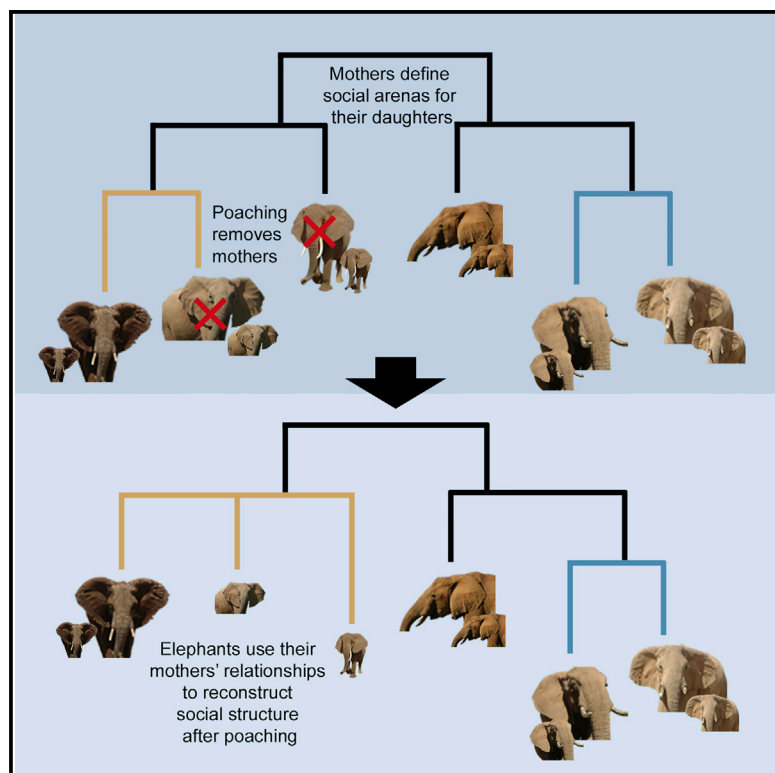


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Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks

Graphical Abstract



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In Brief

Goldenberg et al. show that elephant social networks are robust to removal of structurally important matriarchs. Daughters actively regenerate ties within the social arenas defined by their mothers, highlighting the importance of social structure to this species despite population changes and demonstrating evolved mechanisms of network resilience.

Highlights

- Poaching targets older elephants, removing key social individuals
- After poaching disruption, elephants maintain hierarchical social structure
- Daughters leverage their mothers' prior social context to reconstruct networks



Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks

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SUMMARY

Network resilience to perturbation is fundamental to functionality in systems ranging from synthetic communication networks to evolved social organization [1]. While theoretical work offers insight into causes of network robustness, examination of natural networks can identify evolved mechanisms of resilience and how they are related to the selective pressures driving structure. Female African elephants (*Loxodonta africana*) exhibit complex social networks with node heterogeneity in which older individuals serve as connectivity hubs [2, 3]. Recent ivory poaching targeting older elephants in a well-studied population has mirrored the targeted removal of highly connected nodes in the theoretical literature that leads to structural collapse [4, 5]. Here we tested the response of this natural network to selective knockouts. We find that the hierarchical network topology characteristic of elephant societies was highly conserved across the 16-year study despite ~70% turnover in individual composition of the population. At a population level, the oldest available individuals persisted to fill socially central positions in the network. For analyses using known mother-daughter pairs, social positions of daughters during the disrupted period were predicted by those of their mothers in years prior, were unrelated to individual histories of family mortality, and were actively built. As such, daughters replicated the social network roles of their mothers, driving the observed network resilience. Our study provides a rare bridge between network theory and an evolved system, demonstrating social redundancy to be the mechanism by which resilience to perturbation occurred in this socially advanced species.

RESULTS AND DISCUSSION

Network topology determines process direction and strength, from information flow on the internet and electrical transmission on power grids [6] to eco-evolutionary processes like sexual

selection [7], disease transmission [8], and cultural exchange [9]. Network perturbations threaten connective integrity, with implications for functionality and the benefits that individual components derive from structure [1, 10]. Targeted removal of nodes may lead to destabilization, a shift in structure reflective of shifting optima, or regeneration of original structure [8, 11–13]. Although theoretical work has demonstrated that redundancy in complex networks [5] and redirection of ties following removal of highly connected nodes can lead to structural resilience [13–15], whether these or alternative processes occur in evolved systems requires investigation. There is evidence for functional collapse after the removal of key social hubs in the few animal studies on perturbation in complex social networks [12, 13]. However, these studies of natural networks are often short term or conducted in captive systems. In situ and longer-term studies will illuminate how natural networks respond to perturbation.

Elephant populations have experienced a resurgence in ivory poaching over the last decade, which has targeted older cohorts for their larger tusks [4, 16]. The importance of older elephants is well recognized, raising concerns about the impacts of age-selective poaching on population function [3]. Using the context created by this selective harvest, we investigated emergent grouping patterns among individually identified adult female elephants in northern Kenya's Samburu and Buffalo Springs National Reserves (0.3°–0.8° N, 37°–38° E) over a 16-year period [4, 16]. Elephants maintain complex societies, characterized by clearly detectable social tiers (strongly cohesive core groups nested within moderately cohesive bond groups, which in turn are nested within less-cohesive clan groups) [2] and heterogeneously distributed social ties, with older females serving as connectivity hubs [3]. Removal of older elephants is analogous to the targeted knockout of highly connected nodes in other networks [5, 12].

We investigated network properties in our study population across three sampling periods representing different ecological and harvest conditions: the moderate-productivity, low-poaching period T1 (June 1998–May 2001), the high-productivity, low-poaching period T2 (June 2001–August 2004), and the moderate-productivity, high-poaching period T3 (June 2012–July 2014). A severe drought in 2009 was an additional source of disruption prior to T3 [16]. Despite the population changes over time (Figure 1), agglomerative clustering of elephant pairs (dyads) revealed hierarchically structured social organization across the study, with distinguishable core and bond groups with similar group size and association index (AI) values

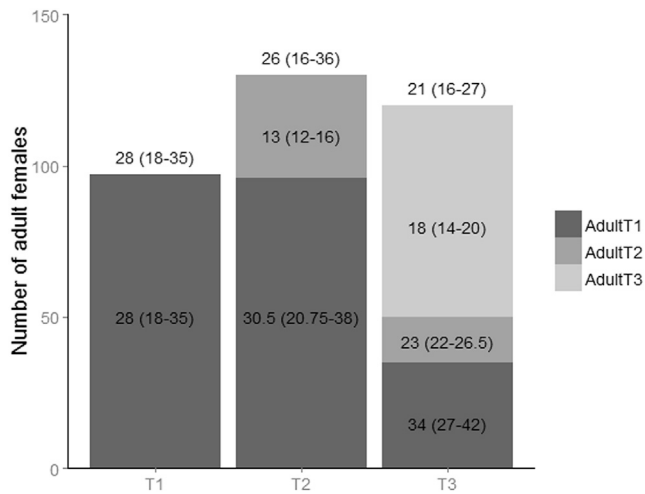


Figure 1. Study Females Changed with Time Due to Maturation and Mortality, with a 70% Turnover in the Population's Adult Females over the Study and a Resulting Downward Shift in Age

Cohorts of females are shaded based on when an individual was first present in the analysis. Median ages (with interquartile ranges) for cohorts (within bars) and overall (above bars) are presented.

(Experimental Procedures; Figure S1; Table S1) [2]. Structure was conserved despite ~70% turnover in the population's adult females and a significant decline in average age between T1 and T3 ($\text{age}_{T1} - \text{age}_{T3}$: $\chi^2 = 6.47$, $df = 1$, $p < 0.05$). The matrilineal composition of core and bond groups, however, changed over the study, particularly where previously distinct matrilineal groups fused after groups were affected by mortality (Figure 2). Eight of nine females that fused into a different core group in T3 had lost their mothers, and seven of nine core groups that fused into different bond groups in T3 lost their matriarchs (defined here as the oldest member of the group) between T2 and T3.

In contrast to core and bond groups, the inability to detect clans in T3 may suggest that this structure was not beneficial during the disrupted period, or that clans are a manifestation of lost links among older age cohorts. It has been suggested that as young females reach breeding age, resource competition within groups becomes more intense and older females lead permanent fissions of core groups into discrete core groups that together comprise a bond group (or fissions in bond groups into discrete units that comprise a clan group) [2]. The altered age structure after poaching reduced the number of connected multi-generational lineages, potentially severing the foundational connections necessary for clans to emerge.

In this population, the relationship between age and network position appears to be relative: the oldest individuals available have higher degree and betweenness centrality. Degree, the number of contacts per individual, was significantly positively correlated with age in all sampling periods (T1: $r = 0.308$, $p < 0.01$; T2: $r = 0.335$, $p < 0.01$; T3: $r = 0.281$, $p < 0.01$). Betweenness, the number of shortest paths that go through an individual within the larger network, was significantly correlated with age in T2 and T3 (T1: $r = 0.137$, $p = 0.180$; T2: $r = 0.212$, $p < 0.05$; T3: $r = 0.221$, $p < 0.05$). Thus, the oldest individuals in the population tended to serve as social bridges (higher betweenness) and

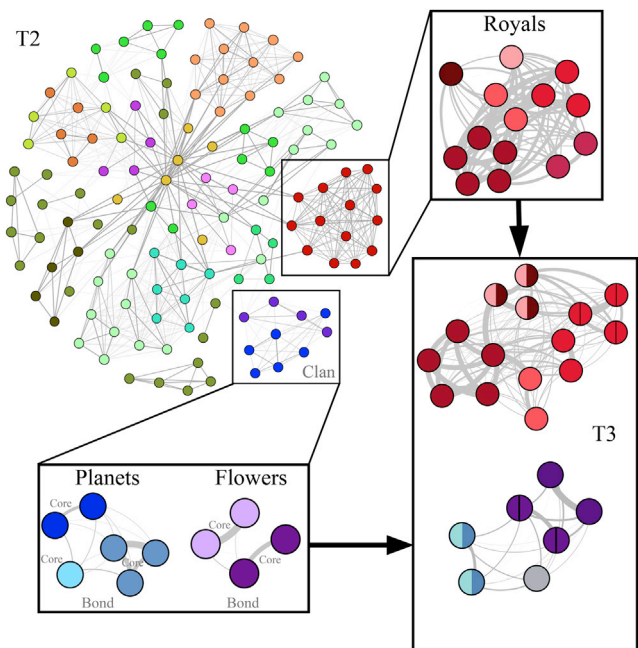


Figure 2. Despite Changes in Matriline Composition over Time, Core and Bond-Group Structure Are Maintained in Elephant Society

Nodes in the T2 population network (top left) represent individual female elephants, width of edges between nodes represents association index strength, and colors differentiate bond groups. Insets of three of these bond groups (the Royals, a group that experienced low adult mortality, and the Flowers and Planets, groups that experienced high adult mortality) are shown. Matching nodes represent distinct core groups, where hybridized nodes represent fusion of matrilineal and black lines through nodes represent core groups that fissioned after T2. Gray indicates matrilineal groups that were not a part of either bond group in T2. The Flowers and Planets merged into one bond group by T3. Gray words distinguish the nested tiers of female elephant society. See also Figure S1 and Tables S1–S3.

hubs (higher degree). In extreme cases, we witnessed this clustering even within highly disrupted families, where surviving relatives coalesced around the oldest female in the group even if she was a juvenile. These findings indicate that the overall structure of female elephant society is resilient regardless of age composition.

To investigate the role that older individuals play in structuring social environments, we examined the relationship between the social positions of daughters and their mothers [17] or their bond-group matriarchs using Mantel tests of dyadic AI. We first tested associations among individuals present in more than one period to determine whether elephants are socially consistent over time. Second, we tested whether mothers' associations with each other were correlated with their daughters' relationships. AI of individuals over time and in mother-daughter pairs both within and between sampling periods were all significantly correlated (Table S2), indicating that individual contact patterns were consistent over time and that closely associated mothers have daughters that are also closely associated. This correlation held even after a mother died. To assess the possibility of the alternative hypothesis that daughters' social positions are more a function of their broader social environment than that of their mothers, we also compared the social associations of

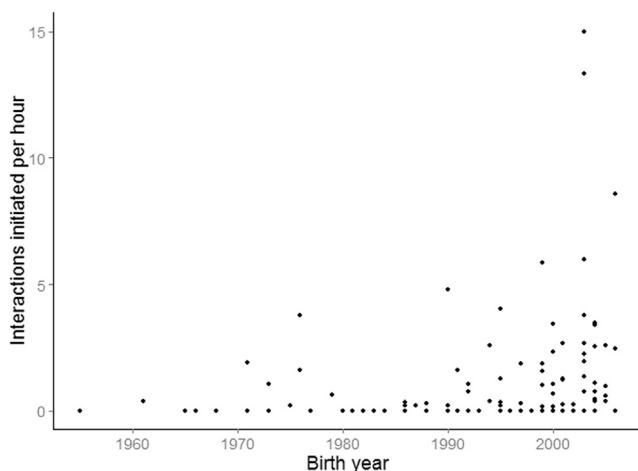


Figure 3. Younger Elephants Initiate Affiliative Interactions toward Non-Core-Group Members at a Higher Rate Than Older Elephants
See also Tables S2 and S3.

these daughters with those of their oldest bond-group member outside of their core group. Although significant, the correlation was considerably lower than that between mother-daughter pairs (Table S2).

Similar to Mantel tests, generalized linear models (GLMs) showed that mother betweenness in T2 was the strongest predictor (significantly positive) of daughter betweenness in T3 (Table S3). Network position was unrelated to mother death. Age was positively correlated with social position but was not as important in predicting daughters' positions. While age was significantly correlated with social position in our univariate analysis at the population level, the GLM was a multivariate analysis focused on a narrower age distribution (11- to 27-year-olds rather than 9- to 58-year-olds). Collectively, these results suggest that the conserved structure in elephant social networks was a function of individuals maintaining their social positions over time and daughters replicating the contact patterns of their mothers.

While lineage-replicated behavior was a key component in network resilience, active contact building revealed the extent to which this replication is learned. Birth year was positively correlated with initiation of affiliative behaviors toward non-core-group members ($\rho = 0.45$, $p < 0.01$; Figure 3), indicating that social exploration was primarily conducted by younger elephants. Juveniles actively built their contacts within the context created by their mothers, which is likely the means by which daughters replicated the network positions of their mothers. This mechanism allows individuals whose mothers' close contacts are gone to strengthen bonds, conserving the general network properties that they experienced before disruption. Fusions of previously distinct matrilineal groups occurred in groups where removal of most adult elephants meant daughters could not replicate the social networks of their mothers (Figure 2). This active contact building often involved strengthening bonds with elephants that were distant contacts in their mothers' networks.

The remarkable stability in elephant population structure across periods of demographic change was attributable to the

ability of young elephants to emulate the contact patterns of their mothers within a hierarchically clustered context. The social arena set by the grouping decisions of matriarchs may buffer network collapse by providing maturing females with social opportunities from which they can build their own contact structure. Our finding that younger females are more interactive with individuals outside of their immediate core group underscores the active role that they take in shaping their own contacts and suggests that this emergent property is more a function of learning than of classic inheritance [18]. Thus, the apparent inheritance of social position appears to be an interaction between the tiered sociality defined by older relatives and the active maintenance and generation of social ties by younger females [19]. We did not explicitly assess the role of primary productivity here, but ecological dynamics are likely important in structuring networks, as elephant associations are known to reflect seasonal changes [2]. Further analysis of the relationship between productivity and network structure merits investigation. Although this study demonstrates structural resilience in elephant society regardless of age composition in the population, further study is needed to understand the fitness repercussions of family mortality and loss of matriarchs. Our work highlights the potential that empirical systems offer for understanding of social network evolution and function and demonstrates the mechanism by which network integrity is maintained in this social species.

EXPERIMENTAL PROCEDURES

Data Collection

The unfenced study system was semiarid savannah receiving approximately 350 mm of rain annually in two wet seasons [20]. When elephants were encountered along four established reserve transects, the date, time, GPS coordinates, group size, individuals present, and observation accuracy were recorded. Elephants were considered to be associating when behaviorally coordinated and spatially cohesive within 500 m of an observer-estimated center [2]. Focal interaction data were collected for 30 min or less in a sampling day, during which all interactions with conspecifics were recorded [21]. Data were collected across all seasons. Observations were conducted noninvasively (IACUC 12-3414A) and with permission of the Kenya Wildlife Service, the Samburu and Isiolo County Councils, Colorado State University, and Save the Elephants.

Data Analysis

To ensure observation consistency and quality, we only included observations for which all breeding females present were identified and only used observations conducted by three primary observers. We limited analysis to parous females, where females were considered parous starting in the month in which they had their first calf. We compared age distributions of females across periods using Kruskal-Wallis chi-square tests. We used the simple ratio index as an association index (AI) to measure strength of association between pairs of females: $AI = N_{AB} / (N_A + N_B + N_{AB})$, where N_{AB} is the number of observations for which both individuals were in the same group, and N_A and N_B are the number of observations when A was without B and B without A, respectively [22]. A modified approach was applied where AI values were calculated only during periods when dyad members were parous and alive on the date of the observation, thereby controlling for demographic changes over time [23, 24]. We calculated AI separately for each of the three sampling periods.

To limit bias introduced by small sample size, we only included females observed ten times or more within a sampling period ($N_{T1} = 97$, $N_{T2} = 130$, $N_{T3} = 120$) [25]. We used AI values to examine structure at the individual and population scales using ego networks and cluster analyses, respectively. We constructed distance matrices (distance = $1 - AI$) and clustered individuals using Ward's linkage rule [2, 26]. We plotted the cumulative number of bifurcations for each 0.05 increment in cluster tree height to locate points of structural

change, where significant slope changes on the cumulative bifurcation plot (using Mann-Whitney U tests) were identified as points at which clustering patterns change [2, 27]. All individuals represented on a unique, contiguous branch below the identified knot value were considered a group (Figure S1).

We first performed this procedure with all females in each sample to determine core-group structure. We then determined the oldest female (matriarch) of each core group and conducted a separate cluster analysis using matriarchs as representatives of core groups to more clearly delineate higher-order structure that may be dampened by the strong associations within core groups when all individuals are included [2]. Because bond and clan groups are most apparent during the wet season [2], we recalculated AI between matriarchs using observations during the wet season, where wet season was defined for the study system using threshold-normalized difference vegetation index values [28]. As with previous AI calculations, we excluded matriarchs seen fewer than ten times ($N_{T1} = 39$, $N_{T2} = 49$, $N_{T3} = 39$).

We constructed networks from AI values, where nodes represent females and ties between nodes represent AI strength [29], visualizing networks using Gephi (v0.8.2) [30]. We then calculated ego-network metrics using the statnet package for R [31]. Because elephants are long lived and age is associated with increased group survival [3], we used Pearson correlations to compare metrics to age, where age at the midpoint of each sampling period was used. p values were Bonferroni adjusted where multiple comparisons were used. Statistical analyses were performed in R (v3.0.3) [32].

Identification of Mechanisms Driving Structure

We used Mantel tests to compare matrices of AI values to understand whether behavior is consistent within individuals and within mother-daughter and other pairs. We conducted four sets of comparisons: (1) AI among individuals present in two adjacent sampling periods, (2) AI among mothers and AI among their daughters within the same period, (3) AI among mothers in one period and AI among their daughters in the following period, and (4) AI among daughters in T3 and among oldest bond-group members outside daughters' core groups in T2. The third category was subdivided for the T2-T3 test using mother-daughter pairs for which the mother was dead in T3 and for which the mother was alive in T3 to illuminate whether association indices are correlated with a history of family mortality. For all generational tests, the order of daughters in matrix rows and columns corresponded to the ordering of the older generation matrix, so that corresponding cells in the two matrices represented relevant matched pairs. We ran 1,000 permutations for each Mantel test.

To address the mechanisms related to node-level metrics, we implemented generalized linear models (GLMs) predicting a female's degree, betweenness, and clustering coefficient using Poisson, gamma, and beta regressions, respectively, on a subset of females from T3 for which mothers were known to be alive in T2 and covariates were available ($N = 67$). We used a quasi-GLM to correct for overdispersion in the Poisson model, adjusting coefficient standard errors by the overdispersion parameter [33]. Explanatory variables included age in T3, mother's age in T2, core-group size in T2, core-group size in T3, bond-group size in T2, bond-group size in T3, number of calves in T3, mother's degree in T2, mother's betweenness in T2, mother's clustering coefficient in T2, and whether the mother was alive in T3.

To further investigate behavioral mechanisms, we used focal follow data of affiliative behaviors directed toward conspecifics in T3. For each female observed for at least one hour while feeding, we combined all follow data and calculated the rate at which she directed affiliative behaviors (e.g., body rubbing, trunk touching, greeting) toward non-core-group members. We conducted a Spearman correlation of affiliation rate with birth year to elucidate whether age structures social initiative.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure and three tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.11.005>.

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