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

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Abstract

We present here, the first detailed study of 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. 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 than with 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 test strengths against age-peers 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.

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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). Interactions between males in such species, especially if the species is polygynous, 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 between males in species with female-philopatry are expected to be uncommon and occur primarily in the context of coalitions to defend or contest access to females (for example, Saayman 1971 in baboons, Schaller 1972, 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, all-male groups are formed during foraging in some polygynous species, usually in the non-breeding season (for example, Lettevall *et al.* 2002 in sperm whales, Mooring *et al.* 2003 in desert bighorn sheep, Fischhoff *et al.* 2009 in plains zebras, Chiyo *et al.* 2011, 2012 in African savannah elephants). Male associations in such groups may be motivated by 1) the opportunities available for social learning (possibly African savannah elephants, Chiyo *et al.* 2012), 2) the presence of age-mates, possibly to test their strengths against each other (mouflon sheep, Bon *et al.* 1993, African savannah elephants, Chiyo *et al.* 2011), 3) increased efficiency in obtaining food resources (river otters, Blundell *et al.* 2002), or 4) improved defense against predators (Cape ground squirrels, Waterman 1997, sperm whales, Cure *et al.* 2013). However, there has been little study on male association patterns in mammals overall.

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

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are expected to compete intensely. Therefore, male-male affiliative associations in the species are expected to be very weak. Male African savannah elephants have been shown to have weak associations but 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, 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 correlated with a different male social structure than 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 might be based on opportunities available for a) social learning from older individuals and/or b) testing strengths. 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

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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

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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. 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.

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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 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 (<1 year), 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

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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 10 m (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. Males could indulge in sparring during their associations, but if males, upon encountering each other, displayed only aggressive interactions and moved away, they were not said to be associating.

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

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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 possibile 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

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procedure for randomising associations found in Whitehead (2008, pg. 124, following the method of Bedjer *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

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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 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, $AI_{AB(F_abs)}=N_{AB(F_abs)}/(N_{A(F_abs)}+N_{B(F_abs)}-N_{AB(F_abs)}$, 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

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female presence and absence to their Poisson expectation (expected for a 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 $AI_{AB}=AI_{BA}$) 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

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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 2015). 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

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avoidances (Whitehead 2015). 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 1). 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 with male age

Based on sightings in which all adult males were aged and identified, there were a total of 96 identified elephants (see Supplementary material 1, 2). 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

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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). 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 3).

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

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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;

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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). The time 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 4).

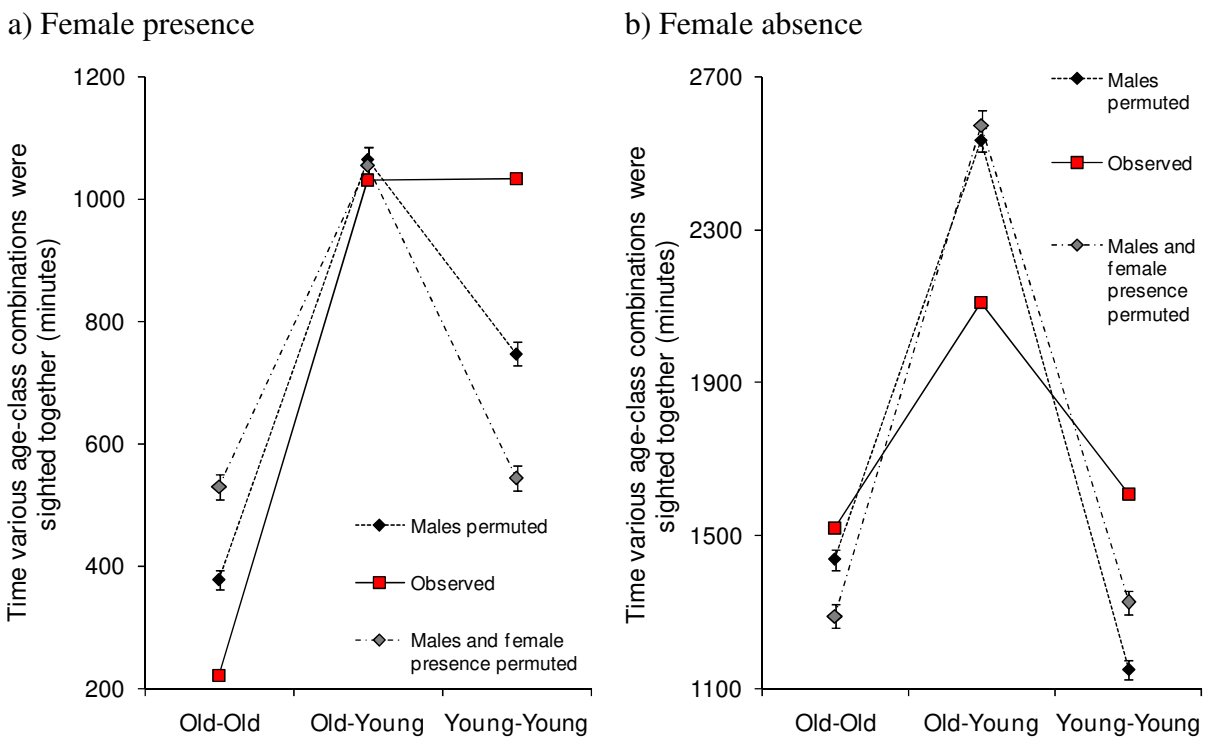

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Figure 1. Permuted and observed values of time spent together by adult males of the same and different age-classes in a) female presence and b) female absence. Old males are >=30 years and young males are 15-30 years old. Please note that the Y axis 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: $N_{F_presence}$=33 pairs of males, $N_{F_absence}$=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).

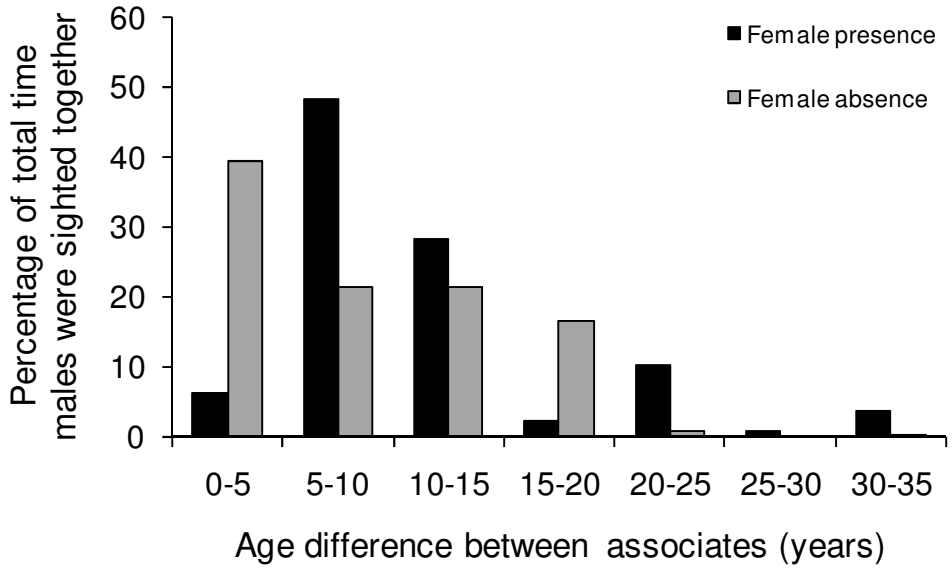

Figure 2. Percentage of total time in female presence and absence that males of various age differences spent together.

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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 5). 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).

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

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 6). The modal experienced group size (counted as the number of adult males) was 1 (Supplementary material 6). 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

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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).

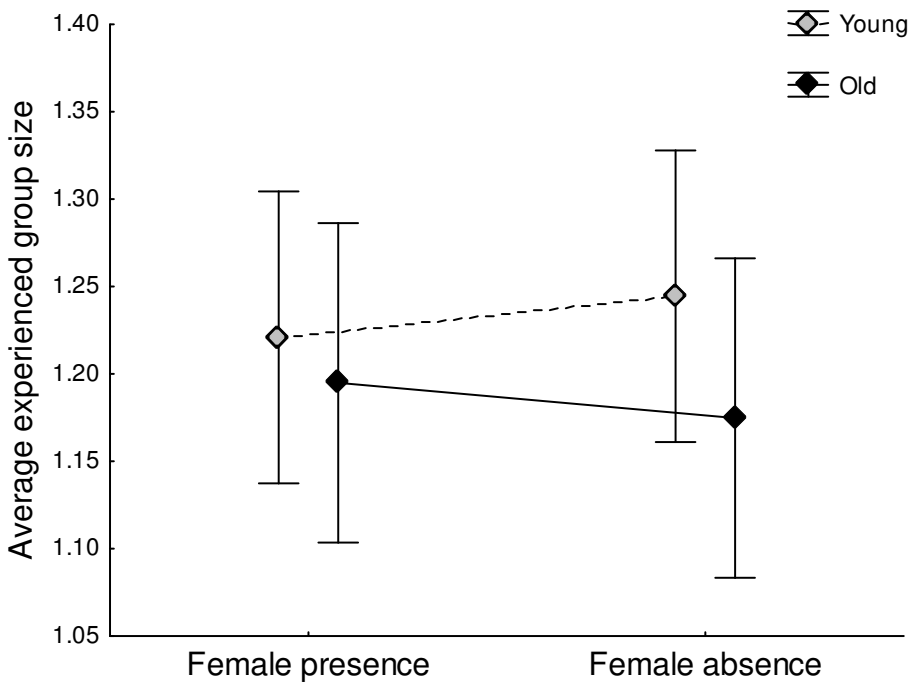

Figure 3. Average experienced group size (number of adult males) experienced by common males of both age-classes, in female presence and absence. Error bars are 95% CI.

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 7). 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.

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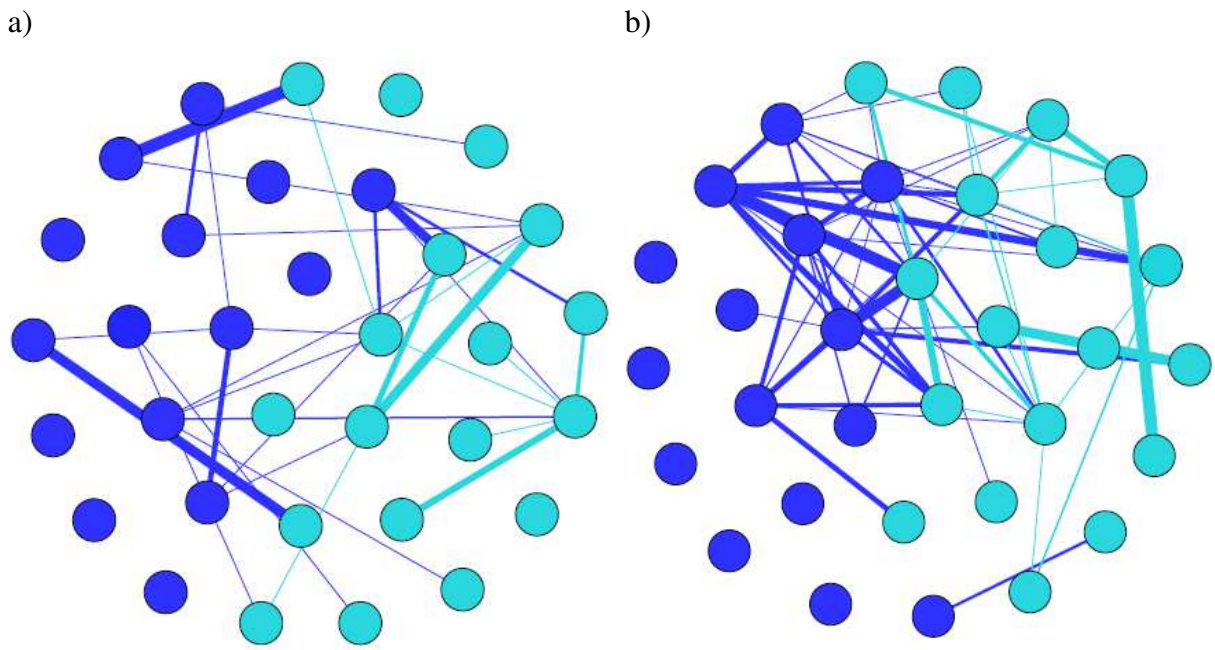

Figure 4. Undirected association networks of adult males (33 males seen on >=5 different days each in female presence and absence) in a) female presence and b) female absence. Nodes representing males >=30 years are coloured dark blue and those representing 15-30 year old males are coloured light blue. 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 $\text{difference}_{\text{random}} \geq \text{difference}_{\text{observed}}$) / 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)

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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 6). 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 8). 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 8).

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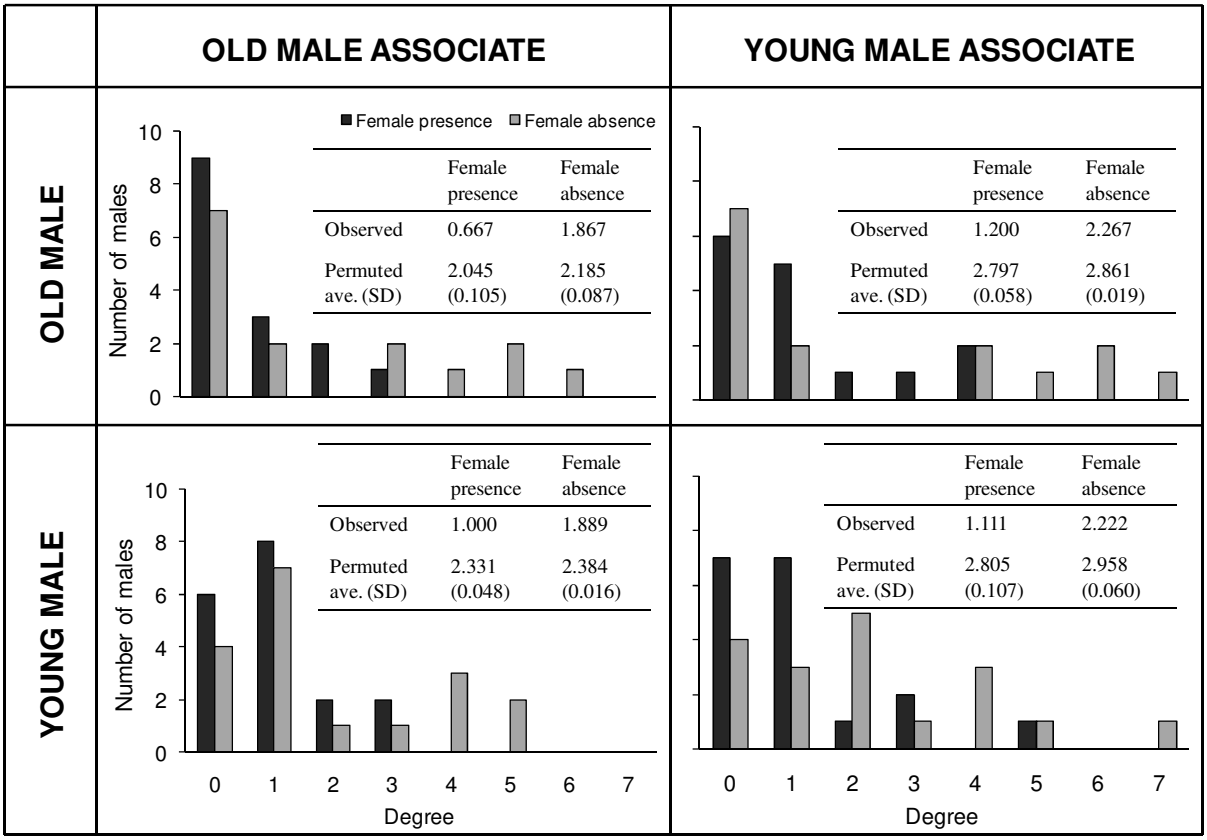

Figure 5. Degree distributions in female presence and absence of (clockwise from top left) old males with old males, old males with young males, young males with young males and young males with old males. The average degrees, based on the observed and permuted datasets, are shown inside each panel. 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 9). 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).

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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 8), 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 10). 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 11).

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

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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}	Median AI_{Top}, AI_{Others}	P	N_{Top}, N_{Others}	U, Z_{adj}	Median AI_{Top}, AI_{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 adult male associations 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 1). The percentage of time spent alone (without females or another adult male) was greater in Kabini (~54%) than in Amboseli (~18%). Not only was the percentage of time spent in all-male groups lower in Kabini than in African savannah

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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 12). 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) 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). 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.

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. Adult males of older age-classes (35+ years of age) had been sighted more frequently with female groups than adult males of younger age-classes (15-25 and 25-35 year age-classes) during a study in the neighbouring Mudumalai Wildlife Sanctuary (Daniel *et al.* 1987), which has tall grass (that elephants feed upon) areas and greater grass biomass (Sivaganesan 1991, Baskaran *et al.* 2010) than in our study area (Gautam *et al.* 2017). However, the average group size of adult males (including solitary males) was only 1.1 in Mudumalai Wildlife Sanctuary also (Daniel *et al.* 1987), as in our study. The maximum all-male group size was 2 in Mudumalai (Daniel *et al.* 1987) compared to the maximum group size of 6 we observed in Kabini. However, the latter was observed only for 65 minutes (0.13% of the total female absence time), therefore, it is not surprising that a shorter study may not have observed these larger groups. A maximum adult male group size of 5 was observed in Gal Oya in Sri Lanka (McKay 1973) and the maximum group size in Amboseli was 18 (Chiyo *et al.* 2011). 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

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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).

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

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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. In fact, 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 4). 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). The greater social role of older males in the African savannah elephant compared to the Asian elephant

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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 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. 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, 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 -

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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. 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. 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

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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). 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

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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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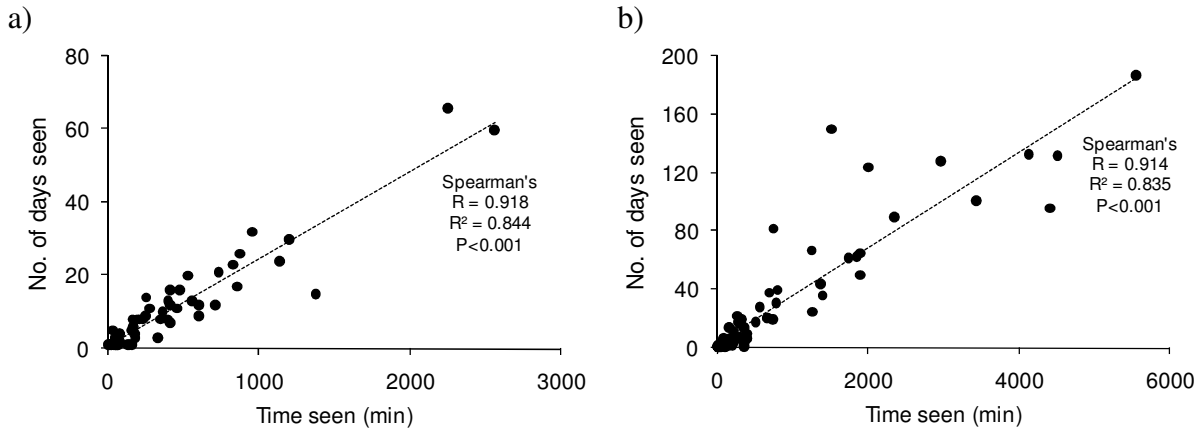
Supplementary Material

Supplementary Material 1. 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 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.

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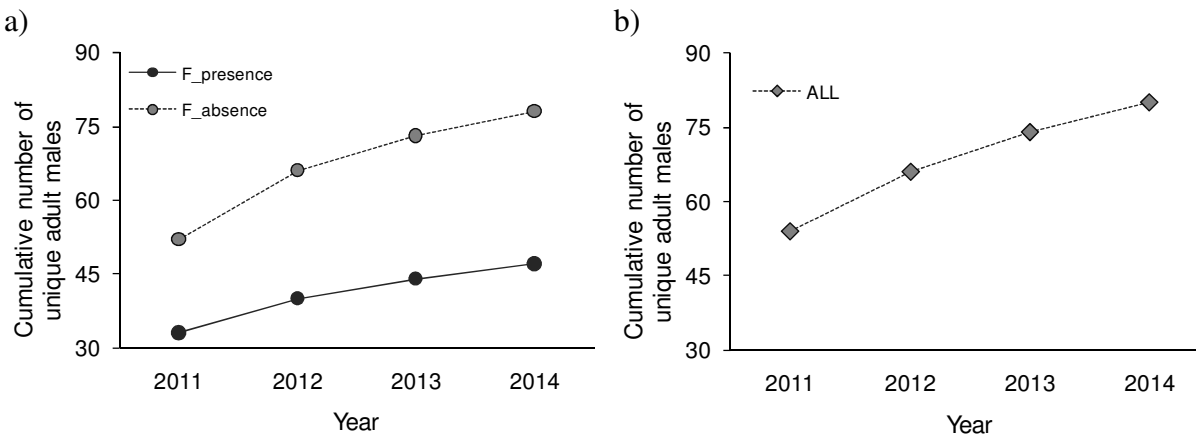
Supplementary Material 2. Cumulative number of males identified.

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 2, 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).

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Supplementary Material 3. 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 3, 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.

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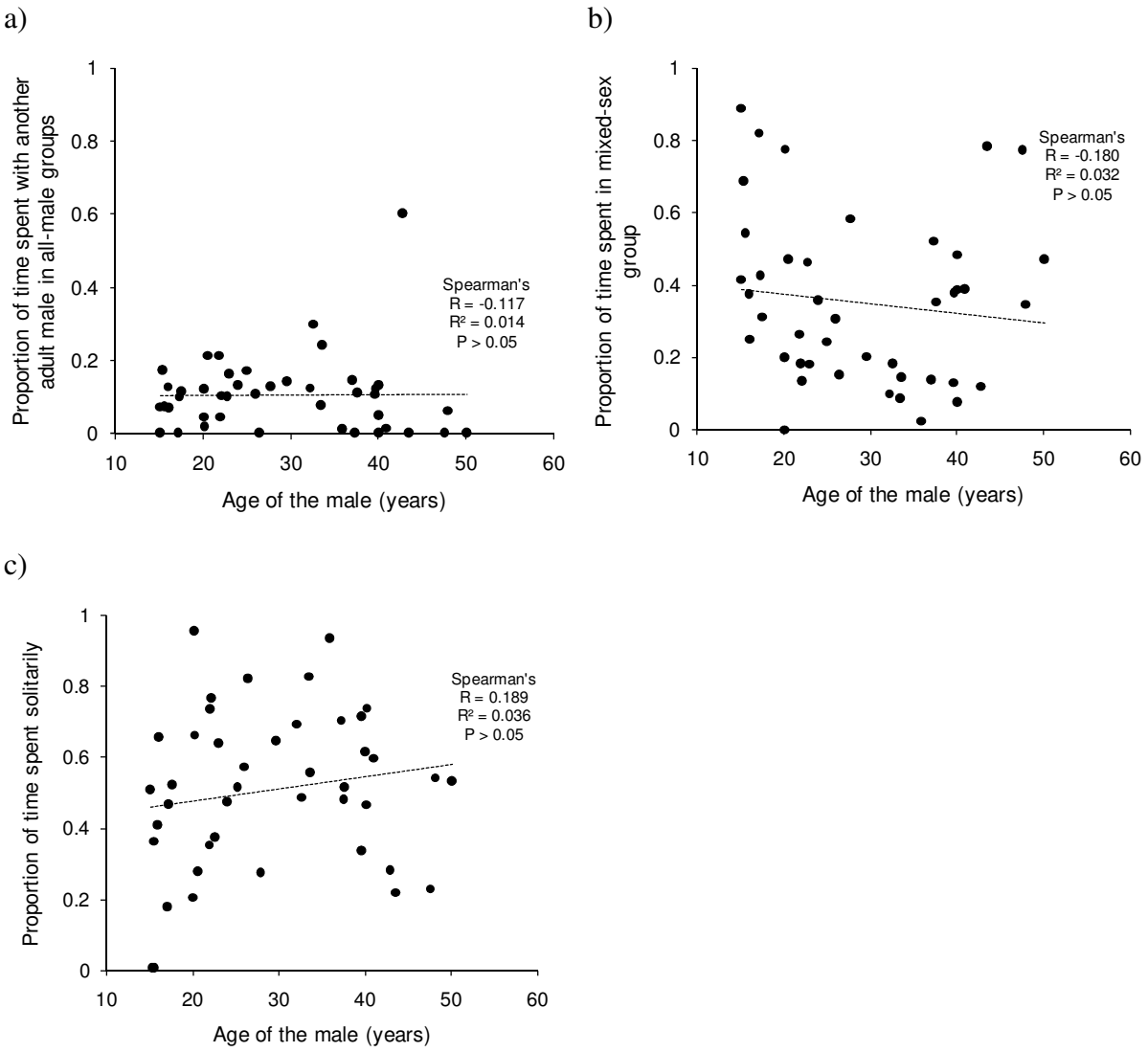

Supplementary material 3, Figure 1. Proportion of total time spent in a) all-male groups with multiple adult males, b) mixed-sex groups, plotted against male age and c) solitarily.

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).

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Supplementary material 4. 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.

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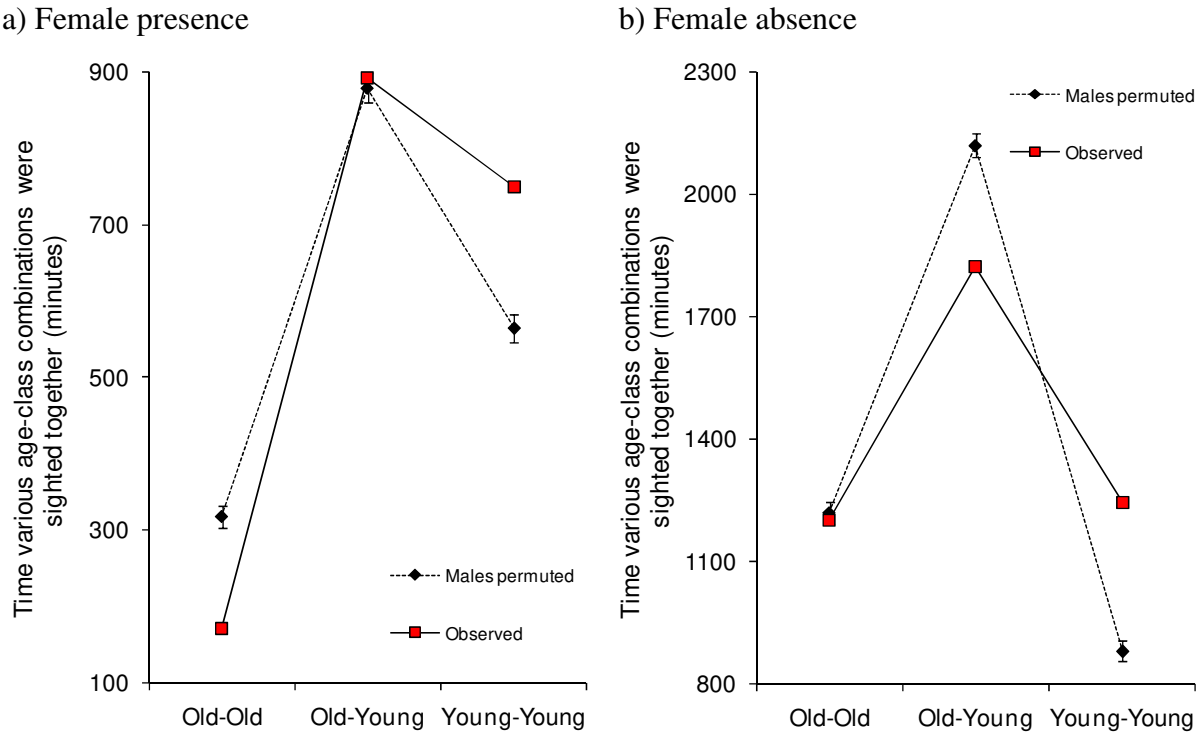

Supplementary material 4, Figure 1. Permuted and observed values of time spent together by adult males of the same and different age-classes in a) female presence and b) female absence. Please note that the Y axis scales differ across the two panels.

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Supplementary Material 5. ANCOVA results on proportion of time a male spent with other males, in female presence and absence, using the actual proportion values.

Supplementary material 5, 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	-	-

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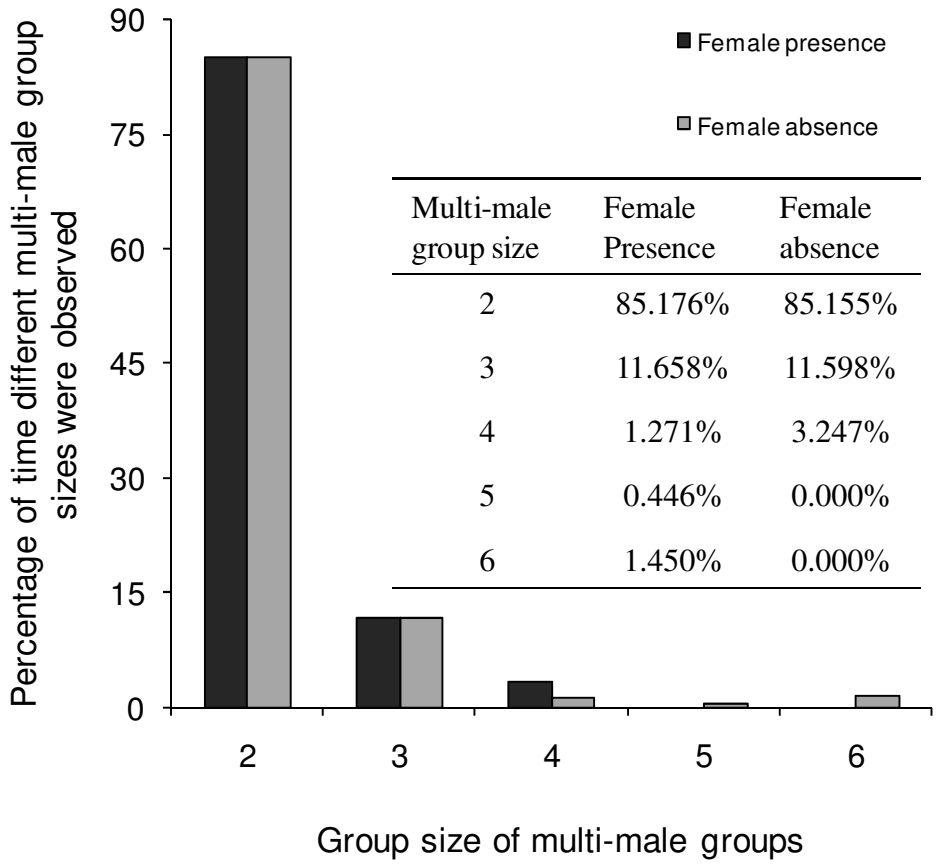
Supplementary material 6. Group size distributions of multi-male groups and experienced group sizes of males in female presence and absence.

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

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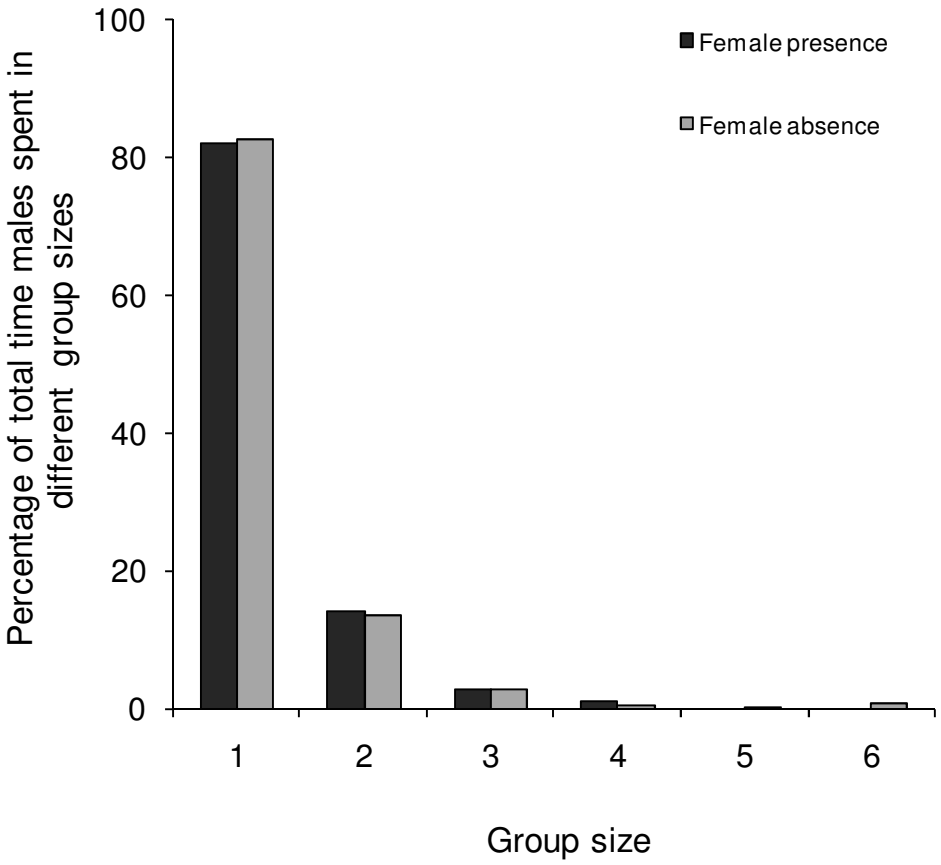

Supplementary material 6, Figure 2. Percentage of the male's total time spent in groups of different sizes (different numbers of adult males) in female presence and absence. Groups in female absence include solitary males and all-male groups, while groups in female presence include mixed-sex groups.

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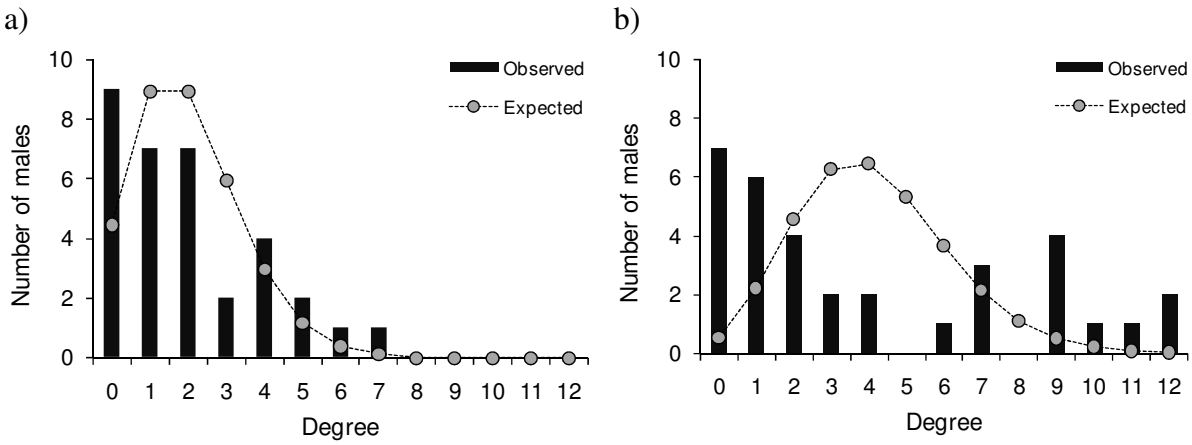
Supplementary Material 7. Degree distributions of association networks in female presence and female absence.

We compared the degree distribution of our observed networks to Poisson distributions (expected for a 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 7, Figure 1. Observed (bars) and expected (lines) degree distributions of male association networks in a) female presence and b) female absence.

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Supplementary Material 8. 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 magnitude 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 8, Table 1. AI between associates, within and between age-classes, in observed and permuted female presence and female absence datasets. *P*=(number of times $\text{difference}_{random} \geq \text{difference}_{observed}$) / 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

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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 8, 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**

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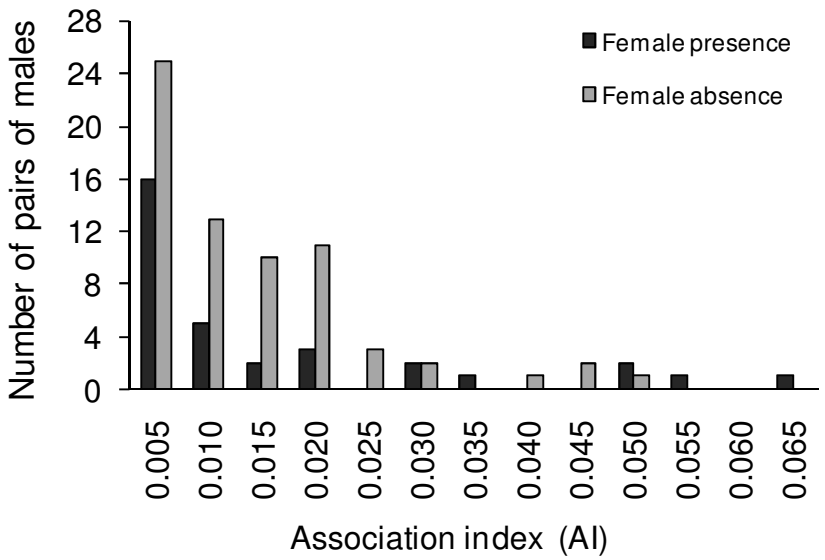
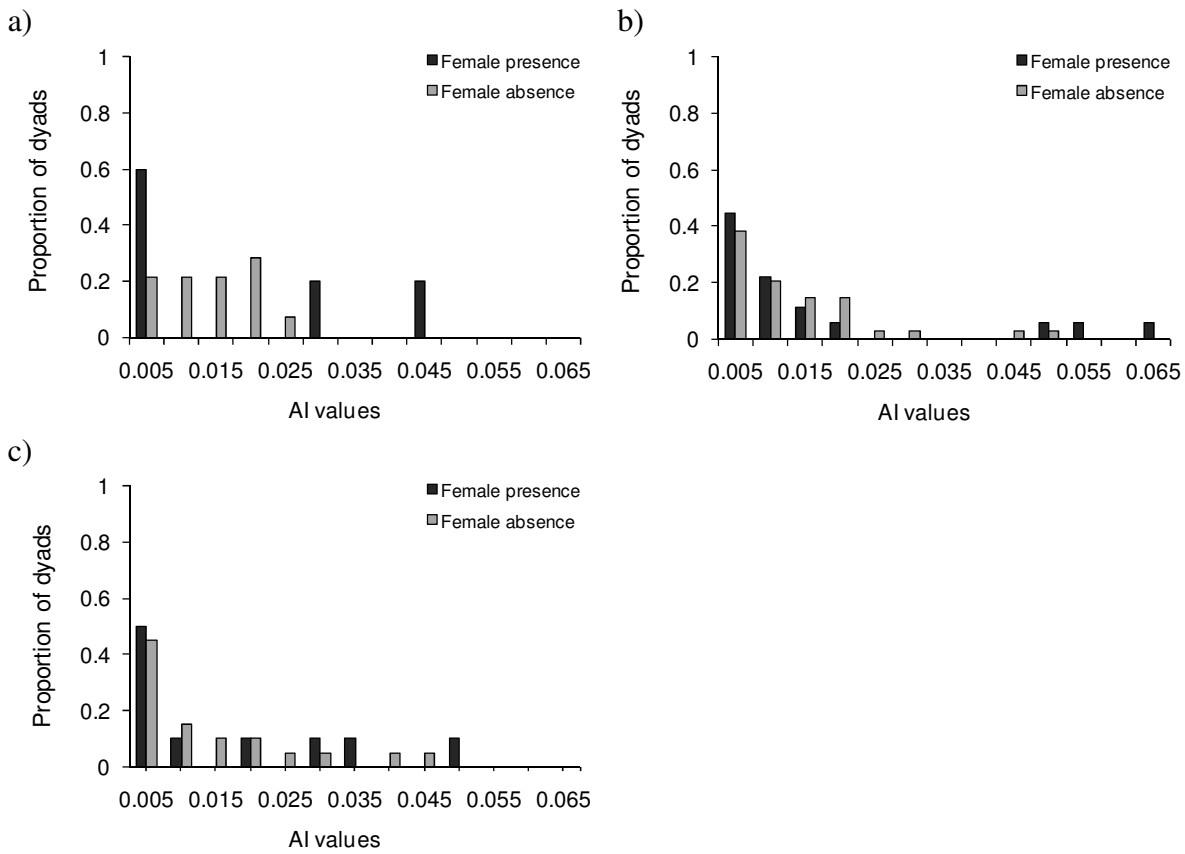


Supplementary material 8, Figure 1. Distribution of non-zero AI values between males (seen on >=5 days each in female presence and absence, *N*=33) in female presence and absence.



Supplementary material 8, 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

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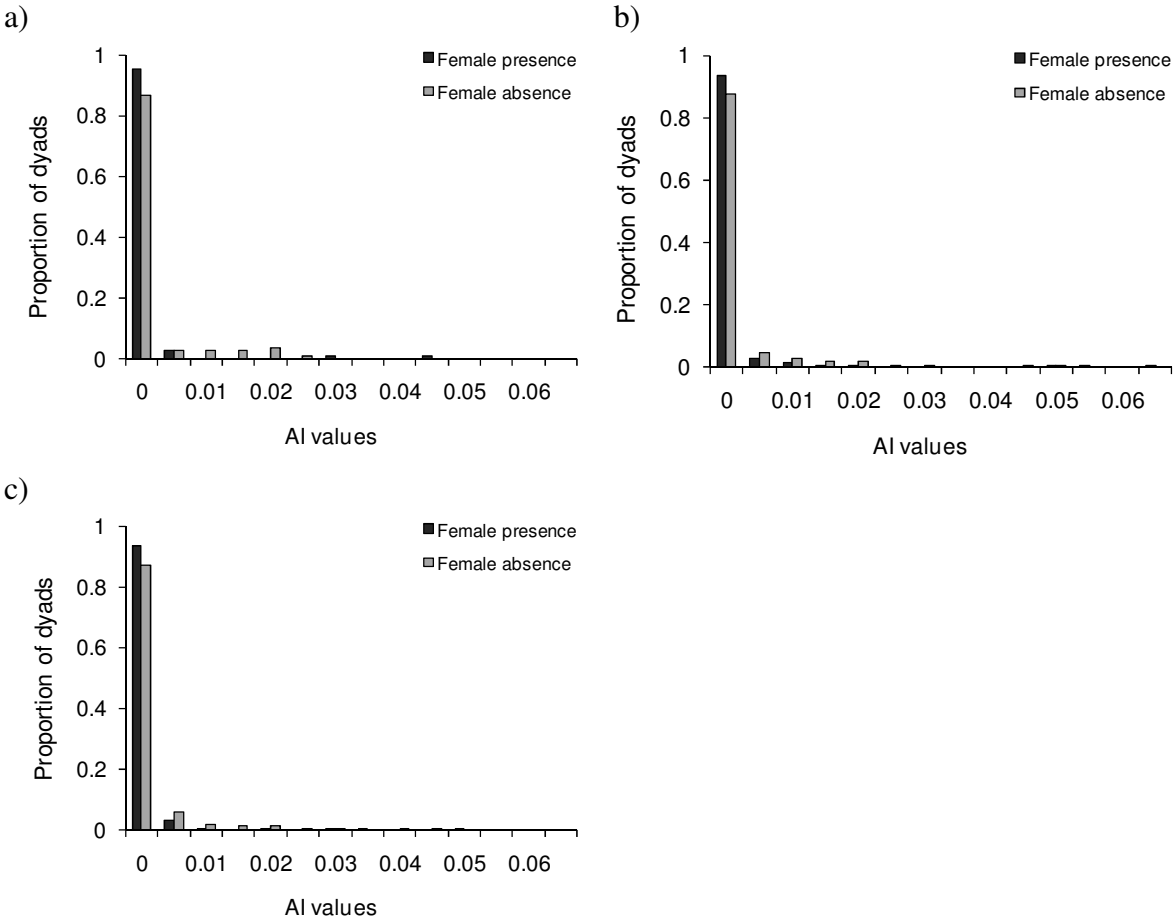
15-30 year old males, in female presence and absence.



Supplementary material 8, 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.

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Supplementary material 9. 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 9, 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**

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Supplementary Material 10. 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. The results of the permutation tests are tabulated below (Table 1).

Supplementary Material 10, 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. 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

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Supplementary material 11. 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 11, 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**

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Supplementary Material 12. 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 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 12, 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

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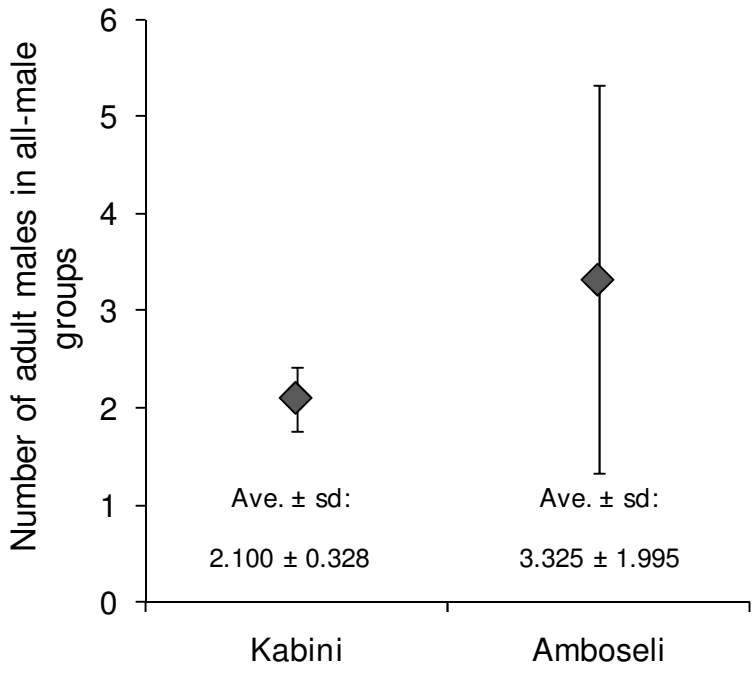
Minimum	2	2
Maximum	18	4



Supplementary material 12, Figure 1. Group sizes of adult males in all-male groups in Amboseli and Kabini, when each male was sampled once a day.

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