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Title

Simulated poaching affects connectedness and efficiency in social networks of African savanna elephants

Authors

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Abstract

Poaching of mature and socially influential African savanna elephants for their prominent tusks alters the structure of their social networks. To learn if targeted poaching affects the functioning of elephant associations, we simulated network formation and disturbance via 'poaching' experiments in one wild and 100 virtual populations. To simulate virtual networks, we built an individual-based model guided by empirical association trends. After poaching of 1) the most mature or socially central individuals or 2) individuals selected at random, we evaluated network connectedness and efficiency. The networks never broke down, suggesting structural robustness. Unlike in age-specific deletions, eliminating individuals with the highest topological centrality decreased network connectedness and efficiency. The simulated networks, although structurally stable, became less functionally resilient when subject to poaching-like stress. Our work may offer new insights into elephant behavior vis-à-vis anthropogenic pressure, and inform conservation efforts focused on translocation of social species or trophy hunting practices.

Keywords

Loxodonta africana; social network analysis; connectedness; global efficiency; poaching; socioecological experience

Introduction

In wild animals, the loss of experienced or otherwise influential individuals through natural or anthropogenic causes may be detrimental to their conspecifics (Borg et al., 2015; Krofel et al., 2015) and to the population as a whole (Jesmer et al., 2018; Shannon et al., 2013). In taxa with multi-level social structures, such as some passerines, cetaceans or proboscideans, individuals may buffer the consequences of losing socially valuable partners by restructuring their social networks (Firth et al., 2017). African savanna elephants (*Loxodonta africana*) have one of the most complex social systems described in nonhuman animals (McComb et al., 2000). After targeted removal of most senior conspecifics, savanna elephants (from now on referred to as elephants) seem to restructure their social networks, incorporating prior and novel associations (Goldenberg et al., 2016). Still, much remains unanswered about the functional characteristics of their seemingly resilient social landscapes.

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As a multi-level society, elephants navigate across several social tiers, ranging from large aggregations of distant kin to small units of closely related conspecifics. On a day-to-day basis, they operate in matrilineal herds of adult females and their immature offspring (Wittemyer and Getz, 2007), or in transitional groups consisting of post-dispersal males of varying ages (Chiyo et al., 2011; Murphy et al., 2019). Similarly to other long-lived, widely ranging species (Brent et al., 2015; Canteloup et al., 2020), older elephants of relatively dominant social rank possess more experience than their younger conspecifics (McComb et al., 2001). For instance, compared to herds traveling with relatively subordinate matriarchs (Exposito 2008), herds led by dominant matriarchs experienced higher calf survival rates (Lee et al., 2016) and used better quality resources, frequently in protected reserves (Wittemyer et al., 2007). As another example, Slotow and his collaborators (Slotow et al., 2000) reported that juveniles maturing in populations without seniors entered musth prematurely and exhibited aberrant hyper-aggressive behaviors; however, these behaviors ceased after the reintroduction of adult males. These examples demonstrate the role mature elephants have on the development and modification of a range of adaptive behaviors by younger group members, particularly their social interactions and responses to a rapidly changing physical environment, both natural and human-induced.

Human degradation of traditional wilderness areas makes once inaccessible elephant habitats susceptible to poaching (Graham et al., 2009). Ivory poachers target the individuals with the most prominent tusks (Wasser et al., 2015), resulting in the elimination of the largest and oldest group members (Chiyo et al., 2015). Most studies exploring the effects of poaching have focused on demographic changes in vulnerable populations (Bradshaw and Schore, 2007; Gobush et al., 2008) and movement behavior near poaching hotspot proxies (Goldenberg et al., 2018; Ihwagi et al., 2015). Another more pernicious consequence may be the loss of decades of knowledge about resource distribution and phenology, and about complex social dynamics, that the poached elephants presumably held in memory (McComb et al., 2011). Although the impact of poaching on information transfer to surviving group members remains ambiguous, one research group has shed light on how poaching of mature elephants changes the topology of social interactions in re-established herds (Goldenberg et al., 2016).

Analyzing a dataset spanning periods of low and high poaching pressure, Goldenberg and her team (2016) found that although poaching altered the composition of elephant herds, the structure of their social networks remained largely unchanged. In addition, the female offspring of the previously most socially connected members became the new social centers. Instead of a linear, age- and size-determined dominance hierarchy (Archie et al., 2006; Hollister-Smith et al., 2007), the elevated social roles of the orphaned females may have been a byproduct of operating within the same social landscape as their mothers (Wittemyer and Getz, 2007). Nonetheless, it is unlikely that relatively young females would possess the same wealth of ecological experience as did their poached mothers and aunts. The consequences of such an experience void may include reduced fitness among survivors, as well as an impairment of the species' keystone activities (Pellegrini et al., 2017) and its role in wildlife-based tourism (Naidoo et al., 2016). It is therefore important to evaluate whether re-established elephant social networks, although structurally resilient, are comparable in their functional resilience to their pre-poaching state.

The functionality of a social network can be defined as the likelihood of a fault-tolerant and efficient exchange of socially available information, through individual observation of, or interactions with, more knowledgeable conspecifics (Claidière et al., 2013; Puga-Gonzalez et al., 2019). In schooling golden shiner, individuals moving near the periphery of the group, or those with few, strong social connections, appear most informed about the external environment and social dynamics (Rosenthal et al., 2015). In contrast, in systems structured around lifelong

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interactions, individuals at the center of their social networks tend to assimilate valuable information more efficiently than their peripheral counterparts and are more attractive as social partners (Kulahci et al., 2018). For example, in three tit species, socially central individuals were most efficient at discovering novel foraging patches (Aplin et al., 2012). Removal of such individuals resulted in less efficient information exchange in simulated systems (Puga-Gonzalez et al., 2018) and also in empirical networks of bottlenose dolphins (Lusseau, 2003). Whereas in elephants, fragmentation of established social dynamics, after the culling of mature conspecifics, left juvenile survivors unable to recognize age- and dominance-specific vocal cues from their distant kin (Bradshaw and Schore, 2007; Shannon et al., 2013); for consequences of natural network disturbance in other species see (Linklater et al., 1999).

As an important indicator of socioecological competence in many gregarious species (Brent et al., 2015; Carter et al., 2013; Lee and Teichroeb, 2016; Shier, 2006), and elephants in particular (McComb et al., 2011; Murphy et al., 2019; Shannon et al., 2013), age may be functionally parallel to traditional measures of social centrality. Hence, poaching-induced removal of the oldest elephants from their social networks may result in the reduced transfer of socioecological information, as would be expected in the removal of the most socially connected network members in long-lived, social species. Establishing whether age-targeted poaching alters information transfer characteristics within reestablished social networks requires a long-term record of behavioral, demographic and poaching-induced mortality data to be collected simultaneously. In elephants, few such data are collected, mostly opportunistically and with little to no spatial and temporal replication. Moreover, record sharing is restricted due to the species' vulnerable conservation status (Chase et al., 2016) or intellectual property concerns (Campbell et al., 2015). Instead, to study the functioning of elephant social networks subject to increased poaching stress, we used a virtual approach, informed by an empirical association record and tested via simulation modeling. Although the technique we used in this research is well established in the field of social network analysis, the novelty of our work is in assessing the functional effect of poaching of the most competent individuals across 100 network replicates. Importantly, the large number of replicates likely represents the variability of demographic and social conditions found in real elephant populations.

To ensure the validity of our assumptions and for replicability, our study was carried out in two stages, first by evaluating one empirical association dataset, and later 100 virtual datasets. Initially, in the empirical portion of our study, we assembled one social network by modifying association data on a free-ranging elephant population inhabiting Amboseli National Park (NP) in Kenya (Archie et al., 2006). Within this context, we determined the maturity level of associating members according to their age (McComb et al., 2001, 2011; Wittemyer and Getz, 2007). We also defined the most socially central network members according to two established network topology metrics, namely betweenness and degree centrality (Farine and Whitehead, 2015; Sueur et al., 2011). Next, we conducted a series of deletion experiments as proxies for poaching events by either incrementally deleting 1) the oldest or the most central group members, or 2) by removing individuals randomly without regard for their age category or centrality scores (Kanngiesser et al., 2011; Manno, 2008). To quantify the change in information transfer characteristics within the deletion-altered networks, we evaluated four global-level indices reflective of network connectedness and its efficiency (Pasquaretta et al., 2014).

To set the empirical results in the context of a large-scale variation in demographic and social dynamics, we generated 100 virtual elephant populations. To simulate social network formation in our virtual populations, we built a non-spatially explicit, individual-based model. The rules of this model were informed by dyadic association trends, within or between groups, evident in the Amboseli dataset (Archie et al., 2006; Wittemyer et al., 2005). Specifically, the

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probability of an association between any given dyad of individuals was based on their kinship and age category. The process of defining centrality metrics, conducting deletion experiments and quantifying network-wide deletion effects was similar to that used in the empirical portion of our study. An experiment unique to the virtual portion of our research involved filtering out the 'weakest' associations prior to deletion experiments to further understand the nature of network response to deletion-induced stress (Granovetter, 1973; VanderWaal et al., 2016). The 'strength of weak links' is a concept commonly used to evaluate if social currency passes through the network by means of repeated socialization within clearly defined social units, or through rare interactions between several distinct units. It is, therefore, a useful approach for examining the fission-fusion dynamics of elephant multi-level society.

To our knowledge, continuous data featuring network reorganization after poaching do not yet exist for elephants in the wild, so building a time-varying model to predict the consequences of poaching-related stress on network functionality would be purely theoretical. Therefore the rules we developed to guide our modeling process depend on a static set of empirical association data. As a result, the predictions we tested were focused on the functional changes to elephant social networks occurring immediately after deletions. We predicted a more pronounced decrease of information transfer characteristics in networks subject to targeted deletions of the oldest, or the most central members, relative to random deletions. In addition, we expected this pattern to increase as a function of increasing deletion proportion, resulting in eventual network breakdown. Lastly, we anticipated that the deletions performed according to age category and the two centrality metrics would produce similar results in the empirical and virtual networks respectively.

We discuss the results of our study in the context of fission-fusion dynamics characterizing elephant sociality and our modeling approach. We also reflect on the potential of data sharing among researchers interested in elephant social behavior and show how collaboration in this field may help us better understand the effects of poaching, or poaching-related stressors, on elephant sociobiology. Lastly, we consider the utility of our work in relation to established conservation and management strategies used in group-living species that are vulnerable or in negative interactions with humans (Krause et al., 2007; Snijders et al., 2017).

Methods

We studied whether poaching of the most influential network members, defined according to their age category- or social centrality-related experience, reduces information transfer characteristics in elephant social networks. To do so, we performed a series of deletion experiments using one social network derived from association data on a free-ranging elephant population and 100 virtual networks mimicking the empirical one. Details of these experiments are described in the following subsections.

Empirical data

Specifying empirical population composition

To gather baseline information about demography and social dynamics characterizing elephant sociality, we considered two dyadic association datasets originally published elsewhere (Archie et al., 2006). During the original data collection, the authors inferred the dyadic associations at two separate social tiers: among individuals within 10 separate, core groups (within core group - WCG) and between 64 core groups (between core group - BCG), where each group was treated as a single social entity. However, we had a different goal — to examine the effect of poaching on social network functioning across the whole population. To represent associations

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that occurred within each core group in the population, we used the unaltered WCG association data according to the following association index (AI) formula: $AI_{i,j} = x_{i,j} / x_{ij} + d + (n - d - x_{i,j})$. In this formula, x_{ij} is the number of times individuals *i* and *j* were seen together; *d* is the number of times neither individual was seen; *n* is the total number of times a group was observed; and by extrapolation ($n - d - x_{ij}$) represents the number of times either individual *i* or *j* was seen. Whereas to express the dynamics occurring between individuals from different core groups, we assembled a dyadic association matrix by combining the WCG and BCG data (Cairns and Schwager, 1987).

Although the original dataset included 64 groups, we could only focus on 10 groups for which both WCG and BCG data were available (labeled AA, CB, DB, EA, EB, FB, JAYA, GB, OA, and PC). To reflect the typical, multi-tier structure of an elephant society (Wittemyer et al., 2005), we aggregated the 10 core groups into eight bond groups [i.e., B1 (core group AA, including 10 individuals), B2 (FB, 6), B3 (EA, 9 and EB, 10), B4 (DB, 4), B5 (CB, 6 and OA, 10), B6 (GB, 11), B7 (PC, 9) and B8 (JAYA, 8)] and three clan groups [i.e., K1 (bond groups B1, B2, B3 and B4), K2 (B5, B6 and B7) and K3 (B8)] using genetically determined relatedness indices and long-term, behavioral associations inferred by the authors ((Archie et al., 2006); Lee P., personal conversation substantiated by the Amboseli Elephant Research Project long-term data, March 2019)).

Inferring population-wide social dynamics and assembling one social network based on empirical association data

We calculated the fraction of all sightings when an individual *i* from core group *G* was seen in that group according to the following formula: $f_{i,G} = average\ n_{i,j,G} / (n_G - average\ d_{i,j,G})$ where the averages are over all the other individuals *j* in group *G*. In this formula, $n_{i,j,G}$ represents the number of times individuals *i* and *j* were seen within group *G*; $d_{i,j,G}$ is the number of times neither individual *i* nor individual *j* was seen within group *G*; and n_G is simply the number of times group *G* was observed. The denominator is, therefore, the average number of times group *G* was observed with either individual *i*, individual *j* or both present, and $f_{i,G}$, which falls in the interval {0,1}, can be thought of as the average fraction of these occasions when they were both present or an index of the overall sociability of individual *i*. This process was repeated for every individual in the population.

Using the information available for the BCG association data, we calculated the fraction of all sightings when group *G* was seen with group *B* according to the following formula: $f_{G,B} = n_{G,B} / (n_G + n_B - n_{G,B})$. Here, $n_{G,B}$ indicates the number of times groups *G* and *B* were seen together; n_G indicates the number of times group *G* was seen without group B; and n_B indicates the number of times group *B* was seen without group G. Thus the denominator is the number of times groups *G* and *B* were seen individually. This process was repeated for every pair of groups in the population and can be thought of as the probability of seeing a given pair of groups together. Finally, we derived a symmetric, weighted matrix consisting of probabilities of dyadic associations between individuals from two different groups, for instance, individuals i_G and a_B from groups *G* and *B* respectively, by using the following formula: $p(i_G, a_B) = f_{i,G} \times f_{a,B} \times f_{G,B}$.

From this empirical association matrix, we constructed a network of associations and quantified two individual-level metrics of centrality, namely betweenness and degree (Farine and Whitehead, 2015). We chose these metrics because they help identify which individuals have the most control over the flow of social currency in the network, at a local and potentially global level. The definitions for these metrics are detailed in Table 1. From this point onward we may refer to these metrics as centrality metrics, and to individuals with high centrality as the

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most central individual. Given our interest in age-related socioecological competence, we also considered the age category as a metric indicative of an individual's ability to hold or pass information. The four age categories we considered included 1) young adults (individuals younger than 20 years old), 2) prime adults (between 20 and 35 years old), 3) mature adults (older than 35 years) and 4) matriarchs (the oldest females in their core groups) (Laws, 1966).

Conducting deletion experiments using modified, empirical social networks

To assess how disturbance affects the functioning of elephant social networks, we carried out a sequence of targeted deletion experiments by selecting 20 percent of the oldest or most central network members (together referred to as 'deletion metrics') and deleting them in a random sequence in increments of two percent. In removing up to 20 percent of members we were motivated by evidence that complex biological networks are organized around a few, highly connected individuals, important for network development and stability (i.e., 20 percent of individuals are involved in 80 percent of associations — (Barabasi and Albert, 1999)). In addition, by eliminating up to a fifth of the most influential network participants we attempted to parallel the level of stress likely imposed on many wild populations by intensive poaching (Hauenstein et al., 2019). We compared the effect of targeted deletions against a null model by also deleting 20 percent of network members randomly (together referred to as 'deletion types') in increments of two percent (collectively referred to as 'deletion proportions'). Each deletion proportion was replicated 1000 times for both deletion types (Puga-Gonzalez et al., 2018). After each deletion proportion, in each deletion type, we quantified a number of network-level indices diagnostic of information transfer.

The indices we used included the clustering coefficient, as well as unweighted and weighted measures of diameter, global efficiency and modularity (Table 1). Each of these heuristics expresses a unique, functional characteristic of a social network, and should change drastically after the deletion experiments we undertook in this research. The clustering coefficient and modularity of a network help discern its connectedness and partitioning, or the pattern and degree to which individuals within and across disparate 'communities' or modules associate with one another. For example, a network with a high clustering coefficient (numerous associations where three individuals associate with each other) and low modularity (numerous associations between individuals from disparate modules) represents a social landscape where many associate with many. The other two indices, namely global efficiency and diameter, help determine the capacity for fast and fault-tolerant information exchange in a network. A network with many, direct connections is more efficient and has a smaller diameter than a network with few such connections. Weighted variants of these indices express relative values, and this perspective matters when network members associate differently with different conspecifics (e.g., more frequent associations with an older individual rather than a juvenile). Weighted modularity highlights the fact that some associations are more consequential in connecting remote modules in a network. Whereas weighted global efficiency and diameter often indicate that particular association pathways have a greater capacity to transfer information across the network in a flexible and timely fashion.

We predicted that relative to random deletions, targeted deletions of the most central and the oldest individuals would result in a marked decrease in clustering coefficient and global efficiency indices, and an increase in diameter and modularity indices. In addition, we anticipated this trend to increase as a function of the proportion of deleted individuals, with eventual network breakdown (Table 1). Finally, we expected that the experiments performed according to all three deletion metrics (i.e., age category, as well as betweenness and degree centrality) would produce similar trends.

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We assessed the mean value of each network-level index as a function of the proportion and type of deletion. Each deletion condition (e.g., targeted deletion of two percent of the most mature network members) was repeated 1000 times — a process theoretically unlimited in the sample size. Therefore, instead of using a comparison of means statistical test informed by a biological distribution, we quantified the difference in the effect size between respective means using Hedge's g test (Table 1S; (Fritz et al., 2012)). We expressed the differences in the mean values between all corresponding conditions using the 95 percent confidence interval. Finally, to assess the relationship between both metrics of centrality and age, per each network-level index evaluated, we used the Pearson correlation test (Table 2S).

Table 1. Definitions of individual-level centrality metrics and network-level indices used in this publication, as well as expected outcomes for network-level indices measured after incremental deletion of the most central individuals in targeted deletions, or in random deletions without consideration for individual centrality scores; [1]shortest path - the path with the minimum number of connections between two most isolated individuals; [2]triplet - three individuals connected by either two or three connections, referred to respectively as open and closed triplets; [3]path weight - the inverse of the weight of a connection, where connections with heaviest weights are equivalent to shortest paths (Archie et al., 2006; Blondel et al., 2008; Ek et al., 2015; Farine and Whitehead, 2015; Iacobucci et al., 2019; Laws, 1966; Li and Schuurmans, 2011; Newman, 2006; Phan et al., 2013; Singh et al., 2015; Sueur et al., 2019; Wey et al., 2008)

Individual-level metric	**Definition**	
Betweenness centrality	the number of shortest paths[1] passing through an individual; high values indicate high social connectedness an individual has	
Degree centrality	the number of connections between an individual and its neighbors; high values indicate that an individual has a high number of social partners in a symmetric social network	
Age category	a segment of the population within a specified range of ages (e.g., a young adult - an individual < 20 years old), used when categorical consideration of age is desired, or when data on absolute age are not available; in the empirical population the age ranges are based on demographic record (i.e., year of birth); in the virtual populations, the ager range distribution was modeled to parallel the empirical distribution	
Network-level index		**Predictions**
Clustering coefficient	the number of triplets[2] divided by the total possible number of triplets; high values indicate a high degree of connectedness across the network and resilience against random network damage	deletion proportion: 0 > 0.2 deletion type: random > targeted
Diameter	the longest path among the shortest path lengths across all dyads; high values indicate slow transfer of information across the network	deletion proportion: 0 < 0.2 deletion type: random < targeted
Diameter weighted	the path with maximum weight[3] among the shortest path lengths across all dyads; high values indicate a slow transfer of information	deletion proportion: 0 < 0.2 deletion type: random < targeted

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Global efficiency	the average of the inverse of the shortest path lengths across rall dyads; high values indicate high network efficiency (and information transfer)	deletion proportion: 0 > 0.2 deletion type: random > targeted
Global efficiency weighted	the inverse of the network's GE; high values indicate high network efficiency (and information transfer)	deletion proportion: 0 > 0.2 deletion type: random > targeted
Modularity	the density of connections within a module, relative to the density of connections between modules; high values indicate a low degree of information transfer and potential breakdown	deletion proportion: 0 < 0.2 deletion type: random < targeted
Modularity weighted	the density of connections within a module in a weighted network relative to the density of connections between modules; high values indicate a low degree of information transfer and potential breakdown	deletion proportion: 0 < 0.2 deletion type: random < targeted

Virtual data

Specifying virtual population composition

To characterize the impact of poaching pressure on the functioning of an assortment of elephant social networks, we generated 100 virtual populations based on empirically determined information about the species' demography and social dynamics (Archie et al., 2006). Based on the trends observed in the Amboseli population, and generally consistent with reports about other free-ranging populations, each virtual population consisted of female individuals in the four, previously detailed age categories (Laws, 1966). We also categorized members of each virtual population into four social tiers (Table 2), namely core, bond, clan and non-kin clan group (Wittemyer et al., 2005). To show the parallels between the virtual and the empirical populations, we present the distribution of the average dyadic association indices across all age categories and social levels in both population types (Figure 1S).

Characterizing association properties in virtual populations

For guidance, we evaluated the distribution of mean association indices in the empirical network, according to age category and kinship, and noticed the following patterns. 1) Individuals of any age category were most likely to associate with conspecifics within their core group. In addition, they were more likely to associate with kin from the same bond group than from other bond groups; then with individuals from their clan; and lastly with non-kin from other clans (Poole et al., 1988). 2) Within a core group, individuals of any age category were more likely to associate with conspecifics from older age categories (Figure 1Sa). Since these patterns are generally consistent with the dynamics described in many elephant populations (genetic relatedness — (Poole et al., 1988; Wittemyer et al., 2009); multi-level structure — (Archie et al., 2006); spatial proximity — (Charif et al., 2005; Esposito, 2008)), we used the resulting association ranges to assemble our virtual populations (Figure 1Sb).

Simulating virtual social networks

To simulate 100 virtual social networks, we used a non-spatial, individual-based model at two social levels, first between core groups and then between pairs of individuals or dyads (Figure 2S). The range of probabilities of association between two groups, or individuals, in this simulation were drawn from a triangular distribution calibrated to mimic observed empirical data.

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At each time step, each core group would have the opportunity to associate with all remaining groups based on the ranges of kinship-based association indices. Once a core group association was determined to occur, then a dyadic association would be assigned according to age-based association ranges. At the end of each time step, the number of times a specific dyad had been observed in an association was updated (i.e., increased by one if the association had occurred, or remained the same otherwise). The simulated networks had started to reach a plateau after 500-time steps (Figure 3S). However, to study how deletion experiments may affect the functioning of networks at different stages of establishment, we stopped the simulation at different stages of network development, focusing on 100-, 200-, 300-, 400- or 500-time steps. From these networks, we quantified betweenness and degree centrality metrics (Table 1) and noted the age category of every participating individual. To compare their structure, we provide graphs of the empirical social network and an example virtual network selected for its similarity in size to the empirical network (Figure 1). Both networks appear similar in terms of their age category makeup and WGS associations. As for differences between them, the empirical network has fewer BCG associations and more uniformly distributed betweenness centrality values.

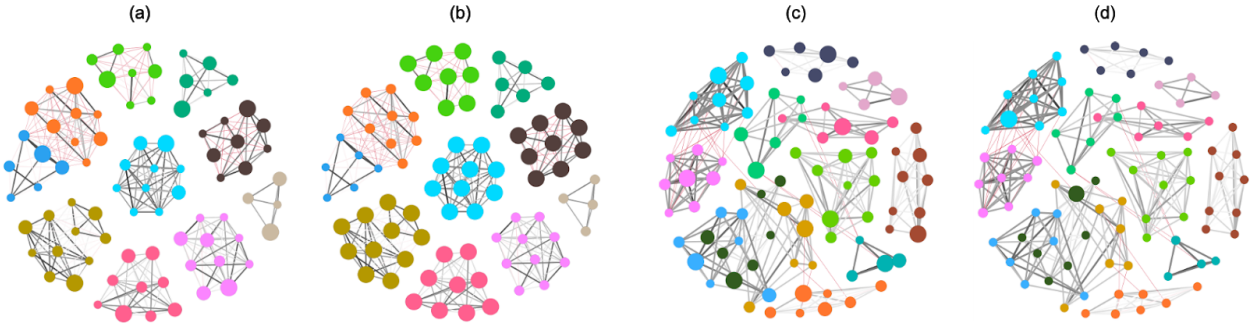

Figure 1. Social network graphs of 1) the empirical population with color partitioning according to a core group, considered from the perspective of either **(a)** age category or **(b)** betweenness centrality; and 2) an example virtual population with color partitioning according to a core group, and either **(c)** age category or **(d)** betweenness centrality; in both population, the nodes are ranked by size where the largest node indicates either the oldest age category or the highest betweenness centrality; the links are ranked according to their relative weight or the number of times a dyad had associated out of the total number of opportunities for association; the color scheme depicting the weight of each link ranges from red (small) to beige (medium) to dark grey (high weight); links with weight less than 5 percent were filtered out for the purpose of visual clarity

Deletion experiments using virtual social networks

To measure if the disappearance of the most socially influential individuals changed the connectedness and efficiency in the virtual populations, we performed a series of targeted and random deletion experiments using 100 virtual networks (Table 2). Individuals were deleted in four percent increments, ranging from zero to 20 percent. In targeted deletions, 20 percent of individuals selected for removal had the highest centrality measures (i.e., individual betweenness and degree centrality) or belonged to the oldest age category. During each random deletion, the same proportion of individuals as in targeted deletions was removed randomly, disregarding their metrics of centrality or their age category. After every deletion proportion, we recalculated the following network-level indices: clustering coefficient, as well as unweighted and weighted diameter, global efficiency and modularity (Table 1). As in the empirical portion of our study, we used the Hedge's g test to quantify the difference in the effect

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size between the means of all network-level indices across 1) the deletion proportion spectrum, 2) deletion type, 3) simulation time step and 4) deletion metric (Table 3S) (Fritz et al., 2012).

Based on preliminary assessment indicating a high degree of resilience to fragmentation after the deletion of the oldest or most central members, even at early stages of network formation (i.e., 100-time steps), we explored if simulated networks would break down when subject to elimination of relatively weak associations. During this process, we manipulated only the most robust networks (i.e., 500-time steps) by filtering out the 'weakest association links'. To do so, we divided the value of each link in the association matrix by the highest link value and eliminated the links with values up to three percent of the highest link in increments of one percent. After each elimination step, we carried out the deletion experiments as described above.

The social network quantification and analysis of both the empirical and virtual data were performed using the R statistical software, version 3.2. (R Core Team 2017). Visualization of the social networks was performed in Gephi software, version 0.9.2 (Bastian et al., 2009).

Table 2. The summary composition of 100 virtual populations with the numbers of clan, bond and core groups, as well as individuals per population; the number of bond and core groups, and individuals per clan; the number of core groups per bond group; and the number of individuals per bond and core groups; the distribution of age categories within each core group was the following: young adults (mean = 2 individuals, min = 1 , max = 5); prime adults (mean = 2, min = 0, max = 7); mature adults (mean = 1, min = 0, max = 3); and matriarchs (mean = 1 , min = 1, max = 1); the composition of the empirical population (i.e., = 10 core groups including a total of n= 83 individuals) evaluated in this study is included as a reference (Archie et al., 2006; Laws, 1966)

Demographic group	Minimum	Maximum	Median	Empirical contrast
Clan groups per population	1	8	5	3
Bond groups per population	1	28	14	8
Core groups per population	5	86	40	10
Bond groups per clan group	1	5	3	4,3,1
Core groups per clan group	1	20	9	5,4,1
Core groups per bond group	1	5	3	1,1,2,1,2,1,1,1
Individuals per population	95	760	350	83
Individuals per clan group	10	175	74	39,36,8
Individuals per bond group	1	45	25	10,6,19,4,16,11,9,8
Individuals per core group	4	15	8	10,6,9,10,4,6,10,11,9,8

Results

Empirical network

Contrary to our expectations, the results of targeted deletion experiments in the empirical portion of our study revealed disparities in almost all network-level indices between the age category versus betweenness and degree centrality deletion metrics (Figures 3 and 4). The indices resulting from age category-specific deletions were never correlated with either those from betweenness- or degree centrality-specific deletions. The latter two were correlated across several indices (Table 2S).

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Overall, results of age category-targeted deletions, along the deletion proportion axis, revealed an increase in network efficiency and resilience to fragmentation (i.e., an increase in clustering coefficient and global efficiency, both weighted and unweighted, as well as a decrease in weighted and unweighted modularity). Whereas indices pointing to the speed of information flow through the network, instead of decreasing markedly, remained unchanged (i.e., nearly constant diameter values, both weighted and unweighted) (Figure 2). Although targeted deletion patterns differed from those observed in random deletions, the effect size statistics estimating the mean difference between them were rather small (Table 1S).

The targeted elimination of individuals with highest values of betweenness (Figure 3) and degree centrality, as a function of deletion proportion, led to a decrease in network efficiency and resilience to breakdown (i.e., a decrease in clustering coefficient and global efficiency, both weighted and unweighted, as well as a decrease in weighted and-unweighted modularity). The speed of information flow decreased noticeably but only when we considered the weights of dyadic associations (i.e. an increase in weighted diameter values, but nearly constant values in unweighted diameter). Given that the results for degree centrality-specific deletions were qualitatively and quantitatively similar to those seen in deletions according to betweenness centrality (Figure 3), we only include the graphical representation of the latter.

Finally, in contrast to age category-related deletions, in betweenness- and degree-specific deletions the effect size statistics estimating the mean difference between targeted and random experiments across most indices evaluated were large and consistent with our expectations (Table 1S).

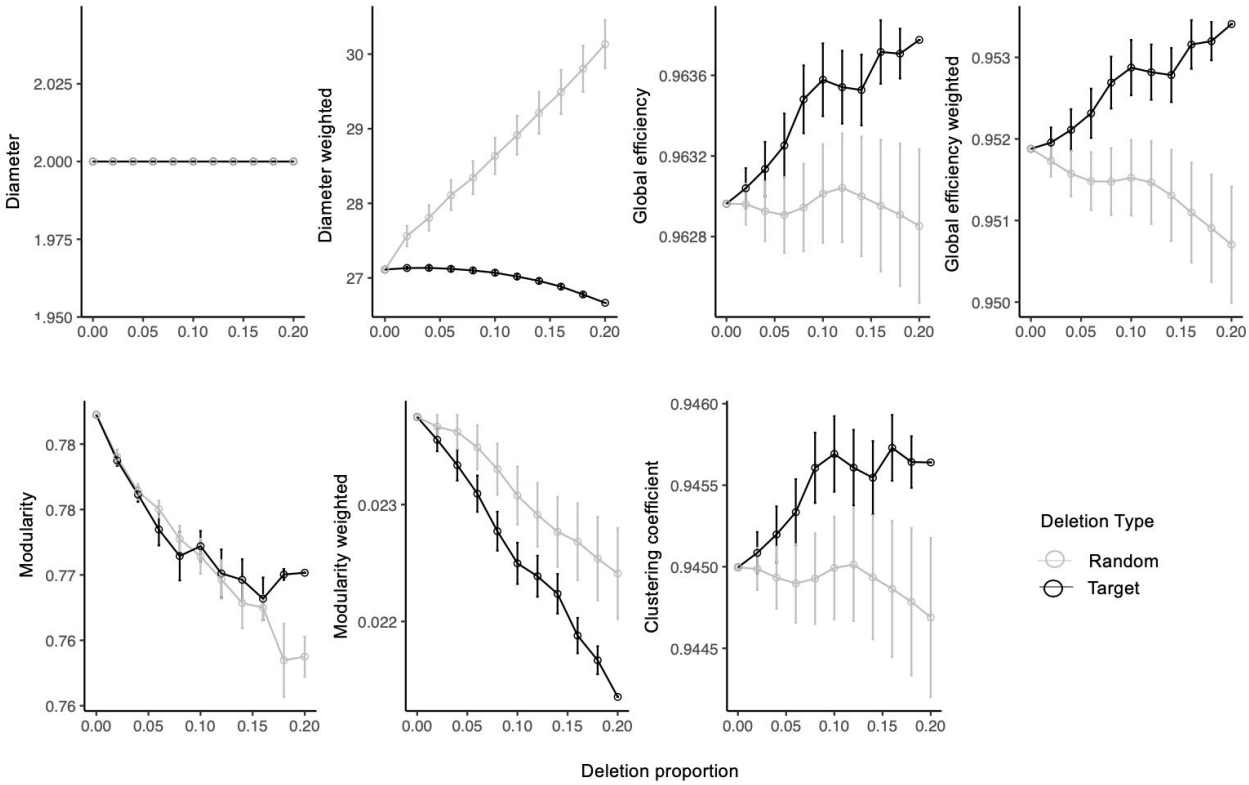

Figure 2. Graphs representing results of deletions according to age category, with the mean value and 95% confidence interval per the following network-level indices: weighted and unweighted diameter, global efficiency and modularity, as well as clustering coefficient, for studied combinations of deletion proportion and type, in the empirical network

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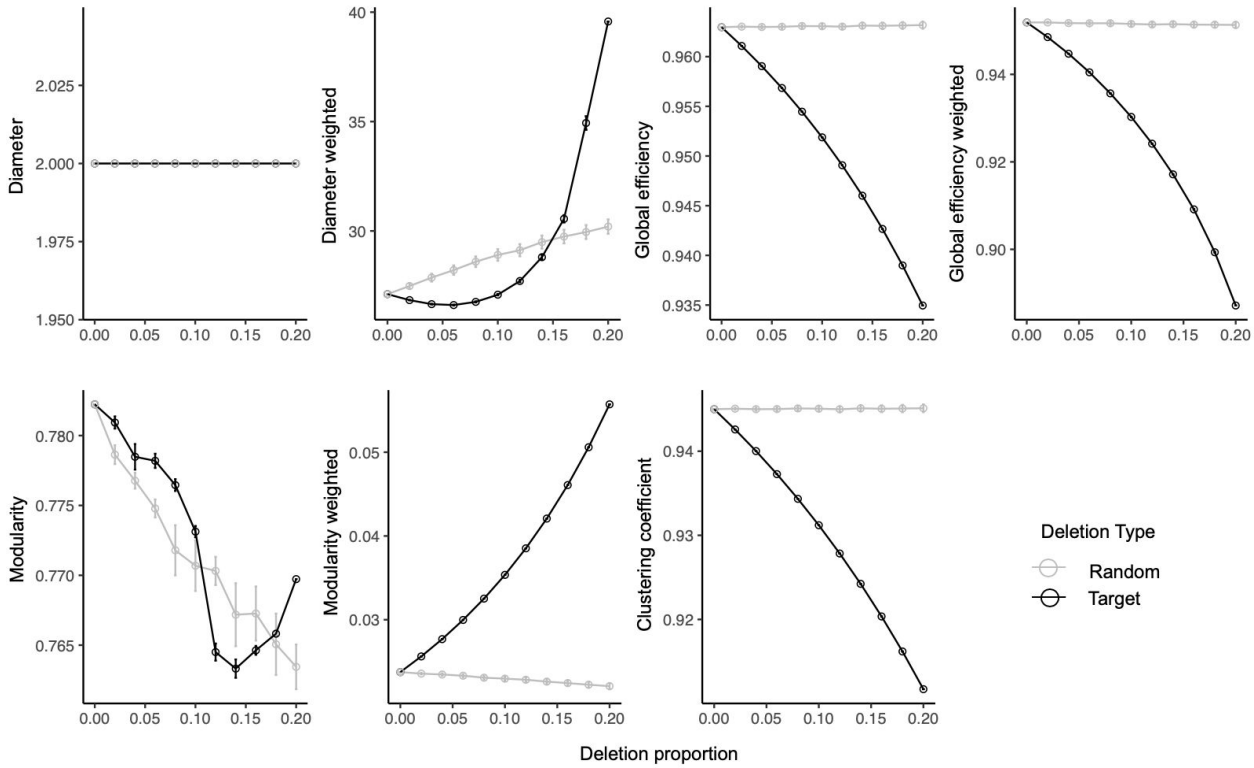

Figure 3. Graphs representing results of deletions according to betweenness centrality, with the mean value and 95% confidence interval per the following network-level indices: weighted and unweighted diameter, global efficiency and modularity, as well as clustering coefficient, for studied combinations of deletion proportion and type, in the empirical network

Virtual networks

The results in the virtual portion of this study were similar to those from the empirical portion (Table 3S). There was a notable difference between deletions performed according to age category versus betweenness and degree centrality in how they impacted all network-level indices.

When age category was the metric of choice, network efficiency and resilience to fragmentation in targeted deletions increased as a function of deletion proportion and simulation time step, but this pattern was not consistent across all indices diagnostic of these two characteristics (i.e., 1) an increase in clustering coefficient and weighted and unweighted global efficiency, as well as a decrease in weighted modularity versus 2) a decrease in unweighted modularity). However, the speed of information transfer did not change meaningfully (i.e. a slight decrease in weighted diameter, but not in unweighted diameter which remained nearly constant). Although the effect size statistics estimating the mean difference between the results of targeted versus random deletions were large, specifically for indices of network efficiency and resilience to breakdown, they were inconsistent with our predictions (Table 3S). In contrast, when targeted deletions were performed according to betweenness and degree centrality, network efficiency and resilience to breakdown decreased notably as a function of both deletion proportion and simulation time step (i.e., a decrease in clustering coefficient and weighted and unweighted global efficiency, as well as an increase in modularity, both weighted and unweighted). The speed of information transfer was also negatively affected by targeted deletions (i.e., an increase in weighted diameter, with unweighted diameter remaining almost constant). Moreover, effect size statistics evaluating the mean difference between targeted and

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random deletions, across all indices, except for the diameter, were large and consistent with our predictions (Table 3S).

Elimination of association links with values up to two or three percent of the highest link led to a breakup into at least two modules in four and 99 percent of the 500-time step networks respectively. Given their 'premature' disruption, these networks were excluded from the subsequent deletion experiments. The results of the deletion experiments performed on the remaining network are summarized in Table 4S. While evaluating these outcomes according to the deletion metric and type, we observed that when age category and degree centrality were the deletion metrics, random deletions caused more damage to the virtual networks than targeted ones. On the other hand, when betweenness centrality was the focus of the deletion experiments, targeted deletions were much more damaging to the virtual network. In addition, we noticed that, although the weakest associations were rather evenly distributed between individuals of various age categories, they occurred most often among individuals from different clans and non-kin clan tiers of social organization (Figure 4S).

Discussion

We characterized the functional properties of simulated elephant social networks subject to poaching-like removal of the most socially competent network members. Besides the topological metrics of social competence (i.e., betweenness and degree centrality), we considered age category — an important determinant of ecological experience and social influence in elephants, and a factor in poaching risk. We anticipated that poaching-like disturbance would 1) perturb network cohesiveness and the efficiency of information transfer, 2) increase as a function of removal intensity leading to eventual network breakdown and 3) lead to similar effects between all three indicators of social competence. By drawing conclusions from the trends seen in empirical and virtual data, we provide a unique perspective on the immediate functional effect of poaching that may be occurring in real elephant populations.

Contrary to our predictions, the results of empirical and virtual poaching simulations conducted according to age category revealed that removal of the oldest group members improved network performance as information nexus and marginally enhanced its robustness against the disappearance of seniors. By contrast, targeted elimination of individuals with the highest metrics of betweenness and degree centrality led to an overall decrease in information transfer efficiency and network connectedness. Although we expect the resulting networks to have fewer channels for frequent associations and information exchange, we did not anticipate the importance of rare associations — a phenomenon often referred to as the 'strength of weak ties'. The crucial role of such association channels in preventing network fragmentation became apparent in deletion experiments performed on filtered virtual networks, particularly when considered from the perspective of individual betweenness centrality. In this context, rare association links among distantly related conspecifics or non-kin appeared most important in preventing network breakdown. However, the age category alone was not an important factor.

Although our results do not support our expectation that age category and established metrics of centrality are equivalent in estimating the value of social competence in network performance, they validate our concern about conflating the structural resilience in poached networks with their functional resilience and the passage of socioecological information. In addition, while the differences between results of the targeted and random deletions are objectively small, the effect size estimates of these differences are large and likely important, particularly in the context of the two topological metrics. Therefore it is prudent to discuss the potential biological drivers of the disparities between deletion experiments per age category versus the established metrics of social centrality.

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One could attribute this discrepancy to age category being an accurate metric of social competence within core elephant groups but less so at the population level. This idea, however, contradicts what we know about the multi-level nature of elephant sociality and its dependence on context-specific engagement by all members in the population, ranging from mother-calf units to distant juvenile kin to dominant adults of different kinship (Murphy et al., 2019; Poole et al., 1988). The high degree of gregariousness and indiscriminate play behavior by relatively young elephants may lead them to interact with a range of conspecifics of different age categories and kinship (Lee and Moss, 2014; Webber and Lee, 2020). This propensity, in turn, should provide the opportunity to gain invaluable social experience without directly relying on close senior kin and maintain the structural resilience of the social networks at the population level (Goldenberg et al., 2016; Wey and Blumstein, 2010). On the other hand, similarly to aging individuals in other highly social species (Almeling et al., 2016; Wrzus et al., 2013), senior elephants may be more selective in their choices of social partners (Archie et al., 2006). Given the wealth of social information and unique ecological experience, the interactions that older elephants have with closely related, younger conspecific during daily group activities must facilitate the transfer of invaluable information such as about resource phenology — a process that cannot occur through bouts of occasional social engagement. Whereas, less frequent interactions with distant kin or non-kin, unlikely to be initiated by young individuals still expanding their social awareness and recall, preserve population-wide affiliations.

This type of network organization where the structural stability and transfer of socioecological experience are mediated by different categories of individuals may be an example of a decentralized system, perhaps to avoid the destabilizing effect of prolonged fission or more stochastic events such as drought-induced mortality or poaching. Otherwise, the networks where the two roles are dependent on one category of individuals may be jeopardized, or result in an outright system collapse, in the event of their death or disappearance. In fact, the proportion and type of depredated or otherwise lost group members, as well as the initial size and connectedness of the networks, may help explain why some poached elephant populations take exceptionally long to recover from member loss (i.e. depauperate fitness in Mikuma NP in Tanzania — (Gobush et al., 2008); tusklessness in Addo Elephant National Park, South Africa — (Whitehouse, 2002)), while other populations recover much quicker (i.e. increasing population numbers after the most recent poaching crisis in East Africa — (Schlossberg et al., 2020)).

Another factor that may have contributed to the diametrical differences between trends in age category deletion experiment vis-à-vis the other two centrality metrics may be intrinsic to our methods. While assembling empirically-based probabilities of dyadic associations to simulate population-level network formation in the empirical and virtual portions of our study, we combined subsets of WCG and BCG data. Due to coding of the original datasets, we were unable to ascertain if the number of times individuals *i* and *j* seen together for some total number of times had been out of the same number of times that individuals *i* and *k* were seen together. To allow for joint treatment of WCG and BCG data, we averaged the number of times each individual was observed in its core group and used the average values to derive a probability matrix of dyadic associations between individuals from different core groups. The averaging of individual sociability may have reduced the variation in association rates between individuals of different age categories. This, in turn, may have led to small effect size in most index estimates of the mean difference between targeted and random deletions performed according to age category. Whereas results of the experiments using the traditional centrality metrics, where most effect size statistics were large, may stem from the fact that these metrics do not depend on weights of specific associations among individuals of different age categories.

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The key to advancing research into the functional consequences of poaching on elephant sociality may depend on 1) simulating a process by which individual elephants transfer either social or ecological information to others while associating and 2) allowing for network reorganization after each poaching event. Simulating such a process may, for instance, be accomplished through incorporating a memory decay function where older, more experienced individuals would have lower memory decay than their younger conspecifics (Bracis et al., 2015; Polansky et al., 2015). In this context, a dyad may have to associate a set minimum number of times for the information to be considered as transferred. Relative to social information passage among distant kin or non-kin, this minimum should be higher for ecological information passage from seniors to their younger, close kin. In addition, allowing a simulated population to age and senesce would allow for acquisition of long-term knowledge and prevent it from ever reaching a completely informed state. In sum, this approach may remedy the potentially overinflated importance of juveniles as information holders on par with their mature conspecifics. However, data to parametrize such a dynamic model are rare and seldom shared due to collection challenges, the vulnerable conservation status of many wild species (i.e. elephants) and the concerns over losing competitive advantage. It is for that reason we encourage more collaborative engagement among scientists with access to empirical data featuring the dynamics of elephant social networks and those pursuing social network data to build modeling tools for hypothesis testing and for forecasting.

Although our focus was on improving the understanding of elephant social behavior in areas where poaching is an ongoing threat, our work may be of use to translocation practitioners working with other vulnerable species (Mengak, 2018; Muller et al., 2019). In the past, translocation specialists put their efforts into the optimization of the demographic (Miller et al., 1999) and genetic (Weeks et al., 2011) properties of target populations, as well as attributes of habitats intended for translocation (McCoy et al., 2014). Recently, more attention has been given to social behavior to improve translocation outcomes (Goldenberg et al., 2019). This trend stems from the empirical realization that in social species the structure of a population and social roles of its members affect individual survival and fitness through interactions with, and learning from, more competent conspecifics (Mueller et al., 2013). For example, in black-tailed prairie dogs, juveniles exhibited poor establishment at new sites if translocated without the most mature network members (Shier, 2006). Besides conservation efforts, our work may also inform wildlife management approaches focused on prescribed culls or trophy hunting (Feber et al., 2020). These approaches continue being used as alleged conservation income generators or means of population control. However, if applied without consideration for the species' sociobiology, they may destabilize social dynamics, exacerbate human-wildlife conflict and lead to decline of wild populations, particularly in vulnerable species. For instance in African lions, hunting of pride males contributes to infanticide by nonresident males or risky movement of distressed lionesses outside of protected areas. By offering an insight into how anthropogenic stressors, such as poaching, affect social cohesiveness and information transfer across social networks, our model may motivate research into other testing platforms, for translocation- or culling-related hypotheses difficult to test in field conditions (van der Ploeg, 2017).

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Data Availability Statement

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The analysis code will be made available upon submission. Empirical association data used in this study may be obtained upon request from the Amboseli Trust for Elephants.

Supplemental Materials

Supplemental information is included in a separate file.

Author contributions

Maggie Wiśniewska conceived the idea and experiments. M. Wiśniewska**,** Ivan Puga-Gonzalez and Cédric Sueur designed and performed the experiments. M. Wiśniewska**,** I. Puga-Gonzalez, C. Sueur and Simon Garnier contributed analysis tools. Phyllis Lee and Cynthia Moss contributed long-term association data. M. Wiśniewska and I. Puga-Gonzalez analyzed the data and prepared figures and tables. C. Sueur served as the Chateaubriand Fellowship host. S. Garnier, I. Puga-Gonzalez, Gareth Russell and C. Sueur served as the Fellowship mentors. M. Wiśniewska wrote this manuscript. All authors reviewed drafts of this manuscript.

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