A Comparison of Social Organization in Asian Elephants and African Savannah Elephants

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Abstract Asian and African elephant species have diverged by *ca.* 6 million years, but as large, generalist herbivores they occupy similar niches in their respective environments. Although the multilevel, hierarchical nature of African savannah elephant societies is well established, it has been unclear whether Asian elephants behave similarly. Here we quantitatively compare the structure of both species' societies using association data collected using the same protocol over similar time periods. Sociality in both species demonstrates well-defined structure, but in contrast to the African elephants of Samburu the Uda Walawe Asian elephants are found in smaller groups, do not maintain coherent core groups, demonstrate markedly less social connectivity at the population level, and are socially less influenced by seasonal differences in ecological conditions. The Uda Walawe Asian elephants, however, do maintain a complex, well-networked society consisting of ≥2 differentiated types of associates we term ephemeral and long-term affiliates. These findings imply we must broaden our recognition of multilevel social organization to encompass societies that fall along a gradient of nestedness, and not merely those that exhibit hierarchical nesting. This in turn suggests that multilevel structures may be more diverse and widespread than generally thought, and that phylogenetic comparisons within species-rich clades, such as that of primates, using the methods presented can provide fresh insights into their socioecological basis.

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Introduction

Among the diversity of social organizations, multilevel societies with hierarchical nesting of social levels have emerged in several disparate taxa: humans (Hamilton *et al.* 2007), nonhuman primates (Kawai *et al.* 1983; Kummer 1968), proboscideans (Wittemyer *et al.* 2005b), cetaceans (Connor *et al.* 1992), and birds (Hegner *et al.* 1982). In such societies, social affiliations among individuals are stratified into different tiers, which can be defined based on patterns of association among them (Wittemyer *et al.* 2005b). Multilevel societies with hierarchical patterns of association among individuals defined on the basis of spatial proximity are conceptually different from societies with hierarchical dominance structures resulting from age, size, fighting ability, or other characteristics of individuals and social feedbacks (Chase *et al.* 2002), though societies with hierarchical dominance structures may also exhibit multilevel organization (Archie *et al.* 2006; Wittemyer and Getz 2007). Hierarchically stratified societies are similar in that they often exhibit fission–fusion social dynamics (Connor *et al.* 1992; Dunbar and Dunbar 1975; Kummer 1984), but fission–fusion societies are not necessarily stratified hierarchically (Cross *et al.* 2005). Known mechanisms driving the emergence of hierarchical societies include responses to predation pressure (Dunbar and Dunbar 1975), male infanticide (Grueter and van Schaik 2010), and interaction across multiple socially facilitated behaviors, e.g., group territory or resource defense, mating opportunities, information exchange, etc., that emerge at different group sizes and composition (Rubenstein and Hack 2004; Wittemyer *et al.* 2005b). As such, the formation of hierarchical relationships appears to be a response to the costs and benefits associated with the social context and consequences of group size and composition.

Currently, theory regarding the factors driving hierarchical social stratification is poorly developed and not explicitly addressed by socioecological frameworks (Emlen and Oring 1977; Wrangham 1980). Where multiple studies of the same species have been conducted, i.e., humans, methodology to define social structure often varies or is difficult to apply across different contexts. Research on nonhuman hierarchical societies typically focus on single, well- studied populations, with little attempt at cross-comparison among populations or species (*cf.* Hill *et al.* 2008). There is good reason for this, as it is often difficult to replicate studies across localities or taxa, each with their own particular observational and methodological constraints. Nevertheless, replicated studies across populations or species are necessary if we are to identify mechanisms driving the emergence of behaviors of interest (Symington 1990), which necessarily precede theoretical treatment (Chapman *et al.* 1995). Comparative population- or species-level studies of the factors related to the formation or dissolution of hierarchical social tiers can offer deeper insight to the mechanisms driving the emergence of such societies. Here we compare social aggregation behavior between 2 related species, African savanna elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*).

African elephant social organization is well described, with the fundamental social unit typically being sets of related females and their dependent offspring (Buss 1961; Buss and

Smith 1966). These family units often demonstrate repeated association with other family units to form extended groups, also typically kin-based, which have been described as kinship groups (Douglas-Hamilton 1972) or bond groups (Moss and Poole 1983). This description was recently refined based on quantitative analysis of their fission–fusion associations, empirically delineating 4 social tiers: tier 1 units are defined as a breeding female and her sexually immature offspring (mother–calf units); tier 2 units comprise regularly associating tier 1 units and are classically referred to as family or core groups; and tier 3 units corresponding to kinship or bond groups are composed of multiple tier 2 units, which in turn are nested within tier 4 groups (Wittemyer *et al.* 2009, 2005b). These social units are part of a 5th tier subpopulation, probably as a function of geographic features, which in turn is nested within a 6th tier population, also geographically defined.

In contrast to African savanna elephants, few studies of Asian elephant social organization are published and less is known about the occurrence of hierarchical organization in this species. Males disperse on reaching adulthood, but females and calves are usually found in small groups (de Silva *et al.* 2011a; Eisenberg *et al.* 1990; Fernando and Lande 2000; Vidya and Sukumar 2005). Fission–fusion dynamics in these smaller, female-based social units have been observed (de Silva *et al.* 2011a). The species uses a wide range of tropical habitats with seasonal rainfall and is a generalist that occupies a similar niche to African elephants as the largest herbivore in its environment (Campos-Arceiz and Blake 2011; Campos-Arceiz *et al.* 2008; Fernando *et al.* 2008; Leimgruber *et al.* 2003). The two clades have nevertheless diverged by at least 6 million yr (Shoshani and Tassy 1996).

Here we analyze individual-based, social affiliation data collected from two wild populations of African and Asian elephants. We collected these data over a 2-yr period, following comparable protocols. Our aims here are 2-fold: 1) to offer a direct comparison of social organization in the two species and 2) to explore the sensitivity and strengths of different quantitative methods for defining multilevel societies to facilitate effective analysis of social behavior in other species. We apply three approaches to define properties in the individual affiliation data: 1) network path properties, 2) hierarchical clustering patterns, and 3) association index threshold analysis. We expected, based on the previous studies (de Silva *et al.* 2011a; Wittemyer *et al.* 2005b), that both distributions would show positive skew but that the Asian population would tend to have fewer strong relationships than the African. We then examine the effect of this on higher-order structure. Results demonstrate the strongly nonrandom nature of social organization in both species, but also highlight substantial differences in the strength and uniformity of social bonding across the two populations. We discuss the implications of these findings with respect to the ecological contexts in which the two species have evolved and offer suggestions for further theoretical and empirical treatment of multilevel societies.

Methods

Data Collection

Samburu-Buffalo Springs National Reserves (SBSNR) Samburu and Buffalo Springs national reserves in northern Kenya (0.3–0.8°N, 37–38°E) are primarily semiarid

savanna with a riparian woodland and cover a combined area of 220 km^2. Individuals in this elephant population have been monitored since 1997 (Wittemyer 2001). This semiarid region is dominated by Acacia–Comiphora savanna. The reserves are centered on the Ewaso Ngiro River, which is the only permanent water source in this semiarid region and, as such, a focal area for wildlife. Rainfall averages approximately 350 mm/yr and occurs during biannual rainy seasons generally taking place in April/May and November/December. For purposes of the analyses presented here, we defined seasonal transitions using spatially explicit remotely sensed Normalized Difference Vegetation Index (NDVI) data, a longitudinal metric of vegetative productivity (Goward and Prince 1995), as described by Wittemyer *et al.* (2007).

We collected the data presented here from January 2001 through December 2002, representing a period including *ca.* 4 wet seasons and 4 dry seasons. We recorded the presence of individual elephants (all elephants that use the reserves are known), location, and time during weekly travel along 4 established transects (*ca.* 20 km long) in the protected areas (Wittemyer *et al.* 2005a). The focal elephants are not always present in the national reserves (Wittemyer *et al.* 2007), which represent <10% of the subjects' known range (Wittemyer *et al.* 2005b); therefore sampling was opportunistic. As a result of heavy tourist use of the parks, the focal elephants are habituated to vehicles, enabling easy observation.

Association data are compiled from 1483 observations of elephant aggregations (888 dry season and 595 wet season observations), where aggregations are defined as all elephants within a discernable grouping typically within a radius of 500 m (Wittemyer *et al.* 2005a). Only observations for which the observer was confident of registering all associating breeding females are included. The analysis presented focuses on breeding females in the resident subpopulations (Wittemyer 2001), which totaled 112; juveniles and adult males are not analyzed. Each individual's aggregation was recorded only once per day to avoid nonindependence of observations. In all instances of multiple observations per day, the first observation was retained to avoid potential observer (preordained) bias regarding the location or social context of individuals.

Uda Walawe National Park (UWNP) We consider only observations within Uda Walawe National Park (UWNP), Sri Lanka, where human activity is least likely to affect behavior. This park encompasses 308 km^2 between latitudes 6°25′–6°34′N and longitudes 80°46′–81°00′E, at an average altitude of 118 m. Habitat includes open savannah-like grasslands, dense scrub, riverine forest, secondary forest, a permanent river, seasonal streams, and water holes as well as large human-made reservoirs. Rainfall measured using a standard U.S. Weather Bureau rain gauge ranged from 1293 to 1726 mm annually. Dry months (January–February and May–September) received on average 45.5 mm of rain and wet months (March–April and October–December) received on average of 230.4 mm, corresponding to 2 annual monsoons (Zubair *et al.* 2008). Human disturbance within the park was minimal and subjects were well habituated to tourists.

The data collection protocol matched as closely as possible that of Wittemyer *et al.* (2005b). The study began in May 2006, but the data presented span 259 field days (20 mo) from 2007 to 2008, or 3 d/wk on average. This constitutes 5 seasons: 2

wet, 2 dry, and 1 transitional. We typically entered the park between 06:00 and 07:00 h (sunrise), remaining continuously inside until 17:30–18:30 h (sunset). Driving routes were varied such that all accessible parts of the park were covered in a week. Locations where elephants were closest to the road were marked on a hand-held Garmin GPS unit. We observed 286 breeding and postreproductive females along with their young during the course of the study. We individually identified all of them using photographs of natural markings (de Silva *et al.* 2011b).

We compiled data from 1366 observations of elephant aggregations (687 dry season and 511 wet season observations), where aggregations were defined to be subjects grouped together within a 500-m radius, described by de Silva *et al.* (2011a) and Wittemyer *et al.* (2005b). We recorded all observations, even if all adult females were not clearly visible. We excluded aggregations containing only unidentified individuals from further analyses. Where at least one adult female was known, we typically identified ≥80% of the individuals present. Because UWNP contained large tracts of tall grass habitat, most observations occurred in areas of high visibility. Moreover, spending ≥30 min with the same group of elephants minimized the chances that individuals remained obscured by vegetation. We always noted the location, identities, and age classes of all individuals, not only the first encounter with any individual. We recorded data using an HP ipaq hand-held PDA with custom software.

Data Analysis

We reduced data sets to include only individuals that were seen ≥20 times over the course of either study to avoid distortions to the measures of association due to temporary migrants or individuals that were rarely seen. The resulting sample sizes were 105 adult females for the Asian population and 110 for the African (2 of the original 112 died in the middle of the period analyzed and we removed them from analysis).

Data collection protocols were identical except that we defined association of individuals in the African population by group composition in the first observation of the group in a given day. In contrast, we considered individuals in the Asian population to be associated if we observed them in a group together at least once in a day. We combined multiple sightings of an individual with any other individual within the same day, thereby indicating a single association event. We considered each day to be an independent interval. We converted associations into the Simple Ratio Index of association (henceforth Association Index or AI), which is a symmetric index reflecting the proportion of times we observed a pair of individuals together out of the total number of times we observed either of them (Cairns and Schwager 1987; Wittemyer *et al.* 2005b). These matrices of association form the basis of all further analyses. We examined both study sites using full data sets as well as partitions containing only wet or dry seasons, in which we pooled all wet months or dry months respectively.

Lower-Order Structure—Basic Properties of Association Matrices We first test the null hypothesis that associations are completely random. This addresses whether properties of the data having nothing to do with sociality could lead

to the observed data structure, e.g., the number of observations per individual, observed aggregation sizes, or number of sampling intervals. For each real data set we generate 1000 randomized data sets that preserved these qualities of the original data sets, but simply reassign individuals randomly to groups using the swap method (Bejder *et al.* 1998; Sundaresan *et al.* 2007a, 2009). We make 100,000 swaps to generate a single randomized data set and use the mean AI as the test statistic.

We then compare the AI distribution of the African population to that of the Asian population. We expected the Asian population to have fewer strong relationships than the African. This property is quantified by the kurtosis of a distribution. We test the null hypothesis that the two distributions are not significantly different from one another using the 2-sample permutation test with 10,000 permutations and kurtosis as the test statistic (Sokal and Rohlf 1995).

We explore structural properties using social network analyses. In social networks each individual is represented as a node and, in this analysis, connections between nodes correspond to interindividual AI values (Wasserman and Faust 1994). We offer a general comparison of three network path properties as a qualitative overview of the two populations: egonetwork size, clustering coefficient, and distance weighted reach. An egonetwork is the set of individuals a subject is directly connected to, i.e., those that are 1 step away (Wasserman and Faust 1994). Clustering coefficient is the proportion of actual ties among an individual's companions to the number of potential ties that could exist if they all associated with one another (Wasserman and Faust 1994). Distance weighted reach is a weighted sum of the reciprocal of the path length from the subject to all others in her network (Borgatti *et al.* 2002; McDonald 2007). Path properties are calculated for each node and averaged over all individuals. We test the significance of observed differences in estimated mean values using the 2-sample permutation test, with 10,000 permutations.

Higher-Order Social Structure We use hierarchical cluster analysis (Wittemyer *et al.* 2005b) to examine whether the Asian population exhibits social tiers similar to that of the African. Dendrograms are generated using average, Ward's, single, and complete linkage clustering methods. The method that best captures association topology is determined using the cophenetic correlation coefficient (Sokal and Rohlf 1962), with values >0.8 signifying little distortion in interindividual relationships. We then analyze dendrogram structure by looking at characteristics of the tree bifurcation rate. Significant changes in the slope of cumulative graphs of trees' bifurcation rates are used to identify social tiers (Wittemyer *et al.* 2005b). The points where slopes demonstrate the maximum rate of change, termed knots, are identified by comparing the distribution of bifurcations per stepwise increment above vs. below the knot values using the Mann–Whitney U test (Wittemyer *et al.* 2005b). Knot values are compared across seasons and species.

We also explore social stratification by assigning individuals to clusters using the Girvan-Newman algorithm, which finds the most appropriate way to divide a network into n clusters based on network topology (Girvan and Newman 2002). This algorithm does so by finding the subsets in which individuals have more connections to one another than to those outside their subset, irrespective of edge weights. However, a network can be partitioned into any arbitrary number of subnetworks in

this manner. The modularity quotient Q is an objective way of determining how many clusters is suitable (Clauset *et al.* 2004). We take the partition that maximizes Q to be the most appropriate way of clustering a network. If more than one partition yields identically high values of Q, we measure the number of clusters to be the average of the two. For instance, if a network could be divided into 16 or 17 clusters we assigned a value of 16.5. The actual placement of individuals within clusters does not matter for ensuing analyses, in which we are concerned only with changes in the number of clusters.

To incorporate edge weights in defining network structure in addition to topology, we next implement a thresholding procedure. We remove all edges below a particular value as well as isolated individuals, recluster the remaining individuals as described in the preceding text, then record the number of clusters. We repeat this procedure, sequentially removing ties at or below increments of 0.02 (0.02, 0.04, 0.06, … 0.9) and plotting the resulting number of clusters against the increment value. This procedure is described in detail by de Silva *et al.* (2011a). We also perform this procedure for data sets generated through randomization to assess whether simple constraints of the data structure having no relation to social behavior could produce similar clustering.

To examine whether these curves show regions of structural change indicative of social levels, we test the significance of local slope changes around any given point by using a sliding window spanning 0.2 AI increments (0.1 above and 0.1 below the point). We apply the Mann–Whitney U test to compare slopes for stepwise increments above a point to those below it, within this window. Significance levels for other window sizes are provided in the electronic supplementary material (ESM) figures.

Implementation and Ethical Note

We performed statistical analyses, dendogram plots, and Girvan-Newman procedures primary ly using Matlab v.7. We visualized SRI matrices as social networks using Netdraw and calculated network measures with UCINET (Borgatti *et al.* 2002). Plots use the graph-theoretic layout with node repulsion (Borgatti *et al.* 2002). This research complied with the Institutional Animal and Use Committee of the University of Pennsylvania, and was conducted with the permission of the Kenya Wildlife Service and Department of Wildlife Conservation, Sri Lanka.

Results

Regardless of season, African savannah elephants at SBSNR (henceforth African population) are observed in groups with greater numbers of breeding females —a surrogate for group size— than Asian elephants at UWNP (henceforth the Asian population; Table I and Fig. 1). The African population also shows a significant increase in the number of breeding females per group and levels of association during wet seasons compared to dry seasons, whereas the Asian population does not (Table I). Association matrices for the African population were correspondingly less sparse than those for the Asian population (Table I). Associations among individuals were highly nonrandom for both populations, in all seasons (randomization test, $p<$

Table I Summary data

	Average aggregation size (SD)		% Nonzero values		Kurtosis	
Partition	*Elephas maximus*	*Loxodonta Africana*	*E. maximus*	*L. africana*	*E. maximus*	*L. africana*
Full	3.07 (2.34)	5.03 (4.61)	20.8	82.75	10.35	27.59
Dry	3.10 (2.36)	4.44 (3.29)	16	45.93	8.59	16.55
Wet	3.03 (2.33)	5.91 (5.96)	13.05	79.15	8.29	23.52

The average numbers of breeding females per group (aggregation size) are significantly higher in the African population for all seasonal partitions. The number of breeding females per group is significantly higher during the wet partition for the African population (2-sample permutation tests, $p<0.0001$), but not for the Asian population ($p=0.28$). Association matrices of the African population are less sparse than that those of the Asian. The AI distributions of the African population have significantly higher kurtosis compared to the Asian in all partitions and also differ significantly across seasonal partitions within the African population (2-sample permutation tests, $p<0.0001$), but not within the Asian population ($p=0.45$)

0.001; Fig. 2). Moreover, the AI distribution of the two populations also differed from one another significantly, with that of the African population always having higher kurtosis than that of the Asian population (2-sample permutation test, $p<0.0001$, Fig. 2 and Table I).

Striking differences in structure between populations are evident from network path properties (Table II). Individuals in the African population are directly connected to many more individuals than those in the Asian population, given by egonetwork size (Table II). As a result, it is more likely that the associates of a female African elephant are also associated with one another than those of a female Asian elephant, captured by each node's clustering coefficient (Table II). This also means that an African elephant is connected to more individuals in fewer steps than an Asian elephant, captured by the metric of distance weighted reach (Table II). In fact, all individuals in the African population are within 2 steps of any other individual in the population. But in the Asian population, none are within 2 steps of all others. Rather, 38 individuals (36%) are within 3 steps, and the remaining 67 are within 4 steps.

Only dendrograms generated with average linkage had cophenetic correlation coefficients >0.8 for both populations; therefore we take them to have the least distortion and present only these (Fig. 3). Replicating a previous study (Wittemyer *et al.* 2005b), the tree for the African population shows a significant knot at a bifurcation distance of 0.23, identifying a core, 2nd-order social tier. The Asian
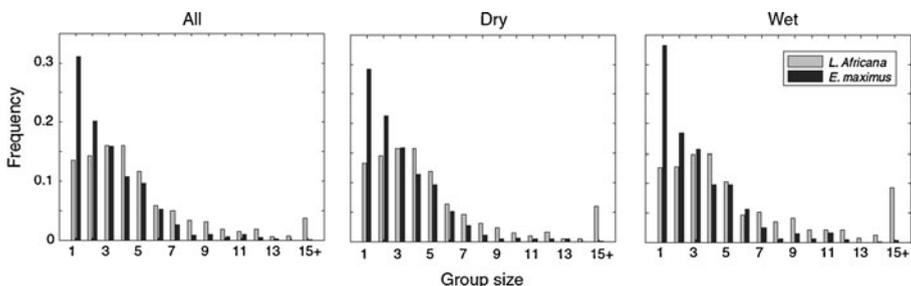
Fig. 1 Distributions of observed numbers of adult females per group by season in each population.
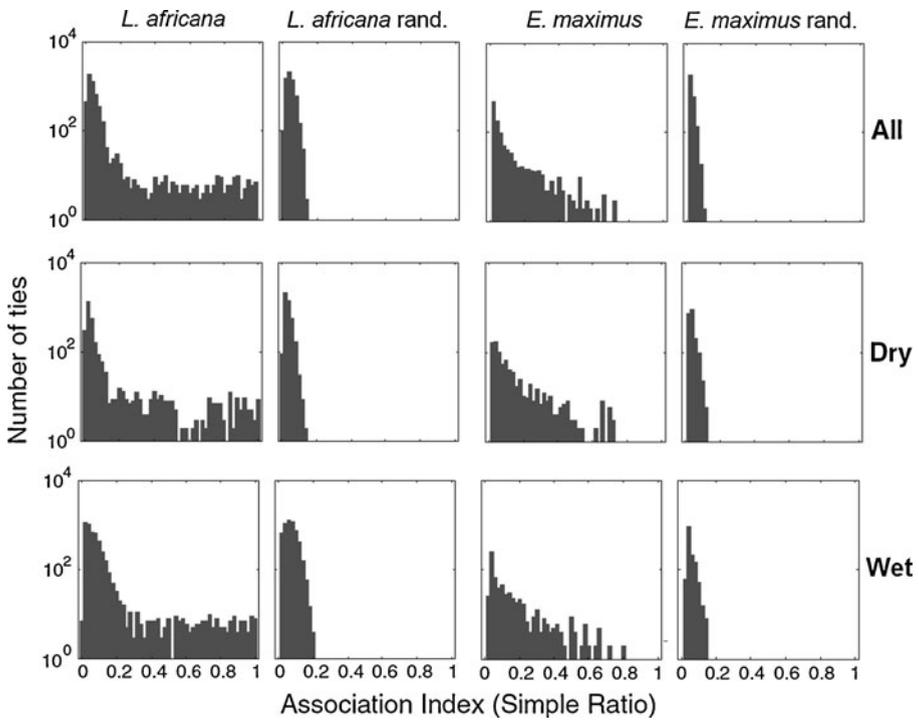
Fig. 2 Distributions of nonzero association index values by population and season. Actual data sets are significantly different from randomized data sets (permutation test, $p<0.001$). Observed associations have more high values than permuted data sets. The African population has a greater number of strong ties than the Asian population (Table I).

population shows no such difference, with social units diverging at very high bifurcation distances, loosely corresponding to low AI values. In other words, associations among these Asian elephants are not clearly stratified into hierarchical social tiers. This does not mean, however, that individuals associate only with a small group of companions.

The relative sparseness of the AI matrices for the Asian population vs. the African population (Table I) is reflected in the appearance of their respective social networks

Table II Network path properties

	Egonetwork size		Clustering coefficient		Distance-weighted reach	
	$\overline{X}$	(SD)	$\overline{X}$	(SD)	$\overline{X}$	(SD)
Loxodonta Africana	88.87	(16.00)	0.88	(0.04)	99.94	(7.96)
Elephas maximus	22.53	(11.85)	0.63	(0.13)	59.46	(9.04)

Egonetwork size is the number of individuals directly connected to an individual. The clustering coefficient is the proportion of an individual's associates directly associated with one another. Distance weighted reach is a weighted sum of the reciprocal of the path length (geodesic distance) from an individual to all others in the network. All measures are significantly higher for the African population (2-sample permutation test, $p<0.0001$)
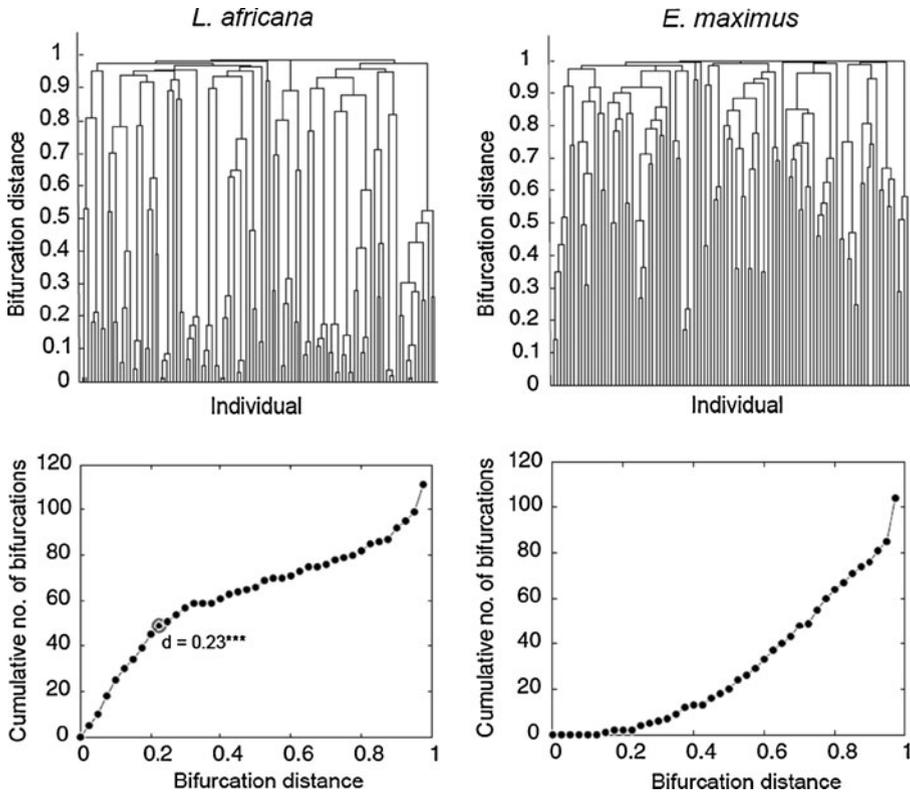
Fig. 3 Dendograms and knots through hierarchical cluster analysis, using average linkage. The dendogram for the African population has branch lengths that are initially short but increase with bifurcation distance, whereas the dendogram for the Asian population shows the reverse, which is reflected in the curves of cumulative bifurcation rates on the bottom panel. The African population shows a significant decrease in bifurcation rate distinguishing 2nd and 3 rd tier structure (circled point, $U=4.35$, $p<0.0001$). Such tiers are indistinguishable in the Asian, where bifurcation rates gradually increase rather than decrease.

(Fig. 4). These differences are quantified in Table II and Fig. 5. The thresholding procedure shows that network substructure differs between the populations (Fig. 5). The African population shows two regions of structural change, indicating higher-order social stratification, with differences in the position of these regions between the wet and dry partitions; in contrast, the Asian population consistently shows one region of structural change, indicating two different types of social affiliates. Despite this, the Asian population also exhibits an extensive network in which the whole population forms a large unit with many interconnected subcomponents. Analogous plots for randomized data are included in the ESM figures for reference.

Discussion

In this study we provide a quantitative comparison of the social structure of populations representing two extant elephant species. Observed association behavior
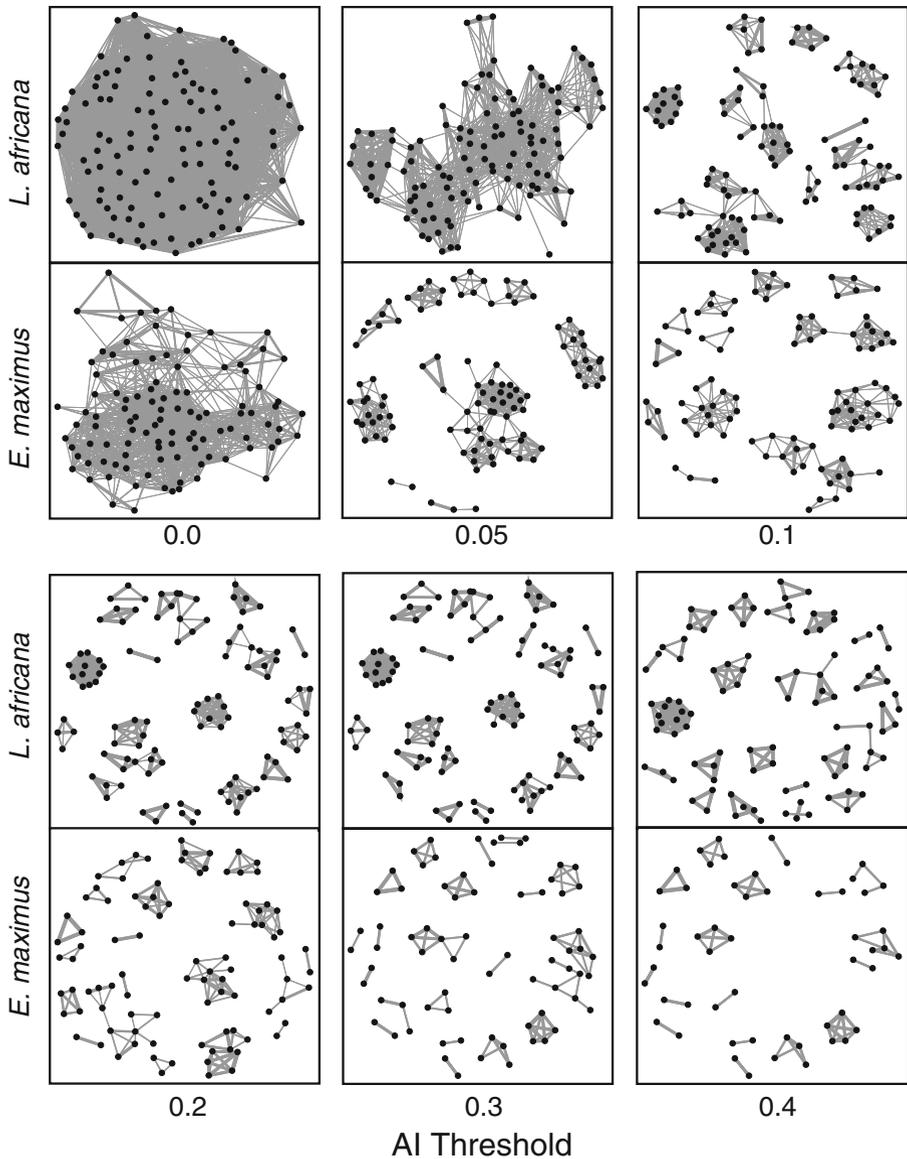
Fig. 4 Snapshots of network fragmentation. The Asian network is less interconnected than the African network, contains fewer strong ties, and fragments more quickly when ties are sequentially removed. This is visible most clearly at the AI threshold of 0.05, in which clusters are already more differentiated in the Asian network than in the African.

differed significantly from randomized data sets for both populations, demonstrating that the observed patterns for both species are not simply the result of constraints of the data structure. Because we have only a single population for each species, we cannot assert whether the differences observed are due to phylogenetic or ecological reasons, but we can characterize differences observed. As expected, individuals in the African population tend to be more gregarious than those in the Asian population
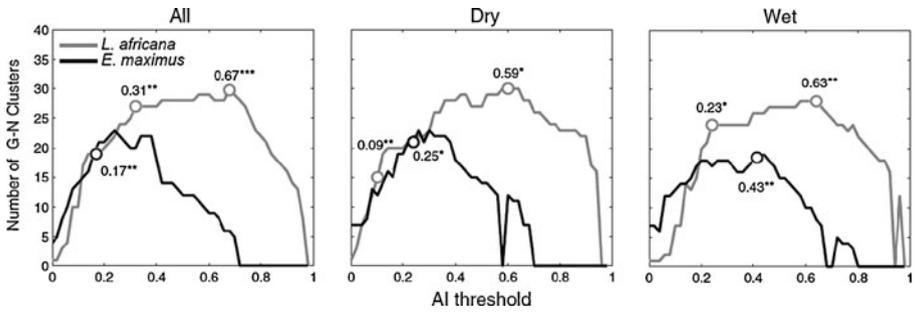
Fig. 5 Social network substructure after thresholding. Both elephant populations exhibit peaked curves but the Asian population has fewer clusters at its peak than the African, and declines more rapidly. Curves for the African population each show 2 points of structural change, whereas those for the Asian consistently show only 1, indicated by open circles labeled with the corresponding threshold value (stars indicate significance level according to the test described in the "Methods", where *$p<0.05$, **$p<0.01$, and ***$p<0.001$). Analogous curves for randomized data have very different profiles and do not exhibit any significant points of structural change (see ESM).

in two important respects: they form larger groups and are much more strongly associated with their social units as well as with the population in general than those within the Asian population. This has a number of consequences. Without a large number of strong ties, the degree of possible stratification among the Asian elephants is limited. A tier structure requires that individuals in a social unit within the nth tier associate more strongly than those within units at the level above it. Where individuals associate weakly overall, there is less potential for hierarchical stratification. Moreover, if some social units form higher-order associations but others do not, differentiation among tiers is more difficult. As a result, the cluster analysis method using dendrogram branching rates to define levels did not identify hierarchical structure in the Asian population. This precludes data reduction analysis as used in Wittemyer *et al.* (2005b) to differentiate higher-order tiers. Such a procedure is appropriate only when an individual can be used to represent her entire family or social unit, such as with the African population where individuals within units are tightly associated. Lower rates of association within the Asian population imply that individuals cannot be substituted for one another in this way.

Social networks are much more interconnected in the African population than in the Asian population. This greater interconnectedness is reflected by simple network metrics. In addition, the thresholding procedure implemented in this article captured some aspects of the multitiered structure found previously using this same data set for the African population using hierarchical cluster analysis (Wittemyer *et al.* 2005b), including multiple levels and expansion of threshold values during ecologically richer wet seasons. The points at which structural levels are defined using the thresholding procedure, however, are more sensitive to changes across seasonal partitions than those previously defined using hierarchical cluster analysis. As a result, the individual compositions of structural levels are less consistent when defined using the thresholding procedure. Usefully, this sensitivity allowed identification of multilevel structuring in the Asian population that was not apparent with the other clustering approach. As such, this approach can identify differentiation in association patterns (strategies) among individuals comprising loosely cohesive social

units, an analytical property that is likely to be of use in other species demonstrating high social lability.

The *multilevel* society of this Asian elephant population is different from the *multitiered* society of the African elephant population, providing a useful example of possible variation in multilevel structuring. Any society in which an individual differentially associates with more than one set of companions is in essence a multilevel society. The ego networks of Asian elephants are smaller than that of African elephants, but they are still far bigger than the group sizes observed in the field (de Silva 2011b). Where association patterns are different from random, it may be constructive to view social stratification along a continuum of potential relations, not as a discrete feature of societies that is simply present or absent (Fig. 6). In some systems the levels may be distinct and biologically meaningful, whereas in others, levels may transition more gradually. Strict definition of multilevel societies only as
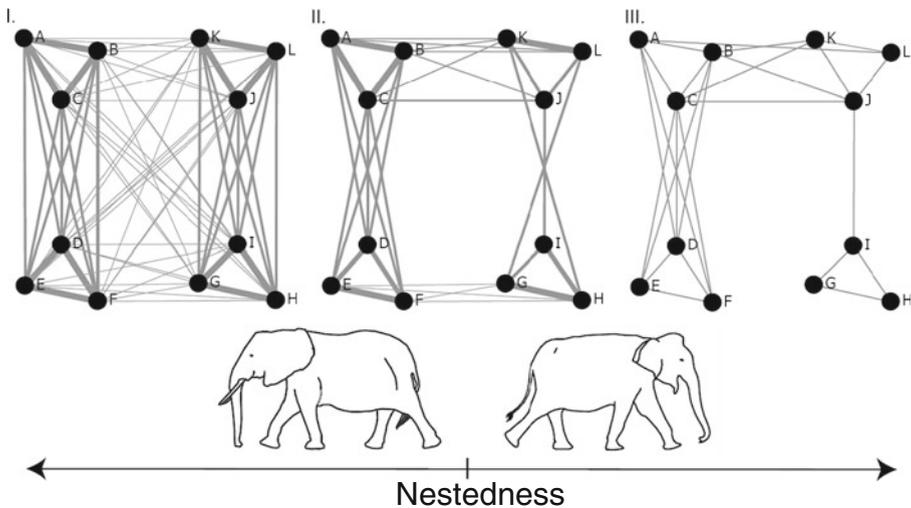

Fig. 6 Types of hypothetical networks. I. Completely nested clusters: Clusters are distinguishable only through edge weights rather than topology because everyone is as equally connected as everyone else. Results when individuals associate very strongly with their core unit (idealized when AI=1, e.g., ABC). This necessarily implies that they collectively associate with other units. Both sets of individuals are entirely nested within the resulting higher-order cluster, creating clear social tiers, e.g., individuals ABC and DEF form a larger cluster, or higher-order social unit, ABCDEF that associates less frequently so that AI values among them <1. A single individual, e.g., a matriarch, can represent her entire set of immediate companions. II. Incompletely nested clusters: Data set is more sparse; therefore connections among units are fewer. Clusters are distinguished on the basis of both topology as well as edge weights. Such societies may results when individuals do not associate strongly with their own social unit; thus links among units depend on a few bridging individuals. Single individuals cannot represent an entire social unit. Tiers cannot be strictly defined because all constituent members of a unit do not participate in higher-order interactions, though some units may still be nested. III. Topological clusters: Connections between units are incomplete and all edges have equal value. Clusters are distinguished only on the basis of network topology. Results when individuals do not show any preference among companions at all. There may still be units nested within others; ABC and DEF still form a larger cluster. A, B, and C do not associate more strongly with one another than with the rest of the network, but are simply more central structurally. Both I and III are logical extremes that would be unlikely to emerge in real animal societies. The African population tends toward I while the Asian population tends toward III, as displayed in Fig. 4.

those exhibiting nestedness may limit understanding of multilevel structuring and its evolution. Moreover, societies exhibiting multilevel structure along this continuum may be more widespread than initially supposed (Wolf *et al.* 2007).

Environmental differences between the two systems may drive observed differences in social behavior. Although both Asian elephants and African savannah elephants occupy seasonal environments, Asian elephants tend to be found in areas with higher absolute amounts of rainfall, and hence primary productivity. In this study, the two sites are of similar size but differ greatly in the amount of rainfall. Differences in productivity create different levels of competition among conspecifics, a strong driver of social patterns even intraspecifically (Silk 2007), as well as among species with similar mating systems and diet requirements as is the case in this study (Chapman and Chapman 2000). The two populations also differ in that elephants in Sri Lanka historically have had no predators other than humans. Gregariousness is often hypothesized to be an antipredator strategy as a by-product of cover-seeking among animals living in open environments (Hamilton 1971). This is supported by large-scale phylogenetic analyses, which find that herbivores living in open environments tend to be more gregarious (Caro *et al.* 2004). Social facilitation of antipredator behavior includes both dilution (Foster and Treherne 1981; Krause 1993), and cooperation among individuals from one or more social groups in active defense (Arnold 2000; Feh *et al.* 2001; Graw and Manser 2007). With lions taking calves on occasion in Samburu (Wittemyer *et al.* 2005a), predation pressure may contribute to differences in the observed behavior. Unfortunately, these factors cannot be teased apart without detailed studies of populations in other ecological and predation regimes.

Rather than ecological drivers, social factors alone may motivate the formation of groups as well as higher-order structures (Silk 2007). Alloparental care has been documented in African elephants (Lee 1987) and also observed in Asian elephants (de Silva *unpubl. data*). Mating competition and avoidance of inter- or intrasexual aggression also mediate social relationships in a diverse range of taxa (*Pan paniscus*: Hohman and Fruth 2003; *Equus grevyi*: Sundaresan *et al.* 2007b; *Poecilia reticulata*: Darden *et al.* 2009). Another very important benefit of aggregating for animals that forage on the move is the potential for sharing or responding to information, though the type of information being processed is itself more often ecological (McComb *et al.* 2011; Zuberbühler, 2009) than social (McComb *et al.* 2001). Information transfer may not require active communication or social affiliations *per se* (Sumpter *et al.* 2008); therefore truly social groupings must be distinguished from those resulting from the passive transmission of cues.

Phylogenetic comparisons of social network metrics as described in this article may provide fresh insights as to the factors shaping different kinds of multilevel societies. To take these investigations further, we need additional comparative studies of social organization among species as well as populations of the same species in different environments (Rubenstein *et al.* 2007; Sundaresan *et al.* 2007a; Symington 1990). Only then can we develop general theories that address not only the formation of social groups, but also the conditions driving the formation of groups of groups, resulting in a diversity of multilevel societies. The proboscidean clade alone has too few extant branches with which to test these hypotheses, but it would be possible to do so with other species-rich clades such as those of primates or birds.

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