



## Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*



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The drivers of social affiliation may vary over time as individuals change their goals with respect to changing environments or physical condition. Studies of companion preference rarely consider shifts in motivational state, despite the potential importance of such shifts in structuring association and population processes. Ignoring state dependence in social behaviour may weaken the ability to recognize social properties and identify their underlying drivers. Modifying established approaches, we apply a state-specific analysis to investigate social properties in male African elephants, which are thought to be weakly social. Specifically, we delineate associations during distinct sexually active and inactive periods and quantify common social metrics (network size, density, betweenness and the number and age of preferred companions) to examine how sexual states may relate to male elephant social relationships. We found that state-dependent association index values were higher and quantitative definitions of preferred companions were more conservative than those derived when sexual state was not taken into account. Preferred companions tended to be closer in age among sexually inactive dyads relative to sexually active dyads, indicating that bulls seek out age-mates when sexually inactive. Networks were larger and denser when sexually inactive. By accounting for dynamic behaviour in social systems, this study demonstrates that male African elephants show more social preference than had been previously thought.

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### Background

In social systems with contest polygyny, males attempt to monopolize receptive females, and male–male relationships are often competitive (East & Hofer, 2001; van Hooft & van Schaik, 1994). Despite this expectation of competitive relationships, preferential association has been demonstrated among males in polygynous taxa (e.g. ibex: Villaret & Bon, 1998; chimpanzees: Langergraber, Mitani, & Vigilant, 2007). Empirical work has linked companion preference among males to reproductive success when coalitions or coordinated displays facilitate copulations (Connor,

Heithaus, & Barre, 2001; Ryder, Parker, Blake, & Loisel, 2009; Schülke, Bhagavatula, Vigilant, & Ostner, 2010). In societies in which reproductive benefits of association are not apparent, reports of preferential associations among males are rare (Fischhoff, Dushoff, Sundaresan, Cordingley, & Rubenstein, 2009).

Motivational state is highly relevant to the structure of social relationships. Male interactions often vary in relation to the reproductive status and distribution of females (Emlen & Oring, 1977). During mating periods, competitive or coalition-based interactions likely dominate whereas the influence of reproductive competition may be less apparent during periods of sexual inactivity. Social interactions while sexually inactive may provide benefits including information exchange (e.g. McComb, Moss, Durant, Baker, & Sayialel, 2001; Sonerud, Smedshaug, & Bråthen, 2001), predator defence (e.g. Hamilton, 1971), foraging facilitation (e.g. Baird, Ryer, & Olla, 1991), or resolution of dominance

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hierarchies (Beacham, 2003; Evans & Harris, 2008; de Villiers, Richardson, & van Jaarsveld, 2003). Understanding one's status in a hierarchy can prevent future contest among competitors, which is especially beneficial for species with weaponry (Rowell, 1974). Investigation of social preference is potentially confounded by such shifts in behavioural states (sexually active to inactive). Few studies of sociality assess differences in structure across behavioural states, despite the potential difference in cost/benefit ratios (but see Fischhoff et al., 2009; Lusseau, 2007; Patriquin, Leonard, Broders, & Garroway, 2010).

African savannah elephants engage in contest polygyny, with females coming into oestrus for 4–6 days once every 4 years (Moss & Poole, 1983). Mature males have distinct periods of sexual activity and inactivity throughout the year (Poole, 1987). Because females can come into oestrus at any time of year (Poole, 1989), mature male elephants undergo sexually active periods asynchronously (Hall-Martin, 1987; Poole, 1987; Rasmussen, 2005). Grouping behaviour reflects these periods, as males often are found among all-male groups when sexually inactive and found among mixed groups when sexually active (Poole & Moss, 1981), suggesting that the motivation to associate with conspecifics changes between states (Fischhoff et al., 2009).

Quantifying relationships among males necessitates a framework that accounts for this marked difference in motivational state. Dyadic association indices incorporate observations when one individual is seen without the other as rejected opportunities to associate (Cairns & Schwager, 1987; Ginsberg & Young, 1992). Previous studies using association indices have found weak or random relationships among male African elephants (Chiyo et al., 2011; Croze, 1974; Moss & Poole, 1983), but have not accounted for the dynamic and individual-based schedules of sexual activity that may drive association. Collapsing multiple states into one category potentially distorts values by including males as potential associates when they may be predisposed towards avoidance (i.e. one is seeking female associates while the other is seeking male associates), limiting understanding of what may be driving social behaviour. Here, we control for mixed motivational states by conducting state-based calculations of association indices in a population of free-ranging elephants in Samburu, northern Kenya. We investigate male–male associations and the social network metrics that arise from those associations to gain insight into the strength of bonding and the drivers of male sociality.

Assuming the distribution of females is the primary driver of male conspecific association during sexually active periods (Emlen & Oring, 1977), but that it plays a limited role during sexually inactive periods, we expect associations among male elephants to be structurally different in relation to their reproductive state. Males may use sexually inactive periods to assess competitors (of close stature/age) and resolve rank to mitigate potentially costly contests (Beacham, 2003), or male–male bonding may be driven by other non-contest-related benefits such as information exchange across male age classes (Chiyo et al., 2011; Evans & Harris, 2008) or predator defence (McComb et al., 2011). If males use sexually inactive periods to foster bonds that confer benefits like shared knowledge similar to those found among females in the species (McComb et al., 2001; Wittemyer, Douglas-Hamilton, & Getz, 2005), we expect evidence of preferred companionship. The structure of preferred companionship may provide insight into the benefits of such affiliations. To assess the importance of incorporating state in social analyses, we compare elements of social structure (association index values and social network metrics): (1) disregarding behavioural states and (2) differentiating state-based social properties. We present individual-based comparisons of state-dependent differences in social metrics. We investigate relationships among age, association and social network structure

across states to provide insight regarding possible drivers of observed social patterns. Finally, we relate our findings to previous work on male elephant society (Chiyo et al., 2011; Evans & Harris, 2008).

## METHODS

### *Study Population*

This study is a part of an ongoing long-term monitoring project that has maintained individual-based records of the elephant subpopulation that uses the unfenced Samburu and Buffalo Springs National Reserves in northern Kenya (0.3–0.8°N, 37–38°E) since 1997 (Wittemyer, 2001; Wittemyer, Daballen, & Douglas-Hamilton, 2013). The reserves are located along the Ewaso N'giro River, the only permanent water source in this semi-arid savanna ecosystem and thus a focal area for wildlife. Because of the sparse, semi-arid vegetation, good visibility at the study site enables researchers to detect groups and solitary individuals easily. The elephants that use these reserves are habituated to vehicles, allowing detailed behavioural observation, but move in and out of the reserves regularly; they are a part of a larger population that ranges within the Laikipia/Samburu ecosystem (Wittemyer, Daballen, Rasmussen, Kahindi, & Douglas-Hamilton, 2005).

### *Data Collection*

Between August 1999 and November 2003, observations of elephants were collected while performing established transects on a daily basis within Samburu and Buffalo Springs National Reserves that resulted in complete coverage of the parks at least once per week (see further description in Wittemyer, Douglas-Hamilton, et al., 2005). Observations were also collected opportunistically outside of the reserves where few roads exist, making systematic surveys impossible; elephants were located during opportunistic surveys through the use of radiotracking collars (Rasmussen, 2005). When elephants were encountered the identities of all individuals over 18 years old in the group (younger males were often difficult to distinguish and therefore noted by age rather than identity), the GPS location, date, time and group activity were recorded (Wittemyer, Douglas-Hamilton, et al., 2005; Wittemyer et al., 2013). Individuals were identified using unique ear patterns and tusk shape (Douglas-Hamilton, 1972; Moss, 2001). Bulls were considered a part of a group if they were spatially clustered (within a 500 m radius of an observationally estimated centre) and coordinated in movement and activity (Chiyo et al., 2011; Wittemyer, Douglas-Hamilton, et al., 2005). The presence of musth signalling (i.e. temporal gland secretion and urine dribbling) was recorded (Poole, 1987) and used to verify model accuracy in defining states of sexual activity and inactivity (see *Delineating States* below). For days when a bull was observed more than once, only the first observation of the day was included in analyses (Rasmussen, 2005; Wittemyer, Douglas-Hamilton, et al., 2005). Bull ages were estimated using established criteria, including shoulder height, tusk girth and head shape (Moss, 1996), the accuracy of which was established using molar dentition from dead or immobilized individuals (Rasmussen, Wittemyer, & Douglas-Hamilton, 2005).

There were 154 bulls identified over the course of the study. It is common to use the most frequently observed individuals in analyses to minimize effects driven by poor sampling (Whitehead, 2008). We defined our focal bulls ( $N = 32$ ) as those seen at least 20 times in the sexually inactive state because we anticipated social interactions to be strongest during the sexually inactive state, when mate competition would not structure interactions. The number of observations in the sexually active and inactive states of these focal

bulls was similar (median: inactive = 42; active = 45). There were 3473 observations of focal bulls in known states in 2018 distinct aggregations over the 4-year study. Focal bulls were estimated to be between 21 and 41 years old at the midpoint of the study. To analyse the relationship between age and strength of association, we divided pairs of individuals (dyads) into four categories in which 'age-mates' were defined as individuals born 5 or fewer years apart. Age classification was determined by the youngest member of the dyad, for which 'old' bulls were at least 30 years old and 'young' bulls were younger than 30 years old. The 30-year cutoff criterion was based on the age of musth onset in the study population (Rasmussen, Ganswindt, Douglas-Hamilton, & Vollrath, 2008). Therefore, our four categories were 'age-mates (old)', 'non-age-mates (old)', 'age-mates (young)' and 'non-age-mates (young)'.

### *Delineating States*

When sexually active, mature males overtly musth-signal whereas younger males typically do not overtly signal their state (Ganswindt, Rasmussen, Heistermann, & Hodges, 2005). Therefore, we applied a hidden Markov model (HMM) (Rabiner, 1989) to characterize individual males' sexual state to allow state delineation based on behavioural traits other than overt musth signalling (see [Supplementary material](#)). In this model, the frequency of association type (mixed-sex group, bull group, lone bull) served as the observable signal with state-specific probabilities, and sexual state served as the unobservable (hidden) state (Rasmussen, 2005). Model parameters (i.e. state transition and observable signal probabilities) were optimized on temporal sequences from multiple bulls simultaneously to avoid model overfitting that might arise from individual-based model optimization. While the time series of group type was used to define an individual's state, this state categorization was independent of male–male dyadic relationships and preferences that occur in mixed-sex and all-male groups (males associate with other males when sexually active and inactive). The HMM state assignment does not predict the strength of relationships among males in either state, and it was these male–male associational preferences that were the focus of the analysis conducted using permutation tests exclusively structured on male–male properties of aggregations (see below, [Permuted Data Sets to Test for Random Association](#)).

The model was first applied to bulls older than 35 years with regularly occurring musth periods and concurrent visual signals to determine whether model-defined sexually active periods based on association type accurately distinguished these periods, which are associated with reproductive activity (Poole, 1987). When this cross-validation procedure confirmed HMM assignments, the same modelling steps were applied to temporal sequences of younger bulls without regularly occurring musth periods. Finally, a combined model was optimized for all bulls. Although varying numbers of states were tested, the best combined model included two states, assigning bulls to state 1 (sexually inactive, in which the probability of association with females was low) or state 2 (sexually active, comprising musth and sexually active nonmusth, in which the probability of association with females was high). The combined model preserved most of the state designations from the age-specific models (91–99%). Models were fitted using Mathematica (Wolfram Research, 2004). For further details on model definition and results, see Rasmussen (2005), Rasmussen et al. (2008) and the [Supplementary material](#).

States were assigned for each day on which a focal bull was seen for all but 61 occasions over the 4-year study. A bull seen consecutively in the same state less than 28 days apart was assumed to be in that state for the days between sightings. If two consecutive sightings of a bull were within 28 days but he was in different states

on those days, the interim period was split evenly between the two states. If two consecutive sightings of a bull were more than 28 days apart, his state during that period was considered unknown, during which the individual was excluded from state-based calculations (see below).

### *Calculating Association Indices*

Association indices measure the strength of association between two individuals (Cairns & Schwager, 1987). Because bulls in our study system were as likely to be identified when apart as they were when together and because all individuals within a group were registered, we used the simple ratio index (hereafter 'AI') to determine the strength of dyadic bonds:  $AI = N_{AB}/(N_{AB} + N_A + N_B)$ , in which  $N_{AB}$  is the number of times that individuals A and B were seen together, and  $N_A$  and  $N_B$  are the number of times that individual A or B was seen without the other, respectively (Cairns & Schwager, 1987). AI was only calculated for dyads that comprised focal bulls. The number of observations per dyad ranged from 0 to 211 for sexually inactive dyads (median = 28) and from 0 to 146 for sexually active dyads (median = 22).

To evaluate the effect of including motivational state, we calculated AI using three approaches: (1) using all observations of focal bulls regardless of group type or sexual state (the 'all-data sample', median<sub>obs</sub> = 95), (2) using only observations of bulls in all-male groups (the 'all-male sample', cf. Chiyo et al., 2011, median<sub>obs</sub> = 38) and (3) using only data for which the members of the dyad were both categorized with identical sexual states (i.e. observations on dates when the members of a dyad were in different states or when one member was in an unknown state were not included in calculations). AI values for dyads were calculated independently for both the sexually active (median<sub>obs</sub> = 45) and inactive states (median<sub>obs</sub> = 42). Association index data were non-normal even after arcsine transformation. As a result, nonparametric statistical approaches were used to compare the distributions of AI values derived from sexually active and inactive data. We also tested for any association between the AI value of a dyad and their absolute age difference using the Mantel test (Mantel, 1967) implemented in the package 'ade4' for R (Thioulouse, Chessel, Dolédec, & Olivier, 1997). All analyses and associated statistical tests were performed in R v.2.15.1.

### *Permuted Data Sets to Test for Random Association*

Permuted data sets can be used to provide a distribution of random association against which to compare observed data (Manly, 1995). We used the swap method described in Bejder, Fletcher, and Bräger (1998) to generate random associations from our observation data, in which the number of times a bull was seen and the group structure in terms of number and sizes of observed groups were maintained (i.e. the column and row totals). We additionally excluded all observed groups that were composed entirely of nonfocal individuals before permutation in order to increase the statistical power of the permutation tests while maintaining biological validity. This approach, which we will henceforth refer to as Permutation I, effectively retains the observed data structure and controls for variation among bull sightings (Bejder et al., 1998; Whitehead, Bejder, & Ottensmeyer, 2005). Two individuals from two distinct groups, for which each individual was only present in one of the groups, were randomly selected and swapped. Our modification accounting for different motivational states was to swap two bulls only if they were in the same sexual state on both dates on which the groups were observed (state 1 for sexually inactive random matrices and state 2 for sexually active random matrices), thereby keeping the state-specific social

attributes the same (Croft, Madden, Franks, & James, 2011). As such, randomly chosen bulls that were in different states were not available for swaps. This contrasts with the all-male and all-data approaches, in which bulls could be swapped despite being in different states. Although AI was only calculated for dyads composed of focal bulls, swaps could occur among all known bulls in the population, distributed among 2018 observations of distinct groups. Observed dyadic association strengths higher than those derived from permutations suggest the existence of social preferences.

Two thousand permutations of 1000 swaps each were completed and dyadic AI calculated for every permutation for each of the four samples (all-data, all-male, sexually active or sexually inactive). The distributions of observed and random AI values were therefore derived from the same data set, regardless of subsampling structure. This large number of swaps served to decrease autocorrelation among AI values between permutations. All AI values derived from permutations were grouped according to sample size (i.e. the sum of the observations of bulls A and B:  $N_S = N_A + N_B + 2N_{AB}$ ; see [Supplementary material](#)). The sample-size-specific distributions of AI values were then compared to observed AI values, which were considered significant when greater than or equal to the 95th quantile of the sample-size-specific distribution of randomly generated AI values. We controlled for sample size in this way to avoid bias potentially introduced by subsampling by state and consequent reductions in sample sizes. Because there were few randomized values corresponding to the highest and lowest sample sizes, a function for the sample size and corresponding 95th quantile value was fitted using nonlinear least squares and used to predict the significance cutoff value for the highest and lowest sample size distributions that had too few values for empirical estimation. We chose a one-tailed distribution because we were interested in preferred companions. These procedures were implemented in R v.2.14.0 (R Development Core Team, 2010).

### Modular Structure

To determine whether bull social networks were modular (i.e. whether bulls associate more closely with a subset of individuals), we constructed undirected weighted networks in which nodes representing individuals were linked by edges whose thicknesses were proportional to AI values. We then analysed these networks using established techniques (Newman, 2006) to identify structural components that may relate to the drivers of male–male associations. We examined structure using the Walktrap community detection algorithm in iGraph v.0.6.5 for R (Pons & Latapy, 2005), which accounts for weighted edges. This approach uses a short random walk to identify nodes that are more tightly connected to one another than to those outside, which are henceforth referred to as ‘modules’. We tried 3, 4 and 5 steps for each state-based network, choosing the partition that maximized modularity (Newman, 2006). To determine whether the observed partition was likely to occur by chance for each state, we compared the observed maximum modularity to the distribution of modularity maxima obtained for the 2000 permuted data sets obtained via Permutation I, described in the previous section. Departure from what would be expected at random suggests the existence of modules in the population.

### Network Metrics

We compared nodal metrics from ego-networks (graphs consisting of the immediate neighbours of each focal individual, in which neighbours share an AI > 0 with the focal individual) for

each bull across states to assess how individual bulls differ from one another socially. We created ego-networks using the ‘statnet’ package for R. Three primary network metrics were examined for each individual and compared across the sexually active and inactive states as a means to infer differences in their social drivers: (1) ‘ego-network size’ (also known as degree centrality, the number of direct connections to the individual), which directly measures the number of companions an individual has had, (2) ‘ego-network density’ (sometimes referred to as clustering coefficient, the proportion of an individual’s companions that are also connected to one another), which is a measure of community integrity defined as the propensity of a subject’s companions to associate with one another and (3) ‘betweenness centrality’ (the number of shortest paths in the entire network that pass through an individual), which indicates how centrally embedded the subject is within the full network (Wasserman & Faust, 1994). Individuals with higher betweenness are structurally important to the integrity of networks since they tend to bridge different social groups (Lusseau & Newman, 2004) and can be biologically relevant by facilitating information exchange or maintaining social cohesion (Chiyo et al., 2011; Williams & Lusseau, 2006). For a subset of analyses we also computed a related measure, ‘eigenvector centrality’, which is also influenced by the centrality of an individual’s contacts themselves.

To test the null hypothesis that network measures do not depend on sexual state, we generated 10 000 permuted samples of the sexually active and sexually inactive data sets, respectively. This procedure, henceforth referred to as Permutation II, preserved associations among individuals on any given day, the sizes of aggregations in which they were observed and the total number of observations per individual, but it randomly assigned their sexual state (see [Supplementary material](#) for details). The mean values of the three network metrics and differences between the two states for the permuted data sets were computed.

### Ethical Note

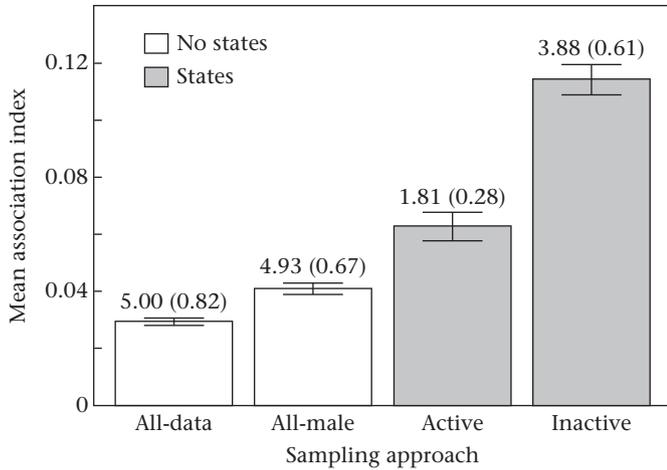
Observations were conducted in a noninvasive manner (ACUC R217B) and with permission of the Kenya Wildlife Service (wildlife authority in Kenya), the Samburu and Isiolo County Councils (local managers of the protected areas) and the University of Oxford and Save the Elephants (host institutions).

## RESULTS

### Comparing Association Index Values across Sampling Approaches, Sexual States and Age Classes

AI values were significantly greater among sexually inactive bulls than among active bulls (Wilcoxon signed-ranks test:  $W = 131465.5$ ,  $N = 414$ ,  $P < 0.001$ ). Because data were nested across the other treatments (all-male or state-based treatments were a subsample of the all-data treatment), statistical comparisons were not appropriate, although it was clear that AI means were higher with state-based treatments. This shift in means was not related to differences in sample sizes across the treatments, as the all-data and all-male treatments showed similar AI distributions, but had markedly different sample sizes. Similarly, the all-male, sexually active and sexually inactive treatments had similar sample sizes, but showed differences in the distributions of means.

Identification of significant dyads varied depending on data treatment (Fig. 1). Dyadic AI was significantly greater than expected by chance for 12.8% of potential dyads in the sexually inactive state (mean AI  $\pm$  SD =  $0.334 \pm 0.118$ ,  $N = 62$ ) and 6.8% of potential dyads in the sexually active state (mean AI  $\pm$  SD =  $0.310 \pm 0.251$ ,  $N = 29$ ). In contrast, 16.1% in the all-data sample (mean



**Figure 1.** Mean dyadic association index  $\pm$  SE among male African elephants based on sampling approach (all-data, all-male, state specific: active, inactive). Numbers above bars indicate the mean  $\pm$  SE number of significant affiliates per bull. Standard errors were determined empirically.

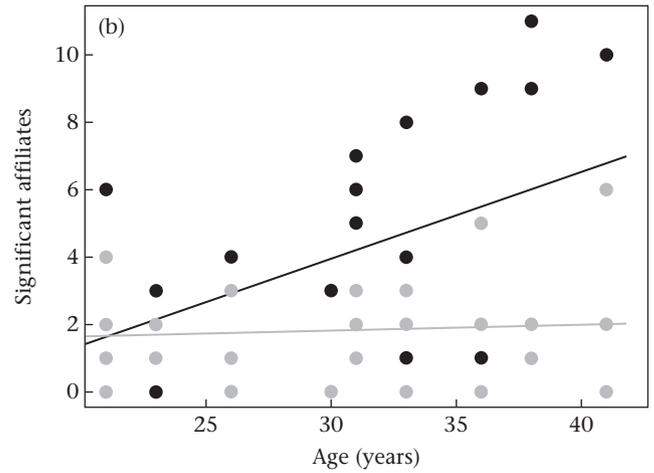
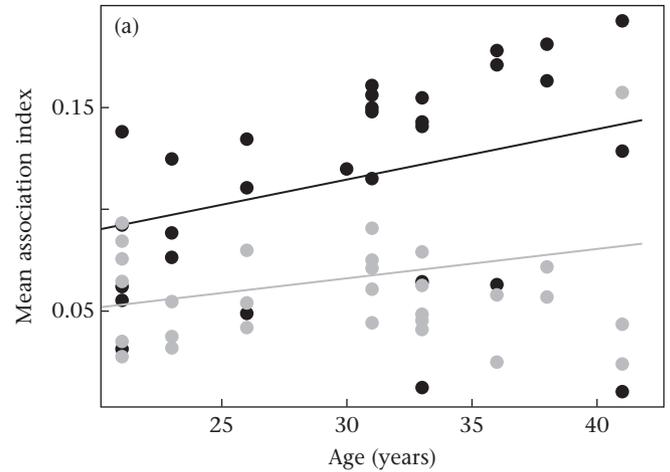
AI  $\pm$  SD =  $0.079 \pm 0.025$ ,  $N = 80$ ) and 15.9% in the all-male sample (mean AI  $\pm$  SD =  $0.117 \pm 0.043$ ,  $N = 79$ ) were significantly greater than expected by chance when disregarding state. Mixing states by randomizing individuals into groups that could not occur biologically deflated the randomized AI distribution relative to when biological constraints were imposed in the randomization procedure. As a result, the threshold above which AI values were considered significant was deflated in the all-data and all-male samples, resulting in more significant dyads.

The average AI for the inactive state and the number of significant dyads per individual when inactive were positively correlated with their age (Spearman rank correlation: AI:  $r_s = 0.422$ ,  $N = 32$ ,  $P < 0.05$ ; significant dyads:  $r_s = 0.472$ ,  $N = 32$ ,  $P < 0.05$ ). However, these relationships were not found among sexually active bulls (AI:  $r_s = -0.014$ ,  $N = 32$ ,  $P = 0.938$ ; significant dyads:  $r_s = 0.028$ ,  $N = 32$ ,  $P = 0.879$ ; Fig. 2). Across both states, significant dyads included age-mates and non-age-mates. The proportion of significant dyads differed by dyadic age category in the inactive state (chi-square test:  $\chi^2_3 = 31.575$ ,  $P < 0.001$ ) but not in the active state ( $\chi^2_3 = 2.157$ ,  $P = 0.541$ ; Fig. 3). Age differences among significant dyads tended to be smaller among inactive dyads (median: inactive: 5; active: 10), with 54.8% and 34.4% of significant dyads composed of age-mates in the inactive and active states, respectively. Of the significant inactive age-mates, 82.4% were older dyads. However, there was no significant relationship between the absolute within-dyad age difference and its AI value in either state (Mantel test: inactive:  $r = -0.1073$ ,  $P = 0.96$ ; active:  $r = 0.0633$ ,  $P = 0.10$ ).

There was a positive correlation in the AI between sexually inactive and sexually active states among dyads for which both could be calculated (Spearman rank correlation:  $r_s = 0.214$ ,  $N = 414$ ,  $P < 0.001$ ). Among dyads for which AI was significant in both states ( $N = 7$ ), 85.7% were composed of bulls over 30 years old at the midpoint of the study. The median age difference among these dyads was 7 years.

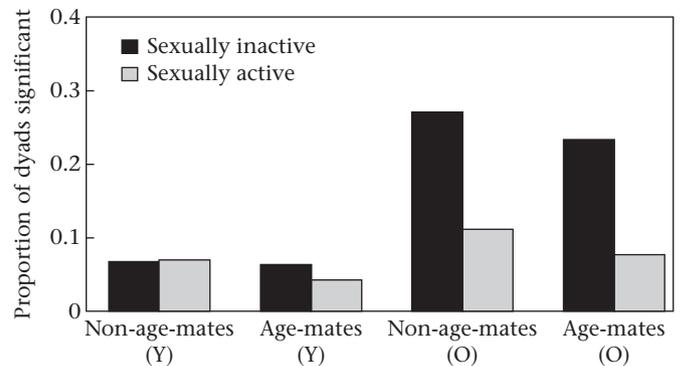
**Module Detection and Network Statistics**

Greater modularity ( $q_{max}$ ) than expected under the null model of chance association was found in both the sexually inactive and active states, with the  $q_{max}$  in the active state higher than that in the inactive state (Permutation I:  $P < 0.0005$ ; Fig. 4). However,

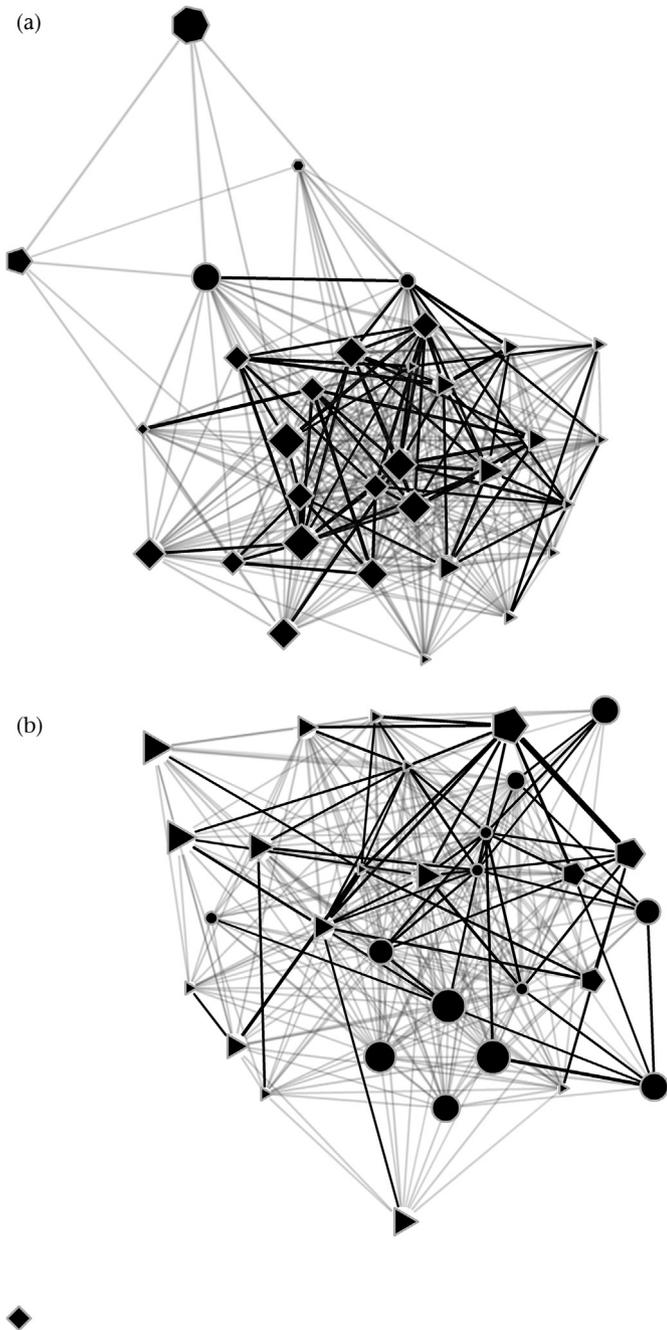


**Figure 2.** Mean (a) association index and (b) number of significant associates for individual African elephant bulls ordered by bull age. Black dots: sexually inactive; grey dots: sexually active. See text for details. Lines show linear fits.

observed values (inactive:  $q_{max} = 0.082$ ; active:  $q_{max} = 0.21$ ) were below the 0.3 threshold taken to indicate meaningful structure (Whitehead, 2008). The composition of modules differed across states. On average, sexually inactive bulls had larger and denser ego-networks but lower betweenness relative to when active (Permutation II:  $P < 0.0001$ ). The ego-network sizes and densities



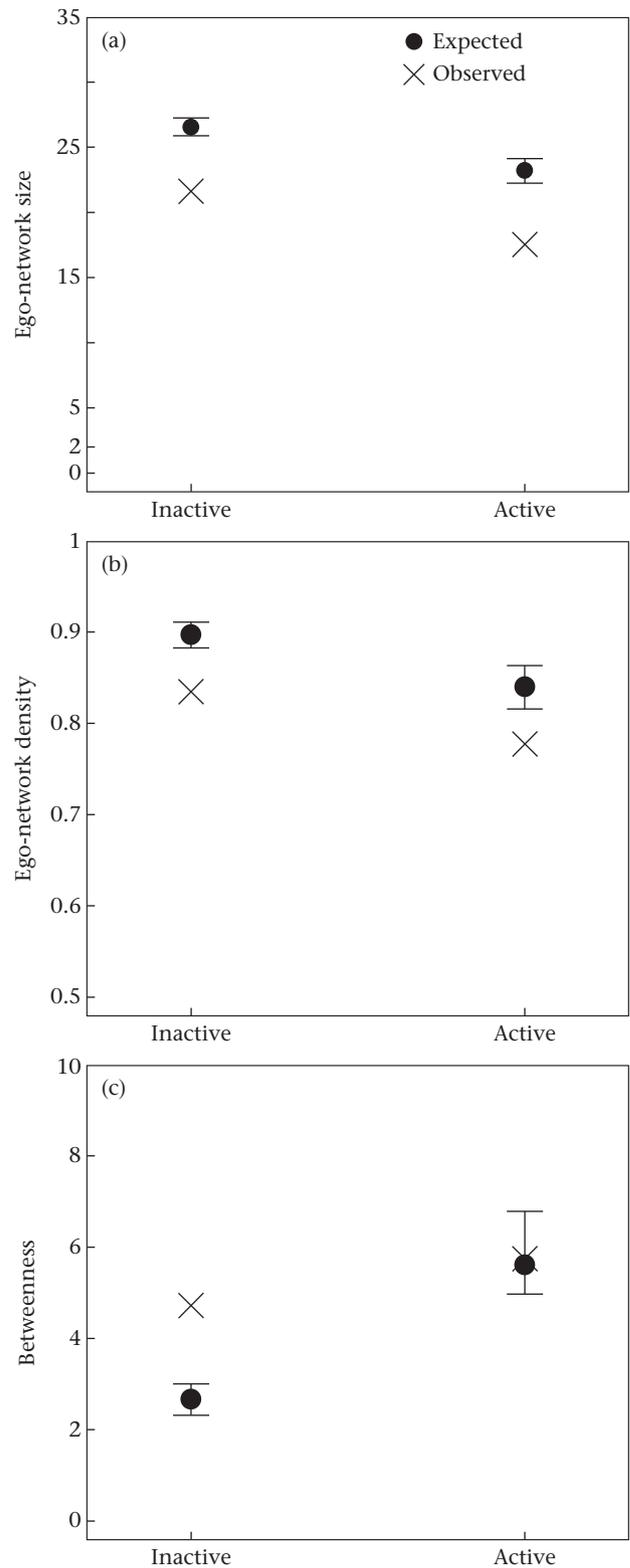
**Figure 3.** Proportion of significant dyads to available dyads among dyadic age categories of male African elephants. Assignment of 'old' or 'young' was determined by the age of the youngest member of the dyad (old:  $\geq 30$  years; young:  $< 30$  years). Age-mates were separated by 5 or fewer years.



**Figure 4.** Social networks of male African elephants when (a) sexually inactive and (b) sexually active, constructed using Fruchterman and Reingold's force-directed placement algorithm. Nodes represent individual bulls, with node size corresponding to age at the midpoint of study, and shape representing module assignment. Edge weight corresponds to dyadic association index value. Edge colour denotes whether the association index value was found to be significant (grey: nonsignificant; black: significant).

observed in either state, as well as betweenness in the inactive state, were unlikely to have arisen through chance association ( $P < 0.0005$ ). Only betweenness in the active state was not different from random (Fig. 5). The relative values of network measures under each treatment are provided in Supplementary Fig. S1.

The relationship between network measures and age varied with sexual state. In the sexually inactive network, density was negatively correlated with age (Spearman rank correlation:  $r_s = -0.49$ ,  $N = 32$ ,  $P < 0.01$ ), but no other measures exhibited a significant relationship. In the sexually active network the reverse was true: density showed a significant positive correlation with age



**Figure 5.** (a) Ego-network size, (b) density and (c) betweenness metrics derived from elephants in the inactive and active sexual states relative to the corresponding permuted values. Expected metrics present the average and confidence interval of the permuted data set averages (mean  $\pm$  95% CI,  $N = 2000$  data sets). Observed metrics present the state-specific averages of the 32 focal bulls (confidence intervals were not computed because there was only one observed data set).

( $r_s = 0.42$ ,  $N = 32$ ,  $P < 0.05$ ), while size and betweenness showed negative correlations with age (size:  $r_s = -0.46$ ,  $N = 32$ ,  $P < 0.01$ ; betweenness:  $r_s = -0.43$ ,  $N = 32$ ,  $P < 0.05$ ). There was no correlation between age and eigenvector centrality in the sexually inactive state ( $r_s = 0.29$ ,  $N = 32$ ,  $P = 0.1129$ ), but there was a significant negative correlation in the sexually active state ( $r_s = -0.44$ ,  $N = 32$ ,  $P < 0.05$ ).

## DISCUSSION

Variation in social interaction among animals may arise from segregation due to reproductive states (as shown here), dynamic environments (Gill & Wolf, 1975), shifts between life history tactics (Bon, Rideau, Villaret, & Joachim, 2001; Fischhoff et al., 2009), or changes in life stage (Patriquin et al., 2010), among other processes. The behavioural state-based analytical approach implemented here on male African elephants provides an effective way to partition and quantify relationships related to different contexts. By accounting for motivational states in our study system, we were able to assess more precisely the social complexity of male African elephants, an animal previously assumed to be relatively asocial. Our results demonstrate that associations among pairs of bulls are much stronger than previously reported in studies in which sexual state was not controlled for (thereby diluting associations by considering behaviourally restricted periods as missed opportunities to associate; Chiyo et al., 2011). However, while association indices were stronger in our state-based treatment compared to standard approaches, we used a more conservative definition of what constitutes significant dyadic affiliation. This is because partitioning data sets for the state-based analyses reduced the denominator of the AI, which can itself result in higher AI values. To account for this, we defined significant affiliates (i.e. those with AI values greater than random) not with respect to the average of the population at large, but relative to dyads that had the same total number of samples ( $N_s$ ) in permutations. We then compared the number of significant dyads relative to those derived from permutations that allowed biologically unfeasible associations (all-data and all-male). Lack of adherence to the assumption that all individuals are equally likely to associate is an acknowledged problem in approaches to social data, often discussed with respect to unrecognized spatial and temporal constraints (Whitehead et al., 2005). This study provides an explicit example of how such problems driven by behavioural state can bias inference.

### *Significant Affiliates, Age and Sexual State*

A surprising result of these analyses was the presence of significant affiliates across behavioural states. In particular, we expected males to be highly individualistic in their sexually active state due to the high levels of mate competition typical of polygynous species. Most of the observations of sexually active males occurred in mixed-sex groups and it is possible these results reflect attraction to the same resource (i.e. oestrous females) among males with overlapping sexually active periods, and consequently may not reflect male–male companion preference (Lee, Poole, Njiraini, & Moss, 2011). Active periods become more consistent as bulls age, and those males that come into musth show a high degree of temporal fidelity in the timing of their musth periods across years (Poole, 1987; Rasmussen, 2005), possibly enhancing the effect of overlapping resource attraction, although such a hypothesis is less applicable to younger, nonmusth individuals.

If male interactions are used to assess the ability of possible competitors (Beacham, 2003; Evans & Harris, 2008; de Villiers et al., 2003) or coalition partners (Connor et al., 2001), persistent relationships among age-mates may be beneficial by facilitating

contest resolution based on previous knowledge rather than potentially dangerous conflict (Rowell, 1974). Such a hypothesis has less relevance to non-age-mates, in which substantial size asymmetries presumably reduce the probability of conflict. The observed difference in median age difference among significant sexually active dyads relative to inactive dyads may be a function of young males shadowing older, more experienced males during sexually active states to gain experience (the information exchange hypothesis of Evans & Harris, 2008) or to access mating opportunities as noncompetitive sneakers (Perrill, Gerhardt, & Daniel, 1978). The drivers of significant sexually active affiliates were not definitive, and further work documenting directions and types of male interactions may provide insight to this question.

The greater proportion of significant affiliates that were age-mates among inactive dyads may indicate that competitor assessment plays a role during inactive periods, possibly by reaffirming dominance hierarchies or renegotiating relations based on dynamic variables like body condition (i.e. repeated assessment of the physical state of competitors). The majority of these were among older dyads (82.4%), potentially in relation to higher benefits of resolved rank among bigger bulls that come into musth during their active periods. However, the tight and extended nature of bonds between males (recorded in GPS radiotracking data reported in Rasmussen, 2005), and the tendency for the proportion of significant dyads to be among older bulls regardless of their being age-mates suggest that other mechanisms besides simple competitor assessment also play a role in male relationships. Disproportionate bonding with age-mates may arise from cooperative benefits as has been documented in other taxa (e.g. Langergraber et al., 2007). Vigilance enhancement or antipredator benefits (Hamilton, 1971) are probably important benefits in the study ecosystem where human predation is relatively high (Wittemyer et al., 2013), and foraging facilitation has been observed among male groups, whereby multiple individuals feed on a resource that was made accessible by joint activity or by a member of the group (Wittemyer, n.d.). Such cooperative relationships may occur more frequently among relatives (Chiyo et al., 2011). In addition, males grow up in highly social female-structured societies before dispersing (Lee et al., 2011). It is possible that the extended significant relationships recorded are not costly and are simply a manifestation of the species' social propensity. Determining the motivations giving rise to these social relationships, which appeared to be manifested over multiple years and were stable despite dynamics in the study system, was beyond the scope of this study.

A positive association between dyadic age difference and AI value was found in a study of all-male groups in Amboseli National Park, Kenya (Chiyo et al., 2011). Sexually inactive males in our study did not show such a trend. This disparity could reflect behaviours that manifest from differences in the age structure of the two populations (Wittemyer et al., 2013). The Amboseli population had a greater spread of age differences in the sample analysed (up to 40 years) than that in our system (up to 20 years). Alternatively, differences may reflect incompatibility across our different analytical approaches, supported by the fact that trends derived from the all-male sample (as conducted by Chiyo et al., 2011) differed from those derived from either the sexually active or the sexually inactive samples. Specifically, older bulls in the present study and in Amboseli were more often observed in all-male groups than were younger bulls (Chiyo et al., 2011); as such, metrics derived from all-male groups alone may exaggerate the role of older bulls within networks.

### *State-specific Network Structure*

We found weak (but higher than expected by chance) modular structure in networks for both states. However, the 32 focal

individuals were partitioned differently in each state and the sexually active social network was more clearly divided into modules. Age-related homophily does not appear to account for the observed modules as each module included bulls in different age groups (Fig. 4). Modularity may be partially due to the use of geographically distinct 'bull areas' (Croze, 1974) during the inactive state (manifested in the study system as an 'east' versus 'west' distinction), when individuals focus on foraging rather than mate searching. Such spatial segregation probably facilitates repeated encounters and the emergence of conspecific preferences, although, by and large, our sample of focal males inhabited the western bull area. In the Samburu system, mature males focused their sexually active states on one of the three time periods coinciding with female receptivity (Rasmussen, 2005; Wittemyer, Rasmussen, & Douglas-Hamilton, 2007). This temporal segregation in sexual activity with attraction to the same resource, oestrous females, also may serve to structure social contacts of males using the same areas. This is consistent with the observation that modularity tends to be higher in the sexually active state. Although modularity values were unlikely to have arisen by chance, they were nevertheless very weak relative to those found in female African or Asian elephants, *Elephas maximus* (de Silva & Wittemyer, 2012), perhaps a manifestation of the lower level of sociality in males (Chiyo et al., 2011; Lee et al., 2011). The weakness of the modularity and the lack of obvious drivers of the structure make inference difficult.

All ego-network metrics, except betweenness in the sexually active state, were significantly different from expectations based on randomizations of association (Permutation I). Individuals formed larger and better connected networks when sexually inactive relative to when active, an outcome that was the opposite of expectations based on randomization by state (Permutation II). Networks are likely to be structured by the different levels of competition and motivations for aggregating across sexually active and inactive periods (discussed above). Although we did not investigate the costs and benefits of grouping among males between sexual states, our finding that most observed ego-network values were unlikely to have arisen by chance indicates that further work targeting such shifting cost/benefit ratios may be fruitful.

Network centrality metrics measure the extent to which an individual is a social hub, and they can potentially be used to discern individuals that are important for the structural integrity of networks. Chiyo et al. (2011) found that network centrality (measured as eigenvector centrality) was positively correlated with age in their study of male sociality in Amboseli National Park, Kenya, suggesting a possible function of older individuals in maintaining social cohesion. In contrast to the Amboseli study, we found a significant negative correlation between age and eigenvector and betweenness centrality measures when bulls were sexually active and found no significant relationship when sexually inactive. The significant negative correlation between age and eigenvector (as well as betweenness) centrality when bulls were sexually active could be due to increasing temporal asynchrony in sexual activity with age that is inherently driven by avoidance of overlap with older, sexually active bulls (whose sexually active periods are more synonymous with aggressive musth).

#### Future Directions

The duration of sexually active periods in male elephants decreases with age as these periods become more synonymous with musth and therefore more energy intensive (Rasmussen, 2005). In addition, younger bulls in the Samburu system that did not experience musth tended to have two sexually active periods annually

whereas older bulls had one (Rasmussen, 2005). This suggests that the duration of overlap in motivational state between two bulls will be dynamic over the course of their lives and, therefore, their potential and motivation to associate may vary over time. State-specific analyses as conducted here are essential to identify and understand such dynamics, and more broadly to parse out the potential drivers of complex behaviours in dynamic social systems. Our analyses suggest that not controlling for inherent structure that influences the ability of individuals to associate can strongly affect the results and interpretation of social dynamics.

Time-ordered network analyses and approaches like the exponential-family random graph model (ERGM) or the multiple regression quadratic assignment procedure (MRQAP) may be particularly helpful for understanding state-dependent networks (Blonder & Dornhaus, 2011; Pinter-Wollman et al., 2014), but such approaches require large volumes of data (beyond that available here). The present study represents a 4-year time window, which is a snapshot considering elephants can live up to 6 decades in the wild (Moss, 1988). More detailed behavioural observations and longitudinal data are needed to address temporal changes in association within a state-based framework and to test alternative hypotheses about their social function. Unfortunately, the Samburu population continues to experience high rates of human-caused mortality that have strongly altered the sex and age class structure, particularly among males (Wittemyer, Daballen, & Douglas-Hamilton, 2011, 2013). As a result, the majority of the individuals in this study are dead, precluding further research into the drivers and structure of long-term bonding among these males. The differences in social properties among age classes documented here and elsewhere (e.g. Chiyo et al., 2011) suggest that such age-selective harvest will impact the social structure of a population. Further work addressing whether and how bulls compensate for the loss of age-mates as they mature may help to elucidate the driving costs and benefits of association among males.

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#### Supplementary Material

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