The socio-ecology of elephants: 
Analysis of the processes creating multi-tiered social structures

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Running Headline: WITTEMYER ET AL.: MULTI-TIERED ELEPHANT SOCIAL STRUCTURE

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Word Count: Abstract = 317, Text = 8,630
ABSTRACT

The socio-ecological hypothesis asserts that ecological factors, particularly the distribution of resources, affect social behaviour. Fission-fusion social organizations are of particular interest for the investigation of the relationship between ecology and social structure because such systems are well suited for comparing ecological variation with social changes. We investigate the formation and function of the multi-levelled, fission-fusion social structure in a free ranging African elephant (*Loxodonta africana*) population.

Applying novel techniques, we quantitatively demonstrate the existence of four social tiers using cluster analysis on individual association data. We assess the affect of season and study period on social structuring and levels of cohesion within and among social units. We found that 2\textsuperscript{nd} tier units, potentially the equivalent of the “family”, were stable across seasonal periods but the number of units increased as the study progressed and the population grew. It appears that these units are sufficiently small not to be influenced by ecologically related factors, such as resource competition, that might otherwise lead to them splitting. On the other hand, 3\textsuperscript{rd} and 4\textsuperscript{th} tier units were significantly affected by season in a way that suggests a trade-off between ecological costs (e.g. from resource competition) and different social and ecological benefits (e.g. from predator defence, territoriality, knowledge sharing and rearing of young). Age structure also appears to influence this multi-tiered social organization with the size of 2\textsuperscript{nd} tier social units being significantly affected by the age of matriarchs: units led by matriarchs likely to be grandmothers (i.e. females 35 years and older) are significantly larger than those of younger matriarchs. A conceptual framework for understanding the emergence of multiple-tier social structure from interactions driven by socio-ecological
processes is presented. This study is the first using rigorous quantitative methods to statistically demonstrate the existence of four hierarchical tiers of social organization in a non-human animal. Additionally, our results elucidate the role that ecological processes play in producing complex social structures.
Ecological constraints, by impacting both mating systems and population structure, are formative factors in the evolution of social systems (Emlen & Oring 1977; Clutton-Brock & Harvey 1977). In combination with their genetic underpinnings, the type and structure of individual-based interactions relates to the abundance and distribution of food or predation (Alexander 1974; Wrangham 1980; van Schaik 1989; Isbell 1991). The socio-ecological hypothesis serves as a framework for studies of this particular relationship between ecological factors and social behaviour (Emlen & Oring 1977; Vehrencamp 1983; Terborgh & Janson 1986; Emlen 1995; Kappeler & van Schaik 2002).

The ecological factors affecting a species sociality vary across time and space. Ecological and social costs and benefits play a role in determining social unit size in fission-fusion societies (Devore & Washburn 1963; Kummer 1968). Fission-fusion societies limit the effect of within unit competition through unit splits during periods of high competition (Dunbar 1992; Kummer 1995) and enhance cooperative effects through unit cohesion when the ecological costs of aggregating are low or benefits of sociality arise (Takahata et al. 1994; van Schaik 1999). Aggregating behaviour is generally thought to be a response to predation pressures (Hamilton 1971). Widely distributed food resources are believed to promote the evolution of fission-fusion social organizations as a response to fluctuations in the costs of feeding competition (Schaller 1972; Altmann 1974; Jarman 1974). However, individual based studies focusing explicitly on the variability of social unit structure in relation to ecological factors are few. Here we use individual association behaviour to assess the impact of season and time on social unit composition and cohesion, looking at the influence of ecological factors on the social organization of a free-ranging African elephant population.
In many animals social relations are enigmatic or cryptic and thus difficult to record (Whitehead 1997). Using Hinde’s (1976) framework for the study of social behaviour based on interactions among individuals, recent work has used association indices to assess the social properties of populations (Cairns & Schwager 1987; Whitehead 1995). The objectives of studies employing these methods are testing the deviation from randomness of animal associative behaviour and identifying preferred and avoided associates (Myers 1983; Whitehead & Dufault 1999; Kerth & Konig 1999).

Despite the importance and variability of social layering in human societies (Freeman 1992; Cummins 2000), little attention has been given to such structuring in animal societies, apart from some work on cetaceans (see Mann et al. 2000). Building on these associative based methods, we used clustering techniques to identify social delineation in elephant society. Our methods empirically substantiate previous inferential descriptions of six hierarchical tiers of organization (Buss 1963; Laws 1970; Douglas-Hamilton 1972; Moss & Poole 1983): mother-calf units (tier 1), families (tier 2), bond/kinship groups (tier 3), clans (tier 4), subpopulations (tier 5), and populations (tier 6). Identification of the form and function of nested social tiers can serve to further studies of sociality in numerous animal species that have more than one level of social organization, such as prairie dogs (Hoogland 1995), cetaceans (Mann et al. 2000, Conner 1992), geese (van der Jeugd et al. 2002), and multiple primate species (Strier 2000). In this paper, we focus on the relationship between socio-ecological forces and the emergence of a multi-tiered social structure that appears to conform to the above 6-layer paradigm. Identification of the primary factors influencing the fission-fusion process at each social tier provides
insight into the ecology of a species and can enhance studies on the evolution of complex
social structures.

Being generalist herbivores with low digestive efficiency, elephants spend 60-
80% of each 24-hour day feeding (Owen-Smith 1988). The patchy distribution of
resources in savannah ecosystems, in combination with their heavy feeding requirements,
makes elephants susceptible to intra-specific competition. Such competition in other
animals limits both social unit size and their proximity to one another (Jarman 1974;
Clutton-Brock & Harvey 1977). Slight variation in forage quality and quantity may have
marked impacts on elephant interactions. In order to explore this, we examine social unit
structural variation across the wet and dry seasons over a four-year study period. Further,
we look at temporal changes in social structure in order to assess social dynamics
occurring due to the longer-term process of population growth. Potential benefits derived
from the described social structure are also discussed. Building upon the socio-ecological
framework, this study focuses on the factors influencing individual social behaviour and
their relation to the fission-fusion social dynamic in a multi-tiered social organization.

METHODS

Study Area

Samburu and Buffalo Springs National Reserves are small, protected areas in the greater
Samburu/Laikipia ecosystem of northern Kenya. These reserves hold the largest elephant
population, numbering approximately 5200 individuals, residing primarily outside
protected areas in Kenya (Omondi et al. 2000). As a result of heavy tourist use of the
parks, the elephants using these reserves are habituated to vehicles, enabling easy
observation of their behaviour. Between November 1997 and May 1999, all elephants
using the two reserves were individually identified and tentatively categorized into two
subpopulations, termed resident and non-resident, based upon their degree of reserve use
(Wittemyer 2001). The parks are unconfined and the primary land use in this semi-arid
region is livestock grazing in communally owned group ranches that have few or no
fences.

The majority of the observations in this study were collected within the
boundaries of Samburu and Buffalo Springs National Reserves between June 1998 to
August 1999 and May 2000 to December 2002. The total study area lies between the 0.3-
0.8° N, 37-38° E. Samburu and Buffalo Springs National Reserves are 320 km²,
comprising less than 2% of the greater Samburu/Laikipia ecosystem and generally 15-
25% of the study elephants’ home range (unpublished G.P.S. radio-tracking data). The
reserves are centred on the Ewaso Ngiro River, which is the only permanent water source
in this semi-arid region and, as such, a focal area for wildlife (for further description of
the study area see Wittemyer 2001).

This region is drought prone and rainfall is sporadic, with the majority of rain
falling during the two wet seasons in April and November. Because rainfall is
unpredictable, seasons were defined using daily rainfall totals collected on the reserve
boundary. Dry seasons were defined as beginning after 30 days of 0 mm rainfall. Wet
seasons were defined as beginning after one week with 15 mm or greater rainfall (the
approximate amount of precipitation required to get a vegetative response). Single day
showers between two-week periods of 0 mm rainfall were not considered to elicit a
seasonal change.
Data collection

For purposes of clarity, we define the following terms used throughout this paper to describe the social context of elephants.

1. Aggregation: A collection of elephants in the wild observed at a particular time to be associated with one another (see below for spatially explicit definition of association)

2. Cluster: structural unit of a tree constructed using clustering methods (Romesburg 1984)

3. Tier $i$ units: social or supra-social units (assemblages of individuals defined from analysis of clustering results following the methods described below) within a hierarchical organization where tier $i$ units are composed of tier $i-1$ units, $i=2-6$. Our study focuses on the social behaviour of breeding female elephants, defined as individuals with dependent calves, because the distribution and organization of females is generally thought to relate to the pattern of resources and risks in their environment, whereas males organise themselves around the distribution of receptive females in time and space (Trivers 1972; Emlen & Oring 1977). All females over 20 years of age in the study population have at least one dependent calf. Generally, a breeding female is associated with her juvenile offspring 100% of the time, though this bond weakens as juveniles mature (10-13 years) with males dispersing from their mother’s social unit after puberty (Douglas-Hamilton 1972; Moss 1988). Such tight bonds result in identical association behaviour between a mother and her calf (tier 1 social units); thus, for purposes of analysis, these mother-calf units were treated as a single entity represented by the mother. Our analysis of social behaviour focused on the
“resident” (5th tier) subpopulation comprising 112 breeding females and their calves, representing 382 elephants and 46% of the total (6th tier) population of breeding females identified within the study area (Wittemyer 2001).

The majority of observations used in this study were collected by observers recording all individuals encountered along one of 4 set routes travelled per day. Routes followed existing roads running the length of the reserves both to the North and South of the Ewaso Ngiro River, where routes 1 and 2 were within 500 meters of either riverbank and routes 3 and 4 were located approximately 5 kilometres from the river on either side. Observations of elephant aggregations during non-transect movements in the study area (opportunistic sampling) were also collected and used in this study. All observations were recorded following the same protocol. Once elephants were spotted, observers approached to within 100 meters or less of the aggregation and recorded the following for each observation: (a) identity of individuals present, (b) accuracy of the observation (recorded in categories: 1) 100% identification of all individuals, 2) identification of all breeding females and males excluding calves, and 3) incomplete identification), (c) location of aggregation (G.P.S.), and (d) the date, time, observer name, and route name. The observer stayed with the aggregation until all individuals were recognized, unless thick vegetation did not allow a complete accounting. The data presented in this study is compiled from 2889 observations of aggregations where the observer was confident of registering all associating breeding females, i.e. observation accuracy 1 and 2. Each individual’s aggregation was recorded only once per day to avoid non-independence 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. The average number of observations per breeding female was 132
(minimum = 73, maximum = 284).

Elephant aggregations, for calculation of association indices, were defined as
individuals estimated to be within a 500 m radius of an observationally estimated
aggregation centre (elephants are generally clustered within a small area, thus social
aggregations are easily recognized). When aggregations exceeded this 500 m radius
definition, we used a modified criteria where an aggregation was defined by being
separated from the nearest other aggregation by a distance greater than its diameter. In
order to standardize observations between the individuals used in the study, aggregation
data were converted into simple association indices between all dyads in the study

\[
X_{AB} \quad N - D
\]

where \(X_{AB}\) is the number of observations
during which A and B are together, \(N\) is the total number of observations, and \(D\) is the
number of observations during which neither A nor B were observed (thus including only
observations when A or B were observed). Because association indices are a ratio of the
total observations of two individuals together and separate, results are robust against
sample size differences between individuals.

**Difference from random structure**

Previous studies of social structure based on individual association behaviour
focused on assessing the differences between observed and random patterns of
association (Manly 1995; Bedjer et al. 1997; Whitehead 1997). We applied these
established methods to our elephant association data in order to verify that observed
elephant associations deviate from random. SOCPROG 1.2 (Whitehead 1999) performs
this analysis by generating random association data sets by switching 1 (associated) and 0
(not associated) values in rows of recorded association data (Bedjer et al. 1997). These random data sets are constrained such that the number of observations per individual and group sizes per observation match the original data, and are then used for comparison with actual indices of association in order to identify non-random properties of the study system (Bedjar et al. 1997). Additionally, SOCPROG 1.2 offers a method for assessing the change in individual association behaviour over time by estimating the probability two animals will associate at the same level across time lags (Whitehead 1995). We ran 20,000 routines to assess the robustness of associations over time, as described in Bejder et al. (1997). In order to evaluate preferences in associations, observation data must be partitioned into sampling periods. A sampling period of 10 days was selected for this analysis, because the primary observer was able to cover all sampling routes at least twice within this period, increasing the likelihood of encountering those elephants present. All possible sample periods were assessed in the analysis of lagged association rates (Whitehead 1995).

Structuring

Hierarchical social tiers were defined through a two-step analysis employed to identify emergent properties of the association data: 1) A cluster analysis—the simplification of multi-dimensional information into a two-dimensional representation—of the raw data was conducted to objectively represent the structure of the study population (Strauss 2001). In order to determine the most appropriate clustering method for our data, we assessed the degree to which cluster results fit the observed data using the cophenetic correlation coefficient (CCC) (Rom esburg 1984). Only clustering results with CCC values >0.8 (the accepted standard—Rom esburg 1984) were used in the
second step. 2) For each of the clustering trees we obtained (Figs. 2 and 4), we created a cumulative graph of the number of bifurcations (branches) occurring per 0.05 bifurcation distance \( d \) increment (the bifurcation distance is the Y-axis of a cluster tree, increasing up the tree as the degree of association between individuals decreases). This cumulative bifurcation graph was then used to identify putative knots, defined as points on the cluster tree where the rate of bifurcations below the knot was significantly different from rates above the knot (see below for further description). Thus, knot values indicate points of structural changes in the cluster method tree and were subsequently defined as social tier delineations.

We created hierarchical trees and cumulative bifurcation graphs for association data on all 112 breeding females in the study subpopulation (Romesburg 1984; Strauss 2001) using four different clustering methods: the Unweighted Pair-Group Method (UPGMA), Ward’s Weighted (Ward’s), Complete Linkage (CLINK), and Single Linkage (SLINK), were compared (Table 1). The Ward’s Weighted Clustering Method yielded the highest CCC value (Table 1) and, consequently, Ward’s results were used in subsequent analyses to identify social tiers. We assessed the significance of all potential putative knots (points around which the slope of preceding and succeeding points changes) in the cumulative bifurcation graph by comparing the distribution of bifurcations per stepwise increment above versus below the knot values using the Wilcoxon rank-sum test. The Wilcoxon rank-sum Z-statistics of all contiguous, significant knots were compared and the putative knots that maximized the Wilcoxon rank-sum Z-statistics were used to delineate social tiers (Fig. 1). The bifurcation value associated with the selected knot was then used to define the social units of the defined
social tier where individuals bifurcating below the knot value were considered to be part of the same social unit (Fig. 2). In order to assess the integrity of the defined social units, the compositions of social units characterized using each of the four clustering techniques independently were compared (Table 2).

Significant knot values ($p<0.05$) separate sets of points that can be fitted with lines of different slope above and below the knot. The formation of units above and below the knot thereby occurs at different rates for a given rate of increase in the bifurcation distance variable $d$. Biologically the knot indicates where the type of affiliation between individuals in merging clusters is changing from that of a tight, high AI value to a looser, lower AI value. Lower AI values are related to longer term fissions of component groups within a cluster or more frequent rates of fission and fusion of these groups. In social systems where individuals associate at random, knots separating clusters into tiers that aggregate at different rates are not expected to be evident (Fig. 3). In our case, the graph is distinctly concave down suggesting the primary social tier (comprised of the greatest number of bifurcations) occurs at a high AI level, followed by more loosely associated upper tiers with fewer bifurcations. Biologically this implies the core social tier is comprised of stable, tightly associated units: potentially coalitions or kinship based groups such as a family. This contrasts with social systems producing concave up graphs where a high density of linkages occur in an upper tier predicated by a few individuals associating in the lower tier level. Biologically this would indicate the primary social structure is a relatively unstable, looser aggregation of individuals, potentially in the form of a loose herd.
After definition of 2\textsuperscript{nd} tier units, the data were reduced to include only associations among the matriarchs of each 2\textsuperscript{nd} tier unit (see below for definition of matriarch) in order to identify higher order social tiers. The strengths of 2\textsuperscript{nd} tier associations inundate the weaker higher order relationships, thus all relationships below the identified 2\textsuperscript{nd} tier knot value were excluded from this subsequent analysis. Ward’s clustering method, subsequently run on the reduced association matrix, was the only method that yielded a CCC value greater than the 0.80 standard (Table 1; Romesburg 1984). Consequently, it was the only method we used in the analysis of defined social units at levels above the 2\textsuperscript{nd} tier. Further, multiple significant knot values emerged in two of the data partitions (described below) from this analysis (the wet season and 1998-2000 data while the other sets did not contain more than one significant knot—See Results and Discussion). Identification of multiple knots followed the same procedure as the analysis conducted for the 2\textsuperscript{nd} tier with the additional method of repeated comparisons of potential knots in order to maximize the sum of Z-statistics for both knots simultaneously. The two significant knots were used to define two social tiers: 3\textsuperscript{rd}-tier units were defined as the consortium of 2\textsuperscript{nd} tier units whose bifurcation points lay below the 1\textsuperscript{st} knot of the matriarch tree, 4\textsuperscript{th} tier bifurcation points lay between the 1\textsuperscript{st} and 2\textsuperscript{nd} knot, and the subpopulation (potentially the 5\textsuperscript{th} tier social delineation) used in this study lay above the 2\textsuperscript{nd} knot (Fig. 4).

For evaluation of ecological and temporal effects on social structure, matrices of association indices from observations during the wet and dry seasons and temporal periods 1998-2000 and 2001-2002 were created. The numbers of aggregations recorded for each partition were (seasonally) 1795 during dry periods, 1094 during wet periods,
and (temporally) 1404 during 1998-2000, 1485 during 2001-2002. Differences in the number of observations in the dry and wet season relate to differences in the length of each season (dry periods are typically longer) as well as the tendency of elephants to aggregate in fewer, larger groups during the wet season. Analyses of both seasonal and temporal association matrices were conducted using the methods described above. Structures from each partition were compared with results from the total data set in order to ascertain the degree of social stability. Social stability was assessed in two manners: 1) individual stability—defined as the number of individuals assigned to the same units as found with the total data set and 2) unit stability—defined as the number of units with identical compositions to those defined from the total data set, where a unit is unstable even if a single individual changes membership (Table 3). These analyses provide information on the variation in social structuring seen across seasons, or ecologically distinct periods, and time, or periods differentiated through demographic changes. Furthermore, the social networks of individuals (the number of total study animals with which an individual was observed to associate) were compared across seasonal and temporal partitions using paired statistics. The matriarch of a social unit was defined, on the basis of behavioural observations, as the individual that was dominant to all other unit members (where dominant individuals physically displaced subordinate individuals from resources). Age estimates of matriarchs were conducted using physical features such as shoulder height, body length, and facial features (Moss 1996). The ages for 16 breeding females have been assessed through molar evaluation (a method with an approximate error of ± 2 years; Laws 1966) either after death or during radio collaring operations (Rasmussen et
al. submitted). Differences between our estimates and molar evaluated ages were minor, averaging 2.5 ± 1.5 years, and estimates were generally greater than molar evaluated ages. Known aged individuals were then used for comparison with estimated individuals.

Correlative Coherence Analysis (CoCA)

Previous studies have used the mean and standard deviation of association index values to look at differences in individual associations (Myers 1983; Gowans et al. 2001). In a population of size $n$, the average is taken over $\frac{n(n-1)}{2}$ pairwise indices. These indices, however, are partially correlated with each other and thus not independent, particularly in social units of closely associated individuals such as those found in 2nd and 3rd tier units.

Correlative coherence analysis (CoCA) (Getz 2003) accounts for the fact that a group of $n$ individuals only has $n - 1$ degrees of freedom when finding a single value to represent the “average” degree of association among $n$ individuals, and thus not susceptible to potential problems with non-independence. CoCA produces a single number that generalizes the concept of association from two to $n$ individuals and was developed to generalize the concept of the correlation between two sets of measurements to the correlation among $n \geq 2$ sets of measurements (Getz 2003). Association indices among pairs of individuals, because they range from 0 to 1, are equivalent to nonnegative correlations among these pairs of individuals. The method for computing the CoC value of an $n$-dimensional associate matrix $A$ is as follows (Getz, 2003): Calculate the $n$ eigenvalues $\lambda_i$ ($i=1, \ldots, n$) of $A$. The CoC value of $A$ is then the solution $r$ to the equation

$$\left(1 + (n-1)r\right)\ln\left(1 + (n-1)r\right) + (n-1)(1-r)\ln(1-r) = n \ln n + \sum_{i=1}^{n} \lambda_i \ln \left(\frac{\lambda_i}{n}\right)$$
We note that if all pair-wise associations in a system had the same value, r, then their CoC value would also be r. In this sense, r is an average measure. We also note that CoC and average AI values are similar in populations where all units have reasonably high levels of association or all units are similarly associated. Whenever the matrix $A$ contains many 0s then the CoC value greatly exceeds the average AI value. This is the reason for the striking differences in AI values and CoC values in the 4th tier and population social levels in Table 4. Intuitively the reason for this difference follows from the fact that for the 3-unit system for which $a_{12} = a_{13} = a_{23} = 1/3$ (i.e. all units associate 1/3 of the time with each other) the CoC value = 1/3, while for the system $a_{12} = 1$, $a_{13} = a_{23} = 0$, the CoC value = 0.702. In both cases, the average value for $a_{ij}$ ($i \neq j$) is 1/3, but in the latter case the measure of coherence should be much higher because we have 2 of the 3 units associating with one another all the time. From this example we obtain an intuitive feel for the reason why CoC values are more appropriate to assess group cohesion than average AI values, particularly in populations where the levels of association among units varies greatly between 0 and 1.

**Statistics**

Statistical analyses and all clustering methods were conducted using the software package S-Plus 6.0. Non-parametric statistical methods were used in this study except for comparison of seasonal social networks. The Wilcoxon paired-sample test was used for comparisons of the seasonal differences in social units’ CoC values and 2 tailed, paired $t$ tests used to compare the distributions of social networks across seasons and temporal periods. Jackknife techniques were used to get estimates of variances for CoC values of non-replicated events (i.e. the wet and dry matrices for the total population and matrices
of a social unit before and after its matriarch’s death) (Shao et al. 1996). Median and
inter-quartile range (IQR) values are presented for data sets compared with non-
parametric techniques, and mean and standard error (SE) values are presented for
normally distributed data.

**RESULTS**

**Differences from random structure**

Using the methodology of Whitehead (1999), we found the association behaviour
of the Samburu elephant population differed significantly from random. Observed
association indices were significantly lower than random association indices (observed =
0.085, random = 0.093, \( p < 0.0004 \)), indicating elephants maintain preferred associations
within 10 day sampling periods constraining the number of dyads associating (Whitehead
1999, Gowans *et al.* 2001). Additionally, the standard deviation of observed association
indices was significantly greater than that of random (observed = 0.145, random = 0.086,
\( p > 0.9999 \); this high \( p \) value for the 2 tailed test specifies a significantly larger observed
value than the random value), indicating elephants maintain preferred associations across
10-day sample periods. Lagged association rates are used to assess the duration of
associations in a population, where the rate decreases across the period of the study if
associations are short lived or remain constant if relationships are stable (Whitehead
1999). We found lagged association rates decreased slightly during the first 7-10 day
sampling periods and were relatively stable for all lagged durations exceeding 10 days
(Whitehead 1995).
Seasonal and Temporal Data Set Analysis

Compositions of defined 2nd tier social units were stable across the four clustering methods compared. Structurally, 50 units were defined from three of the four methods, with 51 identified from the fourth (Table 2). In comparison to the Ward’s methods, which gave the greatest CCC value (Fig. 2; Table 1), only 4 of the 112 individuals were grouped differently in 2nd tier units defined from the combined three other methods. We used a reduced data set composed of only the 50 2nd tier unit matriarchs for identification of higher social levels. Four distinct, hierarchical social tiers emerged from this analysis of interactions among elephants comprising the studied subpopulation; where delineations of breeding females into 2nd tier units, 2nd into 3rd tier units, and 3rd into 4th tier units were defined statistically (Fig. 4; Table 4).

Association data were partitioned by season (wet and dry) and year of study (1998-2000 and 2001-2002), and then analysed independently to allow comparison of results derived from temporal or seasonal effects. The explicit, individual compositions of 2nd tier units, “family units” (Buss 1961; Laws 1970; Douglas-Hamilton 1972), were largely stable across data set partitions. The greatest change occurred in the 2001-2 partition where 6 of 112 individuals changed by splitting off to form new family units (Table 3). Both seasonal partitions demonstrated greater consistency, with 3 (wet) and 2 (dry) individuals changing social units as well as consistent numbers of social units (Table 3).

Our ability to separate 3rd from 4th tier units, defined from relationships among 2nd tier matriarchs, was greatly affected by the seasonal partitioning. The delineation between these two tiers emerged only during the wet season, as neither dry season nor total data
sets demonstrated significant knot values (Table 3). Additionally, this delineation was
evident only during the earlier stages of the study, in the 1998-2000 data set, though at a
coesively weaker level with $d = 1.3$ (Table 3).

Social units of the 4th tier were the least cohesive with the greatest variability at
both the individual and unit level occurring during the dry season, where 10 matriarchs
(20%) were grouped in different 4th tier units and only 5 (62.5%) of identified 4th tier
units were identical in composition to those from the total data set (Table 4).

Additionally, the number of 4th tier units increased by 2 in the dry season in comparison
with the wet season, and increased by 1 in the later half of the study as compared to the
first half (Table 4). The 1998-2000 temporal data set was relatively stable with only 2
individual changes and 75% of units identical in composition to the total data set, while
the 2001-2 data set was less so, with 6 individuals changing social units and 75% of units
identical (Table 3).

Comparison of cohesion between social tiers and among data partitions within
social tiers were conducted using CoCA, offering a method to quantify the average
cohesion of a matrix while taking into account the correlation among matrix elements
(Getz 2003). CoC and average AI values generally depicted the same trends in behaviour
(Table 4), though CoC values are greater than the average AI values especially when
many dyads’ AI values are zero as occurs in the 4th and 5th social tiers (see methods for
explanation of this difference). Previous studies have used the average AI value to
compare social cohesion (Myers 1983; Gowans et al. 2001). As noted in the methods,
however, AI values are not statistically independent. Cohesion, as measured by CoCA,
decreased from the 2nd to the 5th tier, with the highest levels occurring among core 2nd tier
units. Corresponding to the cluster method results, levels of cohesion differed significantly across each tier (Kruskal-Wallis $X^2 = 24.627, df = 3, p < 0.0001$; Table 4).

Across all social tiers, seasonal effects on CoC values were apparent (Table 5). The CoC values of 2nd tier “families” generally increased during the wet season as compared to the dry season, however the difference was not significant ($p = 0.086$). We used wet season definitions of 3rd tier “bond/kinship” units in order to compare unit cohesion, finding significantly greater wet season CoC values than those of the dry season ($p = 0.002$). Significantly greater cohesion was also found in 4th tier “clans” during the wet season than the dry season ($p = 0.0156$). However, 9 out of 50 2nd tier, 4 out of 25 3rd tier and 1 out of 8 4th tier units demonstrated the reverse with greater cohesion during the dry season than the wet. The 5th tier subpopulation showed the same general seasonal affect found in tiers 2-4, with the wet season CoC value exceeding that of the dry season. Like cohesion, social networks increased in size significantly during the wet season when individuals associated with an average of 98 individuals (87.6% of the total study individuals) in contrast to dry season networks averaging 80 individuals (71.0% of the total) (2-tailed, paired $t$-test, $t = 12.152, df = 111, p < 0.0001$). However, social networks were not significantly different across temporal periods of the study (2-tailed, paired $t$-test, $t = 1.285, df = 111, p = 0.201$).

Demographic changes in the size of a 2nd tier unit through time are likely to influence its stability, and one might expect the sizes of 2nd and potentially 3rd tier units to be distributed around some ecologically and sociologically determined optimal size. Interestingly, we found no evidence for this: the distribution of the number of 2nd tier units comprising the 26 3rd tier units was not different from random, in this case a
Poisson distribution of the same mean ($\chi^2=0.19277, \text{df}=2, p>0.900$), while the

distribution of individuals (breeding females and their calves) in the 50 2nd tier units did
deviate from random, but was bimodal (Fig. 5). We choose to organise these data into the
sum of two distributions based on matriarch age (the generation time for elephants is 17.4
years (Moss 2001) so elephants twice the age of the generation time, 34.8 years, are more
likely than not to be grandmothers). Again, the distributions of each category based on
matriarch age did not significantly differ from random (35 years and older: mean=9.85,
$\chi^2=8.363, \text{df}=12, p > 0.500$; less than 35 years: mean = 5.02, $\chi^2=10.142, \text{df}=5, p >$
0.050) indicating an optimal group size did not exist when accounting for units with
different age structure. Matriarchs younger than 35 years, however, lead significantly
smaller families than matriarchs 35 years and older (median$_{\text{younger}}=4$, median$_{\text{older}}=10$:
Wilcoxon Rank-Sum: $N_{\text{younger}}=23$, $N_{\text{older}}=27$, $Z=4.666, p<0.0001$) thus matriarch age does
have an effect on the size of social units.

**DISCUSSION**

Elephants exhibit stable, non-random social behaviour. From cluster analysis of
association data, we were able to delineate four hierarchical social tiers from the
continuum of social interactions. These four tiers have significantly different degrees of
cohesion (Table 4) and responded differently to temporal and seasonal effects.

Individuals generally displayed strong unit fidelity across time and season, but fusions of
lower tier units into higher tier units and fissions of higher tier units into lower tier units
occurred regularly. Variability in unit composition across data partitions was generally
the result of switches by a few individuals across social units (Table 3). Thus, the
majority of individuals’ social relations and the 4 tier social organization were relatively consistent during the study period. Previous studies of elephant social structure describe three social tiers, tier 1-3, and three non-social tiers, 4-6 (Douglas-Hamilton 1972; Moss & Poole 1983). Our study is the first to quantitatively demonstrate this multi-tiered social structure. Our 2\textsuperscript{nd} tier units correspond with the definition of “family unit” (Buss 1961; Laws 1970; Douglas-Hamilton 1972), which are groups of closely associated breeding females, most probably relatives, and their calves. Our 3\textsuperscript{rd} tier units appear to equate with Douglas-Hamilton’s (1972) description of kinship groups, later termed bond groups (Moss & Poole 1983), comprised on average of 2.5 family units and 28 (range 14-48) individuals in Lake Manyara National Park. Similarly, 3\textsuperscript{rd} tier units were comprised on average of 2.0 2\textsuperscript{nd} tier units and 16 (range 6-40) individuals in our study area. The difference in average size may be related to ecological differences between the two study areas, because Samburu is much drier than Lake Manyara. Previous research described a 4\textsuperscript{th} tier organization, termed “clan”, as a spatial population structure, roughly grouping elephants according to overlap in their dry season home ranges (Douglas-Hamilton 1972; Moss & Poole 1983). The emergent 4\textsuperscript{th} tier delineation in our study does not rely on any spatial information and represents a potentially novel tier not previously recognized to be influenced by social fusions of 2\textsuperscript{nd} and 3\textsuperscript{rd} tier units. Further, the dry season home ranges of all 4\textsuperscript{th} tier units overlap and some units’ ranges are not distinguishable spatially, indicating the previous definition of clans (Douglas-Hamilton 1972, Moss & Poole 1983) does not apply to the 4\textsuperscript{th} tier units defined in this study.
This study looks at social structure as a function of behavioural association patterns, though it is likely that spatial properties of the study population influence observed social behaviour. Of particular interest is the influence of spatial interactions on the emergence of 4$^{th}$ tier units. Our observations suggest that 4$^{th}$ tier units are a function of social rather than spatial processes, as the data were collected within or near a small (320 km$^2$), unfenced nature reserve. Elephant movements and resulting social interactions, therefore, appear not to be constricted by distance, landscape features, or any geographical barriers. Furthermore, although some spatial structure is associated with the resource-rich river running through our semi-arid study area, we did not identify any riparian structures that would explain the emergence of as many as eight 4$^{th}$ tier units.

Observations of mutualistic interactions (Mann et al. 2000) among 3$^{rd}$ and 4$^{th}$ tier unit members support our assertion that these tiers are social in origin. Radio tracking data of two 3$^{rd}$ tier associates from different 2$^{nd}$ tier units demonstrate coordinated movements over periods greater than a month within and outside the protected study area (unpublished data). Similarly, observational data of 4$^{th}$ tier associates indicates periods of cohesive movement spanning multiple weeks, both within and outside protected areas. Similar cohesive behaviour for shorter periods (7-14 days) has been recorded for the entire 5$^{th}$ tier subpopulation. Coordinated behaviour such as this has been used to distinguish social from non-social structures in studies of cetaceans (Whitehead 2003). Further, large aggregations (>100 elephants) are assembled in relation to social tiers, where 4$^{th}$ tier members are usually spatially clustered within the larger aggregation and 3$^{rd}$ and 2$^{nd}$ tier units are spatially nested within their 4$^{th}$ tier units. Observations of alloparental care were common within 2$^{nd}$ and 3$^{rd}$ tier units and occurred infrequently.
among 4th tier relations. Specifically, lactating females have been observed suckling another 2nd tier associate’s calf in four different units and a 3rd tier associate’s calf in two different units. Such interactions are rare and were not observed across different 4th tier units. Non-lactating females, however, have been observed to suckle calves within 2nd, 3rd and 4th tier units though such behaviour is generally limited to calves less than 6 months old and is infrequent across higher tiers associates. Although rates of this interaction were not rigorously recorded across the population, the significance of this behaviour has been studied (Lee 1987). Individuals defending their 2nd and 3rd tier counterparts are also common, and coalitions of 4th tier units in response to dominance interactions with outside elephants were observed infrequently. These observations suggest a social rather than non-social mechanism in the formation and maintenance to the 4 tier social organization.

Seasonal effects on sociality

During the dry season, when resource quality and quantity decreases, ecological constraints increase inter and intra group competition (Jarman 1974, Altmann 1974). The socio-ecological framework predicts this increase in competition should shape the social structure of organisms (Wrangham 1980; Isbell 1991). Our results indicate that social cohesion of elephant units decreases across all social tiers during the dry season. However, the effects of the dry season are disproportionate across tiers. 2nd tier units were the most stable across seasonal and temporal partitions (Table 3) and across different clustering methods (Table 2). The number and cohesion of 2nd tier units changed little across season, demonstrating that structural organization at this level was robust against potentially divisive ecological forces.
The effect of season was pronounced on the 3\textsuperscript{rd} and 4\textsuperscript{th} social tiers. In particular, the identification of units in the 3\textsuperscript{rd} social tier was dependent on season and the cohesion of 3\textsuperscript{rd} tier units (defined using the wet season definition) was significantly less during the dry season. This was the only seasonally specific social tier, demonstrating its unique dependence on ecological conditions. The number of units in the 4\textsuperscript{th} tier increased during dry periods and unit cohesion decreased significantly during these periods. This tier, however, was discernable across the seasons and throughout the study. Distinguishing the 3\textsuperscript{rd} from the 4\textsuperscript{th} tier structure in the dry season, when only one higher social tier was observed, was conducted by assessing the similarity in unit numbers and compositions to results from the total data set; results clearly indicated the presence of the 4\textsuperscript{th} tier structure rather than the 3\textsuperscript{rd} tier (Table 3).

Tighter ecological constraints of the dry season thus lead to greater levels of disassociation and splits in higher social units, inhibiting 2\textsuperscript{nd} tier units from coalescing into 3\textsuperscript{rd} tier units for extended periods. As competition increases, individuals tend to spatially separate. Levels of association occur along a continuum and the demarcations between social tiers are affected by interactions across all social levels, thus emergence of one tier can be affected by the state of other tiers. In this case, 3\textsuperscript{rd} tier units with bifurcation distance ($d$) values slightly less than the 3\textsuperscript{rd}/4\textsuperscript{th} tier knot (those which bifurcate just below the knot threshold) are marginally more cohesive than 4\textsuperscript{th} tier units with $d$ values slightly greater than the knot. Demarcation of these 3\textsuperscript{rd} tier units is not possible during the dry season because the rate at which individuals bifurcate in 3\textsuperscript{rd} tier units, particularly those close to the 3\textsuperscript{rd}/4\textsuperscript{th} tier threshold, are no longer statistically distinguishable from 4\textsuperscript{th} tier units (Fig. 4). It is likely that 4\textsuperscript{th} tier units are affected by the
social attraction among the merged 3rd tier units during the dry season, resulting in the lower knot value of $d$ (Table 3). Such changes affect the stability of 4th tier units; in this case splitting some units identified using the total data set into two dry season 4th tier units. Essentially, during the dry season higher order social units may act as a hybrid between 3rd tier inhibited relationships and typical 4th tier associates.

**Temporal effects on sociality**

We also found variability in social structure across the study period (Table 3). The 3rd tier social delineation was distinguishable in the 1998-2000 data partition, though it was absent in the later half of the study so comparison between the study periods was not possible. Prior to the start of data collection in June 1998, the “El Niño” climatic event brought excessive rains to the study area. These excessive rains had a major impact on vegetation growth and it is likely 3rd tier units were able to form year round during this period because of the lag effect on vegetation availability acting to supplement typical dry season diminution, thereby limiting intra-unit competition for resources.

Some of the temporal variability observed in social structure may be related to the two-year sample period of temporal partitions. Elephant reproductive intervals are generally between 3.6 and 4.8 years (Moss 2001; Foley 2002). The reproductive state of breeding females and variability in their calves’ ages and development are likely to affect social unit stability. Females with calves less than a year old (those with potentially greater nutritional requirements) may be affected by intra-group competition to a greater extent than other breeding females, resulting in temporarily lower cohesion between these females (1st tier units) and their 2nd tier units. Alternatively, such females may exhibit periods of increased levels of association in order to gain anti-predation benefits from
their social unit while the calf is of a susceptible age. Predation by lions and humans was a salient cause of mortality in the study population (Wittemyer et al. in review). Periodic rainfall events like “El Niño”, which led to the greatest observed population increase during the study period, may extenuate the effects of reproductive status on social unit cohesion by synchronizing reproduction across social units and across the whole population. Longer term studies may find greater temporal stability if partitions are for periods matching the population’s average inter-birth interval.

Population growth, however, is potentially the major factor affecting temporal variability. The number of units in both the 2nd and 4th tiers increased during the later half of the study, probably in relation to the 3.8% annual growth rate occurring during the study period (Wittemyer et al. in review). Structural changes in the numbers of social units as a function of period of study were most obvious among the otherwise stable 2nd tier social units. The 2nd tier average bifurcation distance (average changes in d) was the lowest for the 2001-2 data partition, resulting in six novel 2nd tier units (Table 3). Interestingly, all six of the new units constituted single mothers and their calves that were subordinate to the matriarch of the group from which they split; three had daughters reaching reproductive age or breeding and three were primiparous. Thus, the effect of unit size on social unit stability appears to be compounded by the age, reproductive state and rank of unit members.

Social unit stability and composition

Although no evidence was found for an optimal group size of 2nd or 3rd tier units, the role and age of the matriarch were found to be salient factors affecting the composition and size of social units (Fig. 5). Potential grandmothers were found to lead
larger family units than younger matriarchs. Thus our results suggest that parous
daughters remain with their mothers while their own progeny are sexually immature,
leading to three-generation families. Because of the stable linear-dominance hierarchies
in elephants (apparently a function of both individual size and age; Foley et al. 2001,
Moss 1988), intra-group competition disproportionately affects subordinates and their
offspring. As females ranked lower than the matriarch of their social unit become
grandmothers, the costs of group philopatry may begin to exceed the benefits derived
from remaining with their mothers. Although few females in the study population live to
an age where they are likely to be great grandmothers (i.e. around 50 years old given the
generation time of 17.4 years (Moss 2001)), those that live to this age do not lead larger
social units (mean size = 8, number of families = 3). Thus, as breeding females become
grandmothers, the increased costs of association may cause them to split from their natal
social units and form new 2nd tier social units. Familial contacts can still be maintained
through 3rd or 4th tier social units while avoiding the costs of high degrees of association.

Previous studies demonstrated a positive correlation between matriarch age and
the fitness of social unit members, offering a potential cause for social unit philopatry
(McComb et al. 2001). After the death of its matriarch, we observed a 2nd tier unit fission
that resulted in three novel 2nd tier units comprising a 3rd tier unit. Before her death, the
social unit’s CoC value = 0.749 ± 0.059 (jackknife estimated SE) and after her death the
social unit was less cohesive with a CoC value = 0.658 ± 0.055 (jackknife estimated SE).
This suggests that 3rd and 4th tiers may well be generated through fissions of 2nd and 3rd
tier units respectively, with the components of the fissioning units retaining stronger ties
than expected at random. Furthermore, social unit composition appears to affect higher
order social interactions. Not all 2nd tier units are members of 3rd tier units during the wet season, particularly larger 2nd tier units. Non-forming 2nd tier units generally have greater numbers of breeding females than those that form 3rd tier units, though this relationship was not significant at the 0.05 level (median_{non-forming}=2.5, median_{forming}=2, Wilcoxon Rank-Sum: N_{non-forming}=12, N_{forming}=38, Z=1.778, p=0.0753). Our observations suggest that 3rd tier units are most likely to be formed from 2nd tier units that have recently split probably as a function of unit size. Higher tier associations may also be in response to predation pressures. The largest 4th tier unit is composed of 17 2nd tier units (2 to 3 times more than other units), half of which have recently lost an older breeding female or the unit matriarch. This is in contrast to the other 4th tier units, of which only one has lost a high-ranking female to natural causes.

Low ranking primiparous females, experiencing the constraints of calf rearing for the first time, may also split from their natal 2nd tier social unit potentially in relation to the changing social costs and benefits of child rearing. One of the three primiparous females that formed a novel 2nd tier unit in the later half of our study left her natal unit after the death of the matriarch, believed to be her mother, but maintained contact with original unit members at 3rd tier association levels. Such observations provide anecdotal evidence of the benefits of maternal derived rank and the cost associated with rank alterations for subordinate individuals. Primiparous females were also observed to join non-natal units more frequently than other breeding females, though such visits were usually short lived. Unit switching may serve to enhance the social knowledge of these relatively inexperienced females.
Cohesive and divisive social forces

Inclusive fitness benefits derived from the survival and propagation of kin serve as the general cohesive force in many social organizations (Hamilton 1964; Vehrencamp 1983; Emlen 1995), though other cooperative benefits from group affiliation, such as enhanced success in territorial or resource defence (Schaller 1972; Harcourt 1992), may serve as the primary cohesive factor and not be based on kinship. While some species may form multiple tiered social organizations where membership is not stable across years or seasons, elephants are believed to remain in natal units throughout their lives (Moss 1988). Genetic studies are needed to elucidate the role of kinship in elephant social structure. Previous studies have provided evidence for inclusive fitness benefits derived from elephant sociality, in the form of allomother effects on calf survivorship (Lee 1987) and fitness benefits relating to matriarch social knowledge (McComb et al. 2001). Our results show 2nd tier units, which are probably the units where inclusive fitness benefits are greatest, are highly stable across time and season. This stability indicates such units are organised below the ecological threshold where variability in the social costs and benefits of units can act to significantly affect unit formation and cohesion (Fig. 6a), though it is apparent social unit age structure and composition affects where this threshold lies.

Expanding the socio-ecological model to multi-tiered social systems can help to elucidate the factors affecting the emergence of different social delineations. Our observations indicate the social benefits derived from multi-tiered social structure are probably inclusive fitness, resource/territorial defence, and anti-predatory behaviour. Other researchers have suggested clans, probably the equivalent of 4th tier units, form in
order to facilitate the exchange of ecological information (Foley 2002) and to attract mates (Moss & Poole 1983). Social tiers are influenced by such cohesive and divisive forces, which act throughout the social continuum but may affect relations at each tier to varying degrees (Fig. 6b). With multilevel fission-fusion societies, the nested hierarchy of social tiers can separate into smaller units, down the hierarchy, during times of constraints and increased competition or fuse into larger units, building up the hierarchy, when facilitated by conditions leading to increased cooperative benefits. Social tiers in which the benefits of forming units are only marginally equivalent to the costs of forming those units will be unstable in time and space when variability drives costs to exceed the benefits of the group (Fig. 6c). Degrees of social interactions among members in the study population are affected by ecological and temporal variability, thus delineations (and in some cases emergence of delineations) between social tiers are not fixed but vary over time, both seasonally and with changes in population size. Thus, the net total costs change over time, and depend on the number of social tiers at which a group is interacting (Fig. 6d).

The formation of higher order social delineations has important implications for the evolution of social systems. Though studies of multileveled social structures are few, our study suggests that each tier emerges in response to a different compilation of cost-benefit tradeoffs (Krause & Ruxton 2002, Whitehead 2003). Furthermore, time spent in different social delineations and their spatial properties (like distances between 2nd tier units when associating in their 3rd tier units) potentially affect social benefits derived from multiple social tiers. In gelada baboons (Papio gelada) inclusive fitness benefits apparently act to maintain families (Hamilton 1964; Vehrencamp 1983) but the cohesion
of multiple families into a higher social tier may occur in response to predation pressures
during periods of increased predation risk (Kummer 1995). Similarly for elephants, while
individuals are essentially always in their 2\textsuperscript{nd} tier units, coalitions of 2\textsuperscript{nd} into 3\textsuperscript{rd} and 3\textsuperscript{rd}
to 4\textsuperscript{th} occur less frequently. Individuals maintain the benefits of their 2\textsuperscript{nd} tier units, and
may incur the benefits while avoiding the costs of 3\textsuperscript{rd} or 4\textsuperscript{th} tiers by coalescing into the
higher order units for limited periods at opportune times. For example, elephants may
derive greater social benefits from larger aggregations during the breeding season
(coinciding with the wet season) by attracting mates (speculated by Moss & Poole 1983),
which may be the reason individuals coalesce into 3\textsuperscript{rd} tier units more frequently during
wet seasons.

Isolating the function of each social tier is difficult in complex animals like
elephants. Our study suggests that as 2\textsuperscript{nd} tier units increase in size, social costs are likely
to cause fissions that create 3\textsuperscript{rd} tier social units, which can potentially lead to the
formation of 4\textsuperscript{th} tier units through the same process. However, 4\textsuperscript{th} tier units were apparent
across seasons and temporal periods in contrast to 3\textsuperscript{rd} tier structures, indicating the
dominant forces affecting these two tiers are different. The costs incurred by 4\textsuperscript{th} tier units
may be diffused by the lower levels of cohesion in this tier. Alternatively, novel socio-
ecological benefits, such as intra-group information exchange hypothesized as the
function of clans by Foley (2002), may serve to maintain these units across seasonal
periods. It is possible, however, that the 4\textsuperscript{th} tier social structure is an epi-phenomenon,
occuring simply as a result of elephants predisposition to socially interact rather than as
a function of socially derived benefits. The levels of cohesion, or time spent with 4\textsuperscript{th} tier
conspecifics, are relatively low, possibly minimizing the ecological costs of such
interactions. Thus 4th tier sociality may have no functional meaning, representing
“runaway” sociality comparable in an evolutionary context to Fisherian sexual selection
(Fisher 1930) or superstimulus responses in mate selection (Basolo 1990). Only with
humans is the function of such higher order delineations clear, for example in the context
of economic and military alliances (Falger 1992). Kinship can also dictate the formation
of higher social levels in humans, as found in pastoralist communities in East Africa
where social tiers are based on patriarchal lineage (Spencer 1965; Teustch 1999). Future
controlled experiments are needed to directly assess the influence of cohesive and
divisive factors on the formation and structure of different social tiers. Identification of
the role and relationships of various social levels can serve to elucidate key socio-
ecological factors affecting a population and, as such, are salient to conservation efforts
and studies of sociality.
ACKNOWLEDGEMENTS

We thank the Kenyan Office of the President and the Kenya Wildlife Service for permission to work in Samburu and Buffalo Springs National Reserves. Additionally, the Samburu and Buffalo Springs National Reserves’ County Councils, wardens, and rangers have been incredibly supportive of our work. We thank J. Smith, P. Cross, H. B. Rasmussen, P. Baxter, E. Lacey, L.E.L. Rasmussen, and P. Starks for comments on this manuscript. Hal Whitehead and an anonymous reviewer offered detailed comments that helped to greatly strengthen the manuscript. David Daballen, Daniel Lentipo, and the rest of the Save the Elephants team were instrumental in the collection of field data for this study. Funding for this work was provided by the National Science Foundation, Lincoln Park Zoo, and private donors of Save the Elephants.
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http://is.dal.ca/~whitelab/index.htm


Table 1: The cophenetic correlation coefficients (CCC) (Romesburg 1984) of four clustering methods compared for selection of the clustering method which best fits the study association data.

<table>
<thead>
<tr>
<th>Method</th>
<th>Total Breeding Females</th>
<th>Matriarchs of 2nd Tier Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>UPGMA</td>
<td>0.874</td>
<td>0.529</td>
</tr>
<tr>
<td>CLINK</td>
<td>0.890</td>
<td>0.575</td>
</tr>
<tr>
<td>SLINK</td>
<td>0.841</td>
<td>0.479</td>
</tr>
<tr>
<td>Ward's</td>
<td>0.965</td>
<td>0.820</td>
</tr>
</tbody>
</table>

Table 2: Results from four cluster methods used to assess the integrity of 2nd tier social unit definitions. Compositions of defined units were robust across clustering methods.

<table>
<thead>
<tr>
<th>Method</th>
<th>Knot Value</th>
<th>N_A</th>
<th>N_B</th>
<th>Z statistic</th>
<th>p-value</th>
<th>Defined Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ward's</td>
<td>0.65</td>
<td>27</td>
<td>13</td>
<td>4.823</td>
<td>&lt;0.0001</td>
<td>50</td>
</tr>
<tr>
<td>UPGMA</td>
<td>0.55</td>
<td>29</td>
<td>11</td>
<td>4.867</td>
<td>&lt;0.0001</td>
<td>50</td>
</tr>
<tr>
<td>CLINK</td>
<td>0.60</td>
<td>28</td>
<td>12</td>
<td>4.816</td>
<td>&lt;0.0001</td>
<td>50</td>
</tr>
<tr>
<td>SLINK</td>
<td>0.50</td>
<td>30</td>
<td>10</td>
<td>4.295</td>
<td>&lt;0.0001</td>
<td>51</td>
</tr>
</tbody>
</table>
Table 3: Social unit definitions from subsets of the data (containing association indices calculated during seasonal and temporal periods) were compared with results from analysis of the total data set in order to ascertain the effects of season (ecological variability) and time (population growth) on social structure. Statistical identification of knot values and subsequent unit definitions were conducted by comparing step-wise changes in the number of bifurcations above the knot value ($N_A$) and below the knot value ($N_B$) (see methods and Fig. 1).

<table>
<thead>
<tr>
<th>2nd Tier Delineation</th>
<th>Knot Value</th>
<th>$N_A$</th>
<th>$N_B$</th>
<th>$Z$ statistic</th>
<th>$p$-value</th>
<th>Defined Units</th>
<th>Individuals Different</th>
<th>Units Identical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>0.65</td>
<td>27</td>
<td>13</td>
<td>4.823</td>
<td>&lt;0.0001</td>
<td>50</td>
<td>3 $^a$</td>
<td>45 $^b$</td>
</tr>
<tr>
<td>Wet</td>
<td>0.6</td>
<td>28</td>
<td>12</td>
<td>4.67</td>
<td>&lt;0.0001</td>
<td>49</td>
<td>2 $^a$</td>
<td>48 $^b$</td>
</tr>
<tr>
<td>Dry</td>
<td>0.75</td>
<td>25</td>
<td>15</td>
<td>4.482</td>
<td>&lt;0.0001</td>
<td>49</td>
<td>5 $^a$</td>
<td>44 $^b$</td>
</tr>
<tr>
<td>1998-2000</td>
<td>0.6</td>
<td>28</td>
<td>12</td>
<td>4.533</td>
<td>&lt;0.0001</td>
<td>49</td>
<td>5 $^a$</td>
<td>44 $^b$</td>
</tr>
<tr>
<td>2001-2002</td>
<td>0.45</td>
<td>31</td>
<td>9</td>
<td>4.586</td>
<td>&lt;0.0001</td>
<td>56</td>
<td>6 $^a$</td>
<td>36 $^b$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>3rd Tier Delineation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
</tr>
<tr>
<td>Wet</td>
</tr>
<tr>
<td>Dry</td>
</tr>
<tr>
<td>1998-2000</td>
</tr>
<tr>
<td>2001-2002</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>4th Tier Delineation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
</tr>
<tr>
<td>Wet</td>
</tr>
<tr>
<td>Dry</td>
</tr>
<tr>
<td>1998-2000</td>
</tr>
<tr>
<td>2001-2002</td>
</tr>
</tbody>
</table>

$^a$ out of 112 individuals

$^b$ out of 50 units

$^c$ out of 50 individuals

$^d$ out of 8 units

Table 4: Comparison of the average association index (AI) value and average social unit Correlative Coherence (CoC) value across social tiers. Average CoC and AI values are similar in tightly associated social tiers, but begin to differ markedly in higher tiers (see Methods for a discussion on the differences between these two measures of association).

<table>
<thead>
<tr>
<th>Delineation</th>
<th>Avg AI $\pm$ SE</th>
<th>Avg CC $\pm$ SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2nd Tier</td>
<td>0.829 $\pm$ 0.017</td>
<td>0.835 $\pm$ 0.018</td>
</tr>
<tr>
<td>3rd Tier</td>
<td>0.627 $\pm$ 0.037</td>
<td>0.706 $\pm$ 0.030</td>
</tr>
<tr>
<td>4th Tier</td>
<td>0.376 $\pm$ 0.058</td>
<td>0.515 $\pm$ 0.056</td>
</tr>
<tr>
<td>*5th Tier</td>
<td>0.053 $\pm$ 0.001</td>
<td>0.281 $\pm$ 0.004</td>
</tr>
</tbody>
</table>

Table 5: Correlative Coherence (CoC) values for the 2nd-5th social tiers’ units were quantified across the wet and dry seasons. The 5th tier CoC values were jackknifed to
obtain standard error estimates. The numbers of units compared ($n$) are less than the actual number of units in 2\textsuperscript{nd} and 3\textsuperscript{rd} tiers because comparisons across seasons were not possible in units composed of single breeding females.

<table>
<thead>
<tr>
<th>Delineation</th>
<th>Wet Median (CoC)</th>
<th>$n$</th>
<th>IQR</th>
<th>Dry Median (CoC)</th>
<th>$n$</th>
<th>IQR</th>
<th>Wilcoxon Z (Exact)</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>2nd Tier</td>
<td>0.875</td>
<td>32</td>
<td>0.780-0.924</td>
<td>0.810</td>
<td>32</td>
<td>0.730-0.882</td>
<td>1.715</td>
<td>0.086</td>
</tr>
<tr>
<td>3rd Tier</td>
<td>0.749</td>
<td>23</td>
<td>0.667-0.824</td>
<td>0.645</td>
<td>23</td>
<td>0.602-0.791</td>
<td>(234)</td>
<td>0.002</td>
</tr>
<tr>
<td>4th Tier</td>
<td>0.536</td>
<td>8</td>
<td>0.478-0.605</td>
<td>0.511</td>
<td>8</td>
<td>0.462-0.544</td>
<td>(35)</td>
<td>0.016</td>
</tr>
</tbody>
</table>

**Wet Mean**

<table>
<thead>
<tr>
<th>Delineation</th>
<th>Wet Mean</th>
<th>Jackknife SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>5th Tier</td>
<td>0.305</td>
<td>± 0.0164</td>
</tr>
</tbody>
</table>

**Dry Mean**

<table>
<thead>
<tr>
<th>Delineation</th>
<th>Dry Mean</th>
<th>Jackknife SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>5th Tier</td>
<td>0.272</td>
<td>± 0.0159</td>
</tr>
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</table>
Figure Legends:

Fig. 1: Cumulative numbers of bifurcations across cluster distances (\(d\)) for the four different types of cluster analysis listed in Table 1 and 2. Identification of knot values signifying social tier delineations was conducted by maximizing Z-statistics from comparisons of stepwise changes above and below the knot value. The 0.65 (\(d\)) knot value for the Ward’s Weighted Clustering Method is indicated, as well as the corresponding regions above and below the knot value (\(N_A = 27, N_B = 13, Z = 4.823, p < 0.0001\)).

Fig. 2: A cluster diagram constructed from the association indices using the Ward’s Weighted method identifies putative group relationships among the 112 breeding females used in the study. Each (o) at the base of the tree represents one breeding female. The bifurcation distance (\(d\)) is the measure of associative distance between individuals, where \(d = 0\) indicates two individuals were observed together 100% of observations (having the same association pattern) and increasing \(d\) values represent decreasing degrees of association among individuals. The solid line indicates the \(d = 0.65\) cut-off used to delineate 2\(^{nd}\) tier social units from higher order social relations (Table 1, Fig. 1). Individuals bifurcating below this line are in the same 2\(^{nd}\) tier unit, while those bifurcating above this line are in different 2\(^{nd}\) tier units.

Fig. 3: The difference between the cumulative number of bifurcations across cluster distances (\(d\)) for actual association data (from the Ward’s clustering method) and the data after randomisation. The randomised data set does not have any significant knot values and is relatively linear indicating no social tiers exist. The actual data has a significant knot value (\(p < 0.05\)) at 0.65 (\(d\)) and is concave down indicating the existence of a social tier.

Fig. 4: The Ward’s cluster diagram and the cumulative bifurcation graph are plotted here for the 50 2\(^{nd}\) tier unit matriarchs (listed as letter and number combinations at base of cluster tree: e.g. R1) using wet season data only. The 3\(^{rd}\) (Region A, 0.65 < \(d\) ≤ 1.05) and 4\(^{th}\) (Region B, 1.05 < \(d\) ≤ 1.85) social tiers are identified by the slope changes in the cumulative graph of bifurcations (Insert). Region C, \(d > 1.85\), is where the 4\(^{th}\) tier units aggregate to form the 5\(^{th}\) tier subpopulation associated with the study site. Social delineations occur at statistically optimised knot values (see Methods) after all points below \(d=0.65\) had been removed (these represented 2\(^{nd}\) tier units based on a cluster analysis of all the data). The significances of the knots are: A vs B: \(Z = 2.527, p = 0.012\); B vs C: \(Z = 3.926, p < 0.001\). A statistically significant 3\(^{rd}\) tier delineation was not distinguishable from the 4\(^{th}\) tier delineation in our analysis of dry season data alone (\(Z = 1.324, p = 0.185\); Table 4).

Fig. 5: In order to assess if the sizes of social units are distributed around an optimum, we compared observed distributions of unit sizes with Poisson (random) distributions of the same means. The observed distribution of 2\(^{nd}\) tier unit sizes (including breeding females and their calves) significantly deviated from the Poisson distribution of the same mean (mean = 7.64, \(\chi^2 = 50.870, df = 11, p < 0.001\)), indicating that the sizes of social units are
not randomly distributed. Distributions of 2nd tier unit sizes after separation into two classes based on matriarchs’ age (< 35 and ≥ 35 years) in relation to elephant generation time (17.4 years), however, did not significantly differ from respective random distributions of the same means (35 years and older: mean=9.85, $\chi^2 = 8.363, df = 12, p > 0.500$; less than 35 years: mean = 5.02, $\chi^2 = 10.142, df = 5, p > 0.050$) indicating that an optimal group size did not exist for either category of social unit.

Fig. 6: A conceptual framework is presented on the effects of the interactions among social and ecological costs and benefits on the emergence of a multi-tiered social organization. Social benefit 1 (e.g. inclusive fitness benefits) decrease as group size increases, while a social cost (e.g. feeding competition) increase with group size (a). The point at which these forces intersect dictates the threshold (maximum not optimal) size of the social group ($N_1$), above which costs exceed the benefits of grouping. Certain cohesive or divisive forces may only be salient at specific group sizes as with social benefit 2 (e.g. territorial defence for large groups), such that combined costs and benefits result in multiple threshold group sizes (b). Additionally, social costs and benefits will vary across time and group context affecting these threshold group sizes. In this example, costs exceed the benefits of the second order threshold group size during certain seasonal periods, impeding formation of the higher order social group during high cost periods (as seen with 3rd tier aggregations in elephants) (c). When the net total value of these forces act across the social continuum, multiple social tiers may emerge in relation to a hierarchy of cost/benefit comparisons in which social benefit 1 out ranks social benefit 2 (d).
Fig. 1

Cumulative Number Of Bifurcations

Region Above Knot-value

0.65 Knot-value Ward’s Weighted

Region Below Knot-value

- UPGMA
- CLINK
- SLINK
- Ward’s

Distance (d)
Fig. 2

Bifurcation Distance (d)
Fig. 3

Cumulative Number of Bifurcations vs. Distance (d)

- Random
- Actual

Distance (d):

0 0.5 1 1.5 2 2.5

Cumulative Number of Bifurcations:

0 20 40 60 80 100

Distance (d) vs. Cumulative Number of Bifurcations
Fig. 4

4th Tier Knot

3rd Tier Knot

Region C

Region B

Region A

Bifurcation Distance ($d$)

Cumulative Number Of Bifurcations

0 0.25 0.50 0.75 1.00 1.25 1.50 1.75 2.00 2.25 2.50 2.75

1.85 Knot-value

4th Tier Structure

1.05 Knot-value

3rd Tier Structure


0 1 2 3 4 5 6

48
Fig. 5

Number of Individuals in Families

Number of Families

- □ Observed
- ■ Expected ≥ 35 years
- □ Expected < 35 years

Number of Families

0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Fig. 6

(a) Values (Costs + Benefits)

(b) Values (Costs + Benefits)

(c) Values (Costs + Benefits)

(d) Total Value

Seasonal Variability In Costs

Group Size

Dry Season

Wet Season

Social Cost

Social Benefit 1

Social Benefit 2