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Original Article

Fission–fusion processes weaken dominance networks of female Asian elephants in a productive habitat

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Dominance hierarchies are expected to form in response to socioecological pressures and competitive regimes. We assess dominance relationships among free-ranging female Asian elephants (*Elephas maximus*) and compare them with those of African savannah elephants (*Loxodonta africana*), which are known to exhibit age-based dominance hierarchies. Both species are generalist herbivores, however, the Asian population occupies a more productive and climatically stable environment relative to that of the African savannah population. We expected this would lower competition relative to the African taxon, relaxing the need for hierarchy. We tested whether 1) observed dominance interactions among individuals were transitive, 2) outcomes were structured either by age or by social unit according to 4 independent ranking methods, and 3) hierarchy steepness among classes was significant using David's score. *Elephas maximus* displayed less than a third the number of dominance interactions as observed in *L. africana*, with statistically insignificant transitivity among individuals. There was weak but significant order as well as steepness among age-classes but no clear order among social units. *Loxodonta africana* showed significant transitivity among individuals, with significant order and steepness among age-classes and social units. *Elephas maximus* had a greater proportion of age-reversed dominance outcomes than *L. africana*. When dominance hierarchies are weak and nonlinear, signals of dominance may have other functions, such as maintaining social exclusivity. We propose that resource dynamics reinforce differences via influence on fission–fusion processes, which we term “ecological release.” We discuss implications of these findings for conservation and management when animals are spatially constrained.

Key words: ecological release, hierarchies, ranking algorithms, social dominance, socioecology, triads.

BACKGROUND

Competition for resources can lead to self-organizing mechanisms, such as the formation of dominance hierarchies, by which individuals minimize the costs and likelihood of conflicts, making foraging or mate searching more efficient (Sutherland 1996; Hemelrijk 1999; Chase et al. 2002; Bradbury and Vehrencamp 2014). Although reproductive dominance (skew) concerns the distribution of reproduction (Vehrencamp, 1983), social dominance is a system for settling nonreproductive conflicts (Hand 1986; Drews 1993). Although social dominance, as well as reproductive skew among males, may be largely governed by individuals' age- or size-related physical ability to monopolize resources or females (Emlen and Oring 1977; Boehm 1999; Clutton-Brock and Huchard 2013),

other system-specific competitive factors are thought to shape female relationships (Kappeler and van Schaik, 2002; Payne et al. 2003). Here, we focus on the structure of social rank hierarchies among females.

Socioecological models originally derived from studies of ungulates and attempted to explain the ecological factors shaping social systems (Geist 1974; Jarman 2010). Subsequently, they have focused on the interaction of predation, intraspecific competition, and social pressures including infanticide in driving both female gregariousness and their dominance relations, particularly in primates (Wrangham 1980; van Schaik and van Hooft 1983; Sterck and Watts 1997; Isbell and Young 2002; Broom et al. 2009; Koenig et al. 2013). Strong hierarchies are expected where resources are monopolizable, and there is strong competition within and between groups, whereas egalitarian systems are expected when resources are non-monopolizable and thus favor individual dispersal, when strong between-group competition favors philopatric resource defense, or both (Sterck and Watts 1997; Koenig et al. 2013). In this

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context, “despotic” societies are those in which social hierarchies are strongly linear, whereas “egalitarian” ones are those in which linearity is statistically insignificant (Hand 1986; Hemelrijk 1999; de Vries et al. 2006). However, linear hierarchies appear to be commonplace across diverse taxa (Shizuka and McDonald 2012) irrespective of foraging ecology, suggesting other critical factors may be at play. For instance, water rather than forage can be a limiting resource for ungulates and thus a key determinant of movements (Rubenstein 1994; Wittemyer et al. 2008; Loarie et al. 2009b; Shrader et al. 2010; Rubenstein et al. 2015), whereas many nonhuman primates seldom need to drink. Gaps in our understanding of how ecological conditions relate to gregariousness and dominance therefore persist despite decades of effort, particularly with respect to the egalitarian end of the spectrum. Broader taxonomic perspective may provide more general insights into the factors that regulate hierarchy formation than clade-specific treatments (Silk 2007; Clutton-Brock and Janson 2012).

Proboscideans present an interesting clade for exploring socioecological models as they share similarities with both primates and ungulates. Gregariousness among African savannah elephants is favored in their relatively open environments due to the vulnerability of calves to large nonhuman predators and that of adult elephants to humans, which have coevolved as their top predators (Power and Compion 2009; Ben-Dor et al. 2011). Asian elephants, which generally occupy more closed environments with historically few direct predators, generally favor crypticity and smaller, less conspicuous aggregations (de Silva and Wittemyer 2012). Females usually do not face harassment from males except during their estrus periods, which are minimally spaced 2 years apart due to lengthy gestation and nursing periods (de Silva et al. 2013) and therefore favors a roving male strategy. Like female-bonded primates, female African savannah elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) maintain extensive networks of social relationships, typically, though not always, among related matrilineal (Fernando and Lande 2000; Vidya and Sukumar 2005; Wittemyer et al. 2005; Archie et al. 2006b; Wittemyer et al. 2009; de Silva et al. 2011; de Silva and Wittemyer 2012). Both species are generalists capable of consuming a diverse diet alternating among graze, browse, and fruit depending on season and geography (Loarie et al. 2009a; Campos-Arceiz and Blake 2011). Like equids, elephants are hindgut fermenters and thus require a constant source of forage. But unlike many ungulates or primates, their dietary flexibility potentially allows greater behavioral flexibility. Although there is no discernible reproductive skew among females (de Silva et al. 2013; Moss and Poole 1983), African savannah elephants exhibit clear dominance hierarchies, which are age-/size based and weakly nepotistic in apparent contrast to expectations under socioecological models (Archie et al. 2006a; Wittemyer and Getz 2007). Therefore, it seems within- and between-group competition is greater than gross foraging ecology would initially suggest. The nature of dominance relations among Asian elephants has not previously been described, presenting an opportunity for understanding what governs hierarchies among large-bodied, non-territorial, wide-ranging species. Here, we compare social dominance behavior in female Asian and African elephants at the individual and population levels.

Elephas maximus are physically and ecologically similar to *L. africana* as mega-herbivores, with an evolutionary divergence time of approximately 6 million years (Shoshani and Tassy 1996). A naive expectation based only on their generalist feeding habits and morphological similarities would be that hierarchies in Asian elephants should resemble those in African elephants, structured either by age

(correlated with size) or by family unit. However, the Asian species occupies habitats that are generally more mesic than the African savannah species, with more predictable rainfall regimes and fewer nonhuman predators. Patchy, scarce resources, as found in more xeric systems, are hypothesized to impose ecological constraints on group sizes (Rubenstein 1994; Chapman et al. 1995; Faulkes et al. 1997; Rubenstein et al. 2015). If group size and stability increases with ecological productivity and stability, one would hypothesize that Asian elephants could form larger aggregations, with more stable intraspecific bonds and dominance hierarchies than African savannah elephants, given their wetter and more predictable environments. However, group living is itself costly (Alexander 1974) due to factors such as increased local competition and higher risk of exposure to pathogens, which must be compensated for by other benefits. Female Asian elephants, in fact, exhibit very dynamic fission–fusion contact patterns where social affiliates are often split up among smaller aggregations at any given time (de Silva et al. 2011), with less discrete stratification than observed in African populations (de Silva and Wittemyer 2012). The greater fluidity of associations among Asian elephants, coupled with the generally higher availability of resources may make despotic relationships avoidable, unlike among female savannah elephants. First, we test whether the outcomes of dominance interactions among individual females are more linear than expected by chance, then we examine whether they are ordered either by age or by social unit. We compare the results from the 2 elephant species, discussing the insights they offer for understanding what drives dominance hierarchies. Finally, we discuss the practical implications for conservation and management of *E. maximus* in the wild and in captivity.

METHODS

Study site

Road-based field observations of Asian elephants were conducted from January 2007 to December 2012 (805 field days) at Uda Walawe National Park (UWNP), located in south-central Sri Lanka. UWNP receives 1510 mm of annual precipitation on average and surrounds a large man-made reservoir and several smaller water sources situated on the Walawe river. All water sources, including the main reservoir, dry out substantially or completely during the dry seasons, which generally occur from May to September. Elephants aggregate periodically during dry seasons to use the dry reservoir bed for forage as well as remnant water and mud. Mature trees or vines bearing large fruits accessible to elephants are rare or absent within the UWNP, however clusters of seed pods produced by *Bauhinia racemosa* are consumed by elephants. At the time of the study, the protected area contained tall grassland and a dense understory shrub community, with small tracts of open-canopy deciduous forest. Leopards are the largest terrestrial nonhuman predators found in Sri Lanka and occur within the protected area but are not known to pose a threat to elephants.

Data collection

The study population consisted of 286 known adult or subadult females and their calves as well as periodic seasonal occupants. Identities of all known individuals within an observed group were recorded on encounter. All individuals were assigned to 10-year estimated age-classes (table 1 and figure 2 in de Silva et al. 2013). Analyses were based on 1923 h of focal animal sampling (Altmann 1974) as well as behaviors among nonfocal individuals

and group-level responses recorded *ad libitum*. Specific behaviors included all forms of social interaction, feeding, water-associated behavior, wallowing, dust bathing, resting, and movement. The majority of dominance interactions occurred among nonfocal subjects and were therefore recorded with all-occurrence sampling (Altmann 1974). We included indicators of dominance as well as subordination where the former were defined as supplants or displacements at localized resources, gestures (trunk over the head, neck or back of the other individual, Figure 1a), and overtly aggressive behaviors (pushing, chasing, grabbing the tail with the trunk, and attempts to bite or poke the other individual; video at <http://youtu.be/yjgtjiBEWuU>). Indicators of subordination were freezing on being approached or touched, headshaking, turning away when approached, looking over the shoulder, backing or moving away, and avoidance at a resource (such as waiting to approach a water source until it had been vacated by another). If a series of interactions occurred during a particular event, the winners/losers were determined only on conclusion of the event, when individuals or groups moved apart.

We compared dominance interaction patterns among female Asian elephants with those of female African elephants at Samburu and Buffalo Springs National Reserves, Kenya, described by Wittemyer and Getz (2007). This savannah ecosystem receives on average 350 mm of rainfall and is situated along the Ewaso N’giro River. Dominance interactions were observed from 2001 to 2003, during 1161 h of focal monitoring for 206 field days (5.5 h/day on average). Sampling focused on between-group interactions and dominance interactions were also recorded *ad libitum* apart from focal observations. General behavioral classifications were analogous to those described above, but only agonistic interactions were used to determine dominance outcomes.

In the Asian data set, both agonistic and submissive behavior included 75 interactions among 74 females aged 11 to less than 60 years (6 age-classes), distributed among 28 social units. The African data set contained 264 agonistic interactions among 66 females aged 12 to 55 years (5 age-classes) and 34 social units. To control for the difference in the number of observed interactions between the 2 systems, we repeated analyses with a randomly downsampled African data set containing 75 interactions, which then included only 53 individuals. We did not match both the number of interactions and the number of individuals, as this would introduce artificial distortion to density of the *L. africana* network.

Data analysis

Binary dominance matrices were constructed for both species by assigning the value 1 to the individual that won the majority of interactions for any given dyad and 0 to the other. Where dyadic dominance status was not clear (because outcomes were tied), the matrix elements were both assigned 0.5 (this occurred only among African elephants). The matrix included only individuals that were involved in at least 1 dominant/subordinate interaction, excluding the majority of individuals in the population. In addition, many matrix elements were empty where individuals were never observed to interact (see Results).

Because sparsity in matrices distorts or precludes standard tests of linearity (de Vries et al. 2006; Wittemyer and Getz 2006; Shizuka and McDonald 2012), we tested dominance at the individual level using network triad motifs (Wasserman and Faust 1994; Shizuka and McDonald 2012) (Figure 1b). Transitivity is a property of triads whereby $A > B$, $B > C$, and $A > C$. Cyclicity is a property of triads whereby $A > B$, $B > C$, and $C > A$. Multiple transitive relations that are consistent with one another yield an orderly linear hierarchy, whereas cycles disrupt linearity. Order and transitivity are related but not synonymous; all transitive systems are ordered, but a system with consistent cycles, such as the rules governing the rock–paper–scissors game, can be ordered but not transitive. Shizuka and McDonald’s (2012) technique examines the network context of dominance interactions, comparing the observed with the expected proportion of transitive vs. cyclic triads through randomization with the expectation that the greater the degree of transitivity, the greater the linearity within a system. We further extended this technique to incomplete triads. For incomplete, two-edge motifs, we assessed transitivity by comparing the proportion of motifs representative of transitive triads (double dominants or double subordinates) relative to those that could represent either cyclic or transitive triads (pass-along motifs). To generate the expected null distribution for each motif, the winner of each pairwise interaction was randomized such that each individual had equal (0.5) probability of winning. Ten thousand randomized data sets were generated, and the frequencies of each type of motif in the observed and randomized data sets through triad census were assessed using the Statnet package in R v.3.03. Mutual edges (tied relationships) were not considered (Shizuka and McDonald 2012). We rejected the null hypothesis that the observed frequencies of triad motifs could be obtained by chance if the Euclidean distance between the observed set of triad motifs and the centroid (mean) of randomized data sets was greater than or equal to the distance between the centroid and 95% of randomized data sets. We used this rather than the simple chi-square test for goodness of fit in order to avoid making assumptions about the underlying distribution. Tests were performed in R v.3.0.03 (R Development Core Team 2012).

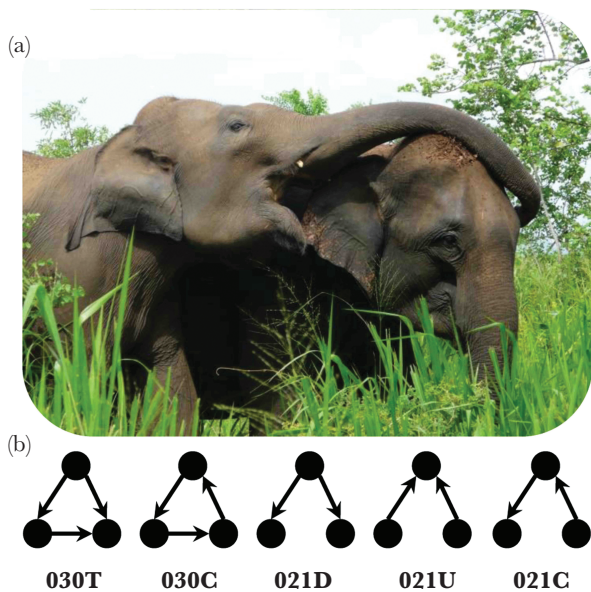


Figure 1
 Dominance behavior and triads. (a) Trunk-over dominance gesture between two adult females. (b) Triad motifs, with MAN labelling scheme (Wasserman and Faust 1994; Shizuka and McDonald 2012). 030T is a transitive triad, whereas 030C is cyclic. Excluding bidirectional outcomes, 021D (double dominant), and 021U (double subordinate) are incomplete triads that would result in transitive triads no matter which way they are completed, whereas 021C (pass-along) could result either in a transitive or cyclic triad with equal probability.

We next tested whether rank orders corresponded to individuals classified by age or social unit. In the African data set “social unit” refers to second-tier units generally understood as families comprising one or more matrilineal units with high rates of association (Wittemyer et al. 2005; Archie et al. 2006b; Wittemyer et al. 2009). In the Asian data set, “social unit” refers to sets of individuals that are statistically clustered together based on their multiyear association rates. Such units also likely consist of maternal relatives (Fernando and Lande 2000; de Silva et al. 2011; de Silva and Wittemyer 2012). The triad-motif test could not be used because there are far fewer classes than there are individuals; the test would therefore have little statistical power. Instead, we aggregated outcomes by class, such that each cell in the dominance matrix represented the sum total of wins by individuals of one class against individuals of another (Supplementary Figure S1). We refer to these as matrices “collapsed” by class. Note that although the original dominance matrices were binary, the collapsed matrices are not, a condition necessary for statistical testing (discussed below). Also, as interactions between members of the same class were discarded in the process of collapsing, the total remaining number of interactions among classes differed between age- and social unit-collapsed matrices.

We assessed hierarchy linearity among classes with h' , the modified version of Landau's h (de Vries 1995). We then tested rank differentiation among classes (age or social unit) by treating them statistically as individuals. We calculated David's score as a basis for evaluating steepness, a measure of the degree of rank differentiation among classes (David 1987, 1988; de Vries et al. 2006). We tested the significance of hierarchy steepness through randomization (de Vries et al. 2006), using a binomial distribution of dyadic winning proportions together with a correction for chance (detailed in Supplementary Appendix 2).

We further devised an alternative statistical test to determine whether there was significant ordering among classes. We reordered the collapsed matrices using 4 different ranking methods: the I&SI method (Schmid and de Vries 2013), the Batchelder–Bershad–Simpson index (henceforth BBS, Jameson et al. 1999), Colley's Rating Method (henceforth CRM, Langville and Meyer 2012), and the Park–Newman Index (henceforth PNI, Park and Newman 2005). The 4 different algorithms were employed to ensure robustness of results. We then calculated the sum-of-reversals (SOR), that is, the sum of entries that fall below the diagonal under a particular order (Supplementary Figure S1). This quantity is the total number of directional interactions that are opposite the overall rank order. The more ordered a system, the fewer reversals it should have. We rejected the null hypothesis that a data set is ordered by class if the observed SOR was less than the SOR obtained in randomized data sets with a one-sided significance threshold after Bonferroni correction for multiple testing set at 0.00625. Henceforth, we shall refer to this test as the sum-of-reversals test or SOR test. For any particular collapsed dominance matrix—observed or randomized—these ranking methods might yield multiple equivalent orderings of classes. In such cases, we calculated the mean SOR from a sample of equivalent orders (Supplementary Appendix 1). To test whether the dominance outcomes we observed were more orderly than expected by chance, we compared the observed SOR for a particular matrix with the SORs obtained through 10 000 randomized data sets, where the SOR values were calculated under each of the 4 algorithms. Linearity, steepness, and SOR tests were performed in Excel using an extended version of DomiCalc (Schmid and de Vries 2013), which is included in a supplementary file. All P values are one tailed.

RESULTS

The distribution of age-classes that participated in dominance interactions was significantly different between the two systems (Figure 2), with the *L. africana* data set lacking individuals in the 60 years and older age-class due to low survivorship in older age-classes (Wittemyer et al. 2013). The direction of outcomes with respect to the age-class of interacting individuals was significantly different between the two populations (Table 1), with the Asian population showing a higher proportion of age-reversed wins (Table 1, Figure 3).

Ordering by individual

The observed frequencies of each triad motif (Table 2) in the Asian data set were no different than expected by chance (randomization test using Euclidean distance among means, $P = 0.64$), whereas they were significantly different for the African dataset ($P < 0.001$). This result was upheld even for the downsampled African data set and driven primarily by the frequency of double-dominant (more common than expected, transitive) and pass-along (less common than expected, could be either transitive or cyclic) triads, whereas both the Asian and African data sets were similar with respect to double-subordinate motifs (Figure 4).

Ordering by class

None of the data sets showed significant linearity either by age or by social unit when assessed with h' . However, steepness (assessed using David's score corrected for chance) collapsed by age and social unit for the Asian data set were both significantly greater than expected (one-sided $\alpha = 0.025$; $P_{\text{age}} < 0.005$, $P_{\text{social}} < 0.01$; Supplementary Table S1). The African data sets were likewise significantly steeper than expected by chance for age and social unit ($P < 0.0001$, Supplementary Table S1). This also held true for the downsampled data set ($P_{\text{age}} < 0.0001$, $P_{\text{social}} < 0.001$).

For the Asian data set, there was agreement among all 4 ranking methods that dominance outcomes were significantly ordered by age ($\text{SOR}_{\text{obs}} < \text{SOR}_{\text{exp}}$, $P < 0.00625$ α -threshold after Bonferroni correction for multiple testing), whereas significant ordering by social unit was indicated by 2 of the 4 ranking methods employed (Figure 5, BBS and I&SI: $P = 0.0001$; PNI: $P = 0.0390$; CRM:

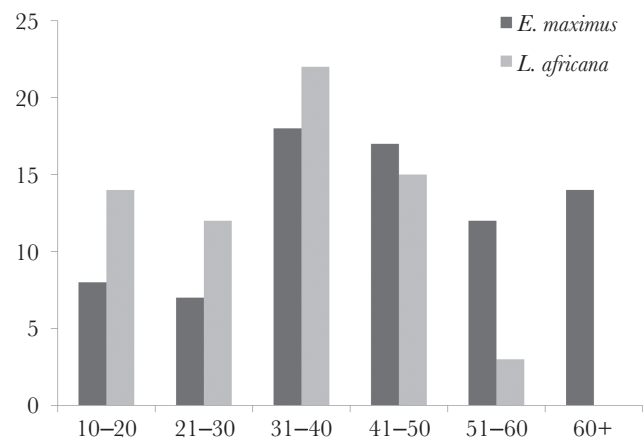


Figure 2

Distribution of age-classes. The distribution of ages among females who participated in at least one dominance interaction ($N = 74$ Asian, 66 African) were significantly different ($\chi^2 = 32.968$, degree of freedom = 5, $P < 0.001$).

$P = 0.0091$). In contrast, the full African data set showed significant ordering both by age and by social unit across all ranking methods ($P < 0.0001$; Figure 5). The downsampled African data set was consistent with these results when ranked by age ($P < 0.0001$), but only half the ranking methods showed significant order by social unit (BBS: $P = 0.0010$; CRM: $P = 0.0007$; PNI: $P = 0.0145$; I&SI: $P = 0.0218$).

DISCUSSION

Many ungulates as well as primates do not readily conform to a simplistic socioecological model in which gross foraging ecology acts as a proxy for the degree of competition individuals experience. Linear dominance hierarchies are commonly observed even among species feeding on seemingly uniform and widely dispersed resources and do not have a clear relationship with levels of agonism, presenting a challenge for socioecological models (Thierry 2008; Koenig and Borries 2009; Clutton-Brock and Janson 2012; Wheeler et al. 2013). Despite their generalist diet, African savannah elephants exhibit strong linear dominance hierarchies within and between social groups where older, taller individuals are more dominant, likely because resource competition among individuals and groups is in fact salient (Archie et al. 2006a; Wittemyer and Getz 2007). However, because group living is inherently costly, one would expect the tendency to fission would be stronger under

ecological conditions that make dispersal easier. In such situations, it would be difficult to exert and maintain strict hierarchies. We tested whether similar patterns hold for an Asian elephant population that shares analogous feeding habits but occupies an environment where forage, water availability, and seasonal predictability of rainfall is greater and where large nonhuman predators are absent.

The most striking quantitative and qualitative difference between the taxa at the individual level was the rarity of transitive motifs within the Asian population (Figure 4). Rather, they demonstrated a distribution of triadic motifs that could not be statistically distinguished from chance. In contrast, the African population exhibited triad motifs consistent with transitivity, as expected based on prior studies (Archie et al. 2006a; Wittemyer and Getz 2007), a result robust to downsampling which matched sample sizes in the 2 data sets. This finding was driven by the disproportionately frequent occurrence of double-dominant motifs (which are inevitably transitive on completion) and relatively infrequent occurrence of pass-along motifs (which could result either in cyclic or in transitive triads) in the African population (Table 2; Figure 4). In contrast, the Asian population shows a disproportionately greater occurrence of pass-along motifs, highlighting the greater potential for cyclic relationships in the Asian system than in the African. Curiously, although double-subordinate motifs are analytically equivalent to double-dominant motifs because they also resolve only in transitive triads, they are not statistically overrepresented. A similar asymmetry between these motifs is observed in the dominance hierarchies of *Diacamma* worker ants (Shimoji et al. 2014), suggesting a widespread pattern in the way that hierarchy is behaviorally expressed that may merit further study.

We tested orderliness beyond the individual level by aggregating individuals into classes by age or social unit. The classical test of linearity, h' , was not significant in data sets collapsed by age or social unit for either species despite expectations to the contrary for the African system. However, outcomes were significantly steep both by age and by social unit, in both taxa. We explored this further by devising the SOR test, which compares the number of reversals observed against the number of reversals expected by chance when

Table 1
Direction of dominance by age

	Dominant older	Dominant younger	Dominant equal age-class
<i>Elephas maximus</i>	42 (56%)	14 (19%)	19 (25%)
<i>Loxodonta africana</i>	157 (59%)	20 (8%)	87 (33%)
<i>L. africana</i> downsampled	47 (65%)	5 (7%)	23 (30%)

The frequency of wins by older individuals vs. younger individuals or those in the same age-class (in 10-year bins, Figure 2) was significantly different between the Asian and African data sets ($\chi^2 = 13.652$, $df = 2$, $P < 0.01$).

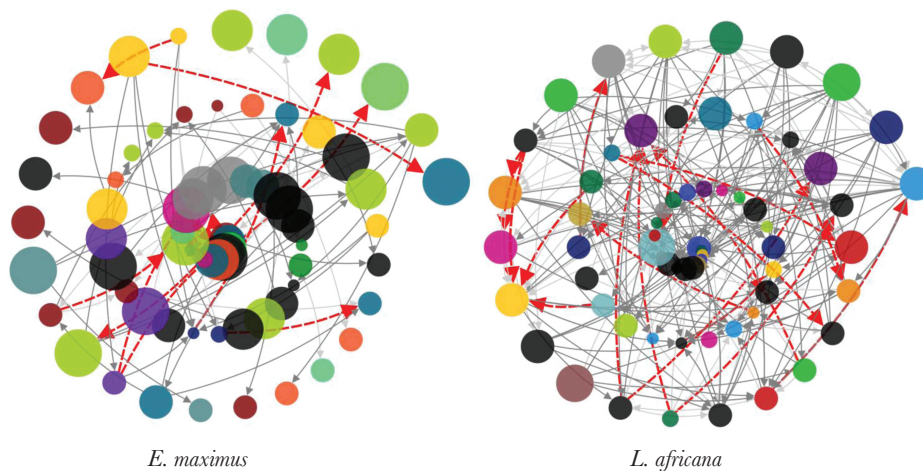


Figure 3
Dominance networks of *Elephas maximus* and *Loxodonta africana*. Nodes are sized by age-class and colored by social unit (black nodes are singletons belonging to units from which no other members were observed in a dominance interaction during the study). Graphs were generated on NodeXL, where nodes spiral outward in the order of increasing out-degree (i.e., nodes with more wins are more peripheral). Dark edges signify interactions in which the dominant was older, light edges signify equal age, and dashed red edges signify reversals. Decreasing node size toward the center in *L. Africana* indicates greater order by age relative to *E. maximus*. *Elephas maximus* exhibit a sparser network with more age irregularities than *L. africana* despite a greater number of total observation hours and an older age structure.

Table 2
Triad census results for known females ($N = 74$ Asian, 66 African)

	021D	021U	021C	030T	030C
	Double dominant	Double subordinate	Pass-along	Transitive	Cyclic
<i>Elephas maximus</i>	39 (28%)	32 (23%)	62 (45%)	5 (4%)	1 (<1%)
<i>Loxodonta africana</i>	512 (37%)	302 (22%)	468 (34%)	91 (7%)	2 (<1%)
<i>L. africana</i> downsampled	85 (41%)	42 (20%)	77 (37%)	2 (1%)	0

Percentages reflect proportion of each motif among these 5 motifs, disregarding others such as null triads (no edges), singles, and motifs with mutual outcomes. Note that the number of transitive as well as cyclic motifs are low simply because there are fewer complete triads than incomplete ones. However, the number of pass-along and cyclic motifs together are disproportionately greater relative to the other motifs in the Asian data set in contrast to the African.

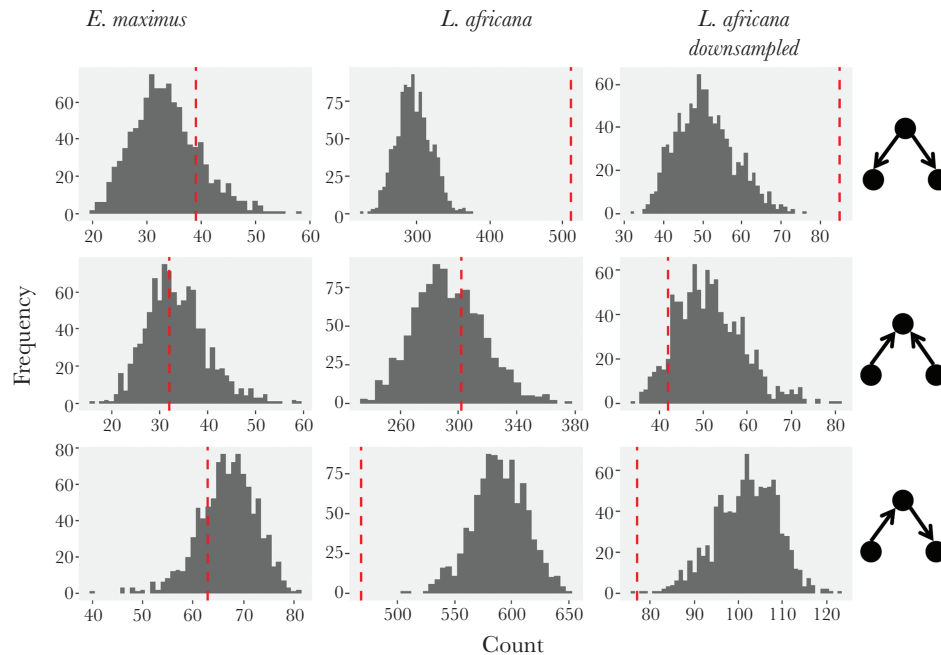


Figure 4

Frequency of triad motifs in observed vs. randomized data sets. The ordinate is the number of times the specified motif appears in a given data set, the abscissa is the number of randomized data sets in which that particular count occurs. The dashed line shows the actual count for each motif observed in respective data sets (see Table 2). Complete triads were rare in the observed data and are therefore not presented.

wins and losses are arranged using ranking algorithms. Multiple ranking indices were in agreement that there is significant ordering by age in both populations, but there was a greater proportion of age-reversed wins in the Asian population (Table 1). Individuals in the oldest age-class are missing in the African sample (Figure 1), unlike in the Asian. One might ask whether observed differences may be explained simply by the difference in the age structure of the populations, as weaker individuals in the oldest age-classes could be dominated by younger females who are in better physical condition (Figure 3). Given the strong correlation between age and dominance in the African system (Wittemyer and Getz 2007), the presence of more older individuals should have reinforced a clearer hierarchy, the opposite of what is seen in the Asian population. In addition, strict order by age was also found in the Amboseli National Park population of African elephants, which did contain individuals in the oldest age-classes (Archie et al. 2006a).

Ordering by social unit was not well-evidenced in the Asian population in contrast to the African, even though more than half of all the observed interactions occurred between individuals belonging to different social units. The artificially downsampled data set

for the African population shows similar results as the Asian, thus results are driven at least in part by the low overall rate of interaction. Archie et al. (2006a) also found that at Amboseli National Park, hierarchies within families were ordered by age rather than matriline, making it a more important determinant of rank. Moreover, in the Asian system, individuals from completely different social units seldom mingled into larger aggregations as they did in the African system, even when range use was highly overlapping (de Silva et al. 2011; de Silva and Wittemyer 2012). On the majority of occasions when individuals from different social units passed by within detectable proximity of one another, they either ignored or avoided each other entirely. Therefore, it is unlikely that null relations between social units could be resolved for truly biological rather than statistical reasons.

Although social dominance is typically assessed in terms of agonism (Francis 1988; Drews 1993; Forkman and Haskell 2004), aggressive behavior need not accompany rank establishment or enforcement even where such exists (Hand 1986; Francis 1988; Drews 1993), and conversely, egalitarianism does not imply an absence of aggression (Strier et al. 2002; Strier, 2007). The

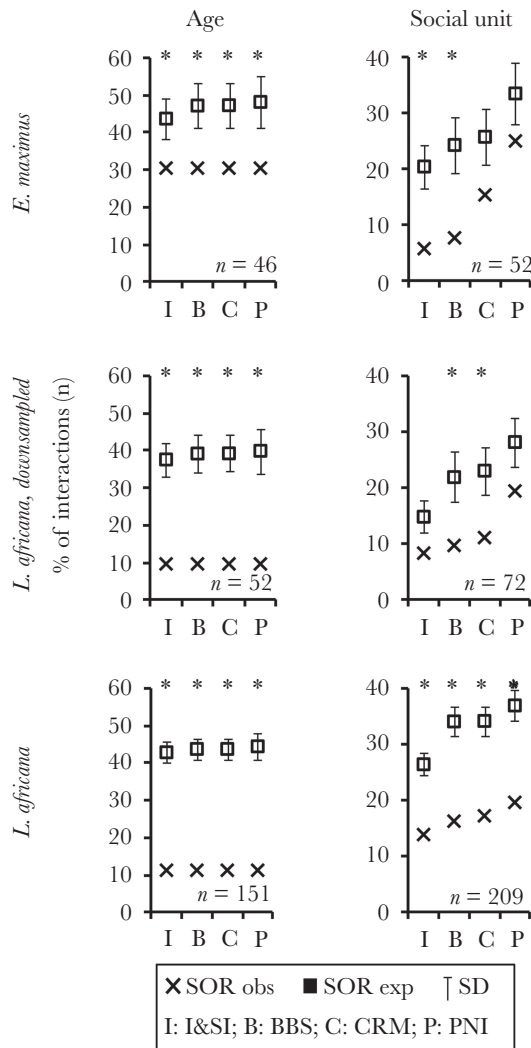


Figure 5 Ordering by age and social unit using 4 ranking methods. Expected SOR values are averaged over all randomizations, with error bars showing standard deviations. “SOR obs” are the observed values, “SOR exp” are the expected values based on 10 000 randomizations. Asterisks indicate significant differences after Bonferroni correction (Asian: $P < 0.00625$; African: $P < 0.0001$). n : number of between-class dominance interactions.

relationship between levels of agonism, hierarchical structure and foraging ecology is therefore not straightforward (Wheeler et al. 2013). Systems characterized as “tolerant” manifest clear dominance hierarchies despite very low levels of aggression, as exemplified by equids (Rubenstein 1994). Among feral horses this is quantified as 0.1 aggressive interaction per hour of observation, which is still much greater than what was observed in the Asian elephants. The Asian data set included all possible behavioral indicators of dominance or submissiveness, not merely aggression, and yet was far sparser than the African data set, which was based solely on aggression. This was not due to a difference in total observation effort, as the Asian data comprised a greater number of observation hours. To obtain a similar number of interactions in the Asian population would require more than 10 years of data collection (Supplementary Figure S2), during which time, some of the subjects will have died. Because association rates among social companions in Asian elephants are generally much lower than among

African elephants, and interactions between individuals belonging to different social units are even less frequent, the lack of rank signaling among Asian elephants seems unlikely to conceal a strong latent hierarchy. The more mechanistically plausible and parsimonious interpretation of these observations is that rarity of dominance interactions reflects a much weaker hierarchy than that of African savannah elephants.

Social and ecological drivers

The maintenance of dominance hierarchies is costly, having consequences for the health and fitness of individuals (Sapolsky 2005). Therefore, one expects them to be favored in the face of competition when they obviate costly conflicts among individuals who repeatedly encounter one another. Where dominance hierarchies reduce overt conflicts, they are likely of greater importance among those who have the opportunity to interact more frequently. For instance, at Amboseli National Park, Archie et al. (2006a) found that agonistic interactions occurred more often among females with higher association indices. Conversely, the ability to segregate spatially may remove or lessen the need for rigid hierarchies, whether among individuals in the same or different social groups (Hand 1986; Drews 1993). Spatial segregation reduces the ability to both to signal and appropriately respond to rank conflicts (Ang and Manica 2010). Scramble competition can occur where resource patches are inadequate to support stable aggregations of conspecifics, or when resources are plentiful in the absence of other factors favoring stable groups (such as predation or sexual harassment). If the former constitutes ecological “constraints,” the latter may be thought of as ecological “release.”

On African savannahs, the dispersed and temporally dynamic nature of resource availability (e.g., fresh forage and water), as well as the presence of predators, enhances the decision-making and resource acquisition value of older, experienced individuals, providing opportunities for exerting dominance as well as leadership (McComb et al. 2001; Foley et al. 2008; Wittemyer et al. 2008; McComb et al. 2011). When errors are less costly, there is less need to rely on knowledgeable individuals, reducing the value of age. Because the protected Asian site has greater absolute rainfall with more predictable seasonality than the African site, no nonhuman predators that pose a serious threat to elephants, and very little poaching, the risks of movement, and dispersal in the Asian site are likely lower relative to the African. Thus, female Asian elephants in this population even with very young calves need not tolerate being socially subordinate and can afford to loosen maternal ties, resulting in the highly flexible contact patterns and low association rates observed. Indeed, solitary adult females were observed far more frequently than at the African site (de Silva and Wittemyer 2012). It follows that this Asian population also lacks clear behavioral (as opposed to genetic) matriarchs, by definition the oldest and most dominant individuals (Archie et al. 2006a; Wittemyer and Getz 2007), perhaps because matriarchal “leadership/despotism” cannot be exerted. The general implications of these observations are that the evolution of strong centralized leadership is not favored under environmental conditions that enable spatiotemporal avoidance and dynamic group membership, reducing competition and impeding hierarchy formation, which we term ecological release.

Encounters among unfamiliar individuals may nevertheless occur even in systems where scramble competition predominates. Among social foragers with non-territorial fission–fusion dynamics, dominance behaviors may be co-opted to enforce social group membership rather than social rank, excluding potential competitors

from one's vicinity whenever direct conflicts arise. If such exclusion is not arbitrary but rather expressing preference for matrilineal kin (Fernando and Lande 2000; Vidya and Sukumar 2005), it is a form of nepotism (Wittemyer and Getz 2007), even if not embedded in a classical hierarchy (Sterck and Watts 1997). Dominance signals in Asian elephants (Figure 2a) may serve this secondary purpose. Although Asian elephants show low rates of aggression among familiar individuals, conflicts including physical aggression can occur especially when individuals from completely unfamiliar units intersect (video at <http://youtu.be/60KxqnVV424>). Although associations among nonrelatives due to early socialization do occur in the Asian population (SdS, unpublished data), and likewise also in African savannah elephants under disturbed conditions (Goldenberg et al. 2016; Pinter-Wollman et al. 2009; Wittemyer et al. 2009), such cases likely represent substitute bonds where immediate kin are unavailable rather than the norm. Aggregations of elephants are therefore fluid, semipermeable, but not amorphous entities, rendering ambiguous such concepts as "group" and "group size" that have been so central to our understanding of social evolution (Robbins et al. 1991; Silk 2007; Snaith and Chapman 2007). Asian elephants possibly share some similarities with human hunter-gatherer societies in which flexible band membership is also a hallmark (Aureli et al. 2008; Moffett 2013; Pennisi 2014) and is a factor thought to inhibit hierarchy formation (Turnbull 1965; Boehm 1999). This suggests that fission–fusion spatial and social dynamics (Aureli et al. 2008) may be key mechanisms behind the development and maintenance of nonhierarchical systems, beyond the absolute abundance or distribution of resources. Although the terms "dominance" and "hierarchy" are often linked together, dominance behavior need not manifest in linear hierarchies. The results of this study suggest dominance hierarchies may be viewed as falling along a gradient of strong to weak ordering, concurrent with the degree of fission–fusion expressed, rather than in terms of despotic/egalitarian or linear/nonlinear dichotomies. We propose that, in appropriately paired comparisons of sister taxa (or multiple subpopulations of the same species), one should expect to see that systems with greater levels of competition should also manifest greater levels of order than expected by chance, whether or not such order is statistically linear.

Conservation and management

Because Asian elephants have substantial range requirements, occupy countries with some of the densest human populations, as well as some of the most threatened ecosystems, this species is extremely vulnerable to range constriction and fragmentation. They are consequently also the focus of intensive management and impacted by development activities. Typically, behavioral considerations do not feature prominently in such decisions. These findings may nevertheless be important for interpreting results of prior management actions and forestalling negative impacts of future interventions.

In particular, practices altering the social organization of populations such as translocations, drives, or roundups (used to move elephants into designated protected areas), may be detrimental (Lahiri-Choudhury 1993; Fernando et al. 2012). It has been assumed that social units consist of only those individuals observed together at any given time and that capturing putative "matriarchs" will draw other family members, ensuring their capture or cooperation (Lahiri-Choudhury 1993). Our findings do not support such assumptions. Such displacements would not only disrupt long-term social bonds because social affiliates may not be close together at

any given time but result in difficulties for the displaced individuals if habitats are already saturated with other elephants. Forced displacement could result in crowding and competition, with likely disproportionately negative impacts to the displaced individuals. Preserving remaining range and its connectivity should be the top priority; behavioral studies could be usefully integrated alongside such interventions and factored into management decisions. Likewise, allowing sufficient space for avoidance will be essential for reducing conflict among individuals confined to captivity.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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