



## Articles

## Association patterns of African elephants in all-male groups: the role of age and genetic relatedness

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Strong social bonds are uncommon among male mammals. In many mammals, however, males form all-male groups, providing opportunities for male–male bonds to emerge. We examined association patterns of male African elephants, *Loxodonta africana*, in all-male groups and assessed the influence of age and genetic relatedness on these associations. We also examined the influence of age and genetic relatedness on the choice of sparring partners in male elephants. Males had many weak and random associations and few valuable relationships. Male associations were positively correlated with genetic relatedness, suggesting that kinship influences patterns of male associations. Male associations were negatively correlated with age disparity, and males were more likely to spar with other males closer in age to themselves. These results suggest that males associate with other males of similar age in part because sparring may facilitate the development and maintenance of motor and psychological responses to sudden and unexpected events that occur during play; this may help prepare males for male–male competition. We also found that older males had high centrality and strength in social networks, suggesting that older males influence the cohesion of male social groups. Consequently, the elimination of older males from elephant populations by poachers or trophy hunters could negatively affect social cohesion in male elephant groups. Finally, we found that age and genetic relatedness were not significantly correlated, suggesting that male associations based on age and relatedness did not overlap. These findings highlight the complexity of male social relationships in all-male groups.

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Male social behaviour is strongly influenced by strategies for gaining access to reproductive opportunities, and hence, male relationships tend to be competitive (van Hooff & van Schaik 1994). Consequently, strong association patterns are relatively rare among male mammals. Most instances of strong male–male associations in mammals occur in species exhibiting either male philopatry (e.g. some primates including squirrel monkeys, *Saimiri oerstedii*: Boinski 1994; hamadryas baboons, *Papio hamadryas hamadryas*: Kumer 1995; chimpanzees, *Pan troglodytes*: Mitani et al. 2000), joint dispersal of males in multilitter siblings (e.g. some carnivores including lions, *Panthera leo*: Packer & Pusey 1982; cheetahs, *Acinonyx jubatus*: Caro & Collins 1987; Marnewick & Cilliers 2006) or

cooperative defence of oestrous females (e.g. bottlenose dolphins, *Tursiops* sp.: Connor et al. 1992).

Despite the rarity of strong and stable bonds between males, most polygynous mammals show segregation between sexes, resulting in the formation of all-male groups for most of the year (Miquelle et al. 1992; Kie & Bowyer 1999; Mooring et al. 2003; Turner et al. 2005; Shannon et al. 2008; MacFarlane & Coulson 2009). Males may benefit in several ways from relationships within these all-male groups, although the patterns of male association that occur in all-male groups have rarely been examined (e.g. elephants, *Loxodonta africana*: Moss & Poole 1983; sperm whales, *Physeter macrocephalus*: Lettevall et al. 2002; plains zebra, *Equus burchelli*: Fischhoff et al. 2009). These benefits may include access to a large pool of sparring partners, access to foraging information from conspecifics and defence from predators.

Male elephants alternate asynchronously between being solitary, in an all-male group, or in mixed group containing both males

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and females. The proportion of time that males spend in all-male groups varies over the life course and as a function of age and reproductive status. In general, older males spend more time in all-male groups and less time solitary than younger males. Older males, when they are in musth, also spend 2–3 months a year in female groups (Poole 1982; Lee et al. 2011). Previous studies observed that male elephants using the same bull area associate frequently in all-male groups, although within a bull area, most male associations appeared weak, but some dyads had particularly strong associations (Croze 1974; Moss & Poole 1983). When in mixed-sex groups, however, Moss & Poole (1983) observed random associations between males. These observations may reflect that male solitariness and associations in mixed and all-male groups play different roles in male survival and reproductive success. Moreover, male associations in all-male groups will be difficult to differentiate from random associations if males have diverse social relationships with nonoverlapping association networks and if the strength of most associations is weak, but closer examination can determine whether males have preferred partners.

In this paper we used observational and genetic data to test several predictions pertaining to patterns of associations of male elephants. First, we tested the prediction that male elephants associate with genetically related individuals or with age peers more than expected by chance. We predicted that this would be so because the risks associated with sparring, competitive feeding interactions or cooperative defence from predators may create a pattern of male–male associations favouring kin-based alliances (Griffiths & Armstrong 2002; Wittemyer et al. 2005; Mathot & Giraldeau 2010).

Second, we tested whether males choose associates and sparring partners that are closer in age and/or genetically related to them. Specifically, we predicted that males close in age and males with higher measures of pairwise genetic relatedness would have higher association indexes and more frequent sparring. Sparring, a play behaviour that is frequent among males and may help them hone responses to physical challenges, poses a risk of escalation to a fight when performed with unfamiliar individuals (Smith et al. 1999). Individuals put themselves at risk by self-handicapping while sparring and sparring with age-mates and relatives may be a way of mitigating sparring risks.

Third, we posited that older males may provide social and ecological information to younger males, as older females do to younger females (McComb et al. 2001; Foley et al. 2008). Consequently, we predicted that males in young age classes would be more attracted to males in the older age classes than to males in their own age class. For the same reason, we also predicted that older males would have a higher network centrality compared to younger males.

## METHODS

### *Study Area and Study Population*

This study focused on the Amboseli elephant population, currently consisting of about 1400 elephants. This population has been intensively studied since 1972 by the Amboseli Elephant Research Project (AERP). All elephants born in the Amboseli population are individually known and are identified using natural tears, notches, holes and vein patterns on ear pinnae (Moss 1996). Elephants are also identified from tusk characteristics (size, shape and configuration, one-tusked, broken or intact), natural body marks and body shape (Moss 1996). We used photographic IDs, maintained by AERP, on all Amboseli males as well as IDs compiled by the first author to confirm individual identities in the field.

This population is free ranging and uses an area of nearly 8000 km<sup>2</sup>, including Amboseli National Park and surrounding Maasai ranches in Southern Kenya (Croze & Moss 2011). The range of the Amboseli elephant population overlaps with the range used by elephant populations from Tsavo and Chyulu in the east and those of Kilimanjaro in the south (Croze & Moss 2011). All known Amboseli elephants have ages assigned to them; elephants born since 1975 have their ages estimated to within 2 weeks, those born between 1972 and 1974 have ages estimated to within a few months, elephants born between 1969 and 1971 have ages estimated to within 1 year, and elephants born before 1969 have ages estimated to within 2–5 years. The known ages are based on the time difference between when a mother was last seen without a calf and when she was first seen with a newborn calf. All age estimations are validated from long-term observations of growth and body shape, as well as from ages based on tooth wear and replacement when dead (Moss 2001).

### *Estimation of Male Association Patterns*

We collected association data of elephants in all-male groups from June to December 2005, 2006 and 2007 using sightings of all-male elephant groups; this was carried out opportunistically because locating elephants was not predictable. We searched for male elephants daily by driving to areas where elephants were likely to be sighted. When we sighted elephants in all-male groups, we recorded the time of the sighting, their location using a Global Positioning System (GPS), and the number and identities of individuals in the group. We defined an elephant group as a spatially cohesive and behaviourally coordinated aggregation of two or more elephants. An elephant group was defined as spatially cohesive if individuals were aggregated within a radius of 100 m and if they were orientated or moving in the same direction. Elephants were considered to be behaviourally coordinated if they had similar activity patterns or interacted during a 10–30 min observation window. To obtain a realistic and an unbiased representation of male association patterns, we chose individuals for whom we had a minimum of 15 sightings when they were in all-male groups during the study period. This produced a sample of 47 individuals (13% of the male population 10 years and older) defined by the following distribution: mean of 45 sightings, median of 39 sightings, mode of 46 sightings and a maximum of 107 sightings. We also chose individuals whose frequent associates were sighted at least 15 times, to eliminate individuals from the sample whose major associates were not sampled intensively. We also restricted our analysis to individuals for whom we had microsatellite genotypes because we wanted to relate association patterns to patterns of genetic relatedness. From these data we estimated pairwise associations for all individual males using a simple association ratio or association index (AI):  $AI = N_{AB}/(N_A + N_B + N_{AB})$ , where  $N_{AB}$  is the number of times that individuals A and B were sighted in the same group, and  $N_A$  and  $N_B$  are the numbers of times that individuals A and B, respectively, were sighted in different groups in the absence of the other.

### *Observations of Sparring Behaviour in Male Elephants*

We collected data on sparring behaviour in males during sightings of all-male groups and from 90 min focal group observations. When we sighted a group of male elephants, we recorded the activity of all individuals in the group at the time of sighting. If we observed any males sparring, we recorded their identities. We also selected focal groups, on a daily basis, that we observed for at least 90 min. We chose a focal group either in the morning if it was

at least the fifth sighting of the morning, or in the afternoon if it was the last elephant sighting of the day.

#### *Genetic Sample Collection and Microsatellite Genotyping*

We collected dung samples from males that were not previously genotyped. We extracted DNA from these dung samples using a QIAamp DNA Stool Mini Kit (Qiagen™, Germantown, MD, U.S.A.) following a modified Qiagen™ protocol (Archie et al. 2003). All individuals were genotyped at 8–11 loci including one dinucleotide locus (LAFMS02; Nyakaana & Arctander 1998) and 10 tetranucleotide loci (LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18, LaT24, LaT25 and LaT26; Archie et al. 2003). We used the PCR protocols detailed in Archie et al. (2003) to amplify DNA from the loci of interest, and the PCR products were separated using Applied Biosystems 3730XL DNA Analyzer and run on Genemapper v.3.7 (Applied Biosystems, Beverly, MA, U.S.A.). Microsatellite alleles were scored using Gene Marker v.1.6. (SoftGenetics, State College, PA, U.S.A.). For each sample, we initially ran the PCR and genotyped each locus twice. If these initial PCR products were both heterozygous, we concluded that the individual was heterozygous at the locus. However, if both of the initial PCR products were homozygous, the PCR was repeated three or four times, to minimize the risk of genotyping error due to allelic dropout. We tested all genotyped loci for Hardy–Weinberg equilibrium and for the presence of null alleles (nonamplifying alleles) using CERVUS software before estimating relatedness (Marshall et al. 1998; Kalinowski et al. 2007).

#### *Estimation of Pairwise Genetic Relatedness*

Genetic relatedness ( $R$ ), for all pairwise combinations of individual males was estimated using RELATEDNESS 5.0.8 (Goodnight 2006). RELATEDNESS employs a regression estimator of  $R$  developed by Queller & Goodnight (1989). This estimator has been demonstrated to perform better than other relatedness estimators such as the estimators of Wang (2002), Li et al. (1993) and Lynch & Ritland (1999) for this study population using the same markers (Archie et al. 2007). We used allele frequencies from 585 individuals typed from previous studies as well as this study to estimate pairwise  $R$  values. We determined the reliability and accuracy of our pairwise  $R$  estimates from genetic data by comparing the mean pairwise  $R$  estimates for pairs of known kinship relationships with the theoretical expectation. These comparisons (Supplementary Material, Table S1) suggest that our pairwise  $R$  values were reliable and comparable to values found for a similar study (Wittemyer et al. 2009).

#### *Correlations between Age, Genetic Relatedness and AIs*

To test whether age similarity and genetic relatedness influence association patterns in male elephants, we performed correlation analyses between the AI matrix and the matrix for either pairwise absolute age difference or pairwise genetic relatedness. We used Mantel tests to assess the statistical significance of these matrix correlations by comparing the observed Mantel correlation coefficient,  $r_M$ , with the null distribution of  $r_M$  values. This null distribution was generated using Monte Carlo simulations of  $r_M$  calculated from 1000 randomized data sets (Mantel 1967). Mantel tests were performed in XLSTAT v.2010.4.01 (Addinsoft, New York, NY, U.S.A.), and for all these tests we report two-tailed probability values.

#### *The Influence of Age and Genetic Relatedness on Sparring Behaviour in Males*

We calculated the absolute age difference between a pair of elephants that we observed sparring and the absolute age

differences between each individual observed sparring with all other individuals in a group in which the male was sighted (i.e. his potential sparring partners). We then compared the mean absolute age difference obtained from all pairs that we observed to spar with the mean absolute age differences from all other potential sparring partners using a randomization test. We used Monte Carlo randomization to generate a mean expectation for random pairwise absolute age differences of sparring partners because these data were dependent. We specifically generated the null distribution of mean absolute age differences by sampling repeatedly at random an equivalent number of dyads we observed to spar from all dyads that were available in the data set. We iterated these randomizations 1000 times and calculated the mean age differences of the random pairs picked per iteration.

#### *Determining the Social Role of Older Individuals in Male Elephant Societies*

To determine whether older males play a pivotal role in male social networks as repositories of social knowledge, we tested two related sets of hypotheses. First, we tested whether males in young age classes associated with males in the older age classes more than expected by chance. Second, we tested whether older males have significantly higher measures of centrality (i.e. association strength and eigenvector centrality) than younger males.

We used a randomization procedure to test whether males in the younger age classes (i.e. 10–19 years,  $N = 16$ ; 20–29 years,  $N = 16$ ) were associated with older males (30+ years,  $N = 15$ ) more than expected by chance. This age classification coincides with important aspects of elephant life history. Ages 10–19 years coincide with the transition period to independence from maternal units (Lee et al. 2011). Elephants in this social class also spend a significant proportion of their time in mixed-sex groups. Age class 20–29 years covers the age range when all males are fully independent: they experience their first musth and become reproductively active (Lee et al. 2011). Age 30 years marks the period when all males are reproductively competitive (Poole 1982; Poole et al. 2011). We calculated observed mean AIs between the 30+ year age class and age classes of 10–19 years and 20–29 years. We generated the expected mean AIs between age classes using a randomization procedure under the null hypothesis that all classes are equivalent in their association patterns. We randomly reshuffled individuals and their AI values across classes, while retaining class size. We iterated this process 1000 times, and, for each iteration, we calculated the expected mean AI between and within age classes. We then used the distribution of these expected AI means to determine the probability that our observed mean AI between and within classes were either larger or smaller than expected by random chance.

To test whether older males have a higher association strength and eigenvector centrality, we calculated the association strength (sum of AIs of each male with all other males), the eigenvector centrality (a composite measure of how connected each male is in elephant social networks) and the number of associates for each individual using SOCPROG 2.3 (Whitehead 2009). Eigenvector centrality ( $X$ ) for the association matrix ( $A$ ) is defined by the equation:  $AX = \lambda X$ , where  $\lambda$  is the largest eigenvalue of  $A$  (for details and alternative formulations, see Bonacich 1987). Individuals with large eigenvector centralities are highly connected because they have high association strength, they have a large number of associates, or they are associated with highly connected individuals. Using these individual network measures, we performed Pearson correlation analyses between age and association strength, and age and eigenvector centrality, while controlling for the number of associates and the total number of groups in which an individual

was sighted. These correlations were performed using the R software (R Development Core Team 2010). We present two-tailed probability values from these analyses.

## RESULTS

### Characteristics of Male Associations

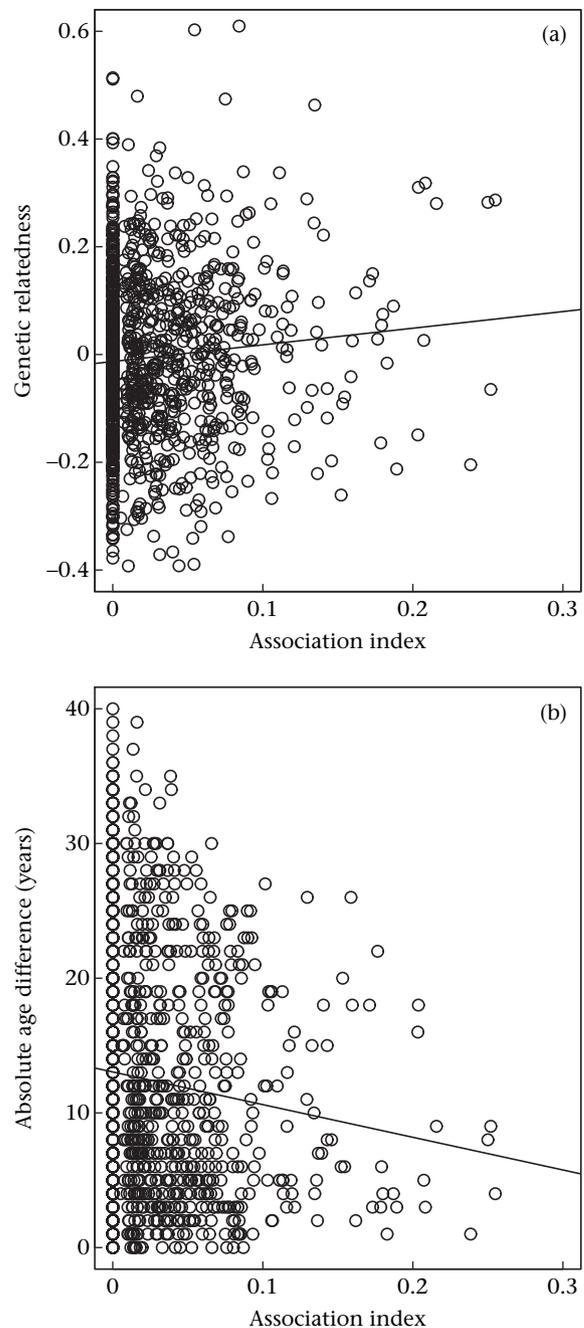
Male elephants (~15 years and older and observed on 15 or more occasions) were most often sighted in all-male groups (mean  $\pm$  SD percentage of sightings =  $63.24 \pm 18.68\%$ ,  $N = 4047$  elephants sighted consisting of 91 males). The rest of the time they were sighted either alone ( $18.39 \pm 11.61\%$  of sightings) or in a mixed-sex group ( $18.36 \pm 16.42\%$  of sightings). Hereafter, we report results of analyses for males in all-male groups only.

Elephants in all-male groups were found in small groups (mean group size  $\pm$  SD =  $3.325 \pm 1.995$ , median = 3, mode = 2, minimum = 2, maximum = 18,  $N = 939$  groups sighted). When we considered all of a male's potential social partners, including those with whom he was never sighted, the mean  $\pm$  SD of the AI was  $0.028 \pm 0.040$  ( $N = 1081$  potential dyads). However, the mean AI calculated among actual social partners (males with whom a male was known to associate with at least once) was nearly twice this value (mean  $\pm$  SD =  $0.049 \pm 0.042$ ,  $N = 614$  dyads observed to associate). Most males had high AIs with relatively few individuals and weak AIs with most individuals they associated with (Supplementary Material, Fig. S1). The weaker associations were similar to those predicted if individuals were associating at random; our results indicate that males have many random associations and few valuable relationships (Supplementary Material, Appendix S1, Fig. S1). A male elephant was associated with an average  $\pm$  SD of  $26 \pm 8$  other males.

### Associations of Elephants in All-male Groups is Influenced by Genetic Relatedness and Age

Male associations were weakly but significantly correlated with pairwise genetic relatedness (Mantel test:  $r_M = 0.0789$ ,  $N = 47$ ,  $P = 0.0095$ ; Fig. 1a). This correlation was significant even when we considered only individuals that associated at least once ( $r_M = 0.090$ ,  $N = 47$  males,  $P = 0.027$ ). Similarly, male associations were weakly but significantly correlated with absolute age differences, both when we considered all males sampled ( $r_M = -0.1019$ ,  $N = 47$  males,  $P = 0.0003$ ; Fig. 1b) and when we considered individuals that associated at least once ( $r_M = -0.123$ ,  $N = 47$  males,  $P = 0.002$ ). Further analyses of association within age classes confirmed association by age. Males in older age classes were more associated with members of their own age class than expected by chance, and association in the younger male age classes was as expected by random chance (observed and expected mean AI: 30+ year age class = 0.045 and 0.028,  $P = 0.006$ ; 20–29 year age class = 0.036 and 0.028,  $P = 0.085$ ; 10–19 year age class = 0.027 and 0.028,  $P = 0.909$ ). Age difference and genetic relatedness were not significantly correlated in the sample of males we studied ( $r_M = -0.045$ ,  $N = 47$ ,  $P = 0.140$ ), suggesting that it was somewhat uncommon to encounter pairs of male elephants that were both close in age and had high pairwise  $R$  values.

Because effect sizes for the correlation between AI and age and AI and genetic relatedness were weak, we conducted further analyses focusing on highly associated pairs using network analyses. We did this because the distribution and magnitude of weak AIs were similar to a randomly expected distribution of AIs, but individual males also had a few high AIs that were not predicted by random association among males, suggesting that these associations represented valuable male relationships. We constructed five



**Figure 1.** (a) Relationship between pairwise genetic relatedness ( $R$ ) and association index (AI) (Mantel test:  $r_M = 0.0789$ ,  $P = 0.0095$ ). (b) Relationship between absolute pairwise age difference and AI ( $r_M = -0.1019$ ,  $P = 0.0003$ ). Data consist of 1081 male dyads from 47 individuals. Genetic relatedness was determined using Queller & Goodnight's (1989)  $R$  estimator; age for all individuals was calculated for August 2007.

directed binary networks based on association ranks determined from the strength of AIs. The first two networks were each based on the association between all males and either their first or second rank associates, and these networks had a mean AI for associated individuals that was larger than the maximum threshold expected if males were randomly associated (Supplementary Material, Fig. S2). The last two networks were each based on associations between all males and either their fourth or fifth rank associates, and each of these networks had a mean AI for associated individuals that was within the AI range expected if males were randomly associated (Fig. S2). Using all five networks and exponential

random graph analyses, we tested whether individuals that associated were likely to be closer in age and whether they were likely to be genetically related (Supplementary Material, Appendix S2, Table S2). These network analyses confirmed our earlier results; genetic relatedness and age proximity positively influenced association patterns for valuable male networks, but they did not influence associations for weak and mostly random male networks (Table S2).

#### *Elephants Preferred Sparring Partners That Were Closer in Age to Them*

We examined 39 elephant groups consisting of 189 potential sparring dyads. The mean absolute age difference between pairs that sparred (5.534 years,  $N = 47$ ) was significantly lower than that for dyads that they could have sparred with but did not (8.696 years,  $N = 142$ ; Student's  $t$  test:  $t_{97} = -3.01$ ,  $P = 0.003$ ). Similarly, dyads that sparred had a lower mean absolute age difference (5.534 years) compared to the age differences expected if they were sparring with other individuals in the group at random (mean age difference for random pairs: 7.922 years; randomization test:  $P = 0.004$ ).

The mean genetic relatedness for pairs of individuals that sparred ( $R = 0.018$ ,  $N = 24$ ) was not significantly different from the expected mean genetic relatedness if they were choosing sparring partners at random with respect to genetic relatedness ( $R = 0.032$ ,  $N = 24$ ; randomization test:  $P = 0.68$ ).

#### *Older Males Play a Central Role in All-male Elephant Social Networks*

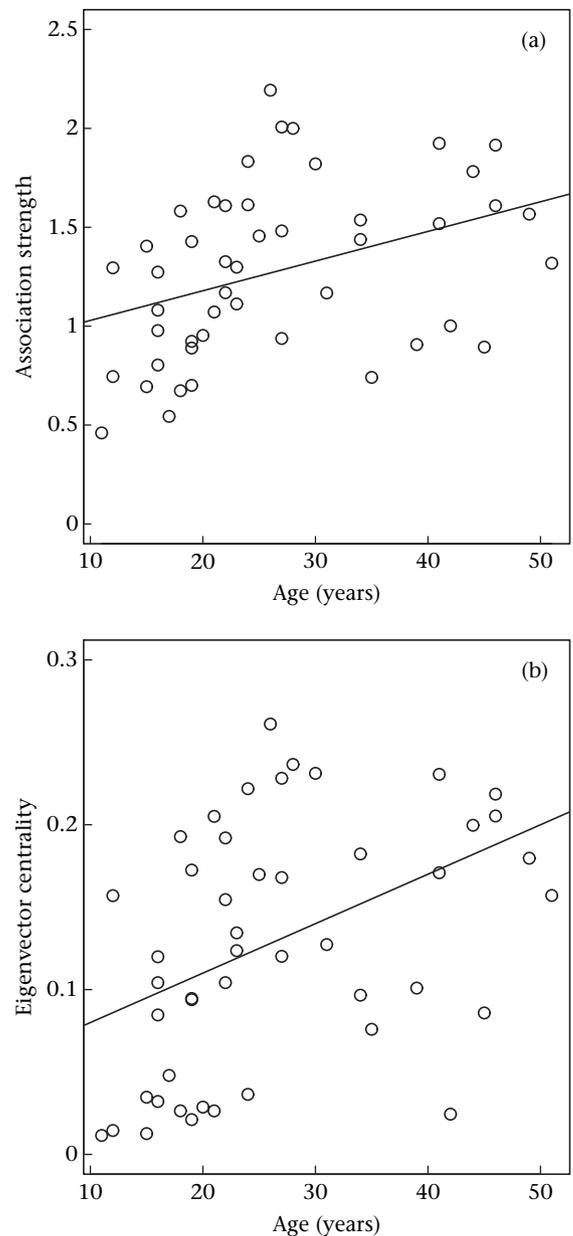
Males in the 20–29 year age class were associated with males in 30+ year age class more than expected by chance (mean AI: observed = 0.03772; random expectation = 0.02789; randomization test:  $P < 0.005$ ). However, males aged 10–19 years were associated with males 30+ years old significantly less than expected by chance (mean AI: observed = 0.01435; random expectation = 0.02791; randomization test:  $P < 0.003$ ).

The correlation between male age and association strength was positive and significant even after controlling for confounding factors using partial correlation analyses (Fig. 2a). In one model, we controlled for the number of times an individual male was sighted (Pearson correlation:  $r_{44} = 0.457$ ,  $P = 0.00066$ ); in another, we controlled for the number of times an individual male was sighted and the number of male association partners an individual had ( $r_{44} = 0.290$ ,  $P = 0.0470$ ). Age was also positively correlated with eigenvector centrality (Fig. 2b) after controlling for individual variation in the number of sightings they were observed ( $r_{44} = 0.414$ ,  $P = 0.0026$ ). However, this relationship became nonsignificant when we controlled for the number of association partners ( $r_{44} = 0.179$ ,  $P = 0.23245$ ). This is because age was also positively correlated with the number of individuals that a male was seen to associate with ( $r_{45} = 0.395$ ,  $P = 0.0043$ ). The number of association partners was also strongly correlated with eigenvector centrality ( $r_{45} = 0.815$ ,  $P < 0.0001$ ) and was the major metric influencing eigenvector centrality.

## DISCUSSION

### *Role of Genetic Relatedness in Male Associations*

In this study, male association was positively correlated with pairwise genetic relatedness. Although this result was weak, it supports recent findings of philopatry in Asian elephants, *Elephas maximus*; males using the same area have been observed to be more genetically similar than predicted by chance (Vidya & Sukumar



**Figure 2.** Relationships between age and (a) association strength (Pearson correlation:  $r_{45} = 0.388$ ,  $t = 2.825$ ,  $P = 0.007$ ) and (b) eigenvector centrality ( $r_{45} = 0.417$ ,  $t = 3.077$ ,  $P = 0.004$ ).

2005). Associations of males based on genetic relatedness have been observed in a number of territorial species exhibiting male philopatry (Packer & Pusey 1982) or male–male alliances to defend oestrous females (Parsons et al. 2003). However, no studies have previously examined association in relation to genetic relatedness in species where males are not territorial or do not show cooperative defence of oestrous females. The benefits of associations based on pairwise genetic relatedness in male African elephants or philopatry in Asian elephants are not currently known. Our hypothesis that males associate with individuals genetically similar to them as safe sparring partners was not supported by our data.

### *Role of Age in Male Associations*

Males in all-male groups tended to associate with individuals that were close to their own age. These results support observations

from several studies in other vertebrates showing that animals associate according to age or body size (Hoare et al. 2000; Bon et al. 2001; Ruckstuhl & Neuhaus 2001; Li & Jiang 2008). Two non-mutually exclusive hypotheses have been advanced to explain this pattern. One hypothesis states that individuals of similar age, size or sex are more likely to associate because they can synchronize their activity budgets and, therefore, maintain group cohesion, because individuals in each age or sex category will tend to have similar energy budgets (Hoare et al. 2000; Ruckstuhl & Neuhaus 2001; Li & Jiang 2008; Jones et al. 2010). The other hypothesis states that individual animals associate with others of similar age, sex or size because they share similar social motivations and behaviours that enhance social cohesion and increased association (Cransac et al. 1998; Bon et al. 2001). Males in all-male groups may share the motivation of avoiding competitive reproductive interactions in mixed groups. Similarly, males may share the need to interact with other males through sparring to increase fighting skills and predation escape skills.

Previous studies on sexual segregation in elephants did not support activity synchrony as a mechanism for association of animals of different sizes or sexes (Shannon et al. 2008). Our result showing that males chose other males closer in age to spar with provides support for the second hypothesis. Sparring between males closer in age has been reported in many species (baboons, *Papio cynocephalus ursinus*; Cheney 1978; bison, *Bison bison*; Rothstein & Griswold 1991; pronghorn, *Antilocapra americana*; Miller & Byers 1998). Sparring plays a proximate role in enhancing the development of rapid responses to physical challenges that occur during play (Spinka et al. 2001; Nunes et al. 2004). Ultimately, these responses may contribute to the development of responses needed for escape from predation or for engaging in male–male contests for dominance (Miller & Byers 1998). However, because sparring poses a risk of escalation to a fight when performed with unfamiliar individuals (Smith et al. 1999), and because individuals put themselves at risk by self-handicapping while sparring (Pereira & Preisser 1998; Petru et al. 2009), males should form stable associations with males that are close to them in age.

Findings from this study also suggest that older males play a pivotal role in elephant male societies. Age was positively correlated with the number of associates that a male had and it was a major metric influencing the eigenvector centrality of males. This is because older males were associated with younger males as well as with members of their age class more than expected by chance. Males in the 20–29 year age class associated frequently with males in the 30+ year age range, but males in the 10–19 age class did so less frequently, presumably because males 10–19 years of age spent less time in all-male groups and more time in mixed groups or with their families (Poole 1982; Evans & Harris 2008; Lee et al. 2011). Possibly, younger males (10–19 years old) facilitate their association with other males while in mixed groups as observed by Evans & Harris (2008) for a different elephant population, but our analyses focused on males in only all-male groups. Centrality measures have been used to demonstrate the social and leadership roles of individuals in animal social networks (Lusseau 2007; Sueur & Petit 2008). In these studies, the more central individuals in the network played a leadership role or were sources of information. The central role that older males play in male elephant social networks suggests that older males are sources of ecological and social knowledge in all-male elephant groups, just as older females are in family groups (McComb et al. 2001; Foley et al. 2008; Mutinda et al. 2011). Foley et al. (2008) observed that survival of elephant calves in family groups led by older matriarchs was higher than that in family groups led by younger matriarchs during a severe drought. These authors concluded that this difference occurred because older matriarchs led their families outside their usual range to areas

with forage and water, using their knowledge of the location of these resources from previous drought experiences. Further studies are needed to confirm similar leadership roles of older males in male social networks.

#### *Weak Associations Reflect Complex Male Social Relationships*

The weak relationships between AI and age and AI and genetic relatedness may reflect one or both of the following processes. (1) Age proximity and genetic relatedness were not correlated in our study, suggesting that it is difficult for males to associate simultaneously with individuals that are both closer in age and genetically similar to them. The inability to pursue both of these preferences simultaneously will weaken the strength of both preferences and suggests that males have different networks for kin and for age peers that do not overlap. (2) Previous research has shown that each male has 2–3 months per year when his top associate is not available as a social partner because his associate is in musth, a period when older males are mostly associating with females (Poole 1982). Top associates also do not have overlapping musth periods (Poole 1982), which makes these relationships appear weaker than they would be in the absence of musth.

#### *Conclusion*

In species exhibiting sexual segregation, and for whom male–male reproductive competition is intense and male alliances absent, the occurrence of all-male groups may facilitate the formation of male–male associations. Our results show that genetic relatedness and relative age influence a male's decisions about who to associate with. In addition, the positive relationship between age and association centrality underscore the importance of older males in male elephant social groups. The removal of older males in the population, preferred targets by trophy hunters and poachers due to their larger tusks, may destabilize the social cohesion of male elephant societies. Taken together, our findings highlight the complexity of male elephant social behaviour and male–male relationships, and indicate that social, developmental and ecological factors contribute to association patterns among male elephants.

#### **Supplementary Material**

Supplementary material for this article is available in the online version at [doi:10.1016/j.anbehav.2011.02.013](https://doi.org/10.1016/j.anbehav.2011.02.013).

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