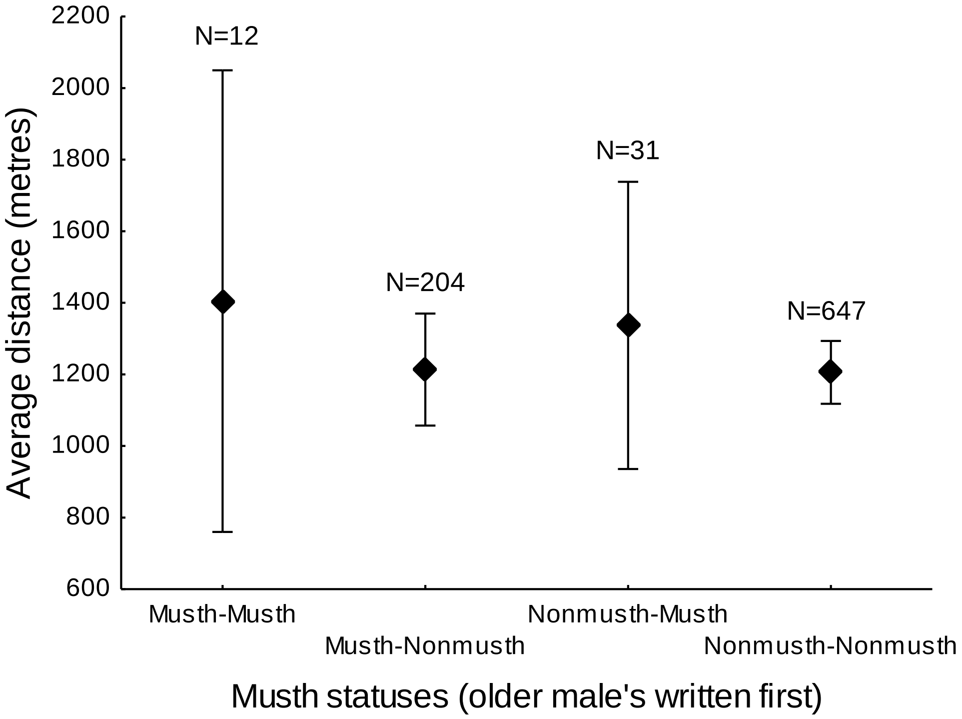


Figure 9. Average pairwise distances between males sighted in the same one-hour time slot, based on their musth statuses and relative ages.

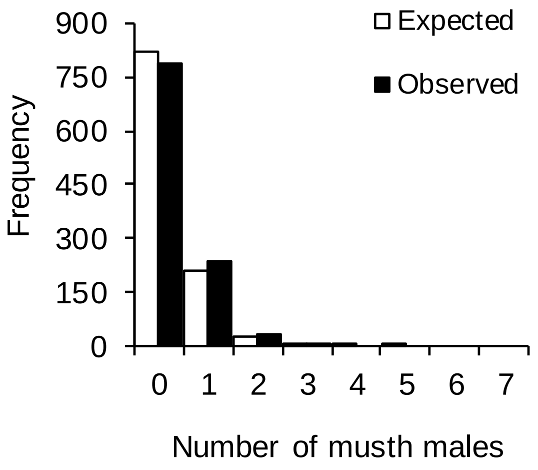


Figure 10. Observed and expected (Poisson) frequencies of number of musth males sighted

per day.

Discussion

This is one of the first studies that examines the phenomenon of musth using long-term data from a free-ranging, wild population of Asian elephants. Over our eight-year study period, we found that the turnover of musth males that were sighted was higher than that of nonmusth males. New males that entered the study area in the latter half of the study period also seemed more likely to be in musth than to not be in musth, although the sample sizes were not large enough for this trend to be statistically significant. These findings are consistent with the prediction that musth may be a roving strategy. They are also concordant with the findings of larger musth than nonmusth ranges of Asian elephants in Rajaji National Park in India and in Sri Lanka (Joshua and Johnsingh 1995, Fernando *et al*. 2008). Larger musth male ranges result in males whose nonmusth ranges are distant from the study area being sighted in the study area during musth alone. Conversely, there were also males in our study area that were sighted only when not in musth. Only 32 out of 156 males sighted in total and 23 out of 58 males seen on at least 10 days (whose home ranges were possibly centred around our study area) were seen both in and out of musth. Thus, musth may allow for secondary social-like dispersal (away from familiar individuals) from a home range in order to find more breeding opportunities, after the initial locational dispersal to a range different from the male’s natal home range. Although our study area and the larger landscape around it has high elephant density (AERCC 2006), roving behaviour may also allow musth males to find unrelated, if not only a greater number of, oestrous females. In African savannah elephants, musth ranges of individual males were larger than nonmusth ranges in some cases (Hall-Martin 1987 in Kruger National Park, Lee et al. 2011 in Amboseli National Park). However, some telemetry studies showed that, while musth males moved more directionally (Whitehouse and Schoeman 2003-Addo National Park) or had longer daily movement (Slotow and Van Dyk 2004- Pilanesburg National Park), the overall musth and nonmusth ranges were not different. Thus, larger musth than nonmusth range is not a consistent feature of male African savannah elephants.

The probability of males being sighted in musth increased with male age, similar to that seen in Kaziranga (Chelliah and Sukumar 2015), and Mudumalai National Parks (Daniel *et* *al*. 1987). This is also in agreement with the model proposed by Whitehead (1994), which suggests that, in species in which males adopt a roving strategy, younger males will delay competitive breeding and instead invest more in growth. In some other species in which males rove, young males are found away from breeding grounds (sperm whale- Best 1979), or are less likely to associate with females during the breeding season (polar bears- Ramsay and Stirling 1986), or are sexually active less often than older males (giraffe- Seeber et al. 2013), once again suggesting that in long lived species with roving males, older males participate more in competitive breeding.

We had also considered that musth might be a conditional strategy for younger males to obtain a temporary reproductive advantage over older males (Hall-Martin 1987), as males can grow indefinitely (Roth 1984, Sukumar *et al*. 1988), resulting in older males being larger and more capable of dominating younger males under most circumstances. If this were the case, we expected that young adult males (15-30 years old) might spend a greater proportion of their musth than nonmusth time in female presence, compared to older males. Instead, we found that young adult males spent a smaller proportion of time with female groups when in musth compared to when not in musth. They spent their time with similarly sized female groups when in musth compared to when they were not in musth. Thus, entering musth seemed to restrict, rather than augment, younger males' access to females. Musth advantage was found to outweigh body size/age advantage during dominance interactions in another Asian elephant population (Chelliah and Sukumar 2013), but we do not know the age-classes at which the younger males benefitted from musth in that study. We did not find an advantage of spending a greater proportion of time with females or spending musth time with larger female groups in the 30-40 year old males compared to the relatively older 40+ year old males either (Supplementary material 5). It would be interesting to examine dominance interactions between males in our study area, although such a musth advantage in young males during dominance, if found, would be puzzling in the absence of it translating into increased time spent with females or increased mating success. In fact, young males in our study had only a small probability of entering musth, in keeping with our findings above. If access to unrelated females is important, the initial gradual locational dispersal of males would allow young males to achieve this (Vidya and Sukumar 2005), while musth might facilitate older males to encounter more unrelated females through roving behaviour. Increased testosterone that characterises musth might even facilitate spatial memory/learning as observed in humans and rats (Driscoll *et al*. 2005, Spritzer *et al*. 2011). Secondary dispersal due to increased breeding opportunities with unrelated females has been seen in primates, black-tailed prairie dogs and lions, although these are species in which males transfer between groups (see Pusey 1992), as opposed to elephants, in which adult males are not attached to female groups.

In African savannah elephants (Poole 1989b) and another population of Asian elephants (Chelliah and Sukumar 2015), female elephants were observed to prefer musth males, rather than nonmusth males, as mates. We cannot rule out the possibility that, while musth serves as a roving/mate searching strategy for old males, it may simultaneously provide some advantage to the young males in terms of female choice, if they encounter a receptive female. Work on vocal communication in African savannah elephants showed that musth males showed more interest than nonmusth males towards calls of oestrous females (Poole et al. 1999), and that males paid more attention to calls of unfamiliar, than familiar, females (Stoeger and Baotic 2017). The roles of vocal communication and female choice in male reproductive behaviour and success remain to be explored in the Kabini population.

Increased association with female groups by musth than nonmusth males has been previously seen in African savannah elephants (Poole 1987, Rasmussen 2001) and Asian elephants (Desai 1987), although the latter was based on short-term study. We found the reverse pattern among young males and only a small positive effect of musth among old males in increasing the proportion of time spent with females. However, we found that old adult males associated with larger female groups when they were in musth compared to when they were not in musth, thereby increasing their chances of finding receptive females. The absence of bull areas and, hence, the lack of spatial separation of nonmusth males and female groups in our study area may contribute to the smaller musth-nonmusth difference in Kabini than that seen in the African savannah elephant. However, based on bulls that were more than 35 years of age, Poole (1987) had found that musth males spent more than 90% of their time in mixed-sex groups (while nonmusth males spent less than 20% of their time in mixed-sex groups), while old (30+) males in Kabini only spent 38% of their musth time (and 16% of their nonmusth time) in mixed-sex groups. The lack of bull areas cannot explain why musth males in Kabini spend a much smaller proportion of their time in mixed-sex groups. One possibility is that the (possibly food-resource based) group size restriction found in female groups in Kabini (Nandini *et al*. 2017) restricts the amount of time male elephants can continuously associate and feed with female groups, thus reducing their association time, although males may still remain in the vicinity of the female groups. Examining the number of receptive females available might also help better understand the time spent by the male elephants of Kabini with mixed-sex groups. It would also be interesting to see if the patterns we find hold in other Asian elephant populations.

We had previously found, by combining data from males of all musth statuses, that old adults avoided age-peers but tolerated young adults when they were associating with female groups (Keerthipriya *et al*. 2018). In the present study, we found that old adult musth males met young adult nonmusth males more often in female presence than in female absence in the current study, suggesting that the tolerance of young (nonmusth) males persisted when old adults were in musth also. Thus, young adult males, when not in musth, had access to female groups irrespective of the presence of older musth or nonmusth males. However, when they were in musth, they were never sighted with another adult nonmusth male in the presence of females. It is possible that young musth, but not nonmusth, males are perceived as a threat by older males and we do not know if young males were avoiding larger groups that might be visited by older males. We found that old and young males spent a smaller proportion of their time in all-male groups when in musth than when not in musth. This resulted in a greater proportion of time spent solitarily by young musth males, while older musth males slightly increased the proportion of time they spent with female groups (Figure 11).Given that young musth males have most of their reproductive tenure ahead of them, escalated contests would be costlier and, hence, it is possible that they avoid encounters with older males when they are in musth. Rasmussen *et al*. (2008b) found that African savannah males face a slump in their reproductive success around the age they start entering musth regularly, and speculated that this could be due to inexperienced young males still learning how to efficiently utilise musth. We cannot rule out the possibility that young males in Kabini may, similarly, be learning how to use musth, resulting in young musth males' decreased access to females, compared to their nonmusth counterparts. In the same population, Rasmussen (2005) observed that the number of females encountered by sexually active nonmusth males and musth males were not different, and that younger (<25 years) males were sexually active 55% of the time (but spent most of that time in sexually active nonmusth state), while older (40+ years) were sexually active 25% of their time (but were almost exclusively in musth).If young males in Kabini also spent time in sexually active nonmusth state, we would expect it to reduce the difference in female encounters between musth and nonmusth states but the reduction in female encounter while in musth is not explainedby young males being in a sexually active nonmusth state. In African savannah elephants, there have been observations of younger males avoiding auditory signals of older musth males (Poole 1999) and it has been suggested that musth in younger male African savannah elephants may be suppressed by older males (Poole 1989a, Slotow *et al*. 2000, Ganswindt *et al*. 2005). Subadult Asian elephant males have also been found to avoid olfactory signals of adult musth males (Rasmussen *et al*. 2002, Rasmussen and Greenwood 2003), although suppression of musth itself has not been studied.. Suppression of younger males by older males is seen in giraffes, which adopt a roving strategy (Bercovitch et al. 2006) and exhibit asynchronous, rut-like, sexually active periods, lasting for a few days (Seeber et al. 2013). It was observed that the presence of other males stimulated the frequency of sexually active behaviours among sexually active males of the oldest age-class, but suppressed it among sexually active males of the youngest age-class (Seeber et al. 2013).

Apart from suppression by older males, if musth is an honest, expensive (Jainudeen et al. 1972a) signal, it is possible that young, growing males simply do not possess the energy reserves to enter or sustain musth, resulting in younger male elephants in Kabini being sighted in musth to a smaller extent than older males (Jainudeen et al. 1972a). Teenage males in a study by Rasmussen et al. (2002) were found to exhibit ‘moda musth’, which was different from musth in terms of chemical composition and associated behaviour (see Rasmussen et al. 2002, 2005). Among the young males sighted in musth in our study, only 4 were below the age of 20 years and they were sighted only on one day each, making our findings on young musth males unlikely to be due to the effect of moda musth.

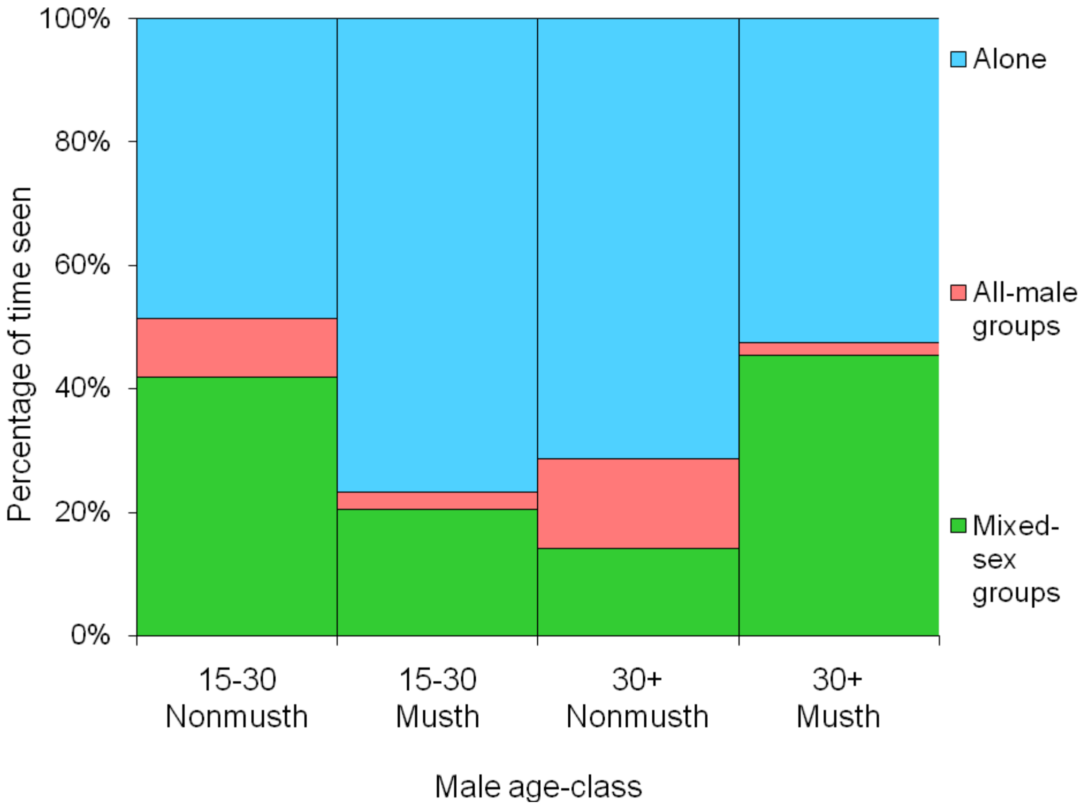


Figure 11. Percentage of time adult males of different age-classes were seen in three types of groups when they were in and out of musth.

Although there might be avoidance of musth males in immediate associations (within ~50m; for instance, two musth males were almost never seen together), we did not find significant differences in the pairwise distances (~1.2 km) of musth-musth, musth-nonmusth, and nonmusth-nonmusth males during 1-3-hour time slots. Therefore, there did not seem to be avoidance between musth and nonmusth males at this spatiotemporal scale. This is also consistent with anecdotal observations of several males coming into musth in the same general area without any apparent aggression (Vidya and Sukumar 2005). However, during our study, we only found a maximum of three males in musth on the same day. The numbers of musth males sighted across days were also not different from the random expectation. Thus, although only one male was in musth during 87% of the days when musth males were seen (see Supplementary material 7), it was due to the low occurrence of musth, rather than any temporal separation between musth males. Old musth males in Amboseli were found to avoid each other through spatiotemporal separation of musth

(Poole 1989a). However, sightings of musth males in that population seem to have been much higher than in ours. It is possible that poaching (males) for ivory in the 1970s and 1980s in southern India that has led to a skewed adult sex ratio in our study population (of about 1 male: 4-5 females; Gupta *et al*. 2016) has decreased male-male competition because of the smaller number males in the older age-classes.

African savannah elephant males have been thought to have a distinct nonmusth, sexually active period (Gandswindt *et al*. 2005, Rasmussen *et al*. 2008a), during which they associate to a greater extent with female groups and have higher levels of testosterone when compared to sexually inactive males. Young males have also been shown to employ alternate reproductive tactics such as sneak mating while not in musth with some moderate success (see Poole 1989b, Hollister-Smith *et al*. 2007, Rasmussen *et al*. 2008b, Poole *et al*. 2011). There are no distinct bull areas in our study area that could result in clearly separated spaces for sexually inactive and active males, and we have not seen distinct sexually active and inactive nonmusth states. However, from our results, it appears that there is an age-specific payoff for musth as a means to gain access to females in the Asian elephant, with musth being too expensive or unnecessary for younger males to invest in. The average group size of females that young males associated with when they were not in musth was higher than the average group size of females that old males associated with when they were not in musth. As mentioned above, young nonmusth males were also tolerated by old musth males in the presence of females. Therefore, in the context of mate searching, it appeared that it was a better strategy for young males to be out of musth rather than in musth. We have seen young nonmusth males mating with females, including one young male who mated with a young female in between two matings of the female by a very large, musth male, who had only walked a short distance (~200 m) away during the time. The young, nonmusth male remained with the female group when the large, musth male returned and did not receive any attention from the large male. Young males (15-20 years old) were also seen to sneak mate in another Asian elephant population (Chelliah and Sukumar 2015). Therefore, we posit that musth in Asian elephants is primarily a conditional strategy for older males to rove and mate search and increase their chances of finding a receptive female, while it may be advantageous in younger males only if it decreases the resistance of females to a mating attempt (if there is a female preference for musth, see Chelliah and Sukumar 2015). Further examination of female responses towards musth and nonmusth males of different age-classes in our study population will shed light on the advantage of musth in old and young males. Although we have used many years of data, we also acknowledge that this is a study based on visual observation of free-ranging animals, and is consequently subject to the limitations of opportunistic observational sampling. For instance, there may be differences in detection probability of different males/group types or they may be behaviours that are exhibited primarily at night, which could potentially bias the results observed. The results and the conclusions from the study are subject to these limitations. More controlled sampling of radiocollared animals might help in this regard.

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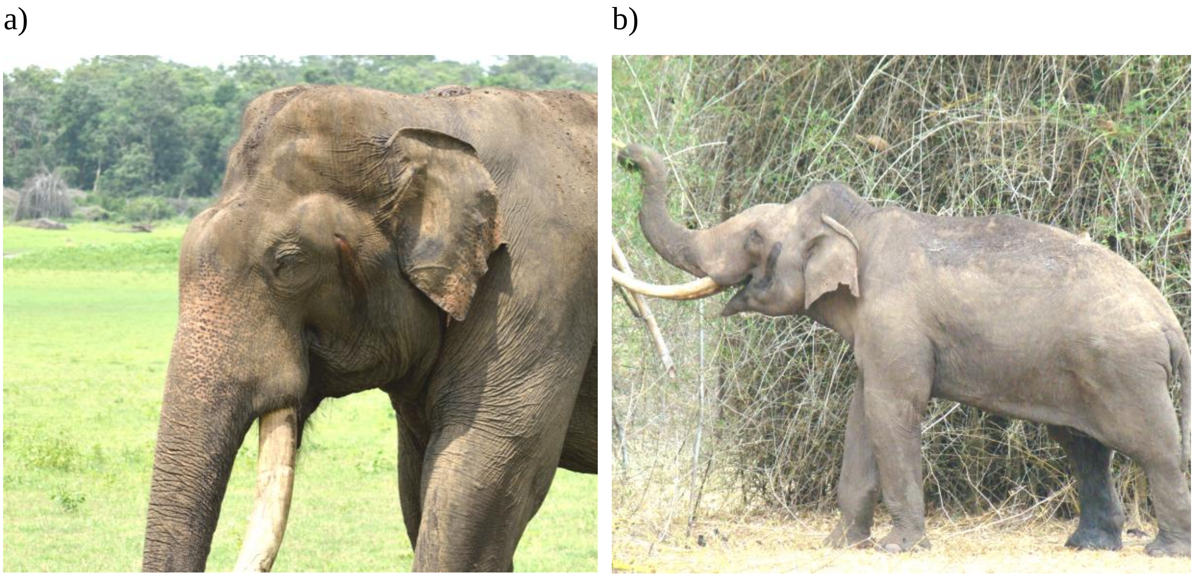
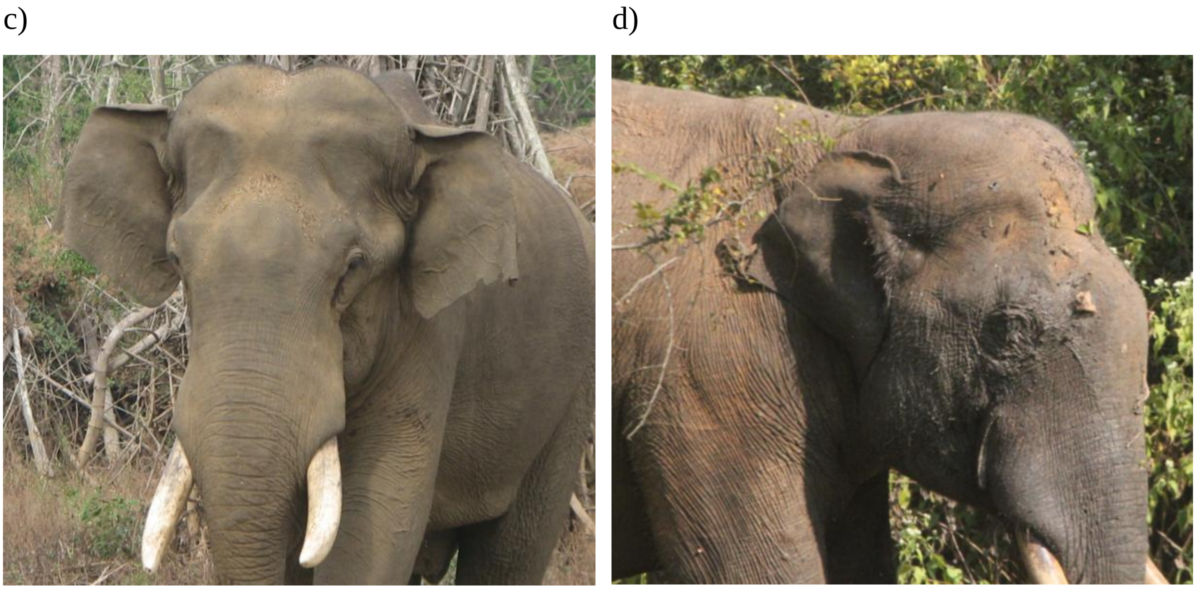
Supplementary material

Supplementary material 1. Males classified by musth status.

As mentioned in the main text, we recorded the musth status of males over 10 years old. We classified males with temporal gland secretion and/or urine dribbling as musth males and those with no temporal gland swelling, temporal gland secretion or urine dribbling as nonmusth males. Ganswindt *et al*. (2005) had found that African savannah bulls could start urine dribbling soon after locating a receptive female and stop the dribbling when a dominant musth male was encountered, but the temporal gland secretion persisted during that time. In Asian elephants also, urine dribbling is not a required criterion to assess a male as being in musth (noticeable temporal gland secretion was used as the criterion by Desai 1987). Males that were too far away (>150-200 m) to evaluate properly and those that had temporal swelling but no secretion or urine dribbling were classified as belonging to unknown musth status (see Figure 1 below).





Supplementary material 1, Figure 1. Males classified by musth status: a) musth male with noticeable temporal gland swelling and secretion, b) musth male with temporal gland swelling and secretion, and urine dribbling (seen as dark stains on the inner hind leg), c) nonmusth male with temporal depression, and d) male whose temporal gland was slightly swollen but was covered in mud and was assigned an unknown musth status.

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Supplementary material 2. Assignment of seasons and number of unique males across years.

The wet season was considered to begin one week after the date of onset of the southwest monsoon, as declared by the India Meteorological Department, and the dry season was considered to begin two weeks after the end of the northeast monsoon (see Nandini *et al*. 2017, Supplementary material 1). We calculated the percentage of identified males who were sighted in musth during the dry and wet seasons and found that season did not affect musth (Keerthipriya *et al*. under prep.). Therefore, we pooled all the musth data for analysis. The numbers of unique males seen in different years are shown in Table 1 below.

Supplementary Material 2, Table 1. Number of unique adult males of different age-classes sighted during different years.

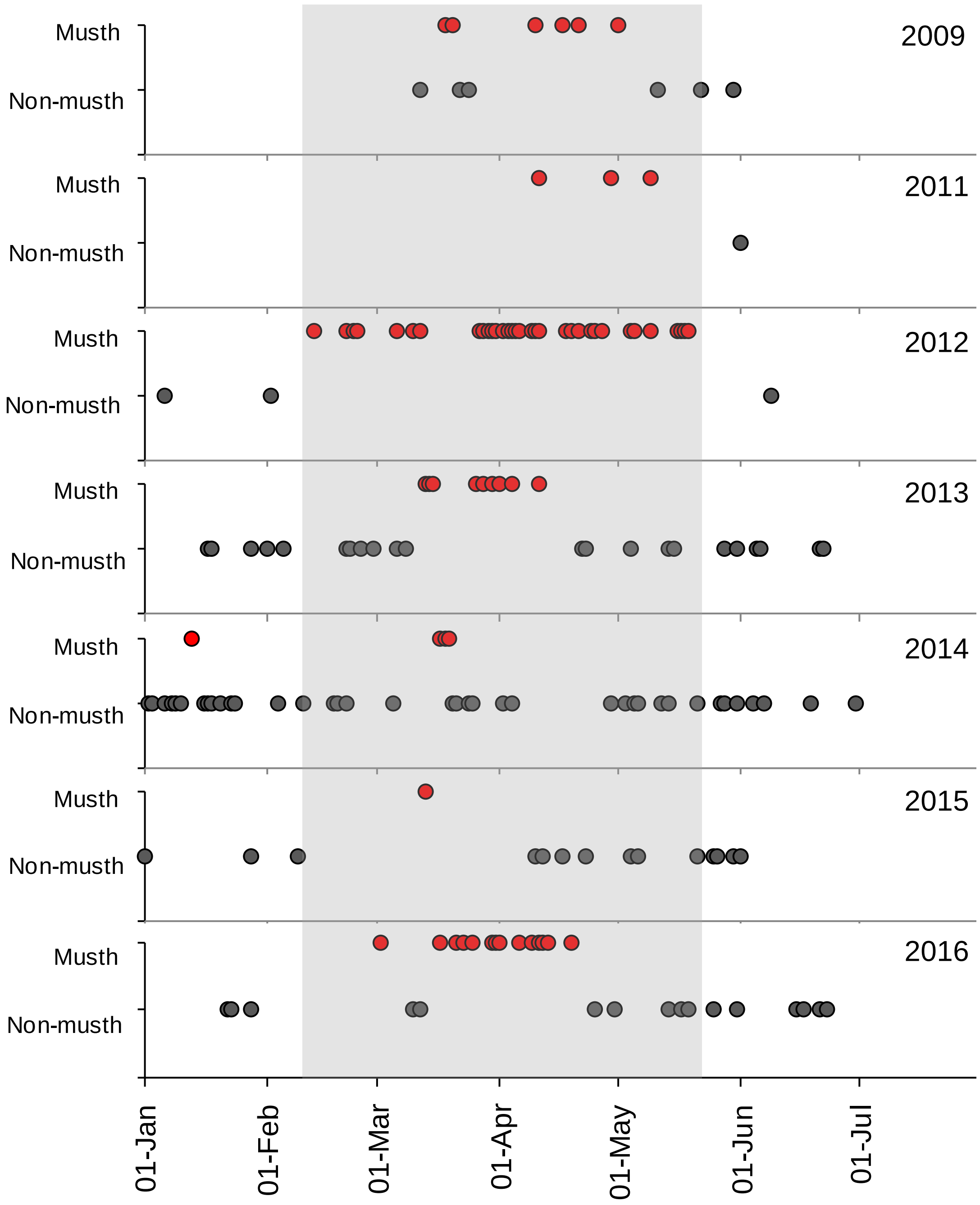
	No. of unique males	
Year	30+	15-30+
2011	26	35
2012	19	37
2013	21	30
2014	19	30
2015	11	25
2016	11	18

References

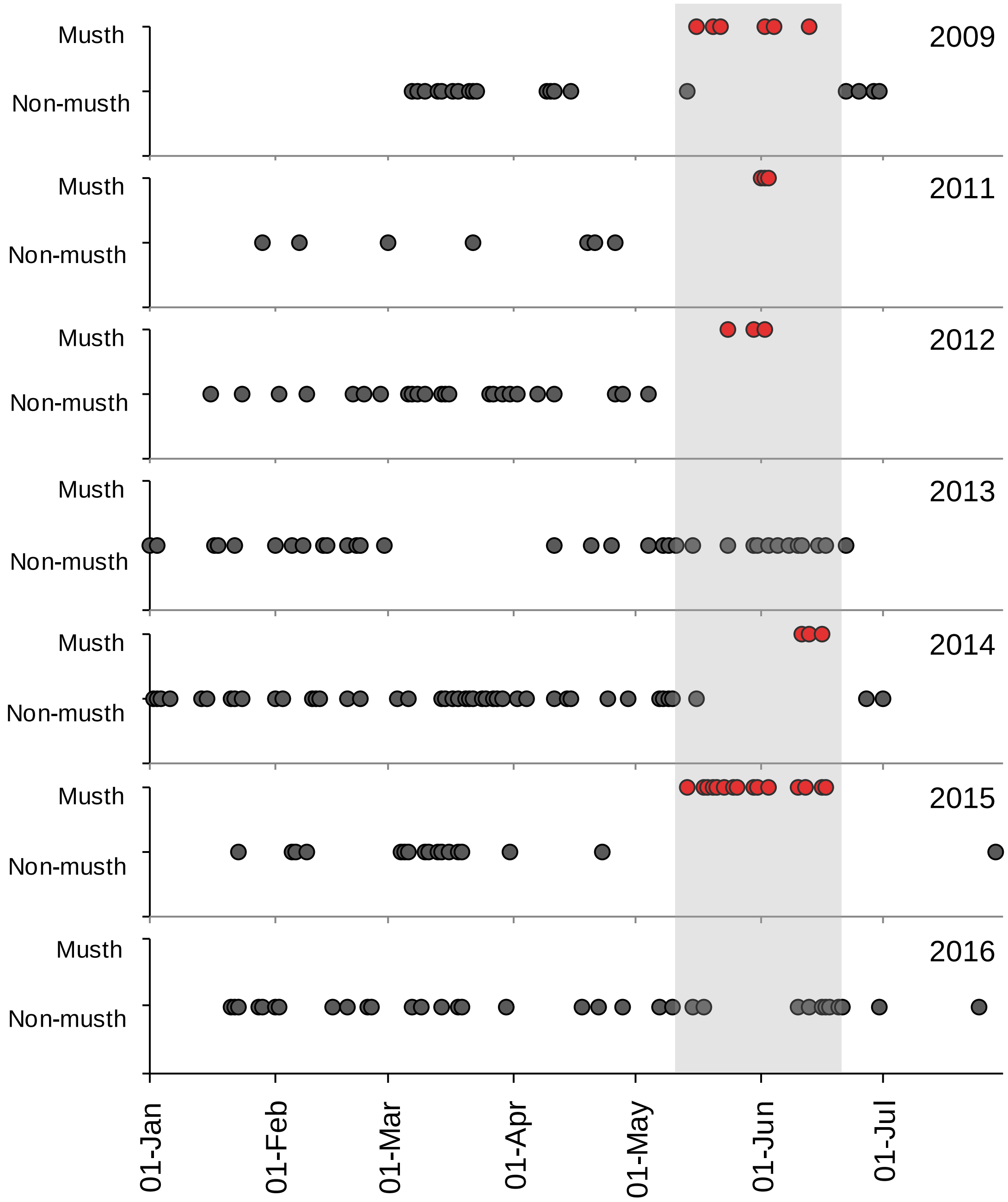
1. Nandini S, P Keerthipriya and TNC Vidya (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.

Supplementary material 3. The timing of annual musth periods of two commonly sighted males.

Horace (aged about 39 years at the midpoint of the study) and Longcross (aged about 41 years) were seen in musth during seven and five years, respectively. The number of days they were sighted in musth differed across years, so did their minimum duration of musth. However, the time of the year when each was sighted in musth remained somewhat consistent across years (see Figures 1 and 2 below). While Horace's musth periods occurred between the second half of February and the first half of May, Longcross' musth periods occurred later, from the second half of May till the middle of June. There were two years (2013 and 2016) when Longcross did not enter musth, possibly because of his body condition.



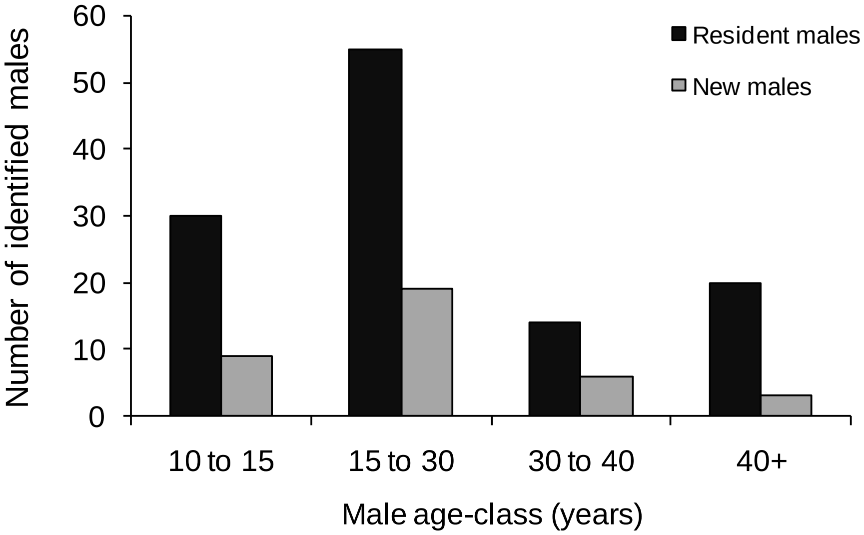
Supplementary material 3, Figure 1. Musth periods of Horace across different years. Red dots represent the days he was sighted in musth and the grey dots represent the days he was sighted when not in musth. The grey area represents the part of the year that the male was sighted in musth.



Supplementary material 3, Figure 2. Musth periods of Longcross across different years. Red dots represent the days he was sighted in musth and the grey dots represent the days he was sighted when not in musth. The grey area represents the part of the year that the male was sighted in musth.

Supplementary material 4. Comparison of ages and occurrence of musth among resident and new males.

In the main text, we had shown that the age-class compositions of males were not dependent on whether they were resident (seen before the mid-point of the study) or new (seen for the first time after the mid-point of the study) males. We had used three age-classes: 10-15 years, 15-30 years, and 30+ years. Since many of the males in musth were above 30 years old, we repeated the analysis using four age-classes – 10-15, 15-30, 30-40, and 40+ years – and found that the results remained unchanged. We found that age-class compositions of males were not dependent on whether they were resident or new males (2x4 *G*-test of independence: $G_{\text{corrected}}=2.159$, $df=3$, $P=0.540$, Figure 1).



Supplementary material 4, Figure 1. The number of unique resident and new males of different age-classes.

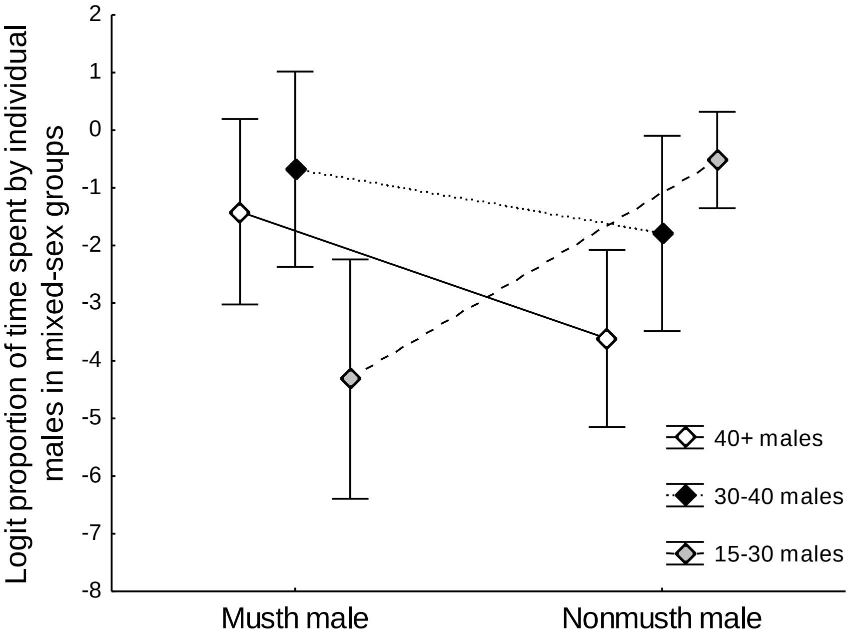
Based on the four age-classes again, the percentages of males in musth showed a trend of being higher among the new males than among resident males in all four age-classes (Figure 2).

Supplementary material 4, Figure 2. Percentages of unique resident and new males of different age-classes who were sighted in musth.

Supplementary material 5. Effects of musth on associations with females and males.

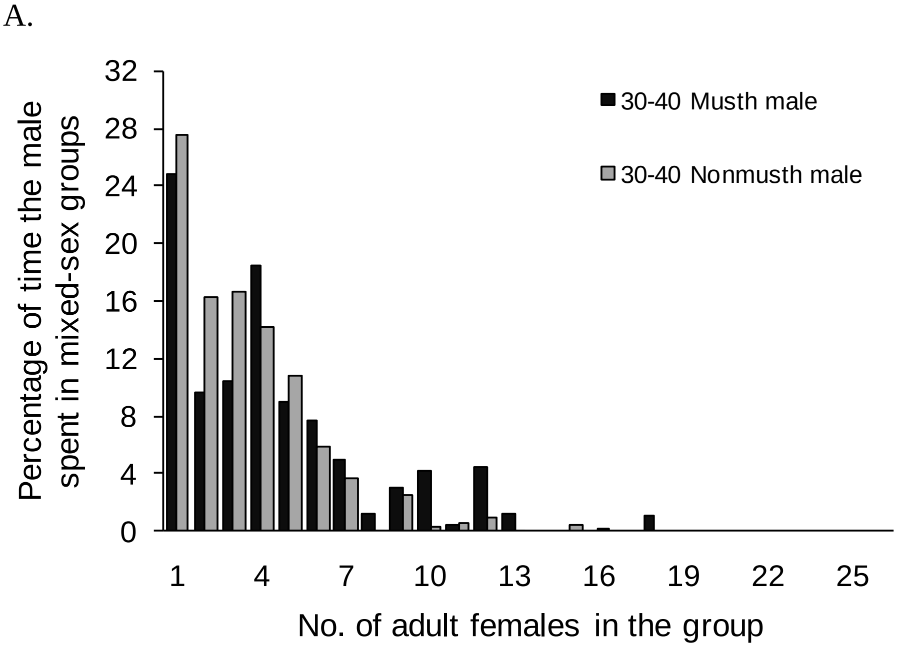
In the main text, we had shown no significant main effect of age-class or musth status on the logit transformed proportions of time (out of the total time in that musth status) that individual males (seen on at least three days in that musth status) spent in association with female groups, but a significant interaction between age-class and musth status. Pairwise Tukey's HSD tests had showed that the proportion of time 15-30 year old males spent with females when in musth (average ± 1.96 SE: 0.118 ± 0.152) was significantly lower than that they spent with females when not in musth (average ± 1.96 SE: 0.440 ± 0.091) (P=0.007), while the proportion of time 30+ year old males spent with females when in musth (average ± 1.96 SE: 0.385 ± 0.129) was not significantly different from what they spent when not in musth (average ± 1.96 SE: 0.159 ± 0.080). We repeated the analysis with only the same males who were seen both in and out of musth for 3 days or more (N_{30+}=11, $N_{15\text{-}30}$=5) and found similar results (Factorial ANOVA: age-class: $F_{1,28}$=0.995, P=0.327; musth status: $F_{1,28}$=2.025, P=0.166; interaction: $F_{1,28}$=5.123, P=0.031). We also repeated the analysis with males seen for 30 minutes or above($N_{30+\text{musth}}$=27, $N_{30+\text{nonmusth}}$=24, $N_{15\text{-}30\text{musth}}$=10, $N_{15\text{-}30\text{nonmusth}}$=54) instead of three days and found similar results (age-class: $F_{1,111}$=0.128, P=0.721; musth status: $F_{1,111}$=0.011, P=0.917; interaction: $F_{1,111}$=5.823, P=0.017).

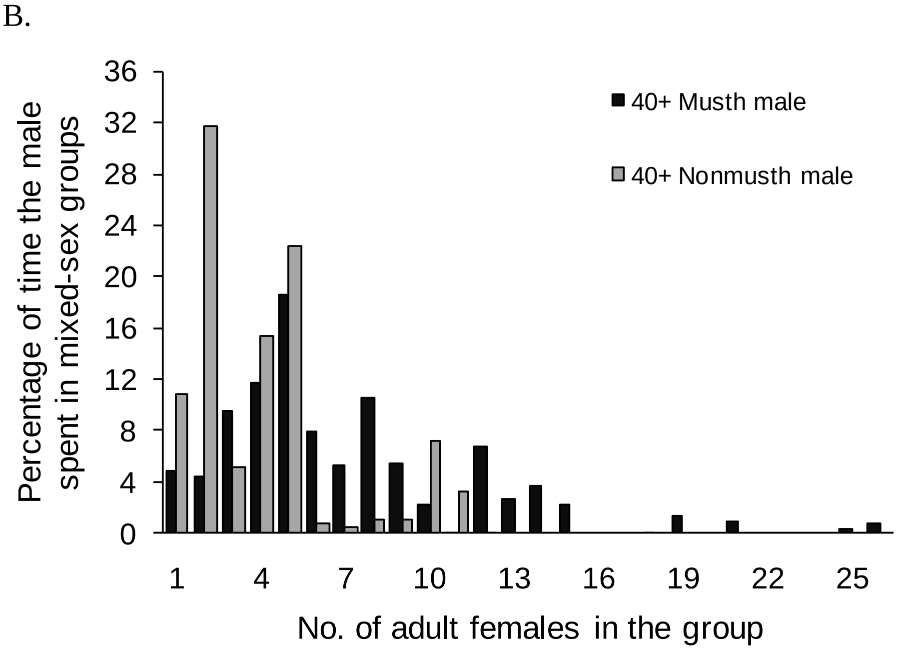
We then analysed males seen on 3 days or more, split into three instead of two age-classes: 15-30 years (N_{musth}=6, N_{nonmusth}=37), 30-40 years (N_{musth}=9, N_{nonmusth}=9), and 40+ years (N_{musth}=11, N_{nonmusth}=10). The logit proportion of time spent in mixed-sex groups were compared, with musth status and age-class as factors. The results were the same, with there being no significant main effect of either musth or age-class, but a significant interaction effect between the factors on the proportion of time spent in mixed-sex groups (Factorial ANOVA: age-class: $F_{2,76}$=1.469, P=0.236; musth status: $F_{1,76}$=0.059, P=0.808; interaction: $F_{2,76}$=8.042, P=0.001; Figure 1).



Supplementary material 5, Figure 1. Logit transformed proportion of time (out of the time that male was sighted in that musth status) spent by individual adult males with female groups across age-classes and musth statuses. Error bars are 95% CI.

In the main text, we had found that young males (15-30 years old) did not differ in the female group sizes that they associated with then they were in and out of musth, while old males (30+) associated with larger female groups when they were in musth compared to when they were not in musth. Here, we examined the group sizes of females that 30-40 year old males and 40+ year old males associated with separately. We found that the sizes (calculated as the number of adult females) of groups visited by 30-40 year old males in musth (average ± SD female group size: 4.400 ± 3.419, *N*=2717 minutes) were significantly larger than the sizes of groups visited by 30-40 year old males not in musth (average ± SD: 3.337 ± 2.410, *N*=5380 minutes) (Kolmogorov-Smirnov's two sample test: *D*=0.157, *P*<0.001, Figure 2). Similarly, the group sizes of female groups visited by musth males of the 40+ age-class (average ± SD female group size: 7.050 ± 4.549, *N*=4326 minutes) were much larger than those visited by 40+ year old nonmusth males (average ± SD female group size: 4.012 ± 2.713, *N*=1223 minutes Figure 2).

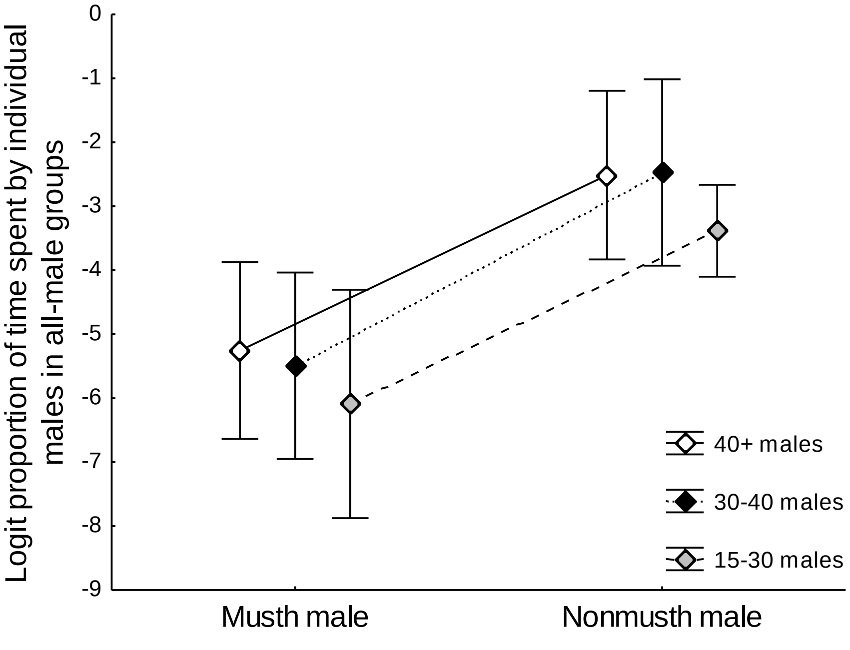




Supplementary material 5, Figure 2. Percentages of time spent by A) 30-40 year old musth and nonmusth males and B) 40+ year old musth and nonmusth males, in female groups of different sizes.

In the main text, we had also shown a significant effect of musth on the logit transformed proportions of time (out of the total time in that musth status) that individual males (seen on at least three days in that musth status) spent in all-male groups (Factorial ANOVA: $F_{1,78}$=22.373, P<0.001), with musth males spending a lower proportion of their time (average ± 1.96 SE: 0.026 ± 0.018) in all-male groups than nonmusth males (average ± 1.96 SE: 0.122 ± 0.044). Neither age-class nor the interaction between musth and age-class affected the proportion of time spent in all-male groups (Factorial ANOVA: age-class: $F_{1,78}$=1.862, P=0.176; interaction: $F_{1,78}$=0.020, P=0.889). We found similar results when the analysis was repeated using males who were seen for 30 minutes or more ($N_{30+\mathrm{musth}}$=27, $N_{30+\mathrm{nonmusth}}$=24, $N_{15\text{-}30\mathrm{musth}}$=10, $N_{15\text{-}30\mathrm{nonmusth}}$=54) (musth status: $F_{1,111}$=19.562, P<0.001; age-class: $F_{1,111}$=2.535, P=0.114; interaction: $F_{1,111}$=0.002, P=0.967).

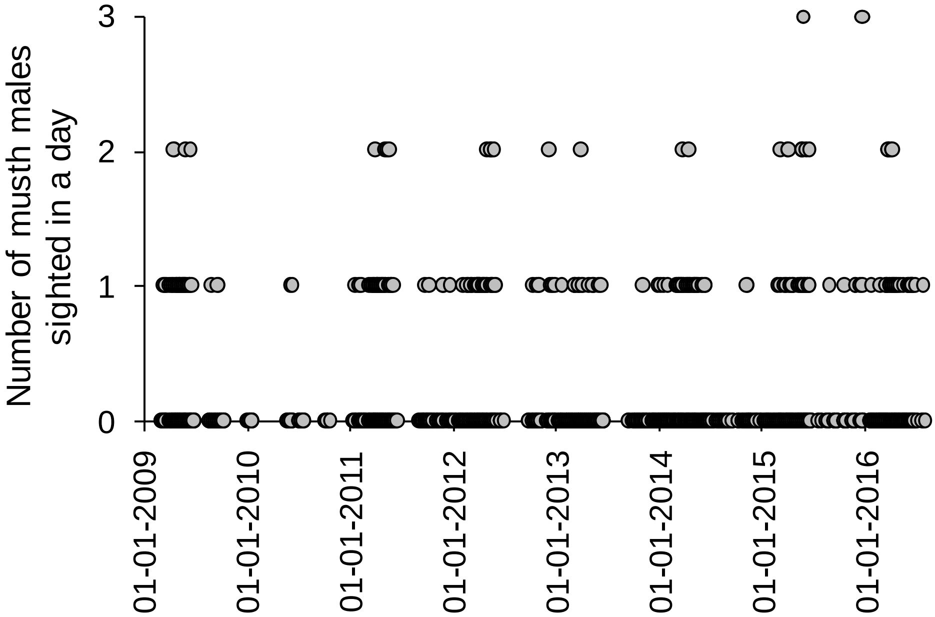
We also analysed males seen on 3 days or more split into three age-classes: 15-30 years (N_{musth}=6, N_{nonmusth}=37), 30-40 years (N_{musth}=9, N_{nonmusth}=9), and 40+ years (N_{musth}=11, N_{nonmusth}=10). The logit proportion of time spent in all-male groups were compared, with musth status and age-class as factors. Again, the only significant effect on the proportion of time spent in all-male groups was the main effect of musth status (Factorial ANOVA: age-class: $F_{2,76}$=0.921, P=0.403; musth status: $F_{1,76}$=24.542, P<0.001; interaction: $F_{2,76}$=0.029, P=0.971; Figure 3).



Supplementary material 5, Figure 3. Logit transformed proportion of time (out of the time that male was sighted in that musth status) spent in all-male groups across age-classes and musth statuses.

Supplementary material 6. The number of musth males seen on the same day.

We sighted 50 unique musth males on 267 different days (out of the 1057 days of fieldwork when any male was sighted). On 233 days (87.3%), there was only one male in musth, on 30 days (11.2%) two musth males were sighted on the same day and on 4 days (1.5%), we sighted three musth males on the same day. The figure below shows the number of musth males sighted on different days.



Supplementary material 6, Figure 1. The number of musth males sighted on the days when sampling was carried out.

CHAPTER 5

A Comparison of Male Population Age-Structure and Occurrence of Musth in the Kabini Elephant Population with Other Populations

Title: A comparison of male population age-structure and occurrence of musth in the Kabini elephant population with other populations

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Manuscript submitted, under review.

Author contributions

TNCV and PK conceived this work. PK collected most of the field data and carried out the analyses. PK and TNCV wrote the manuscript.

Abstract

We collected data on the population age-structure of male Asian elephants and the proportion of sightings of males of different age-classes that were seen in musth in Nagarahole and Bandipur National Parks (Kabini population) during 2009-2016. We compared these with previously published data from Mudumalai National Park and Kaziranga National Park studied by other groups of researchers. The Kabini population had a more skewed adult sex ratio than Kaziranga, but a similar adult sex ratio to Mudumalai when it was studied. However, the male population age-structure was similar between Kaziranga and Kabini while there was a greater proportion of very old males in Mudumalai compared to Kabini. We found the proportion of male sightings in which males were in musth was lower in Kabini than in both Kaziranga and Mudumalai. Thus, the occurrence or duration of musth seems to be influenced by the number of competitors in the area. However, low occurrence of musth due to habitat saturation cannot be ruled out presently. We also found that there was no difference in the frequency or ages of musth males across seasons or months in Kabini, whereas a lower frequency of musth males had been seen during the dry season in Mudumalai.

Keywords

Asian elephant, male age-structure, musth, seasonality, Nagarahole-Bandipur (Kabini), Mudumalai, Kaziranga.

Introduction

The Asian elephant (*Elephas maximus*) is an endangered species and occupies only about six percent of its historic range (Sukumar 2006). Humans have greatly impacted wild Asian elephant populations, through hunting for meat or ivory, and through capture for use in warfare, as a means of transport, or simply a status symbol (Sukumar 2003). In India, which holds the largest population of wild Asian elephants (Sukumar 2006) with around 26,000 to 28,000 wild elephants (Baskaran *et al.* 2011), capturing wild elephants has been regulated (with varying success) since the placing of the Asian elephant under Schedule I of the Wildlife Protection Act (1972) in 1977 (amendment). However, poaching for ivory has been a serious problem. Southern India, which has the largest Asian elephant population within India and globally (Baskaran *et al.* 2011), witnessed a drastic decline in its number of sub-adult and adult males due to ivory poaching (Menon *et al.* 1997, Menon and Kumar 1998, Menon 2002). Despite the CITES ban of international trade in Asian ivory in 1976, a spate of ivory poaching between 1977 and 1986 in southern India is estimated to have killed 100-150 tuskers annually during the period (pp.168, Sukumar 1989). The Indian Government also banned domestic trade in Asian ivory in 1986 and in all ivory in 1991. However, with a rumour of probable downlisting of some African elephant populations in 1997, poaching in India rose sharply again from 1996 onwards (Menon *et al.* 1997). An average minimum number of 36 tuskers were estimated to have been poached each year between 1991 and 2001 in southern India, with almost double that number poached during 1997 and 1998 (data compiled by the Asian Elephant Research and Conservation Centre, Bangalore, and Wildlife Trust of India, New Delhi). As only males carry tusks, ivory poaching in India has led to skewed sex ratios, with different sex ratios in different populations (Ramakrishnan *et al.* 1998, Arivazhagan and Sukumar 2005).

Changes in sex ratio and age-sex structure can affect fecundity (Sukumar *et al.* 1998, Ramakrishnan *et al.* 1998), social structure and various behaviours (Gobush *et al.* 2008, Ishengoma *et al.* 2008, Gobush *et al.* 2009, Sukumar 2006). Changes in sex ratio may also affect musth, which has not been examined previously. Musth is a rut-like state of male Asian (and African savannah) elephants. Males in musth show increased serum testosterone levels, temporal gland secretion, and, sometimes but not always, urine dribbling (Jainudeen *et al.* 1972a,b, Desai 1987). Males come into musth occasionally from the age of about ten years but the probability of coming into musth increases with age and males enter musth more regularly on an annual basis after they are over 30 years old (Jainudeen 1972a, Daniel *et al*. 1987, Desai and Johnsingh 1995, Chelliah and Sukumar 2015, Keerthipriya *et al*. 2018a). The ages of musth males, duration of musth, and paternity have been examined in populations of African savannah elephants with altered age-structures. When young, orphaned elephants were introduced into Pilanesberg (that did not have other, older elephants), males were seen to enter musth earlier than in other populations, to remain in musth for an unusually long duration, and to show aggression and attack rhinos. Musth duration was reduced and the attacks on rhino stopped after the introduction of six older males (Slotow *et al*. 2000). In Tarangire National Park that had been heavily poached, resulting in the age structure shifting towards younger animals, a majority of musth male sightings continued to be of males over 35 years old, and the remaining old males in the population rather than young males fathered the majority of offspring (Ishengoma *et al*. 2008). These studies suggest that the presence of older males might not give the younger males the expected advantage of coming into musth early when the population's age-structure was biased towards younger animals. However, this is expected to depend on the relative numbers of old and young males and the density of individuals, apart from the extent to which young males can be controlled by old males.

We, therefore, wanted to compare patterns of musth in a population of Asian elephants in southern India with those of two other populations in India that had been previously studied and had different sex ratios or age-structures (see Study area below). If the sex ratio was less skewed in a population, we expected to find a greater number of musth male sightings simply because of the greater number of males (and, therefore, male sightings) in the population. However, the proportion of male sightings in which males were in musth would remain the same. If the age-structure of the population was affected by poaching such that there were fewer old males, if old males came into musth more often than young males and one or a few males cannot suppress the others, there would be a greater proportion of male sightings with musth males. We also wanted to compare seasonality in musth, if any, across populations.

Methods

Study area

We carried out our field study in the Nagarahole (11.85304°-12.26089° N,76.00075°-

76.27996° E, 644 km^2) and Bandipur (11.59234°-11.94884° N, 76.20850°-76.86904° E, 874 km^2) National Parks and Tiger Reserves, southern India. Nagarahole and Bandipur lie on the two sides of the River Kabini and form part of the Nilgiris-Eastern Ghats landscape. The habitat primarily includes dry deciduous and moist deciduous forests. Because of a dam on the River Kabini, the area around the Kabini backwaters forms a large, open, grassy habitat for elephants and other herbivores to congregate during the dry season. The Nagarahole-Bandipur population centred around the Kabini (and henceforth called the Kabini population) has a high density of about ~1-2 elephants / km^2 (AERCC 2006). The sex ratio based on animals >=15 years of age in this population was 1 male: 4-5 females based on initial data (Gupta *et al*. 2016) and about 1 male : 3.1 females based on all females and males (>=15 years of age) identified till August 2016 (unpublished data, Kabini Elephant Project).

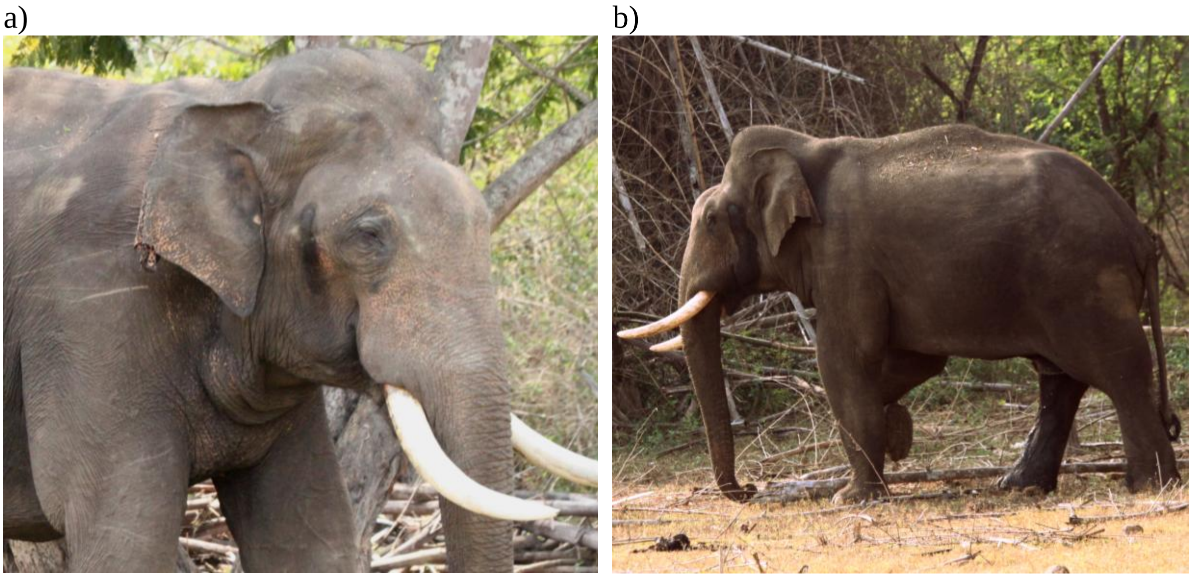
We compared data from the Kabini population with data collected previously by others in Mudumalai and in Kaziranga. Mudumalai Wildlife Sanctuary (when the data were collected; Mudumalai Tiger Reserve now) is also part of the Nilgiris-Eastern Ghats landscape and lies to the east of Bandipur. It has a range of vegetation types from dry thorn through deciduous forests to semi-evergreen forests. Elephant density in the park was ~1 elephant/km^2. Adult male numbers were seen to drop from 1986 to 1988, leading to an adult (>=15 years of age) sex ratio of 1 male : 3.1 females, in Mudumalai (Daniel *et al*. 1987). Kaziranga National Park is located in northeastern India, along the floodplains of the River Brahmaputra. The habitat in the park is primarily riverine, with grassland and semi-evergreen forest. Elephant density was about 1.2 elephants/km^2 in 2011 and the sex ratio of individuals >=15 years of age was 1 male : 2.3 females (KNP Forest Department 2008, 2011).

Field data collection

We collected field data in Nagarahole and Bandipur from March 2009-August 2016, although a large part of 2010 was not sampled due to permit issues. Sampling was carried out in a stratified manner, with greater intensity of sampling around the Kabini reservoir and decreasing intensity away from it in both directions (see Nandini *et al*. 2017). We drove along pre-selected routes (see Nandini *et al*. 2017) and sexed, aged, and individually identified elephants that we encountered. Individuals were placed in age categories as calves (<1 year old), juveniles (1-<5 years old), subadults (5-<15 years old in the case of males and

5-<10 years old in the case of females), and adults (>=15 years old in the case of males and >=10 years old in the case of females; see Nandini *et al*. 2018). Ageing of adults was carried out based on body and skull size, using semi-captive elephants of the forest department in the same area as reference (see Vidya *et al*. 2014). Males from the age of 5-20 years were placed in five-year age-classes and those above 20 years old, into ten-year age-classes, and all of them were assigned a probable date of birth based on (usually) the median age of the age-class and the date of first sighting. Adult males were also grouped into two broad age classes of 15-30 years and >=30 years for some analyses as these age classes were found to have different patterns of male-male associations (Keerthipriya *et al*. 2018b). Identification was carried out based on various natural physical characteristics (see Vidya *et al*. 2014).

Males that were at least 10 years old were assessed for their musth status and classified as being in musth if they had temporal gland secretion and/or urine dribbling and as nonmusth if they did not have either of these (Figure 1). For the purpose of musth status, sightings of males were counted once a day. Males, when sighted, were also classified as being solitary, being part of a mixed-sex group, or being part of an all-male group. A male was part of a mixed-sex group when he was within 10 m of a female group. Males were part of an all-male group if they fed within about 50 m of each other and there were no females in the vicinity.



c)

Figure 1. Male 'Horace' showing different musth statuses: a) in musth with temporal gland secretion, b) in musth with temporal gland secretion and urine dribbling (note the stained inside of the hind leg), c) not in musth. Males with temporal swelling but no secretion or urine dribbling or those that were wet or far away were classified as being of unknown musth status and not used for analyses.

Data analyses

Age structure of populations and age-class-specific proportions of musth male sightings

We compared the age-structure and age-class-specific proportions of musth male sightings in Kabini with those in Kaziranga based on data from Chelliah and Sukumar (2015), and with those in Mudumalai based on data from Daniel *et al*. (1987). Chelliah and Sukumar (2015) had provided the unique number of males of various age-classes that were identified in Kaziranga. We classified our data similar to theirs (based on male age at the midpoint of the study) and compared the age-structures of the two populations by performing a *G*-test of independence (Sokal and Rohlf 1981) on the numbers of unique males of various age-classes in the two populations. Data on the unique number of males of different age classes were not available for Mudumalai. Instead, we obtained the number of sightings of adult males of various age-classes in Mudumalai from Daniel *et al*. (1987) and compared them with those in the same age-classes in Kabini using a *G*-test of independence. As the number of sightings in Mudumalai was obtained from graphs in the paper (Daniel *et al*. 1987), they are approximate (but accurate within ± 2 units).

If the age structures were different across populations, it would not be correct to directly compare the numbers of musth males of different age-classes in the different populations. Therefore, we used the age-class-specific proportions of musth male sightings (total number of musth days of males of an age class divided by the total number of days when males of that age-class were seen) for comparison. The proportions of musth male sightings were available for different age-classes in the Kaziranga population (Chelliah and Sukumar 2015; termed capture probability in that paper). We calculated the proportions of musth male sightings for the same age-classes from the Kabini population and compared the proportions of musth males in Kaziranga and Kabini separately for the 15-20, 20-30, 30-40 and 40+ age classes using tests for differences between two proportions in Statistica 7 (StatSoft, Inc. 2004). The percentage of sightings in which adults of different age-classes were sighted in musth was also provided by Daniel *et al*. (1987). Therefore, we compared the proportion values with those for the same age-classes in Kabini, again using tests for differences between two proportions.

Temporal variation in musth

We examined the occurrence of musth during the dry and wet seasons. Dry and wet seasons in Kabini were assigned based on the arrival and retreat of monsoon rainfall received in that year. The wet season was considered to begin one week after the date of onset of the southwest monsoon, as declared by the India Meteorological Department, and the dry season was considered to begin two weeks after the end of the northeast monsoon (see Nandini *et al*. 2017). The dates thus calculated, based on data collected from HD Kote Taluka office, for the different years are shown in Table 1. In order to find out whether season affected musth in Kabini, we calculated i) the proportion of adult males of an age-class (out of the number of unique males of that age-class that were sighted, either in or not in musth) that were seen in musth during the dry and wet seasons, and analysed the logit proportions of males in musth, using a factorial ANOVA with age-class and season as factors.

Further, since the dry season in Kabini had high densities of elephants around the backwaters and the adult sex ratio could vary across months with the movement of female groups (Gupta *et al*. 2016), we examined musth in elephants within dry seasons. We split each dry season (from 2011-2016) into five months (January till May) and performed a repeated measures ANOVA (with month as the repeated measure and year as replicate) to examine differences in the logit proportions of males in musth across months. For analyses performed using individual months (for each year), we only retained those months in which at least seven days were sampled. All 30 months (January-May) from the years 2011-2016 were sampled for more than seven days (average ± SD: 20.433 ± 5.184). We also compared the logit proportion of males seen in musth during the probable conception peak (probably March to June, unpublished data, Kabini Elephant Project) with that during the rest of the year (July-February; for each year from 2011-2016) using a factorial ANOVA with age-class of the male and the two sets of months (Mar-Jun, Jul-Feb) as fixed factors. ANOVAs were performed using Statistica 7 (StatSoft, Inc. 2004).

Table 1. Dates of onset of the southwest (SW) monsoon and end of the northeast (NE) monsoon, and dates marking the beginning of the wet and dry seasons from 2010 till June 2016. Data till the 2014 wet season are from Nandini *et al*. (2017; reproduced with permission, License Number4473260355940, date Nov 20, 2018).

Year	Date of onset of the SW monsoon	Start of the wet season	Date of end of the NE monsoon	Start of the dry season
1	31 May 2008	7 Jun 2008	15 Nov 2008	1 Dec 2008
2	23 May 2009	30 May 2009	15 Dec 2009	1 Jan 2010
3	31-May-10	07-Jun-10	15-Dec-10	01-Jan-11
4	29-May-11	05-Jun-11	15-Dec-11	01-Jan-12
5	05-Jun-12	12-Jun-12	30-Nov-12	16-Dec-12
6	01-Jun-13	08-Jun-13	15-Nov-13	01-Dec-13
7	06-Jun-14	13-Jun-14	15-Nov-14	01-Dec-14
8	05-Jun-15	12-Jun-15	15-Dec-15	01-Jan-16
9	08-Jun-16	15-Jun-16	-	-

In Mudumalai, three seasons had been considered: the ‘first wet season’, including the months of May, June, July and August, the ‘second wet season’, including the months of September, October, November and December, and the ‘dry season’, including the months of January, February, March and April (Desai 1987). We qualitatively compared the results of the effect of seasonality on musth from Kabini with those from Mudumalai. In Kaziranga, field work had been possible only during the dry season and data were not available on seasonality of musth.

Results

In the Kabini population, we identified 118 adult males in all, of which 50 unique males were sighted in musth, on 267 days, and 138 unique males were sighted when not in musth on 1029 days (Keerthipriya *et al*. 2018a). Of the musth males, 38 unique males were seen on 214 days during the dry season and 20 unique males were seen on 53 days during the wet season (Table 2). Of the males not in musth, 113 unique males were seen on 701 days during the dry season and 88 unique males were seen on 328 days during the wet season. The study in Mudumalai by Daniel *et al*. (1987) had been carried out from October 1985-September 1987 and 23 adult males had been identified during the study. The study in Kaziranga (Chelliah and Sukumar 2015) had been conducted during the dry seasons of 2009-2011 (November 2008-March 2009, November 2009-May 2010 and November 2010-April 2011) 132 adult males had been identified.

Table 2. Number of unique adult males of different age-classes sighted during the dry and wet seasons of 2011-2016 and the percentage of those males (seen in those seasons) who were sighted in musth.

Age-class (years)	Year	No. of unique males		Percentage of males sighted in musth	
		Dry	Wet	Dry	Wet
15-30	2011	29	20	0	0
30+	2011	21	17	57.1	29.4
15-30	2012	33	19	3.0	5.3
30+	2012	18	13	27.8	15.4
15-30	2013	27	14	11.1	14.3
30+	2013	20	9	20.0	0
15-30	2014	28	15	7.1	0
30+	2014	17	9	35.3	22.2
15-30	2015	22	16	9.1	18.8
30+	2015	10	8	60.0	50.0
15-30	2016	17	9	17.6	0
30+	2016	10	6	40.0	33.3

Age structure of populations and age-class-specific proportions of musth male sightings

A comparison of the age-structure (based on identified adult males) between Kaziranga and Kabini showed that age-structure was independent of population identity (*G*-test of independence: $G_{\text{corrected}}=1.658$, $df=3$, $P=0.646$; Figure 2). However, a comparison of the number of sightings of males of different age-classes in Mudumalai and Kabini showed that age-structure was not independent of population identity (*G*-test of independence: $G_{\text{corrected}}=78.887$, $df=4$, $P<0.001$; Figure 3).Thus, Kabini and Kaziranga shared similar male population age-structures while Kabini and Mudumalai had different age-structures.

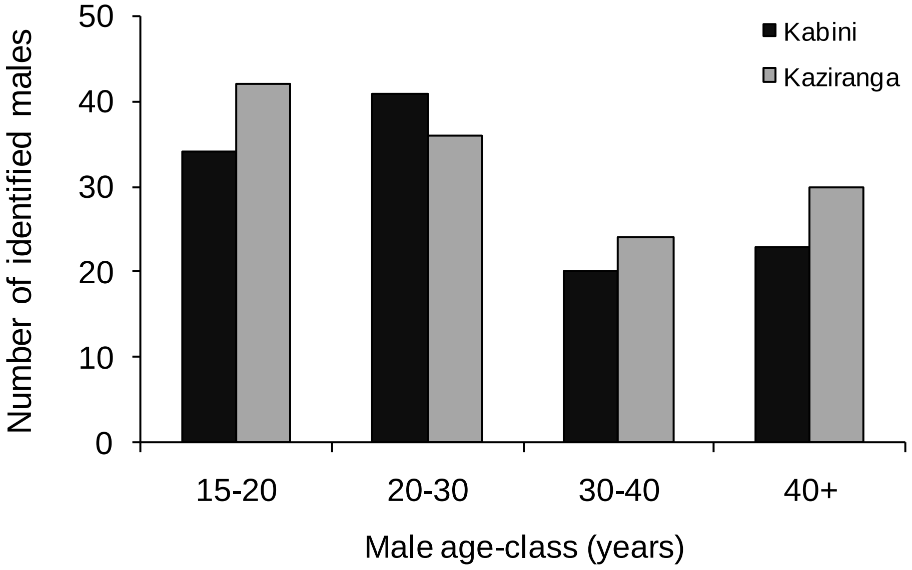


Figure 2. Age structure based on unique males in the Kabini and Kaziranga populations. Data for Kaziranga obtained from Chelliah and Sukumar (2015).

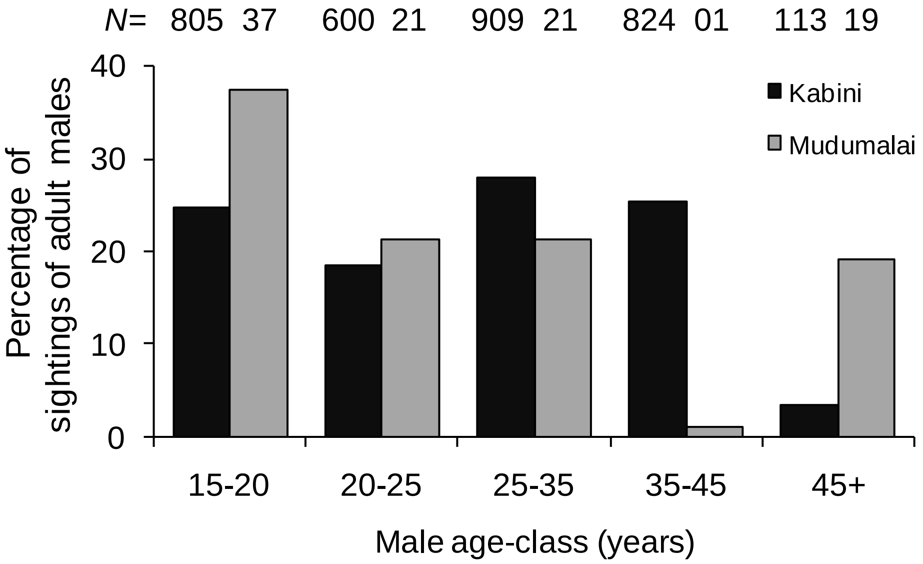
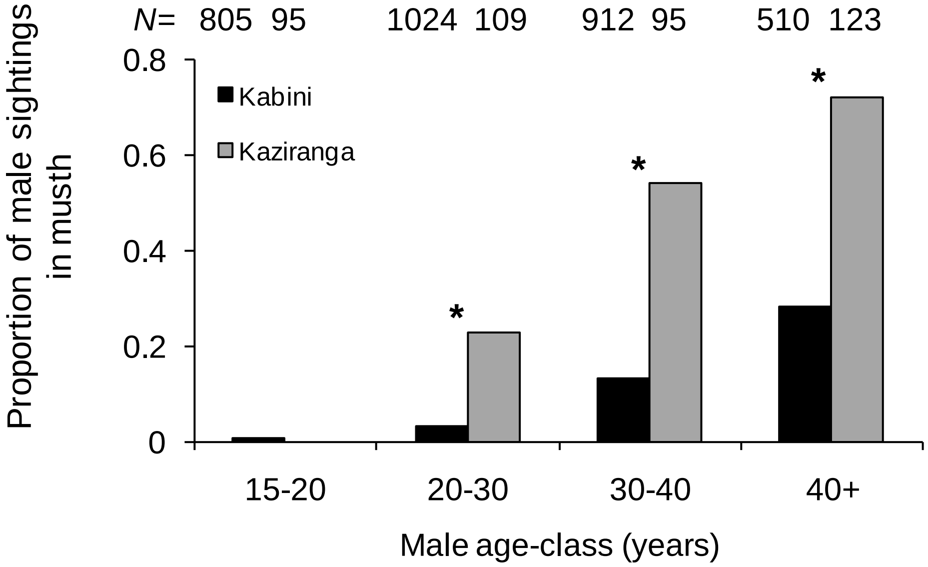


Figure 3. Percentage (out of total sightings of adult males) of sightings of adult males (not necessarily unique males) of different age-classes, in the Kabini and Mudumalai populations. The numbers of sightings are shown above the bars. Data from Mudumalai obtained from Daniel *et al*. (1987).

The proportions of musth male sightings (out of all sightings in that age-class)in different age-classes in Kaziranga and Kabini, respectively, were the following: 15-20 years: 0.00, 0.005; 20-30 years: 0.23, 0.033; 30-40 years: 0.54, 0.132; 40+ years: 0.72, 0.282. Whereas the proportions of musth male sightings for the 15-20 year age-class were not different between the two populations, the proportions of musth male sightings in Kabini for all the other age-classes were significantly smaller than those in Kaziranga (test for differences between two proportions (two sided): $P_{15\text{-}20}=0.490$, $P_{20\text{-}30}<0.001$, $P_{30\text{-}40}<0.001$, $P_{40+}<0.001$; see Figure 4a). The proportions of sightings that males of different age-classes were sighted in musth in Mudumalai and Kabini, respectively, were the following: 15-25 years: 0.175, 0.013; 25-35 years: 0.375, 0.044, 35+ years: 0.760, 0.259. Though we found that the proportion values were much lower in Kabini than the corresponding ones in Mudumalai in all three age-classes (see Figure 4b), as the sample sizes were not provided for Mudumalai, the values could not be statistically compared.

a)



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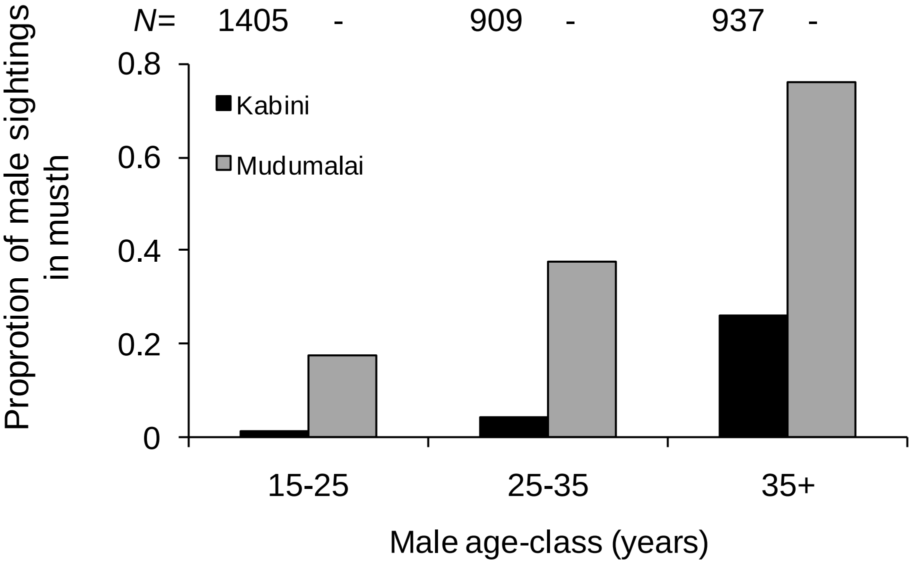

Figure 4. Comparison of proportions of sightings (of males of different age-classes) when males of different age-classes were seen in musth between a) Kabini and Kaziranga, and b) Kabini and Mudumalai. Each male was recorded as having been sighted only once a day in Kabini.

Temporal variation in musth

A factorial ANOVA on the logit proportions of males in musth (out of the unique males in that age-class) with age-class and season as factors showed that there was an effect of age-class on musth ($F_{1,20}$=6.866, P=0.0164), as already known (Keerthipriya *et al.* 2018a), but no effect of season on the proportion of adult males in musth ($F_{1,20}$=2.594, P=0.123) and no interaction between season and age-class ($F_{1,20}$=0.011, P=0.918; Figure 5). Thus, males that came into musth during the dry and wet seasons did not significantly differ in their ages.

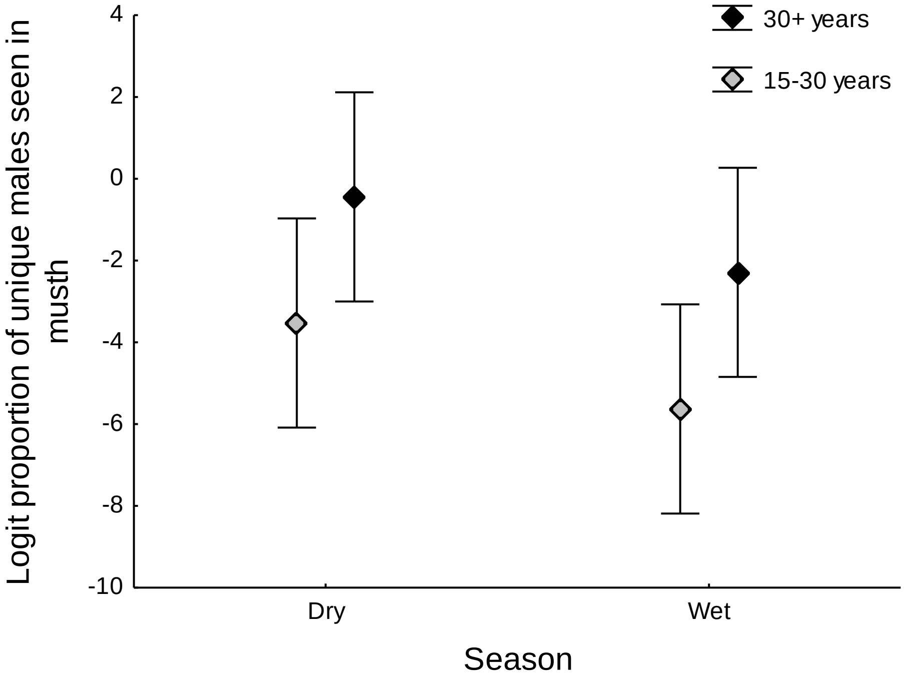

Figure 5. Logit proportion of males in musth during the dry and wet seasons. Error bars are 95% CI.

The repeated measures ANOVA (with month as the repeated measure and year as replicate and age-class as the categorical factor) to examine differences in the logit proportions of unique males in musth across months showed that age-class, again, had a significant effect ($F_{1,40}$=14.599, P=0.003) while the interaction between months and age-class was not significant ($F_{4,40}$=0.572, P=0.684). Though month had a significant main effect ($F_{4,40}$=3.470, P=0.016), none of the pairwise Tukey's HSD tests were significant ($P_{\text{January-February}}$=1.000, $P_{\text{January-March}}$=0.172, $P_{\text{January-April}}$=0.095, $P_{\text{January-May}}$=0.262, $P_{\text{February-March}}$=0.126, $P_{\text{February-April}}$=0.068, $P_{\text{February-May}}$=0.199, $P_{\text{March-April}}$=0.998, $P_{\text{March-May}}$=0.999, $P_{\text{April-May}}$=0.984). The results did not change when the ANOVA was carried out on the logit proportion of all musth male sightings rather than on the logit proportions of unique males in musth. The sex ratio between identified males and females varied between 1 male: 3.025 females in February to 1 male: 4.627 females in May (Figure 6a). The logit proportion of unique males seen in musth was not significantly different between the conception peak and the rest of the year (Factorial ANOVA: sets of months: $F_{1,20}$=0.645, P=0.431; age-class: $F_{1,20}$=9.808, P=0.005; interaction: $F_{1,20}$=0.122, P=0.730; Figure 6b). However, the logit proportion of musth male sightings was borderline significant/non-significant during the conception peak when compared to the rest of the year ($F_{1,20}$=4.354, P=0.050) and age-class, again, had an effect ($F_{1,20}$=19.458, P<0.001).

Desai (1987) found that the percentage of musth males sighted (out of the total number of males sighted) was highest in the first wet season (32.72%), followed by the second wet season (~24%, value read from graph) and was the lowest during the dry season (15.15%) and this difference was found to be significant. As already mentioned, data were collected only during the dry season in Kaziranga and hence this comparison was not possible.

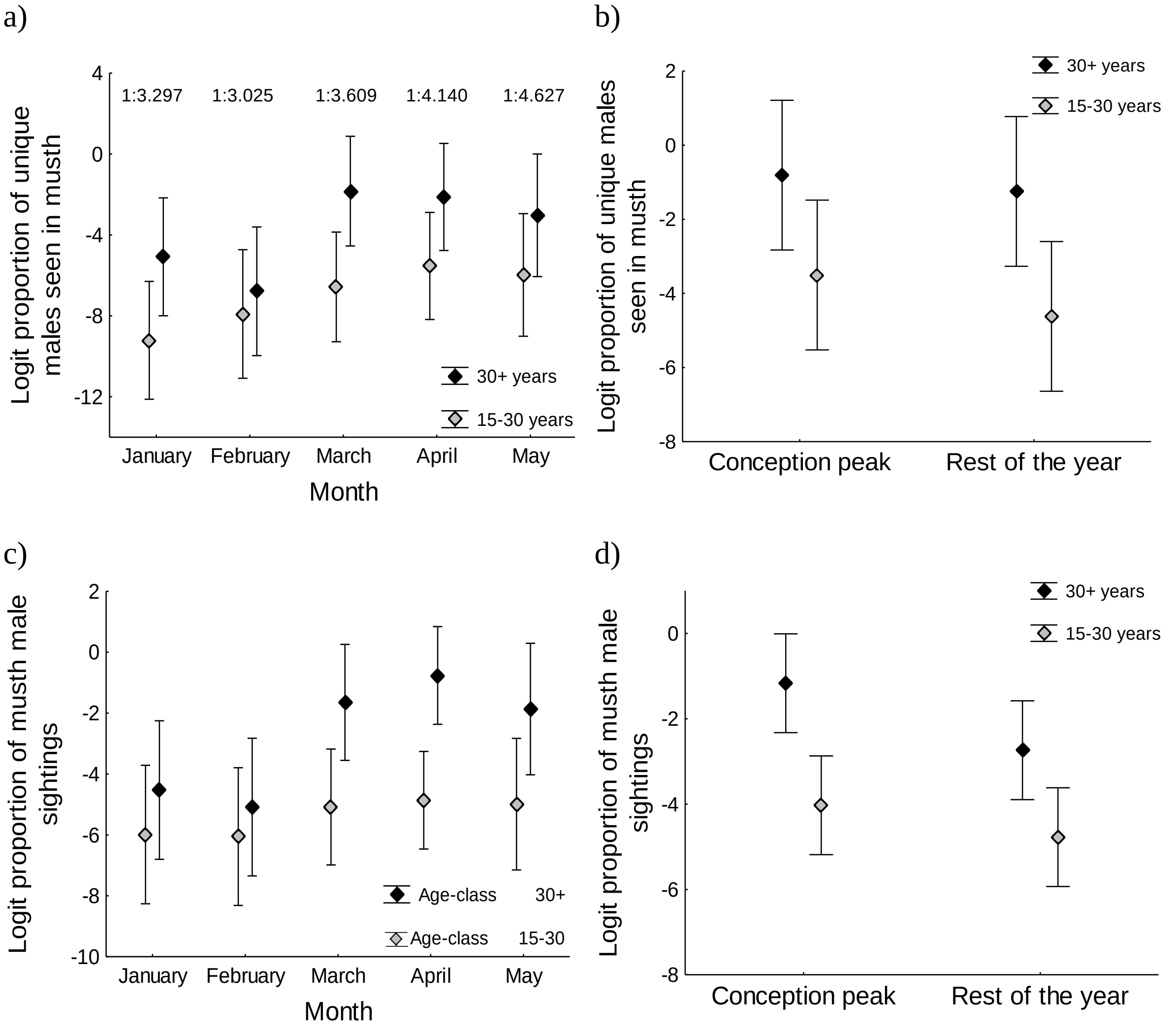

Figure 6. Logit proportion of unique males in musth of two age-classes in a) different months within the dry season (sex ratios between unique males and females >=15 years old sighted during the months, are written as males: females at the top of the graph) and b) during the months when conceptions were probably high (Apr-Jul) and the rest of the year (Aug-Mar) and logit proportion of musth male sightings of the two age-classes of males in a) different months within the dry season and b) during the months when conceptions were probably high and the rest of the year. Error bars are 95% CI.

Discussion

Sex ratio, age structure, and proportion of males sighted in musth

We found that the proportions of male sightings in musth were significantly higher in Kaziranga and in Mudumalai compared to Kabini. Males that were over 40 years old were sighted in musth in over 70% of their sightings in Kaziranga and males that were over 35 years old were sighted in musth in over 75% of their sightings in Mudumalai. In contrast, males that were over 35 or 40 years old were sighted in musth in less than 30% of their sightings in Kabini. Kaziranga had a less skewed adult (>=15 years) sex ratio (1:2.3 from the forest department reports, values provided in Chelliah and Sukumar 2015) than in Kabini (1 male: 4-5 females based on initial data - Gupta *et al*. 2016 - and about 1 male : 3.1 females based on data till August 2016, Kabini Elephant Project, unpublished data) but the male population age-structures were similar between Kaziranga and Kabini. Although the sex ratio in subsequent years became more skewed in Mudumalai (see Arivazhagan and Sukumar 2005), the sex ratio of adults >=15 years old was similar between Mudumalai at the time of Daniel *et al*.'s (1987) study and Kabini during our study. However, the male population age-structure was different between Mudumalai and Kabini, with a much higher proportion of males over 45 years old in Mudumalai compared to Kabini (although a much lower proportion of males 35-45 years old in Mudumalai). A less skewed sex ratio (as seen in Kaziranga) would imply a larger number of males that could enter musth. But since the proportion (and not just number) of male sightings in musth was higher in Kaziranga than in Kabini, increased male-male competition amongst older males perhaps influences the occurrence and/or duration of musth non-linearly. This is consistent with a higher proportion of musth male sightings in Mudumalai, in which male-male competition was possibly high because of the presence of a high proportion of males of the oldest age-class. Such a non-linear effect of competitor presence on the occurrence of musth can be tested by examining the proportion of musth male sightings in other populations with different sex-ratios and populations with different proportions of males in the old age-classes. Within a small range of proportions of 30+ year old males out of the total number of adult males sighted in each year (during 2011-2016), there was a negative correlation between the proportion of old males in Kabini and the proportion of musth male sightings (out of all adult male sightings) (Spearman's rank-order correlation: R=-0.771, R^2=0.594, P<0.08, Figure 7). However, the proportion of 40+ year old males was not significantly correlated with the proportion of musth sightings (R=-0.314, R^2=0.099, P>0.10) and the proportion of 45+ year old males was significantly positively correlated with the proportion of musth sightings (Spearman's rank-order correlation: R=0.886, R^2=0.785, P<0.05, Figure 7). Thus, male-male competition in the oldest age-class might affect the occurrence of musth.

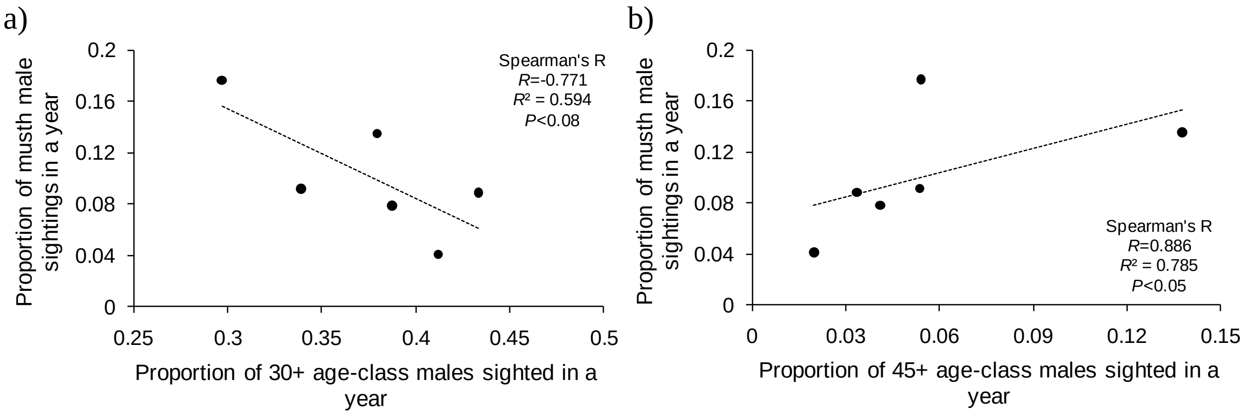

Figure 7. Correlation between a) the proportion of 30+ year old males or b) the proportion of 45+ year old males in the population in a year, and the proportion of musth male sightings in that year.

One trivial possibility to partially explain the results could be that there were differences in ageing animals in the different populations. If the ages of males in Kabini were systematically overestimated, and there were no males in the two oldest age-classes, the proportion of male sightings in musth of the 25-35 year old males in Mudumalai would be similar to the males currently aged over 35 years in Kabini. However, poaching is thought to have affected Mudumalai to a greater extent than Kabini (Arivazhagan and Sukumar 2005) and the percentage of males in the oldest age-class (45+ years) is much smaller in Kabini than that in Mudumalai. Therefore, it is unlikely that male age in Kabini has been overestimated. Furthermore, some of the old males in Kabini had been first sighted by one of us (TNCV) during 2000-2005 and they were already well-grown adult males. Therefore, we had baseline ages and overestimation is unlikely. If the ages were underestimated in Kabini, it would make the proportion of males sighted in musth even smaller in Kabini than in the other populations, warranting an explanation as above.

Another possibility is that Kabini is part of the non-musth ranges of males more than Mudumalai or Kaziranga. One would require radiocollared males in all the three areas to test this. However, this is unlikely because there are annual aggregations of female groups along the Kabini backwaters during the summer, increasing the local density and, therefore, the chance of finding a fertile female. Mudumalai does not have such an aggregation of females. Kaziranga is flooded during the wet season and it is possible that musth is compressed to the dry season. However, since elephants in Kaziranga were not followed during the wet season, we do not have information on this.

A third possibility is that possible resource limitation affects the incidence of musth in Kabini, either directly through male body condition or indirectly, through fertile females not being available because of habitat saturation. Previously, resource limitation was thought to affect female group sizes in Kabini (Nandini *et al*. 2017, 2018), but that was in the context of feeding group sizes which would, therefore reflect the distribution of resources at small spatial scales. If the abundance of resources overall is low, body condition may be poor or the population may no longer be growing, with a limited number of fertile females available. Elephants in the Kabini population are not in very good body condition (Kabini Elephant Project, unpublished data) but this was true of Mudumalai also (in the late 1990s) from personal observations (TNCV). Although the overall densities in the three parks were similar, the relative density (relative to resources available) may be higher in Kabini with the habitat being saturated (especially, with inedible invasive species being abundant and bamboo dying out after mass flowering in early 2011. A study of the population growth rate in Kabini is much needed. Mudumalai, at the time of Daniel *et al*.'s (1987) study did not have a saturated population because we know that it has significantly grown subsequently (Baskaran *et al*. 2010a). Habitat saturation could affect musth through the numbers of fertile females if there is female feedback on the likelihood of males coming into musth. It would be interesting to see if such a feedback exists, whether a feedback in the reverse direction (from musth males to female fertility) exists, whether the density of old males affect musth (amongst other old males; old males are thought to suppress musth in young males), or if only individual male body condition affects musth (of old males).In the Amboseli African savannah elephant population the number of musth males was higher in weeks when the number of receptive females was also high (Poole *et al*. 2011), suggesting that some sort of unidirectional or bidirectional female-male feedback might exist.

Temporal variation in musth across seasons and months

Musth males in Kabini were seen throughout the year and there was no significant effect of season on the proportion of males seen in musth. There was an effect of month on the percentage of musth males seen during the dry season (January-May, when the local sex ratios also varied) but none of the pairwise comparisons yielded a significant difference. This is in contrast to what had been seen in Mudumalai National Park by Desai (1987), wherein musth males were least frequent during the dry season compared to the first wet and second wet seasons. It is possible that the differences between Mudumalai and Kabini in the seasonality of musth sightings might result from seasonal differences in food resources, although the habitat in the two study areas were not very different, except for the Kabini backwaters and the Masinagudi area. Seasonal differences in elephant food resources have been found in Mudumalai (Sivaganesan 1991, Baskaran *et al*. 2010b. While resources are apparently different in Kabini during the dry and wet seasons (Gautam *et al*. 2018), female associations had also been found previously to be largely unaffected by season (Nandini*et al*. 2017). Hall-Martin (1987), when examining the seasonal frequency of musth males in two different populations of African savannah elephants, had found a distinct peak in annual rainfall which coincided with a peak in the number of conceptions in one population (Kruger National Park) but three, smaller peaks in rainfall and no clear peak in the number of conceptions in the other (Addo National Park). This resulted in a peaked frequency of musth males coinciding with the conception peak in Kruger and musth males throughout the year in Addo. In Amboseli, older, high ranking males were seen in musth more than younger, lower ranked males during the time when there were more conceptions (Poole 1989) and the timing of musth of different males was thought to be a balance between high male-male competition during peak conception times and low availability of receptive females in other times of the year (Poole *et al*. 2011). There is, perhaps, no distinct breeding season in Kabini, although this needs to be examined. There was a slight peak in conceptions among identified females in Kabini from March-June (Kabini Elephant Project, unpublished data), but we found no significant difference in the proportion of males seen in musth during this period and the rest of the year. We also found that the ages of musth males were not different either across seasons or months or between the conception peak and the rest of the year (no significant interaction effects between age-class of the male and season/months). A more detailed examination of births at different times of the year and across years in the study population is required in Kabini.

To conclude, we find that the proportion of musth sightings was significantly lower in Kabini than in the other populations examined and think it could have ensued from differences in sex ratio and age-structure (which itself, could have arisen due to poaching). Resource limitation and patterns of resource distribution might also play a role and data from other long-term studies would be useful in examining the various hypotheses we propose about the occurrence of musth.

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CHAPTER 6

Agonistic Interactions among Adult and Subadult Male Asian Elephants and the Factors that Affect their Outcome in Nagarahole-Bandipur, Southern India

Title: Agonistic interactions among adult and subadult male Asian elephants and the factors that affect their outcome in Nagarahole-Bandipur, southern India

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This work was thought of by PK and TNCV. Field data were collected by PK with some help from SN. Video scoring and data analysis were carried out by PK. PK primarily wrote the manuscript.

Abstract

This study examined agonistic interactions involving adult and subadult wild male Asian elephants in Nagarahole-Bandipur, southern India. We found that almost all the dominance bouts between adult males were resolved with a clear winner but dominance bouts between subadult males were less resolved. A greater number of bouts amongst subadults than adults were initiated by the losing male and greater physical contact during dominance was observed in subadults than in adults. Further, subadult males engaged in more dominance interactions with new, different opponents compared to adults. While the proportion of resolved interactions was fairly high even amongst subadults, most pairs of individuals did not interact with one another, making adult and subadult male dominance networks somewhat sparse and a linear dominance hierarchy difficult to uncover. However, the proportion of transitive triads was significantly higher than that expected from random datasets and dominance relationships between adults, subadults, and adult-subadult pairs were unidirectional, indicating orderliness in dominance relationships. When we examined the factors that could be affecting the outcome of nonmusth adult male dominance bouts, we found increased age and better body condition to significantly affect the probability of winning a dominance bout. While we observed tusk use during the dominance bouts, tusk length did not seem to affect the outcome of dominance. Adult and subadult males who associated more also engaged in more dominance bouts with each other, though this was stronger in adults. Dominance bouts involving musth males were not common but musth males almost always won over nonmusth males when they did interact. Thus, musth was a strong but rare advantage in dominance bouts in Kabini. We also found that, unlike nonmusth males, musth males were involved in dominance bouts more often when associating with a female group.

Keywords

Asian elephant, male dominance, age, body condition, tusk length, Nagarahole-Bandipur, Kabini Elephant Project.

Introduction

Agonistic interactions between individuals or groups are common in many mammalian species (for example, see Ellis 1995 for male agonistic interactions, Sterck *et al*. 1997 for female dominance relationships).Agonism among adult males is thought to result primarily from the intrasexual competition males face to procure mating opportunities with the rarer receptive females. Dominance ranks and mating success of males have been found to have a positive relationship (see Dewsbury 1982, Cowlishaw and Dunbar 1991, Ellis 1995). Dominance behaviours are also expected to be shown by younger males in species with high competition and fighting among adult males (Cenni and Fawcett 2018) and males that are not yet reproductively competitive have been found to engage in similar behaviours as adults (see Bekoff and Byers 1998). Though dominance among immature males may face some immediate costs in terms of risk of injury and/or energetic costs, it may lead to delayed benefits, in adulthood. The motor-training hypothesis, offered often as an explanation, posits that such dominance behaviours among immature males help develop motor skills and serve as training or practice for consequential fights during adulthood (Berger 1980). Support for the motor-training hypothesis has been found in several species such as Bighorn sheep (Berger 1980), cats (Caro 1988) and squirrel monkeys (Biben 1998). Dominance interactions amongst subadults or juveniles may also allow for collecting information on future competition (Lee and Moss 2014).

In species with linear dominance hierarchies amongst adult males (for example, Frame *et al*. 1979 in African wild dogs, Packer 1979 in olive baboons, Reed *et al*. 1997 in crested black macaque, Pelletier and Festa-Bianchet 2006 in bighorn rams), various factors may affect the chances of a male winning an agonistic interaction. Age of the male (and consequently, body size, as mammals often grow in size with age) has been shown to have a significant effect on the male's dominance rank. A U-shaped relationship between age and rank, with males moving up the dominance hierarchy as they initially mature and grow older but subsequently falling as they age past their prime, has been seen in many non-human primate species such as olive baboons (Packer 1979) and yellow baboons (Alberts *et al*. 2003). Males may also have certain features which serve as weapons and provide an advantage in physical combat (see Lincoln 1994). In such species, males are expected to use the weapons to gain an advantage in dominance interactions with other males (for example, see Geist 1966, Bowyer 1986, Clutton-Brock *et al*. 1982). Further, males, in some cases, enter a heightened state of sexual activity, when they invest more of their energy into increasing their strength. This includes the phenomenon of rut in ungulates (Lent 1965, Clutton-Brock and Albon 1979) and the rut-like phenomenon of musth in elephants (Jainudeen *et al*. 1972, Poole and Moss 1981, Poole 1987). As physical combat is often risky, especially, but not exclusively, for the loser, males are expected to use various cues and signals to assess their opponents and use them to make choices about engaging in and modulating their contests (Barrette and Vandal 1990, Poole 1999).These cues or signals could be visual, such as body size, weapon size, or rut-related changes in morphology(Lent 1965, Lincoln 1972), auditory, such as calls that are honest signals of the strength of the caller (Clutton-Brock and Albon 1979, Poole 1999, Fischer *et al*. 2004),and/or olfactory, such as pheromones or other chemical compounds secreted in urine or faeces or musth fluid (for example, see Rasmussen *et al*. 2002).

Asian elephants show different female and male societies, with the males leaving their natal herds around their pubertal age (Douglas-Hamilton 1972, Moss and Poole 1983, Desai and Johnsingh 1995) while the females continue to remain in their natal herd along with their female relatives (Vidya and Sukumar 2005). After and during dispersal, male elephants are seen to form associations with other males and with female herds (Keerthipriya *et al*. 2018a,b). Since, elephants are polygynous, with the females being rarely receptive to mating (females are receptive for a few days every five years or so - Moss 1983, Hess *et al*. 1983, Eisenberg *et al*. 1971), and range over large areas, mating opportunities are rare and males are expected to compete fiercely for them.

Elephants show significant sexual dimorphism, with the males being much larger than the females and growing throughout their lifetime (Roth 1984, Haynes 1991, Lindeque and van Jaarsveld 1993, Lee and Moss 1995). While tusks are prevalent in both sexes in the African savannah elephants, only males (and not all males) carry tusks in the Asian elephant. Further, male elephants enter a rut-like state known as musth, which is characterised by higher plasma testosterone levels and aggression (Jainudeen *et al*. 1972, Poole *et al*. 1984, Rasmussen *et al*. 1984, Niemuller and Liptrap 1991, Rasmussen and Greenwood 2003, Ganswindt *et al*. 2005). Musth in the African savannah elephantwas described as a signal of aggressive intent to other males (Poole 1982). In the current study population, we previously found that musth and the age of the musth males affected the associations males made (Keerthipriya *et al*. 2018c).In the Kaziranga population of Asian elephants with roughly equal proportions of tusked and tuskless males, musth was found to override body size which, in turn, overrode tusk presence and length of tusks in determining the winner in a male-male dominance interaction (Chelliah and Sukumar 2013). Age was found to have an effect on the outcome of dominance interactions among adult male African savannah elephants in Amboseli, with older (and hence, larger) adult males tending to win contests unless the younger male had a musth advantage (Poole 1982, Payne 2003). In African savannah elephants in Namibia, male elephants were found to show a linear dominance hierarchy during normal years but not during unusually wet years (O’Connell-Rodwell *et al*. 2011).

In this study, we examined agonistic interactions between males in a population of Asian elephants in southern India. We compared interactions occurring among adult and subadult males. The objectives of the study were the following:

1) To examine how the frequency of dominance bouts changed with male age. As male elephants grow throughout their lifetime, large size differences may be present between subadult and adult males, making dominance relationships between these males very obvious if dominance was size based. Hence, we expected a greater proportions of dominance bouts to occur between pairs of adults and between pairs of subadults rather than between adults and subadults. We compared the observed dominance bouts between males of different age-classes with respect to the age-structure of the population in order to examine this.

2) To examine whether male age affects the nature and outcome of dominance interactions: As subadults are smaller than adults and not reproductively competitive, we expected dominance bouts between subadults to involve lower risk and stakes than those between adults. If the subadults engaged in contests primarily for practice, winning the contest would be less important than participating in it. Therefore, we expected a higher proportion of unresolved bouts involving subadults compared to adults. Moreover, due to the lowered risk involved, we expected more initiation of agonism by the eventual loser of the interaction(s) among subadults compared to adults. We also expected higher levels of aggressive behaviours in resolved subadult-subadult dominance bouts when compared to adult-adult dominance bouts.

3) To test for a linear dominance hierarchy among male elephants. We used multiple methods to test whether male dominance showed orderliness and whether dominance bouts were unidirectional (whether dyads consistently had the same winner).

4) To examine the factors that affect the outcome of adult male dominance. We expected age, body condition, and musth status of the male to have significant effects. Though tusk presence and length were found previously to not have a big effect on male dominance in the Asian elephant population in Kaziranga National Park (Chelliah and Sukumar 2013), there are some differences between the study population and Kaziranga. Musth males were sighted far more frequently in Kaziranga than in Kabini (Keerthipriya *et al*. 2018d). Therefore, we expected musth to play a smaller role in deciding dominance bouts in the current study. Moreover, as our study population has many more tusked males than makhnas, the patterns of tusk use might be different from what was seen in Kaziranga. Therefore, we also calculated the frequency of tusk use and examined the effect of tusk length on the outcome of dominance bouts.

5) To examine whether and how association index, a measure of familiarity, affects the frequency of dominance bouts between unique pairs of identified males. As testing strength against age-peers could be a reason for adult (Keerthipriya *et al*. 2018a) and subadult (Keerthipriya *et al*. 2018b) male associations, we expected males who associated more to engage in more dominance bouts.

6) To examine how female presence affected dominance shown by musth males. As musth is thought to be a signal of aggressive intent and an investment in mating, we expected the musth males to engage in more dominance when in association with a female group than when on their own.

Methods

Field methods

We conducted field work in Nagarahole and Bandipur National Parks and Tiger Reserves, which form a part of the larger Nilgiris-Eastern Ghats landscape in southern India. These parks are primarily comprised of deciduous forests and are separated by the Kabini river.

They have high elephant densities (~2-4 elephants/km^2, AERCC 1998) and the Kabini reservoir (which is built on the river and, when water is released from it during the dry season, has open areas with fresh grass) provides a convenient place during the dry season to observe congregating elephants. Data on dominance interactions were collected on individually identified elephants from February 2011 to July 2014as part of the long term Kabini Elephant Project. We carried out field sampling from about 6:30 AM to 6:00-6:45 PM (depending on daylight hours and field permits).Most of the data on dominance were collected during the time elephants were using the backwaters of the Kabini reservoir as the area provided the visibility to identify and continuously monitor the males engaged in dominance interactions. Whenever we encountered elephants, they were individually identified and aged based on various body characteristics (Vidya *et al*. 2014). Males that were 15 years of age or older were classified as adults, and those between 5 and 15 years of age, as subadults. Males were also classified as tuskers or makhnas depending on whether they had tusks or not. The musth status of males was also recorded and males were categorised as being in musth or not in musth depending on the presence or absence of temporal gland secretion (see Keerthipriya *et al*. 2018c).

Males older than five years of age were said to associate with each other if they fed within 30m of each other in the absence of female groups or fed within 10m of the same female group(s) at the same time (explained in Keerthipriya *et al*. 2018a). If either male was associating with a female group during the interaction, it was said to have occurred in female presence, otherwise it was said to have occurred in female absence. If males approached each other, engaged only in dominance interactions, and left immediately without spending time feeding together or showing affiliative interactions, the males were not said to be associating with each other. Therefore, associations (described in the previous chapter) and dominance did not necessarily have to be correlated. Dominance interactions could occur between males that did not associate and males that associated could engage in dominance interactions but not necessarily so. Behavioural interactions were observed through *ad libitum* sampling and, whenever possible, recorded using a Sony HDR-XR100E video camera. A dominance bout between two males was considered independent of the next one between the same pair of males if there was a minimum interval of 15 minutes between the end of one and the beginning of the next. Each independent dominance bout could contain any number of non-independent dominance interactions and each non-independent interaction consisted of a behaviour, initiated by one male, and a response, if any, of the recipient male. Responses were those behaviours that occurred within 10 seconds of the behavior being initiated; otherwise it was classified as the initiated behavior in the next non-independent interaction. Behaviours such as chasing, displacing the opponent, poking with tusks and placing head on the opponent's back were classified as dominant behaviours. Behaviours such as cowering, presenting backside, unsheathing penis, and walking backwards were classified as subordinate behaviours. Complete lists of initiated behaviours and responses are provided in Supplementary material 1. The initiator was assigned as the winner of that non-independent interaction if the response was subordinance, and no winner was assigned if there was no response. If the recipient responded with even greater aggression than the initiator's behaviour, the recipient was the winner. Sometimes, males initiated subordinate behaviours towards others, in which case, the recipients were the winners of that non-independent interaction. The winner of an independent dominance bout was decided depending on how many interactions in that bout an individual won. If one male won only a slightly greater number of interactions than the other or if an overall winner was ambiguous, the outcome of the bout was scored as unresolved.

Data analysis

Though, the dominance interactions were scored in the field itself, videos recorded in the field were scored in the lab to confirm the behaviours and identities of individuals. The various behaviours seen are listed in Supplementary material 1 and their frequencies are shown in Supplementary material 2.We classified the adults and subadults each into two broad age-classes (5-10 years, 10-15 years, 15-30 years and >30 years; these age-classes were shown to be distinct in their associations in Keerthipriya *et al*. 2018b) for the network analyses. We compared the proportion of independent bouts between different males of different age-classes to the expected proportion based on the number of identified males of the different age-classes, using a test for proportions. We used only bouts between two nonmusth males for comparisons between age-class combinations.

We also examined what proportions of dominance bouts were resolved and whether there were differences in the proportions of dominance bouts that were resolved across age classes, using tests for proportions. We compared the proportion of bouts resolved in female presence for the three age-class combinations, using tests for proportions. If there were no significant differences, we combined data in female presence and absence for further analyses. We also examined whether the age difference between interacting males was greater in resolved than in unresolved bouts, using Mann-Whitney *U* tests for each age-class combination. Age differences for bouts involving identified males were calculated based on their estimated ages while the mid-point of the male's age class was taken as his age if the male was not identified. We compared the number of non-independent interactions in an independent bout, the duration of an independent bout and the proportion of non-independent interactions that involved an aggressive behaviour (after logit transformation) of resolved and unresolved independent bouts using ANCOVAs, with age-class combination and resolution of the bout as fixed factors and age difference between the interacting males as the covariate. Classification of initiated behaviours into different categories is detailed in Supplementary material 1.

We checked if the initiator of the dominance bout was more likely to be the eventual winner of that dominance bout, for each age-class combination, using *z*-tests. We also compared the proportion of bouts won by the male who initiated the dominance bout across the three age-class combination using tests for proportions. We excluded those bouts wherein the first non-independent interaction involved a submissive behaviour, as we only wanted to check whether the male who initiated agonistic behaviour was the eventual winner of the bout.

Adult-adult and subadult-subadult dominance bouts were separately tested for a linear dominance hierarchy using Landau's index *h* (Landau 1951) and de Vries' corrected index *h*' (de Vries 1995).We also used a modification of Landau's index proposed by Singh *et al.* (2003) wherein the proportion of bouts between two males that was won by one male was calculated. Here, each row of the dominance matrix had the proportion of bouts won against all other males by the row's focal male, and the row totals (d_a) replaced the term V_a in Landau's index. The null dyads were assigned values based on the probability that one male would have won in a hypothetical dominance bout; calculated as d_a of the male/(d_a of the male+ d_a of the other male). As we had multiple males in our dataset who had only been observed losing bouts (hence d_a=0), dyads consisting of two such males were assigned 0.5 probability that either male won the bout. Linear hierarchies are characterised by presence of transitivity amongst triads and unidirectionality between dyads. Transitivity occurs if A defeats B and B defeats C, A also defeats C. Since it is possible that a linear dominance hierarchy may not be detected if many individuals do not show agonistic interactions towards one another, we calculated the proportion of transitive triads (out of all the triads in which all three dominance relationships were resolved) in the observed dataset and also calculated triangle transitivity (t_{tri}) (see Shizuka and McDonald 2012; Supplementary material 3) which varies from 0 to 1. We created random datasets by assigning the winner of each observed dominance bout randomly and we created 10,000 such datasets. We compared the observed t_{tri} values with those of the randomised datasets and if the observed value was greater than 95% of the random datasets, we considered the difference to be significant. Similarly, we also looked at triads with two resolved edges and classified them as double dominant, double subordinate (both categories will form a transitive triad 100% of the times) or pass along (which will form 50% transitive and 50% cyclic triads).We calculated the proportion of the first two (double dominant and double subordinate) categories out of the total number of triads with two edges resolved in the observed data. These calculations were done using a MATLAB code. The different kinds of triadic relationships mentioned are illustrated in Supplementary material 3.We also tested for unidirectionality in dominance bouts by ruling out significant reciprocity. Reciprocity was calculated by correlating the dominance matrix with its inverse using a Mantel *Z* test with 10,000 permutations. Some of the analyses to examine the presence of a linear dominance hierarchy (Landau's and deVries' indices) and the test for reciprocity were carried out using SOCPROG 2.6 (Whitehead 2009).

We constructed directed dominance networks using resolved adult-adult and subadult-subadult bouts between identified nonmusth males (*nodes* in the network) with the direction of an *edge* (dominance bout) going from the winner of the bouts to the loser of the bout. Thus, the *out-degree* of a node (an identified male) was the number of males a focal male had won over, while the *in-degree* of a node was the number of males who had defeated the focal male in dominance bouts. Edges could be bidirectional if, in the bouts between those males, both males had won at least one bout against the other. Dominance networks were visualised using Gephi 0.8.2 (Bastian *et al*. 2009). We compared the out-degree (the number of males that the focal male won over) distribution for the networks against an expected Poisson distribution. This was done using distribution fitting in Statistica 7.

Using videos and photos taken of the two males during the time of the bout, we determined whether there was a significant body condition and tusk length difference. Body condition differences were considered significant if there was a difference in visibility of their pelvic and pectoral girdles and their ribcage. A male was said to have longer tusks if the difference in lengths was more than one third of the shorter tusked male's tusk length. We checked whether winners of the independent dominance bouts were generally older than the losers using Wilcoxon's matched-pairs tests in Statistica 7 (StatSoft, Inc. 2004). To see if tusk use was common, we calculated the proportion of non-independent interactions which involved the use of tusks in dominance bouts of difference age-class combinations and compared them using tests for proportion. For this analysis alone, we used all dominance bouts (resolved and unresolved, involving musth and nonmusth males).We used z-tests to see if the factors age, body condition, and tusk length had a significant effect on their own on the outcome of an independent dominance bout. The factors that showed a significant effect were used as predictors in a generalised linear mixed effects model, with the identity of the interacting pair as a random factor. This analysis was performed using the fitglme function in MATLAB, using the Laplace method of fitting (model is fitted by Maximum Likelihood).In each of the resolved dominance bouts, one male was randomly selected as the focal male and the outcome of the bout was scored as 1 if the focal male won and 0 if the focal male lost. The age difference was calculated as the age of the focal male – age of the opponent, the difference in tusk length would be 1 if the focal male had longer tusks, 0 if the tusk lengths were not different and -1 if the opponent had longer tusks, and the body condition was scored as 1 if the focal male was in better body condition than his opponent, 0 if the body condition of both males were the same and -1 if the focal was in worse body condition than his opponent. As the outcome is binary, we used a binomial distribution with a logit link function.

The proportion of associating males who also engaged in a dominance bout were calculated for adult-adult and subadult-subadult associations and the two values were compared using test for difference in proportions. The dominance frequency matrix and AI matrix for adult-adult and subadult-subadult bouts were compared by performing Mantel tests (Mantel 1967) with 5000 permutations. The resolved, independent dominance bouts among identified, wild (excluding the one bout involving a semi-captive camp elephant) nonmusth male elephants were used for this analysis.

We used the bouts between musth and nonmusth males to examine the effect of musth on deciding the winner. We also compared the proportion of bouts involving a musth male in female presence to that in female absence, for the adult-subadult and adult-adult age-class combinations, using tests of proportions.

All statistical analyses including tests for differences between two proportions, ANCOVA, and all non-parametric tests were performed in Statistica 7 (StatSoft, Inc. 2004). Construction of dominance matrices, simple data manipulation, and Mantel tests were done using MATLAB 2011a (The MathWorks, Inc, 1984-2011, www.mathworks.com).

Results

We observed 456 independent dominance bouts involving 43 identified adult and 62 identified subadult male elephants between February 2011 and July 2014. Out of these, 139 bouts were among adult males, 149 bouts between adult and subadult males, and 168 bouts among subadult males (see Table 1 for more details). One of these adult male-adult male bouts and one of these adult male-subadult male bouts involved an identified wild male and two different semi-captive males who were from a nearby elephant camp. The ages of the camp elephants were known and these two bouts were included in all analyses except when we tested for unidirectionality and presence of a linear hierarchy.

Table 1. The total numbers of independent dominance bouts between males of different age-classes and musth status combinations in various group types (female absence and female presence) and, within those bouts, the number of bouts that were not resolved (NR). UN-Unknown musth status

		Nonmusth-Nonmusth		Musth-Nonmusth		UN-Musth		UN-Nonmusth		UN-UN	
		Total	NR	Total	NR	Total	NR	Total	NR	Total	NR
Adult-Adult	Female absence	79	0	8	0	0	0	0	0	2	0
	Female presence	32	2	13	0	1	0	4	0	0	0
	Subtotals	111	2	21	0	1	0	4	0	2	0
Adult-Subadult	Female absence	38	3	4	0	0	0	0	0	0	0
	Female presence	83	12	21	0	0	0	2	0	1	0
	Subtotals	121	15	25	0	0	0	2	0	1	0
Subadult-Subadult	Female absence	23	1	0	0	0	0	0	0	0	0

	Female presence	145	27	0	0	0	0	0	0	0	0
	Subtotals	168	28	0	0	0	0	0	0	0	0
	Grand totals	400	45	46	0	1	0	6	0	3	0

The unique behaviours observed in the context of dominance and responses to agonistic bouts are listed along with descriptions in Supplementary material 1. We found that the behaviours and responses exhibited in independent dominance bouts involving adults and subadults overlapped to a large extent (see Supplementary material 1). The frequencies of different behaviours and responses are plotted in Supplementary material 2.

There were 96 identified males and 105 identified subadult males. Hence, out of the 20100 possible dyads of the 201 males, 0.227 would be adult-adult dyads, 0.501 would be adult-subadult dyads, and 0.272 would be subadult-subadult dyads. If we considered the number of days adult (718 days) and subadult (615 days) males were sighted, then the proportion of adult-adult encounters would be0.290, that of adult-subadult encounters would be 0.497 and the proportion of subadult-subadult encounters would be 0.213. However, among the 456 independent dominance bouts observed, we found that 0.305 were between adults, 0.327 were between adults and subadults and 0.368 were between subadults (Figure 1 compares the observed values to those expected based on the number of identified males).

A greater proportion of adult male-adult male dyads rather than adult-subadult and subadult-subadult dyads were observed to engage in dominance bouts (Supplementary material 4). The proportions of dyads that interacted (out of all possible dyads of males observed engaging in dominance) were 0.191 among adult dyads, 0.084 among adult-subadult dyads, and 0.062among subadult dyads. Twenty-eight per cent of the adult male bouts, but 68.6% of the adult-subadult bouts and 86.3% of the subadult-subadult bouts occurred in the presence of females.

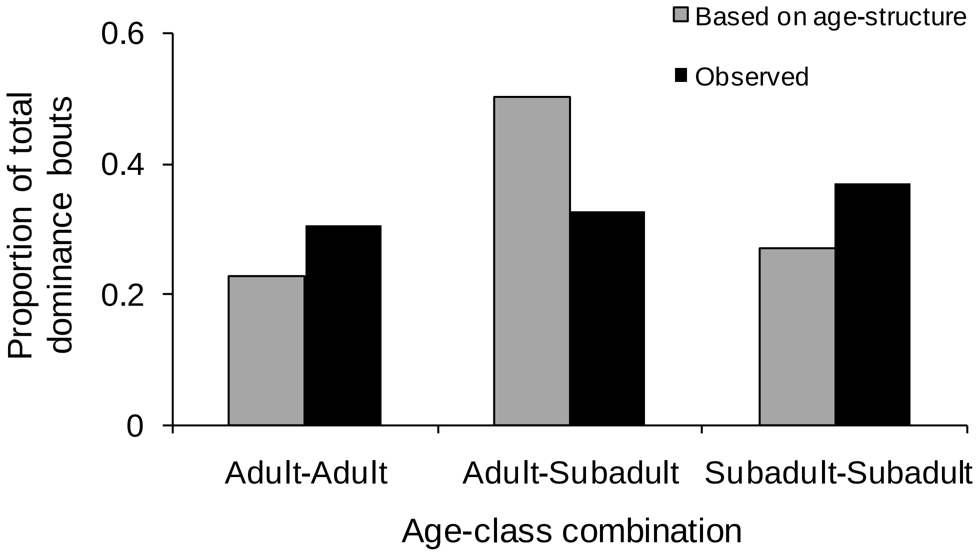


Figure 1. Proportion of dyads of different age-class combination that were expected based on the age-structure and observed engaging in dominance bouts.

Resolution of dominance bouts

We compared the proportions of independent dominance bouts amongst non-musth males of the different age classes that were resolved. Among adult male bouts, only 2 out of 111 bouts were unresolved, thus 98.2% of the bouts were resolved. Among the adult male-subadult male dominance bouts, 87.7% (106 out 121) were resolved, while among the subadult-subadult dominance bouts, 83.3% (140 out of 168) were resolved. The proportion of resolved bouts among adult males was significantly higher than those for the other two age-class combinations, while the proportions of resolved bouts among adults and subadults and among subadults were not significantly different from each other (*P* value for significance after correcting for 3 comparisons is <0.017; test for differences between two proportions (two sided): $P_{\text{Adult\_Adult-Adult\_Subadult}}=0.004$, $P_{\text{Adult\_Adult-Subadult\_Subadult}}<0.001$, $P_{\text{Adult\_Subadult-Subadult\_Subadult}}=0.240$; Figure 2). When we compared the proportion of bouts resolved in female presence and absence in each age-class, none of the comparisons was significant after correction (*P* value for significance after correcting for 3 comparisons: 0.017; test for differences between two proportions (two sided): $P_{\text{Adult\_Adultt}}=0.019$, $P_{\text{Adult\_Subadult}}=0.424$, $P_{\text{Subadult\_Subadult}}=0.091$). Therefore, we combined data of dominance between males in female presence and absence for further analyses.

Figure 2. Percentage of independent bouts among non-musth males that was resolved in the three age-class combinations. Shared letters above the bars indicate no statistical significance in pairwise comparisons (a<b<c).

The age differences between participating males were not different between resolved and unresolved bouts between adult males, adult-subadult male dyads and between subadult males, after flat Bonferroni correction for three comparisons (corrected P: 0.017; Mann-Whitney U tests: Adult-Adult: N_{resolved}=109, $N_{\text{unresolved}}$=2, U=37.000, Z_{adj}=-1.596, P=0.124; Adult-Subadult: N_{resolved}=106, $N_{\text{unresolved}}$=15, U=618.500, Z_{adj}=-1.388, P=0.167; Subadult-Subadult: N_{resolved}=140, $N_{\text{unresolved}}$=28, U=1463.500, Z_{adj}=-2.113, P=0.034). We performed an ANCOVA on the number of non-independent interactions in a dominance bout, with age-class combination and resolution of the bout as fixed factors and age difference between the interacting males as the covariate. There was a significant effect of age difference ($F_{1,389}$=4.980, P=0.026) on the number of non-independent interactions in a bout with an inverse relationship between age difference and number of non-independent interactions. There were no significant main or interaction effects of age-class combination or resolution (ANCOVA: age-class combination: $F_{2,389}$=0.213, P=0.808; resolution: $F_{1,389}$=1.923, P=0.166; age-class combination x resolution: $F_{2,389}$=0.075, P=0.928; see Figure 3) on the number of non-independent interactions within bouts. As the duration of independent bouts was found to be strongly correlated with the number of non-independent interactions in that dominance bout (see Supplementary material 5), we did not separately analyse it.

Similarly, an ANCOVA was also performed on the logit transformed proportion of non-independent interactions that involved aggressive behaviours. Again, age-class combination and resolution of the bout were used as fixed factors and age difference between the interacting males as the covariate.

There was a significant effect of age-difference, with an inverse relationship between age difference and the logit proportion of non-independent interactions with an aggressive behaviour (ANCOVA: age difference: $F_{1,389}$=12.627, P<0.001). There was a significant effect of age-class combination also ($F_{2,389}$=3.424, P=0.033), with the proportion of non-independent interactions with an aggressive behaviour being much higher among subadult-subadult dyads (average ± 1.96 SE: 0.610 ± 0.059) than among adult-subadult dyads (average ± 1.96 SE: 0.307 ± 0.069; Tukey's HSD test: P<0.001) and among adult-adult dyads (average ± 1.96 SE: 0.315 ± 0.065; Tukey's HSD test: P<0.001). The proportions of non-independent interactions with an aggressive behaviour were not different between adult-adult and adult-subadult dyads (P=0.365). There was only a marginally significant effect of resolution (ANCOVA: age-class combination: $F_{2,389}$=3.424, P=0.033; resolution: $F_{1,389}$=3.980, P=0.047) overall on the logit proportion of non-independent interactions with an aggressive behaviour, and the proportion of non-independent interactions with an aggressive behaviour between resolved and unresolved bouts were not different when dyads of the same age-class were considered (Tukey's HSD tests: Adult-Adult: P=0.844; Adult-Subadult: P=0.197; Subadult-Subadult: P=0.273; Figure 4).

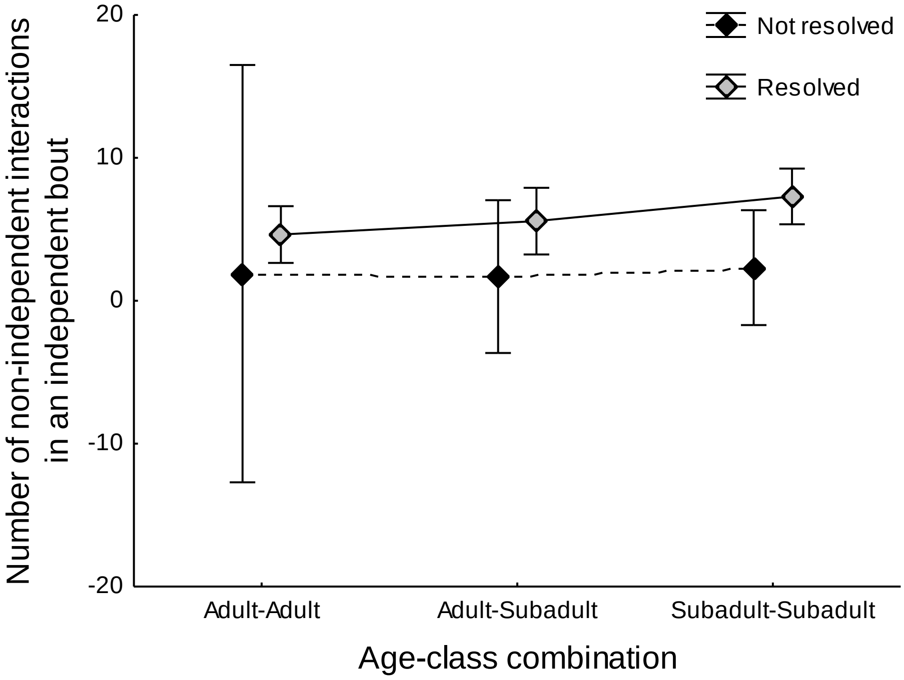


Figure 3. The number of non-independent interactions in an independent bout for resolved and unresolved bouts between males of different age-class combinations. Errors are 95% CI.

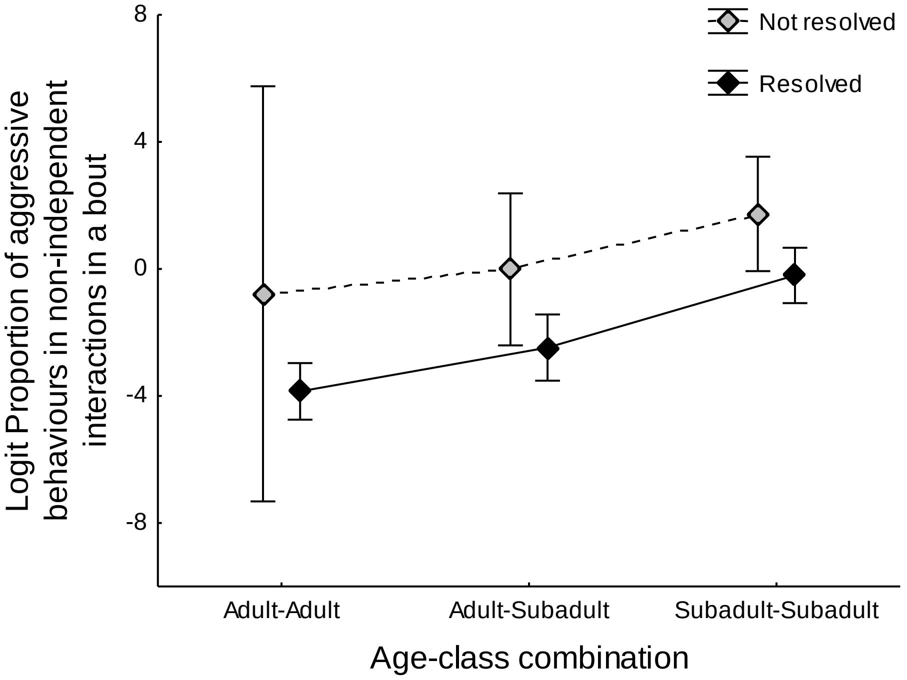


Figure 4. Logit proportion of aggressive behaviours of non-independent interactions in an independent bout for resolved and unresolved bouts between males of different age-class

combinations. Errors are 95% CI.

Among the resolved dominance bouts that began with an agonistic behaviour, we calculated how often the initiator (the male who initiates the first behaviour in the set of interactions of an independent bout) was the eventual winner. The initiator won 96.3% (79 out of 82) of adult-adult dominance bouts, 88.5% (77 out of 87) of adult-subadult bouts, and 77.6% (104 out of 132) of subadult-subadult bouts(all significantly greater than an expected value of 50%, *z*-tests (two sided): $P<0.001$ in all three tests). The proportion of bouts that the initiators won was significantly higher in the adult-adult bouts than the subadult-subadult bouts, while the other two comparisons were not significantly different (test for differences between two proportions: $P_{\text{Adult\_Adult-Adult\_Subadult}}=0.060$, $P_{\text{Adult\_Adult-Subadult\_Subadult}}<0.001$, $P_{\text{Adult\_Subadult-Subadult\_Subadult}}=0.060$; Figure 5).

Figure 5. Percentage of resolved bouts among non-musth males, wherein the first behaviour initiated was non-subordinate, that was won by the initiator. Shared letters above the bars indicate no statistical significance in pairwise comparisons (a<b<c).

Dominance networks and testing for a dominance hierarchy

Despite the adult association network being nonrandom in the absence of females, the adult dominance network was random (the out-degree distribution for the adult male network was not different from a Poisson distribution; χ^2=2.785, *P*=0.248). The subadult dominance network was non-random (out-degree distribution was different from Poisson distribution; χ^2=13.488, *P*=0.004; Figure 6).

We did not find a significant linear dominance hierarchy amongst adult males based on either the Landau's index or the de Vries' index (Landau's *h*=0.044; value expected under random dominance=0.111; de Vries' *h'*=0.134, *P*=0.295 with 10,000 permutations; *N*=26 wild, nonmusth adult males). Similarly, there was no significant linear dominance hierarchy amongst subadult males either (Landau's *h*=0.006; value expected under random dominance=0.054; de Vries'*h'*=0.056, *P*=0.428 with 10,000 permutations; *N*=56 wild, nonmusth subadult males). This was likely because many males did not interact with others, as seen from the low density of both the adult and subadult networks (see Supplementary material 4). When we used the modified Landau's index suggested by Singh *et al*. (2003), the dominance index values increased (adult males: *h*=0.533; subadult males: *h*=0.726).

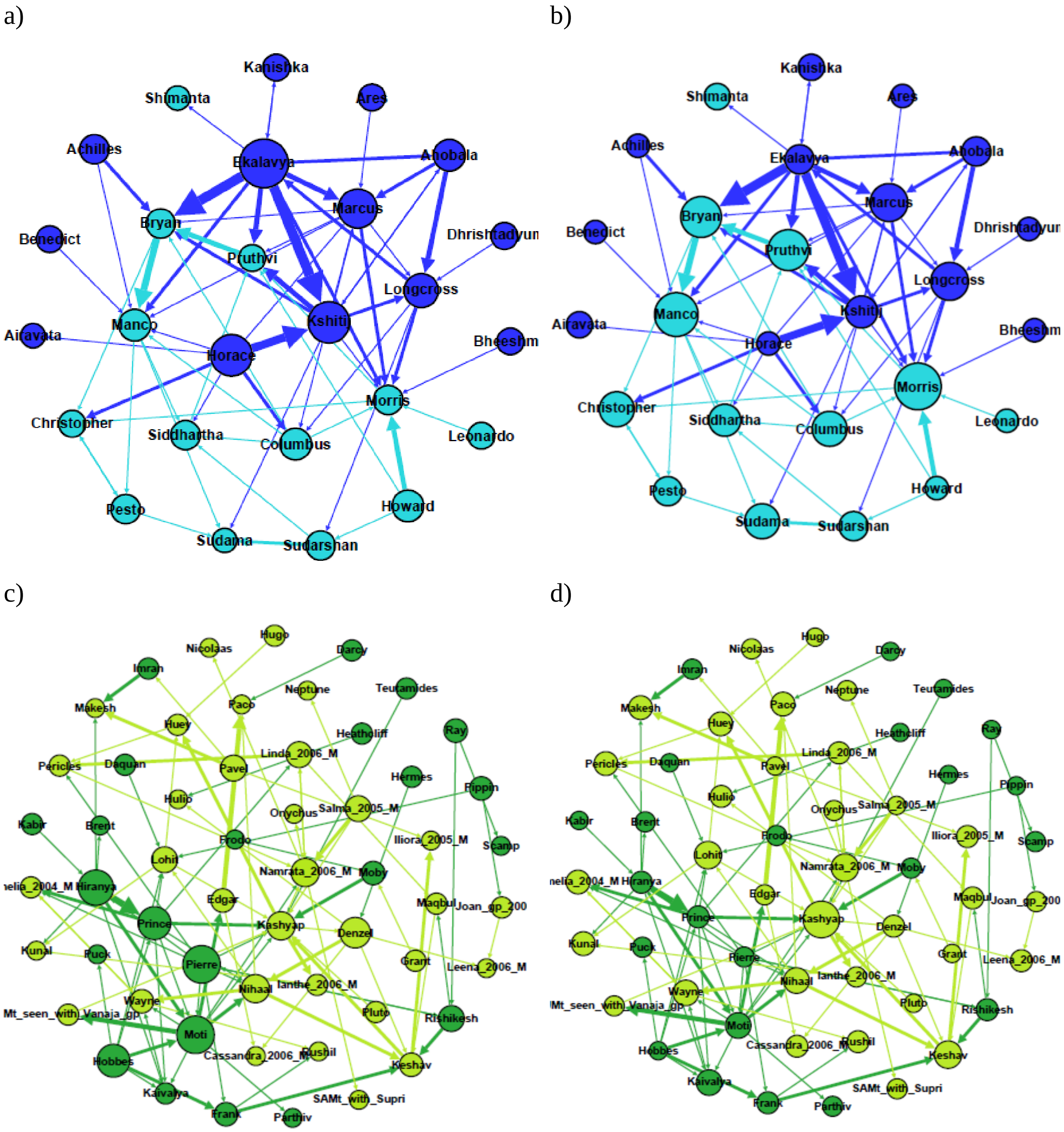


Figure 6. Dominance networks of males in which nodes represent individuals and edges represent bouts. Only independent dominance bouts with a clear winner were used to construct these networks. Nodes representing adultmales over 30 years old are coloured dark blue, those representing adultmales 15-30 years old are coloured light blue,those representing subadultmales 10-15 years old are coloured dark green, and those representing subadultmales 5-10 years old are light green.The panels show a) adult males with nodes sized by out-degree, b) adult males with nodes sized by in-degree, c) subadult males with

nodes sized by out-degree, and d) subadult males with nodes sized by in-degree.

We calculated the different types of triads and found 229 triads amongst adult males wherein two out of the three relationships were resolved (118 double dominants, 94 double subordinates, and 165 pass-alongs) and 44 triads wherein all three relationships were resolved (40 transitive triads and 4 cyclic triads). Thus, only 10.5% of all possible triads had at least two resolved relationships. Amongst subadult male bouts, there were 377 triads with two resolved edges (118 double dominants, 94 double subordinates, and 165 pass-alongs) and only 25 triads wherein all three relationships were resolved (24 transitive triads and 1 circular triad). Thus, only 1.5% of all possible subadult triads had at least two resolved relationships. The t_{tri} values from the observed dataset (adult males: t_{tri}=0.636; subadult males: t_{tri}=0.840) were significantly higher than those from 10,000 randomised datasets, in the case of both adults and subadults (adult males: average ± SD of random values: -0.005 ± 0.333, *P*=0.026; subadult males: average ± SD: 0.002 ± 0.442, *P*=0.016; see Figure 7a). The proportions of triads with two resolved edges that were double dominant or double subordinate were slightly but significantly higher in the observed data (adult males: 0.589; subadult males: 0.562) than in the 10,000 randomised datasets (adult males: average ± SD: 0.5000 ± 0.036, *P*=0.011; subadult males: average ± SD: 0.500 ± 0.029, *P*=0.027; see Figure 7b).

Based on the resolved, independent dominance bouts involving wild, identified nonmusth males, we tested for reciprocity in dominance bouts by performing Mantel *Z*-tests (with 10,000 permutations) between the dominance matrix and its inverse. We found that there was no evidence for reciprocity in adult-adult (*N*=26 adult males, *R*=-0.032, *P*=0.783), adult-subadult (*N*=59 males, *R*=-0.019, *P*=1.000), or subadult-subadult (*N*=56, *R*=0.003, *P*=0.430) dominance bouts. These results indicate that, in all three age-class combinations, the dominance relationships between pairs of males were unidirectional.

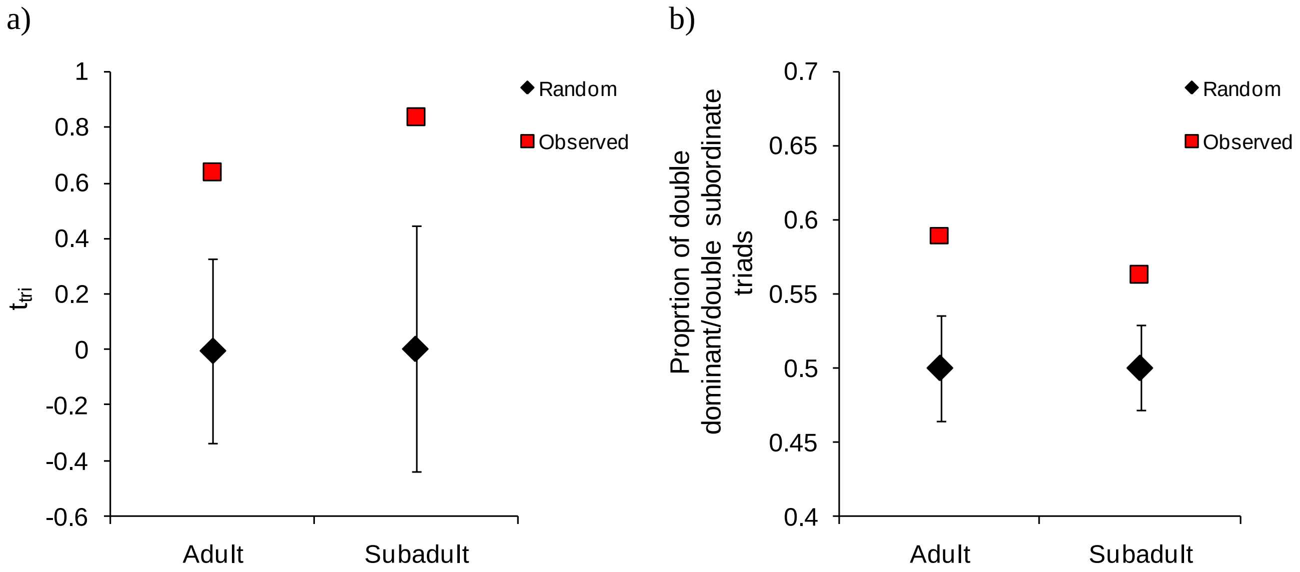


Figure 7. The observed and randomised values of a) the t_{tri}index and b) the proportion of double dominant and double subordinate triads among triads with two resolved edges in dominance bouts between adult males and dominance bouts between subadult males.

Effect of age on winning dominance bouts amongst non-musth males

Older males won 78.9% (86 out of 109) of the adult-adult dominance bouts, 96.2% (100 out of 104) of the adult-subadult dominance bouts, and 74.0% (94 out of 127) of the subadult-subadult bouts. Independent, resolved dominance bouts involving nonmusth males (identified or unidentified but aged) were used to compare the ages of winners and losers, matched fordominance bout. The ages of winners were significantly greater than their corresponding losers in non-musth adult-adult bouts (Wilcoxon's matched-pairs tests: N=109, T=900.500, Z=6.340, P<0.001), adult-subadult bouts (Wilcoxon's matched-pairs tests: N=106, T=32.000, Z=8.836, P<0.001), and subadult-subadult bouts (Wilcoxon's matched-pairs tests: N=140, T=1544.500, Z=6.981, P<0.001).

Factors affecting the outcome of adult-adult bouts

We found that tusks were involved in 17.5% (114 out of 651) of non-independent interactions of adult-adult, 14.4% (74 out of 513) of non-independent interactions in adult-subadult, and 27.5% (342 out of 1242) of non-independent interactions in subadult-subadult dominance bouts. The proportion among subadult males was significantly higher than those for the other two age-class combinations, while the proportions among adult-adult and adult-subadult bouts were not significantly different (corrected P: 0.017; test for differences between two proportions (two sided): $P_{\text{Adult\_Adult-Adult\_Subadult}}=0.162$, $P_{\text{Adult\_Adult-Subadult\_Subadult}}<0.001$, $P_{\text{Adult\_Subadult-Subadult\_Subadult}}<0.001$).As our results indicated that adult-adult bouts were different from adult-subadult and subadult-subadult bouts, with the bouts involving subadults less likely to have a clear winner, we studied the factors that affect the outcome of 108 resolved, independent bouts among nonmusth, wild adult males. This included age of the male (already shown to have an effect in the previous section), body condition, and tusk length. Though musth had already been shown to have a strong effect on the chances of a male winning, musth asymmetry was rare and was observed in only 21 adult-adult bouts. Therefore, we used the bouts wherein musth was not a factor to see how the other potential factors might affect their outcome.

Of the 108 resolved independent dominance bouts involving wild, adult, nonmusth males, the older male won 85 (78.7%, which is significantly different from 50%; z-tests (two sided): $z=5.966$, $P<0.001$) of the bouts and the younger male won the rest (Figure 8). Unlike age, for which all pairs of adult males showed some age difference, significant differences in body condition were observed only in 47 of the 108 (43.5%) interacting pairs. Of these, the male with the better body condition won in 43 bouts (91.5% of the 47 bouts, which is significantly different from 50%; z-tests (two sided): $z=5.689$, $P<0.001$; Figure 8). When we compared the tusk lengths of the interacting males, we found there to be a significant difference in 81 of the 108 bouts (75.0%). Of the 81 bouts, the male with the longer tusks won 43 (53.1%, which is not significantly different from 50%; z-tests (two sided): $z=0.555$, $P=0.579$; Figure 8). Body condition seemed to have the strongest effect, with males in better body condition winning 91.5% of the time. This was also seen from the Generalised Linear Mixed Effects model, in which we used age and body condition (but not tusk length as it did not affect the outcome of dominance) as fixed effects, and the identities of the males in the interacting pair as a random effect (Outcome ~ 1 + Age + Body_condition + (1|InteractingPair); logit link function).Age and body condition both significantly affected the outcome of the dominance bout (generalised linear mixed effects model, binomial distribution, logit link function: $\textit{Estimated coefficient}_{Age}=0.195$, $t_{\text{stat}}=4.101$, $df=105$, $P<0.001$; $\textit{Estimated coefficient}_{Body\ condition}=2.106$, $t_{\text{stat}}=3.447$, $df=105$, $P=0.001$), as did the identities of the interacting pair (*Estimated coefficient*=0.720, $P<0.05$).

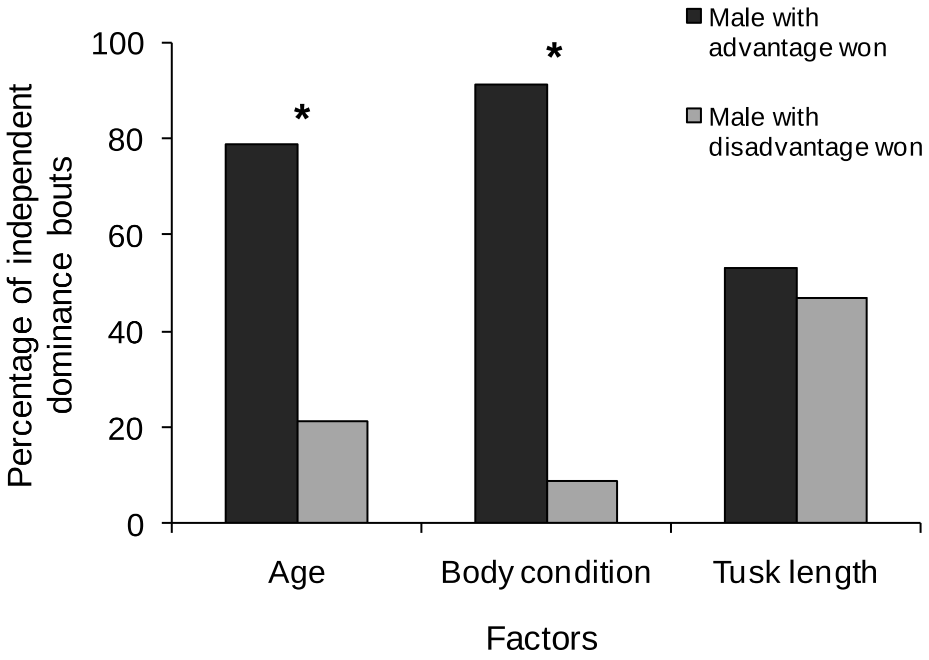
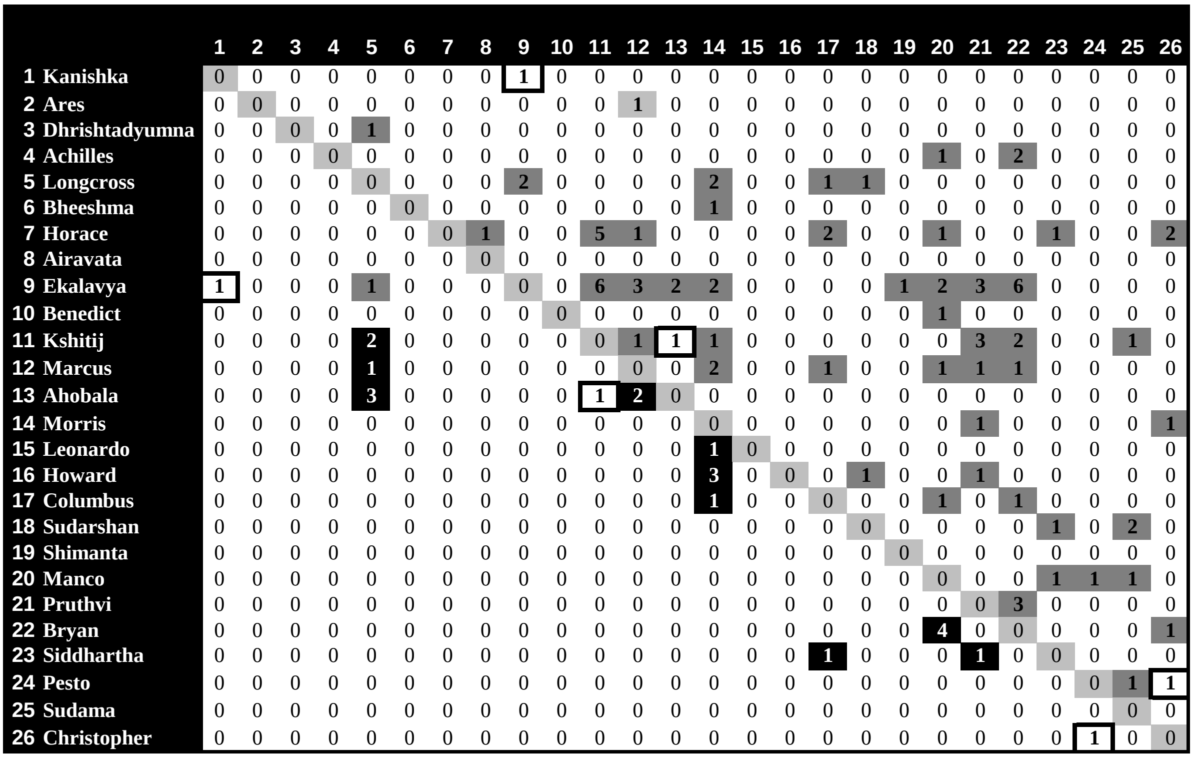


Figure 8. The percentage of independent bouts (with a significant asymmetry between the interacting males with respect to that factor) won by the male with a significant advantage and disadvantage with respect to different factors. The factors where the male with the advantage won significantly more than 50% of the bouts are marked with an asterix.

We also examined age reversals, bouts in which the younger male won, thus going against an age-based hierarchy. The proportion of reversals (entered below the diagonal of the matrix in Figure 9) against age-based dominance was 0.213 (23 out of 108 dominance bouts). Of these 23 reversals, 11 of the younger males had a body condition advantage, another 11 had body condition that was not different from the loser, and the other younger male had the worse body condition of the pair. Of the 62 unique pairs of nonmusth adult males that were observed interacting, the older male won the majority of the bouts in 49 pairs (79.0%), both males won equal numbers of bouts (tie) in three pairs, and the younger male won the majority of the bouts in 10 pairs (0.161 of the total number of pairs).



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Kanishka	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Ares	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 Dhrishtadyumna	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Achilles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0
5 Longcross	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0
6 Bheeshma	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
7 Horace	0	0	0	0	0	0	0	1	0	0	5	1	0	0	0	0	2	0	0	1	0	0	1	0	0	2
8 Airavata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9 Ekalavya	1	0	0	0	1	0	0	0	0	0	6	3	2	2	0	0	0	0	1	2	3	6	0	0	0	0
10 Benedict	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
11 Kshitij	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	3	2	0	0	1	0
12 Marcus	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	1	1	0	0	0	0
13 Ahobala	0	0	0	0	3	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14 Morris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
15 Leonardo	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
16 Howard	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	1	0	0	0	0	0
17 Columbus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0
18 Sudarshan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
19 Shimanta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20 Manco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
21 Pruthvi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
22 Bryan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1
23 Siddhartha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
24 Pesto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
25 Sudama	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26 Christopher	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Figure 9. Dominance matrix for bouts among nonmusth adult males. Males are arranged in descending order of age. The cells where the younger male of the pair won all the bouts are in white text against a black background and the cells where the older male of the pair won all the bouts are shown in black text against a dark grey background. There were four pairs that showed bidirectional relationships, of which three were ties (both males had won an equal number of bouts against the other).These three pairs of cells are shown in black text against a white background and a black border. In the fourth, the older male won the majority of the bouts and hence these cells are coloured dark grey and have black text.

Correlation between association and dominance

In order to examine the correlation between association and dominance, we used data on all independent bouts among identified and wild (excluding the one bout involving a semi-captive camp elephant) nonmusth male elephants. Adult-adult bouts involved 27 unique identified individuals and 63 unique pairs of adult males. We found that a higher proportion of adult males who associated participated in dominance bouts (0.624; 58 out of 93 pairs) when compared to subadults who associated (0.337; 95 out of 282; test for differences between two proportions (two sided): $P<0.001$). There were 5 pairs of adult males and 14 pairs of subadult males who were engaged in dominance bouts but never associated with each other. We compared the number of independent bouts between pairs of these 27 males to the association index (AI) value between them (calculated for the same time period during which the dominance observations were observed) using Mantel test with 5000 permutations and found a significant positive correlation (*R*=0.559, *P*<0.001). The subadult bouts involved 57 unique identified individuals and 109 unique pairs of identified subadults. There was a weak but significant positive correlation (Mantel test: *R*=0.331, *P*<0.001) between the AI values of pairs of the 57 subadults and the number of independent dominance bouts between those pairs.

Comparison of nonmusth male-nonmusth male bouts and musth male-nonmusth male bouts

We observed only 21 independent dominance bouts (comprising 15.9% of the 132 bouts between adult males of known musth statuses) between an adult musth and an adult nonmusth male and 25 independent bouts (comprising 17.1% of the 146 independent bouts between adult and subadult males of known musth statuses) between an adult musth and a subadult nonmusth male. We did not observe any dominance bouts between two musth males. Among the adult-adult bouts, there were only four bouts (19.0% of adult-adult bouts with a musth male) in which the musth male was the younger male of the pair. Of these, only one bout involved a musth male that was more than five years younger than the nonmusth male. Adult males were always the ones in musth in the adult-subadult dominance bouts involving a musth male. All the 46 bouts involving a musth male were resolved. Musth males won over nonmusth males in 20 out of the 21 adult-adult bouts and all 25 of the adult-subadult bouts. In the only instance in which the musth male lost to a nonmusth male, the musth male was older and there was no significant difference in body condition between the two males; therefore, it was not readily apparent why the male lost.

Dominance bouts involving musth males (both adult-adult and adult-subadult) were more common in female presence than in female absence. They also formed a greater percentage of the dominance bouts observed in female presence than those that occurred in female absence. While 28.9% (13 out of 45) of the independent bouts among adults in female presence involved a musth male, only 9.2% (8 out of 87) of those in female absence involved a musth male (test for differences between two proportions (two sided): *P*=0.003; see Figure 10). Independent bouts between an adult musth male and a subadult nonmusth male also seemed more common among the dominance bouts seen in female presence (20.2%; 21 out of 104) than among those in female absence (9.5%; 4 out of 42) but this difference was not statistically significant ($P_{\text{Adult\_Subadult\_F\_absence-Adult\_Subadult\_F\_presence}}$=0.110; see Figure 10).

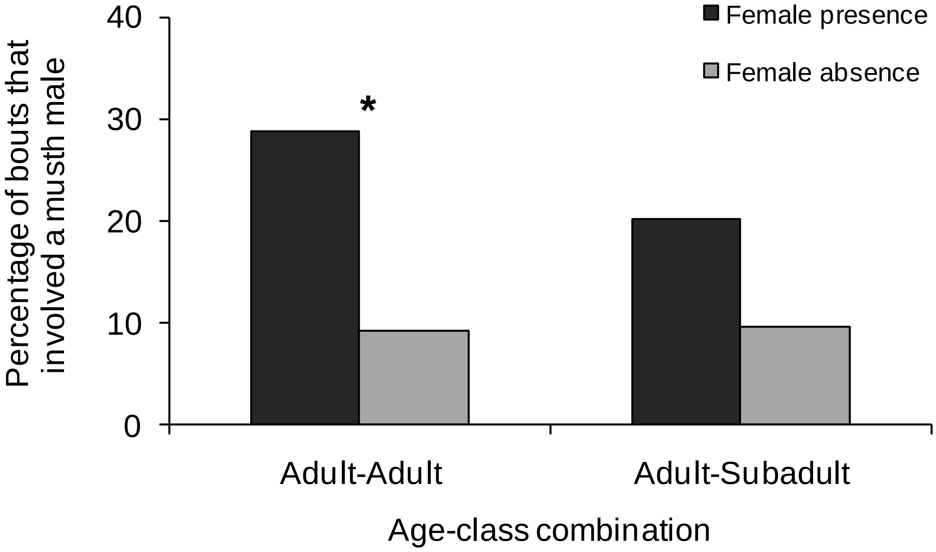


Figure 10. Percentage of independent bouts that involved a musth male in various age-class combinations in female presence and absence. Significant differences are marked with an asterix.

Discussion

We examined dominance interactions among adult and subadult male Asian elephants. This is the first study in this species to compare the dominance interactions of subadults and adults and to analyse adult male dominance above the level of the dyad. This is also only the second study to analyse the factors that affect the outcome of adult dominance bouts. When comparing dominance bouts across different age-class combinations, we used only dominance bouts between nonmusth males and expected bouts among the older, reproductively competitive adult males to be more serious and riskier when compared to the bouts between subadult males. We discuss here, the results of the effects of musth on dominance bouts and examine the factors affecting the outcome of nonmusth adult-adult dominance bouts and compare them to what was seen in the other Asian elephant population in which male dominance has been studied (Chelliah and Sukumar 2013).

Comparison of dominance bouts across different age-class combinations

We found that there was a higher proportion of within age-class (adult-adult and subadult-subadult) dominance bouts and a smaller proportion of between age-class (adult-subadult) dominance bouts compared to what was expected based on the population age-structure. As we had expected, the dyads with the larger age/size differences did not engage in dominance as often as the more evenly matched males. We also found that a greater percentage of all possible pairs of identified males in the adult-adult age-class combination interacted with each other than in the adult-subadult and subadult-subadult age-class combinations. However, even amongst adults, the vast majority of pairs of adult males did not interact. We found that the dominance bouts among adult males occurred primarily (>70%) in female absence, while most of the adult-subadult (69%) and subadult-subadult (86%) bouts occurred in female presence. While analysing male-male associations in the same population (Keerthipriya *et al*. 2018b), we had previously found that subadult males associated to a greater extent with fellow subadult males in female presence than in female absence. Therefore, their greater proportion of dominance interactions in female presence is likely an outcome of their associations.

Dominance bouts among adult males were almost always resolved, with a clear winner, while those involving subadults were less often resolved. As age-differences between participating males, number of non-independent interactions in a dominance bout and physical aggression were not different between resolved and unresolved bouts, it is unlikely that the unresolved bouts are due to the participating males being too evenly matched for a resolution. The dominance bouts among subadults had higher proportions of aggressive behaviours involving physical contact and tusk use than those among adults. Further, adult-adult dominance bouts were won more often by the male who initiated the bout with an agonistic behaviour when compared to the dominance bouts among subadults. Thus, dominance bouts between subadult males were less resolved, involve higher proportion of physical aggression, and the losing (sub-dominant) male initiated dominance more often than in bouts between adult males. This suggests that the outcome may not be as important in these dominance bouts among the young subadults as they possibly are among adults. It is possible that these bouts involve some element of play fighting. Play fighting is expected to involve some degree of reciprocity (though the extent of reciprocity might vary), so that the competition gets attenuated by cooperation (Pellis and Pellis 2017). When comparing aggressive play and agonism in rhesus monkeys, it was seen that aggressive play involves less submissive gestures and more aggression than agonism (Symons 1974). Similarly, Berger (1980) discusses that the head butts of Bighorn sheep lambs are not very risky as they do not have horns, and behaviours signalling play are sometimes missing in their interactions but always present when older animals interacted. When compared to adult dominance, male elephant subadult dominance in Kabini did exhibit some patterns similar to play behaviour. Perhaps subadult dominance is a means to practice for more serious adult fights, in accordance with the motor training hypothesis (Berger 1980). However, the bouts among subadults in Kabini, while seeming to be less serious than those among adults, were also asymmetric and well-defined, just to a smaller extent than adult-adult bouts. For instance, a large proportion of subadult dominance was resolved (83%) and initiating males won the bouts to a high degree (78%). It is possible that juvenile males (1-<5 years of age) in the population may show more symmetric dominance with more play-like features than the subadults do. It would also be interesting to compare how female and male dominance change with age. Females in the Kabini population show fairly high dominance between clans (Shetty 2016).

The high proportion of bouts won by the initiator of the bout indicates that both subadult and adult male elephants are able to accurately assess their relative strength with respect to their opponent even before engaging in the dominance (potentially using visual/auditory/olfactory cues and experiences from previous bouts, if any). This is not a surprising result for a socially complex species like elephants in which males have been shown to use auditory and olfactory cues (Rasmussen *et al*. 2002, Stoeger and Baotic 2016, 2017, Morris-Drake and Mumby 2018).

Testing for linearity and unidirectionality

Dominance bouts in all three age-class combinations were found to be unidirectional and asymmetric. Age had a significant effect on the outcome of resolved bouts in all three age-class combinations; the winners tended to be older than the losers and, as age is related to body size, larger males tended to win more in dominance bouts. There were hardly any age-reversals (where the younger male won over an older male) in adult-subadult bouts, which is not surprising as this age-class combination is likely to have the highest age differences between the participating males. While the Landau's *h* and de Vries' *h*' did not show significant dominance hierarchies, the method proposed by Singh *et al*. 2003 did give much higher values of dominance indices. It is known that the former methods do not work well with sparse networks (networks are likely to be sparse when constructed using data from field studies). The method proposed by Singh *et al*. 2003 did give much higher values of linearity index suggesting that there was some orderliness in the observed data. Among the dyadic relationships that were resolved, we found a higher proportion of transitive triads in the observed datasets than in randomised datasets, in both adult-adult and subadult-subadult dominance bouts. We also found a slightly higher proportion of triads with 2 resolved edges which will give rise exclusively to transitive triads in the observed datasets than randomised datasets. This suggests that there is some 'orderliness' in our dominance networks.

Effect of association index on the frequency of dominance bouts

When we compared the number of independent bouts to the association index between two males, we found that both adult and subadult males interacted more with the adult males with whom they had higher association indices. However, the correlation for subadults was weak. Further, we found that a greater proportion of adult males who associated also engaged in dominance when compared to subadults who associated. Thus, associations seem to facilitate dominance, and the effect seems to be stronger in adult males than subadult males (who may be associating for other reasons than testing strength). When we compared the frequency of bouts between pairs that did interact, adult-adult males had more repeated bouts between the same pair of males than subadult-subadult bouts (Supplementary material 4). Juvenile males in an African savannah elephant population were seen to interact increasingly with unfamiliar males as they grew older (from three years onwards; Lee and Moss 2014). If the subadult males in Kabini were engaging in dominance as practice for future encounters as adults, it would be expected that they compete with different, new opponents rather than repeatedly fighting with the same opponents, which would explain the weak correlation between AI and frequency of dominance, and fewer repeat bouts between the same dyads. In contrast, in the cases of adults, we had speculated that their associations were primarily a way to resolve dominance relationships (Keerthipriya *et al*. 2018a) and the positive correlation between AI and frequency of dominance bouts and repeated bouts between the same pair of males supports that hypothesis.

Factors that affect the outcome of dominance bouts among nonmusth adult males

We used three factors, the age of the male (which has already been proven to have an effect), body condition differences, and tusk length differences to examine the chances of non-musth males winning dominance bouts. We found that, when there was a significant difference in age or body condition, a high proportion of the bouts were won by the male who was older and/or in better body condition. However, males with longer tusks won only about half the bouts when there was a significant difference in tusk lengths. Thus, tusk length did not have a significant effect on the outcome of the bout unlike age and body condition. However, we found that tusk use was not very uncommon in the dominance bouts (17% of all non-independent interactions involved tusk use). Tusks in male elephants in Kabini show a lot variation in their shapes (see Supplementary material 6) and tusk shape might be a better measure of the advantage that tusks provide than tusk length. The shape of the weapon and the effect it has on dominance interactions has been explored in ungulates, where antler shape has been shown to be related to male fighting styles when compared across different bovid and cervid species (Caro *et al*. 2003).

As every pair of interacting males had a non-zero age difference, age had an effect on the greatest number of bouts (even though males with better body condition won more than 90% of the bouts, a significant difference in body condition was observed in less than half the bouts). When we examined age reversals, the younger male had an advantage in terms of body condition in only half the bouts, and there was one instance of a younger male with the worse body condition winning. Thus, a body condition advantage did not seem to be a major factor that allowed younger males to break an age-based hierarchy. The percentage of bidirectional relationships among dyads that we observed interacting (~16%) was much higher than those observed among nonmusth males in African savannah elephants in Amboseli (~4%; calculated from Poole 1982). The percentage of reversals to the age hierarchy of adult males (~21%) in Kabini is close to that of female elephants in Kabini (22%; Shetty 2016).

Comparison with the Kaziranga population

When we compared our observed results with those seen in Kaziranga, the only other Asian elephant population in which male dominance had been studied (Chelliah and Sukumar 2013), we found some similarities and some interesting differences. Both studies found that body size had a significant effect, with larger males winning competitions with smaller males. Although Kaziranga had equal proportions of makhnas and tuskers, unlike the Kabini population that primarily has tuskers, tusk length was not a good predictor of the outcome of dominance bouts in both studies. However, in Kaziranga, Chelliah and Sukumar (2013) found that 80% of the bouts had a musth asymmetry while this was present in only ~16% of the adult-adult bouts in our population. Moreover, 85% of the male dominance bouts in Kaziranga occurred in the vicinity of female herds, possibly because of musth male associations, while <30% of the bouts we observed occurred in female presence. A higher proportion of musth males participating in dominance bouts in Kaziranga was expected due to their higher sighting frequency of musth males when compared to Kabini (Keerthipriya *et al*. 2018d) which might be due to more intense male-male competition or a temporal skew in mating opportunities, leading to multiple males entering musth during that time and, consequently, musth males participating in more dominance. In the Kabini population, there was no seasonal difference or month-wise difference in frequency of musth males (Keerthipriya *et al*. 2018d). The proportion of resolved dominance bouts amongst adults was higher in Kabini (98.5%) than in Kaziranga (88.6% of bouts involving musth and nonmusth males). It is not clear if the lower proportion of resolved interactions in Kaziranga is related to smaller differences in male attributes or the higher frequency of musth. With musth not being a major influence on dominance bouts in our study population, age and body condition are important advantages that help males win in dominance bouts. One more difference between the two populations is in the usage of tusks in dominance bouts. Goring and fencing were apparently not observed in intense tactile interactions in Kaziranga, but 17% of the behaviors initiated in adult-adult non-independent interactions in Kabini involved the use of tusks (this was 27% in subadult-subadult non-independent interactions; however, we have not classified our interactions as intense or not). Perhaps, the difference in tusker to makhna ratio between the two populations has an effect on tusk usage. In our study population, which has more tusked males, males would have had more opportunities to interact with other tusked males and practise using their tusks more from a younger age, possibly enhancing the use of tusks in their interactions as adults.

The role of musth in male-male dominance bouts

Musth had a strong effect on the male winning but a musth asymmetry in dominance interactions was rare. Dominance bouts involving a musth male formed less than 20% of both the adult-adult and adult-subadult dominance bouts. Further, bouts where a younger musth male interacted with an older nonmusth were even rarer (only four instances). Two musth males were never observed engaging in a dominance bout. We had earlier found that pairs of nonmusth males were sighted within the same hour of observation much more often than pairs of older musth and younger nonmusth males and they, in turn, were sighted together much more often than pairs of younger musth and older nonmusth males (Keerthipriya *et al*. 2018c). These relative frequencies were also reflected in the frequencies of dominance bouts between males of various musth status combinations. Thus, musth was a strong determinant of a male's chances of winning a dominance bout but an asymmetry in musth statuses of the participating males was not usually present. We found that adult-adult dominance bouts involving a musth male occurred significantly more often in female presence, while the majority of nonmusth adult male bouts occurred in female absence. We had earlier found that musth males did not spend a greater proportion of their time in female presence when compared to nonmusth males (Keerthipriya et al. 2018c). Thus, musth males seemed to engage in dominance more often when near a female group than when they were away from them. Musth males may be selective about when they express their aggression.

We also found that most of the adult-adult dominance bouts in our population occurred in the absence of females. In one of the studies on African savannah elephants (O'Connell-Rodwell *et al*. 2011) in which male dominance relationships in all-male groups in their 'bull area' had been examined, it had been suggested that dominance in bull areas might occur outside the context of reproduction. It was, in fact, found that the hierarchy formed by males was affected by resource availability; in wet years, the linear hierarchy broke down and the younger, otherwise subordinate males initiated more aggression than in dry years (O'Connell-Rodwell *et al*. 2011). The relationship between resource availability and male dominance has not yet been explored in the Kabini population but, as males and females are not spatially segregated, male dominance in female absence in Kabini might reflect the context of reproduction. Further, male dominance in all-male groups can facilitate males to decide the timing of their musth periods (also discussed in the context of bull areas in Lee *et al*. 2011), which, in turn, might affect other males' movement. We suggest that the dominance we see in female absence in Kabini might help the males establish their dominance relationships, which would then inform their decisions about entering musth and their ranging pattern relative to each other.

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Supplementary Material

Supplementary Material 1. A list of dominance behaviours initiated and the responses to them

We recorded 33 unique behaviours initiated by males and 25 unique responses during dominance bouts. The list of behaviours initiated (Table 1) and the list of responses (Table 2) are below.

Twenty-four of the 32 unique behaviours were seen in adult-adult, adult-subadult and subadult-subadult non-independent interactions and the nine that were not present in all categories were not common behaviours (summed up, those behaviours were exhibited during 1.7% of the total number of non-independent interactions). Similarly, the responses to non-subordinate behaviours in non-independent interactions were also recorded (also listed in Supplementary Material 3) and 16 out of the 25 unique responses observed were seen in dominance bouts of all three age-class combinations. The other nine responses were, once again, rarely seen and constitute 1.6% of the total number of responses to non-subordinate non-independent interactions. Thus, the behaviours and responses in non-independent interactions involving subadult males were similar to those seen in adult-adult interactions.

The behaviours initiated during dominance interactions were classified as ‘Aggressive’ (which usually involved physical contact with the recipient facing the risk of physical injury), ‘Assertive’ (which either involved physical contact or not but did not involve any immediate physical cost to the recipient other than subordinance), ‘Displacement’ (which included displacing or supplanting the recipient from a feeding/drinking/mud splashing site and the recipient incurs a cost only in terms of the resource lost) or ’Subordinate’ (where the subordinate male shows his back or walks away from the other male).

Supplementary Material 1, Table 1. List of behaviours initiated and their category.

Behaviour	Behaviour description	Category
Advance	Walk directly towards opponent	Assertive
Avoid	Move away with no visible threat from the opponent	Submissive
Check	Touch and smell the genital area	Assertive
Chase	Continuously and purposively follow (walk or run after) an individual.	Aggressive
Cower	Cower away with no visible threat from the opponent	Submissive
Displacement	Displace opponent from a feeding/drinking/mud splashing spot	Displacement
Encircle legs with tusks	Convergent or crossed tuskers catching opponent's leg within their tusks and pulling	Aggressive
Head on back	Initiator places his head/trunk on opponent's back	Aggressive
Head on head	Initiator places his head/trunk on opponent's head	Aggressive
Kick	Kick	Aggressive
Looking back and walking	Walking away while turning and looking back with no visible threat from the opponent	Submissive
Lash	Strike with trunk	Aggressive
Pull ears	Pull ears with trunk	Aggressive
Pull leg with trunk	Pull leg with trunk	Aggressive
Poke	Poke with tusks	Aggressive
Push	Push opponent using the head	Aggressive
Pull trunk with trunk	Pull trunk with trunk	Aggressive

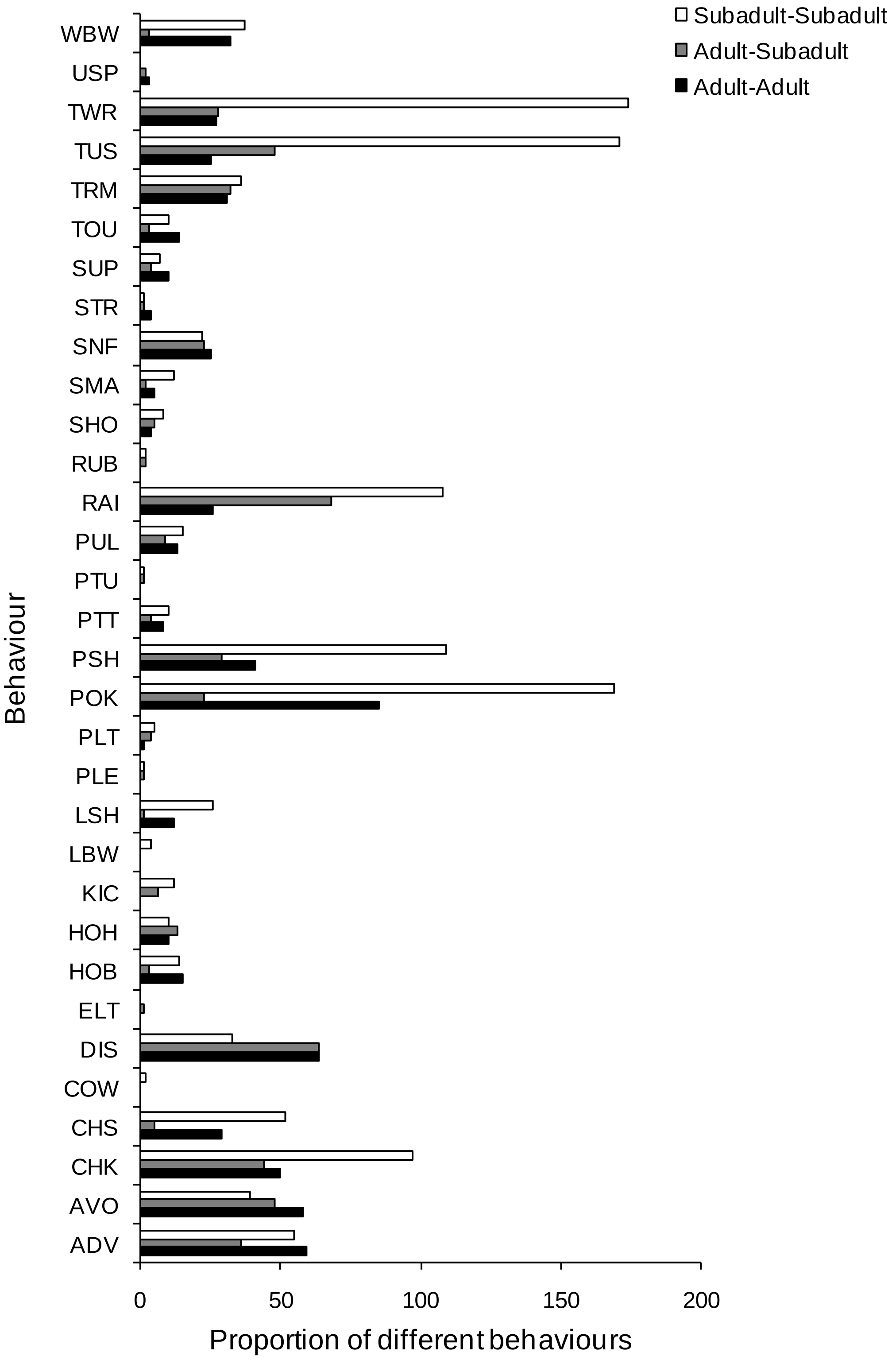
Behaviour	Behaviour description	Category
Pull leg with tusks	Pull leg with tusks	Aggressive
Pull tail	Pull tail	Aggressive
Raise head	Raise head	Aggressive
Rub	Rub against the opponent	Assertive
Shove	Push opponent using the body	Aggressive
Smell anus	Smell anus, mostly with contact	Assertive
Sniff	Smell near the genital area but no contact	Neutral
Strike	Strike using tusks	Aggressive
Supplant	Usurp a feeding/drinking/mud splashing spot from opponent	Displacement
Touch	Touch along the body using trunk	Assertive
Trunk in mouth	Trunk in mouth	Assertive
Tussle	Fencing using the tusks	Aggressive
Trunk wrestling	This involves head butting and trunk wrestling, does not involve tusks	Aggressive
Unsheathe Penis	With no visible threat from opponent	Submissive
Walking backwards	Walking backwards while facing opponent with no visible threat from opponent	Submissive

Supplementary Material 1, Table 2. List of responses to dominance behaviours in non-independent bouts.

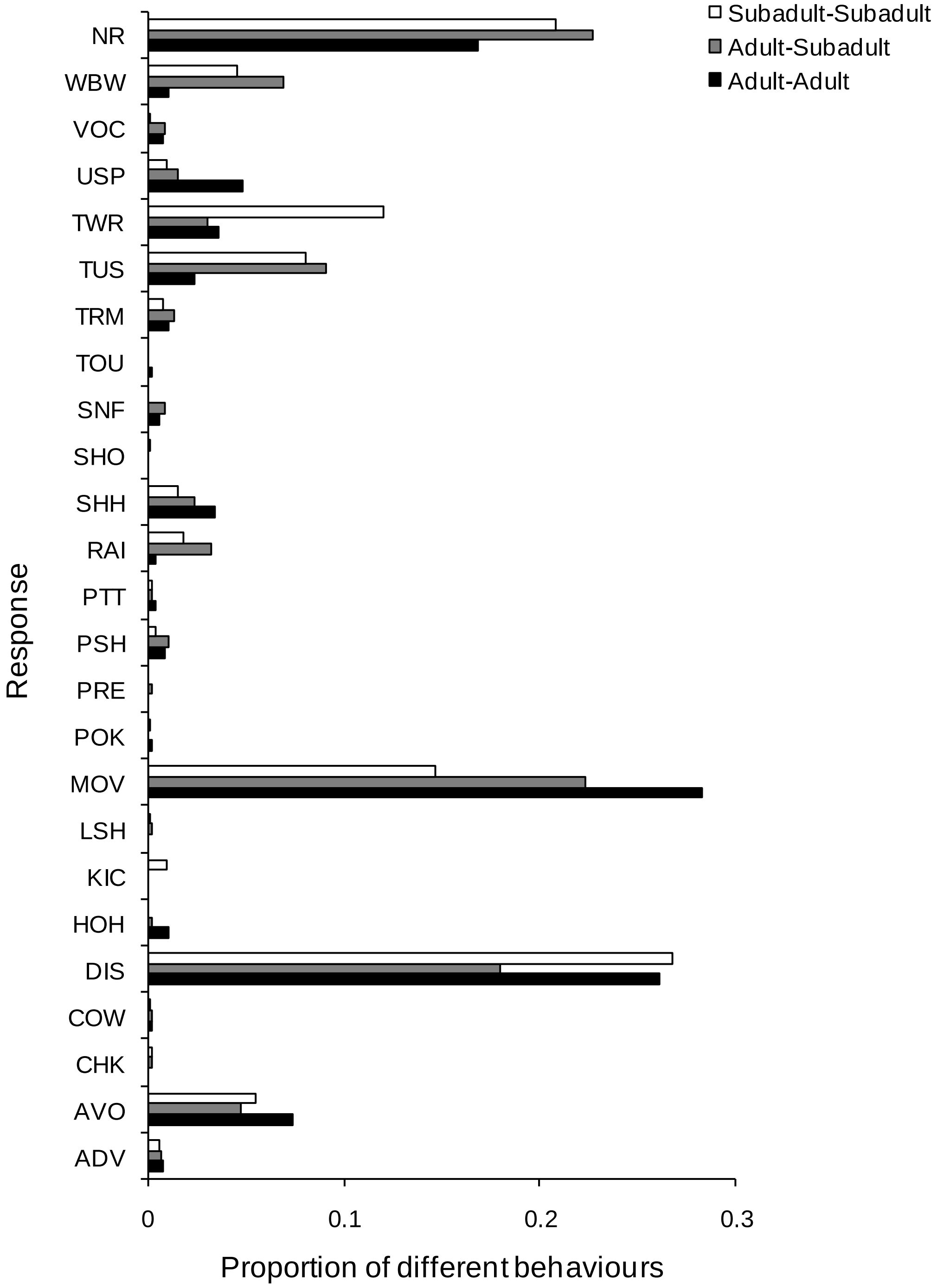
Response	Response description
Advance	Walk directly towards opponent
Avoid	Move away with no visible threat from the opponent
Check	Touch and smell the genital area
Cower	Cower away with no visible threat from the opponent
Distressed	The male keeps fidgeting, not standing still.
Head on head	Male places his head/trunk on opponent's head
Kick	Kick
Lash	Strike with trunk
Move	Move away from initiator
Poke	Poke with tusks
Present backside	Turn around and show back in submission
Push	Push opponent using the head
Pull trunk with trunk	Pull trunk with trunk
Raise head	Raise head
Shake head	Shake head from side to side, disturbed
Shove	Push opponent using the body
Sniff	Smell near the genital area but no contact

Response	Response description
Touch	Touch along the body using trunk
Trunk in mouth	Trunk in mouth
Tussle	Fencing involving the tusks
Trunk wrestling	This involves head butting and trunk wrestling, does not involve tusks
Unsheathe Penis	With no visible threat from opponent
Vocalise	Make noises indicating distress
Walking backwards	Walking backwards while facing opponent with no visible threat from opponent
No reaction	Non-independent interaction was not resolved

Supplementary Material 2. Frequencies of various behaviours and responses



Supplementary Material 2, Figure 1. Frequency of various initiated behaviours in non-independent interactions of different age-class combinations.

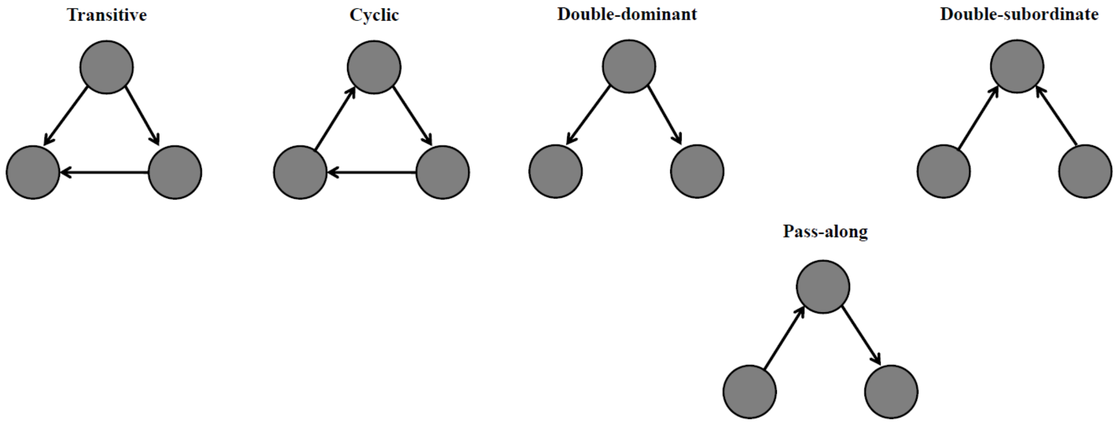


Supplementary Material 2, Figure 2, Frequency of various responses in non-independent interactions of different age-class combinations.

Supplementary Material 3. Various triadic motifs, with two and three resolved relationships.

The different triadic motifs for triads with 3 and 2 resolved edges are shown in Figure 1. Out all possible configurations of triads with 3 resolved edges, 6 give rise to transitive triads and 2 give rise to cyclic triads. Therefore, just by chance, the proportion of transitive triads (P_t) is expected to be 0.75. To account for this, the triangle transitivity (t_{tri}) index is calculated as 4*(P_t-0.75) and varies from 0 to 1. Nodes in a transitive triad can be arranged in a linear hierarchy.

Similarly, for triads with 2 resolved edges, about 50% of all possible configurations form a double dominant or double subordinate motifs (which will lead to a transitive triad regardless of the direction of the third edge) and the 50% form pass-along triads (which can form a transitive or cyclic triad, depending on the direction of the third edge). So, by chance, the proportion of double dominant/double subordinate triads among the ones with 2 resolved edges will be 0.5. This method was proposed by Shizuka and McDonald 2012 as way to analyse dominance datasets where the network is sparse (that is, most pairs of individuals have not interacted with each other), as traditional ways of examining linearity rarely give a significant result with such networks.



Supplementary Material 3, Figure 1. The various triadic motifs with two and three resolved relationships are shown above; arrows go from dominant to subordinate.

References

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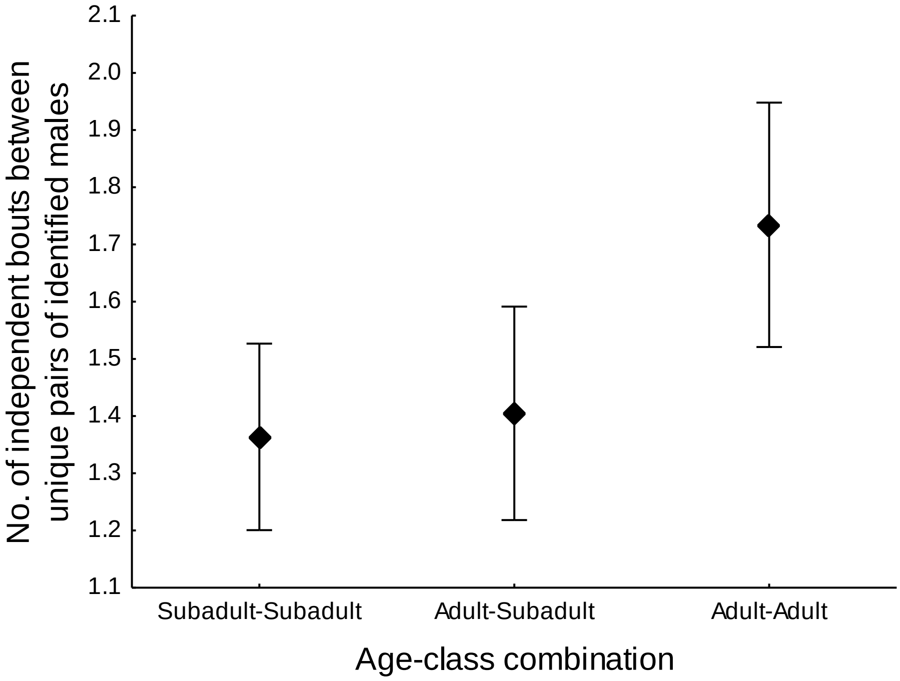
Supplementary Material 4. Percentage of all possible dyads that have interacted and number of bouts between the dyads that have interacted, across age-class combinations

We used the resolved bouts involving wild, identified nonmusth males and calculated the number of unique males and unique pairs of males observed interacting. There were 26 unique males and 62 unique pairs (19.1% of the total number of possible pairs of those 26 males; 325 pairs) among adult-adult bouts, 81 unique pairs involving 30 adults and 32 subadults (8.4% of the 960 total possible pairs) among adult-subadult bouts and 56 unique males and 96 unique pairs (6.2% of the 1540 total possible pairs). We found that the percentage of the total possible pairs that were observed interacting among adult-adult bouts was significantly higher than the values for adult-subadult and subadult-subadult bouts (P value for significance after correcting for 3 comparisons: 0.017; test for differences between two proportions: $P_{\text{Adult\_Adult-Adult\_Subadult}}<0.001$, $P_{\text{Adult\_Adult-Subadult\_Subadult}}<0.001$, $P_{\text{Adult\_Subadult-Subadult\_Subadult}}=0.053$; Figure 1 below). We used the resolved and unresolved bouts among identified, wild males and calculated the number of independent bouts that occurred between each of the unique pairs that were observed to interact. We compared these values using a one-way ANOVA with age-class combination as the factor. We found that age-class combination had a significant effect ($F_{2,255}=4.030$, $P=0.019$) and that the values for adult-adult bouts were marginally significantly higher than those for subadult-subadult bouts while other comparisons were not significant (Tukey’s HSD test: $P_{\text{Adult\_Adult-Adult\_Subadult}}=0.057$, $P_{\text{Adult\_Adult-Subadult\_Subadult}}=0.018$, $P_{\text{Adult\_Subadult-Subadult\_Subadult}}=0.943$; Figure 2 below).

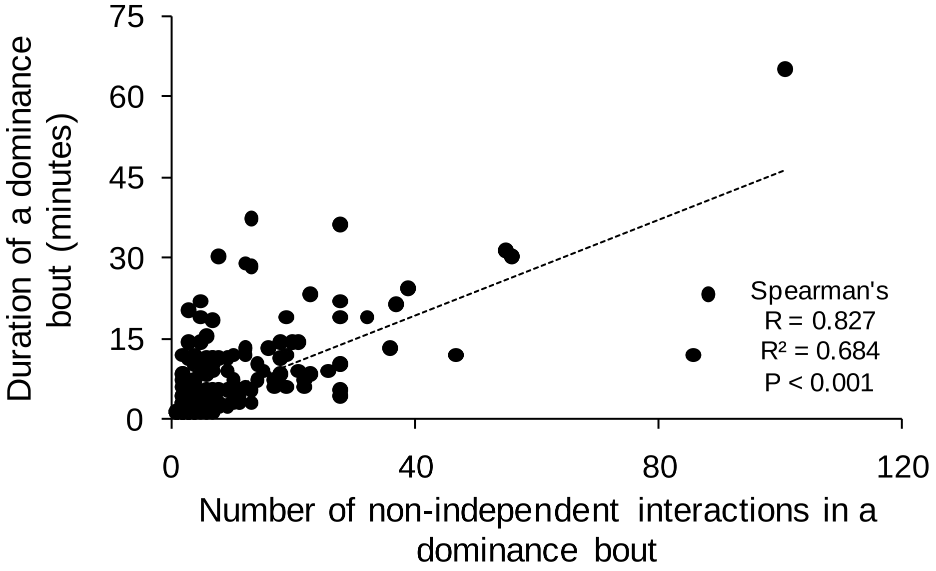
Supplementary material 4, Figure 1. The percentage of all possible pairs of the unique males seen engaging in dominance bouts that were observed interacting.



Supplementary material 4, Figure 2. The number of independent bouts between the unique pairs of males in various age-class combinations. Error bars are 95% CI.

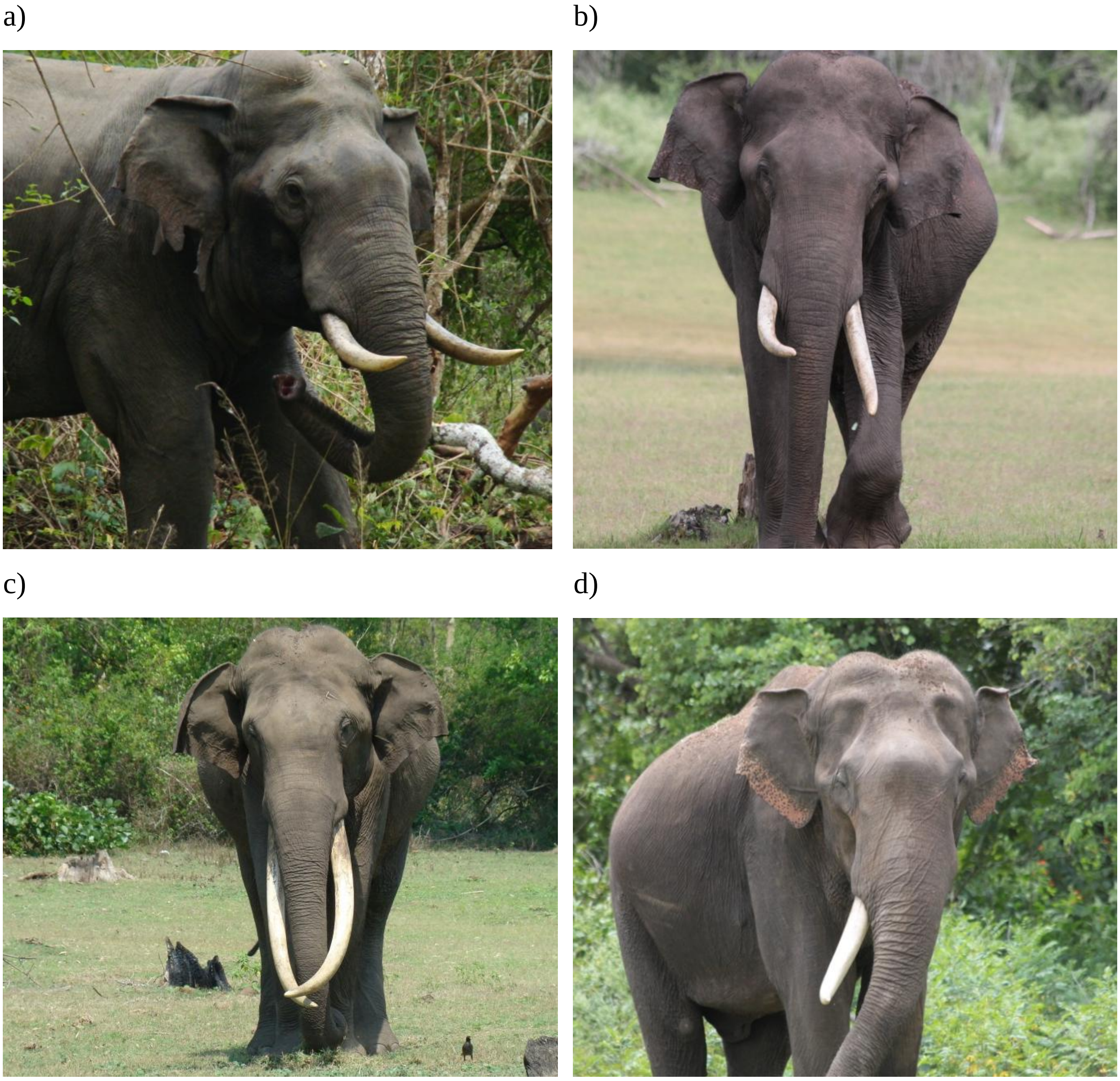
Supplementary Material 5. Correlation between duration and number of non-independent interactions in an independent dominance bout.

For the 400 (resolved and unresolved) bouts between nonmusth males, we correlated the duration of a dominance bout with the number of non-independent interactions in that dominance bout and found that the two values were strongly correlated with each other (Figure 1).



Supplementary Material 5, Figure 1. The duration of a dominance bout and the number of non-independent interactions in that bout. The results of the Spearman's rank-order correlation between the variables are shown.

Supplementary Material 6. Various tusk shapes of adult males in Kabini



Supplementary Material 6, Figure 1. Adult males with different tusk shapes.

CHAPTER 7

Conclusions

Conclusions

This is the first quantitative study of the social structure of female Asian elephants in India. This was the first study to examine in detail, the sociality of adult and subadult male elephants, the agonism between these males, and how musth affects associations and agonism, using various statistical tests, network analysis, and randomisation techniques. I found that male associations were complex and affected by female presence and male age. I also found that the sociality of male Asian elephants is somewhat different from that of the African savannah elephant, which, having been studied intensively, is often used as being representative of elephants in general. While both species show female philopatry and male dispersal, adult male Asian elephants spent a majority of their time solitarily and more time in mixed-sex groups than in all-male groups with other males (only ~10%). African savannah elephants are known to spend a large proportion of their time with other males in bull areas (Poole 1982). Within the time they spent in all-male groups, adult male Asian elephants in Kabini spent more time than expected with their age-class peers, whereas the time the two different age-classes of adults spent together was less than expected by chance. We found that old males were not central in male association networks, and old and young males were equally likely to approach either to associate. These results suggest that social learning from older males is probably not central to the formation of all-male groups of adult males. Thus, in comparison to associations of male African savannah elephants in Amboseli (Chiyo *et al.* 2011), there were fewer associations between males, smaller group sizes, and a limited role of older males in all-male groups in Kabini. These differences might stem from differences in spatiotemporal distribution of food resources in the habitats that the two species occupy. However, in the Samburu African savannah elephant population, when male associations were examined after controlling for their sexual state (inactive and active), there was no relationship between age and centrality in the sexually inactive network and a negative correlation in the sexually active network (Goldenberg *et al*. 2014). Thus, examining associations in all-male groups irrespective of sexual state was thought to lead to an exaggerated role of older males (Goldenberg *et al*. 2014). It would be important to examine social structure in multiple populations in both species in the future.

Male associations in Kabini were influenced to a large extent by male age, with subadults and adults showing differences in associations, and associations varying even within broad age-classes of subadults and of adults. The patterns found seem to reflect the increasing competition expected with male age. Subadults spent about twice the proportion of their time (~75%) in mixed-sex groups as adults did, and this proportion of time spent with females decreased with increasing age of subadults. Similar to adult males, subadult males spent their time in all-male groups with age-peers, and older subadults were not central to association networks. The time spent with age-peers by adult and subadult males seems to be useful in testing strengths and clarifying dominance relationships with similarly aged/sized males. In keeping with the experience that is expected to be gained over time, the agonistic interactions among adult males were almost always resolved, while subadults showed a greater proportion of unresolved interactions, interactions wherein the eventual loser initiated the agonism, and a higher proportion of physical contact.

Male associations in Kabini were also influenced to a large extent by female presence. This effect was different depending on male age. While subadults spent a larger proportion of their time with other subadults in female presence than absence, and association networks of subadults were better connected in female presence than absence, adults spent similar proportions of their time with other adults in female absence and presence, and the association network in female absence was better connected than the one in female presence. These differences would, at least in part, result from subadults not having completed dispersal from female groups. However, there were also differences between age-classes within subadults and adults, the most noticeable being that old (30 years of age and older) and young (15-30 years of age) adults showed differences in associations in female presence and absence. Young adult males did not seem to view each other as competitors and spent more time with other young adults in female presence than expected. However, old adult males avoided one another in female presence while associating with one another more than expected by chance in female absence. Old males did not seem to consider young males a threat and old and young males met each other at random in the presence of females. It is possible that this might provide the young males with opportunities for sneak mating. In African savannah elephants, older musth males achieved more paternity success than younger, nonmusth males (Hollister-Smith *et al*. 2007, Rasmussen *et al*. 2007). However, among nonmusth males, age did not have an effect and nonmusth males of all ages attained a constant low level of reproductive success (Hollister-Smith *et al*. 2007). From the observed patterns of associations and low frequency of musth, it is possible that age would have an effect on male reproductive success of nonmusth males in the Kabini population. It would also be interesting to examine the paternity of calves that were sired when different males associated with receptive females at the same time in the Kabini population.

Since subadult males form more associations with other subadults in female presence than in female absence, associating with their age/sex peers seems unlikely to be the proximate reason for male dispersal from natal groups. An alternate proximate reason for male dispersal from the natal group may include feeding restrictions, which may be disproportionately greater on the larger males than females, while feeding in groups, resulting in males either voluntarily dispersing away or being slowly evicted from the group by females. It would be interesting to examine feeding rates and dominance directed to subadults of both sexes by adult females to evaluate this alternative. Since subadult males spent over 70% of their time in female absence solitarily, resource limitation may be a possibility. Adult males also formed only small all-male groups, with the vast majority of the group sizes being two. Analysis of feeding rates by adult males in groups of different sizes will enable an assessment of feeding constraints.

The influence on male associations in Kabini by female presence is somewhat similar to reproductively active and inactive males associating differently in the African savannah elephant in Samburu (Goldenberg *et al*. 2014). However, in the absence of bull areas in Kabini and the lack of distinct reproductive and non-reproductive states outside of musth, the two are not directly comparable. I found musth to affect male associations, with old adult musth males spending a slightly higher proportion of their time with female groups and associating with larger female groups than their nonmusth counterparts, but young adult musth males spending a smaller proportion of their musth time with female groups than young adult nonmusth males and associating with female groups of similar sizes in and out of musth. While old adult males in musth seemed to tolerate the presence of nonmusth young adult males in female presence, young adult musth males were never sighted in mixed-sex groups with an old adult nonmusth male. Therefore, across these broad age categories, musth was not a means for younger males (which came into musth much less frequently than older males) to temporarily gain an advantage over older males and gain access to female groups. Instead, it seemed to allow the older males to rove and search widely for mating opportunities (see Hall-Martin 1987). In the African savannah elephant, dominance between two musth and two nonmusth males were both decided by body size but when a musth and a nonmusth male interacted, musth, and not body size, decided the winner (Poole 1989). This was also the case in Asian elephants in Kaziranga, in which musth males won almost all the dominance interactions they were involved in, regardless of body size differences (Chelliah and Sukumar 2013). I also found that musth males almost always won over nonmusth males in Kabini, but there were only four interactions between a younger musth male and an older nonmusth male, and only one out of the four involved males with an age difference of more than 5 years between them. The younger musth male won in all four dominance bouts. The proportion of musth males in Kabini was much smaller than those in Mudumalai (Daniel *et al*. 1987, Desai 1987) or Kaziranga National Park (Chelliah and Sukumar 2015), making musth a strong but rare advantage in adult male agonism in Kabini. It is possible that the occurrence of musth is affected non-linearly by the number of competitors present in the area. I also found no evidence of spatiotemporal separation of musth males at scales larger than associations. Radiocollaring subadult and adult males would allow for a much better understanding of male dispersal and musth ranging. In Sri Lanka, a radiocollared male (aged 25-35 years) had been observed during two annual musth periods and, in both cases, the musth range of the male had been much larger than his nonmusth home range, suggesting that musth is a mate searching strategy (Fernando *et al*. 2008).

Among nonmusth adult males in Kabini, age and body condition had a significant effect on the outcome of dominance bouts, but tusk length did not have a significant effect. Similar results were also observed in Kaziranga, but tusks were not found to be used in goring or fencing during intense tactile dominance interactions (Chelliah and Sukumar 2013). As in Kabini, male African savannah elephants also use their tusks to fence and gore during dominance interactions (Poole 1989, Poole and Granli 2011), but the effect of the length of tusks in these interactions was not examined. Agonistic interactions in Kabini usually occurred in the absence of females, unlike those involving musth males, which were more common in female presence. It will be interesting to examine whether adult male dominance relationships resolved under nonmusth condition influences the identities of males who enter musth.

In summary, this thesis provides new information on male sociality and competition and the role of musth by using long-term data on continuously monitored, identified male elephants. In the future, it would be interesting to examine how relatedness affects associations between males and between males and females. Further, by analysing data on dominance and feeding behaviour of females and natal subadult males, we can examine other possible proximate reasons for male dispersal. It would also be illuminating to examine how musth and male age affect the male's interactions with females, whether females respond differently based on these factors, and how all of these translate into reproductive success of the males.

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