

1 **Fission-fusion Processes Weaken Dominance Networks of Female Asian Elephants In A**  
2 **Productive Habitat**

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14  
15 **Abstract**

16  
17 Dominance hierarchies are expected to form in response to socioecological pressures and  
18 competitive regimes. We assess dominance relationships among free-ranging female Asian  
19 elephants (*Elephas maximus*) and compare them to those of African savannah elephants  
20 (*Loxodonta africana*), which are known to exhibit age-based dominance hierarchies. Both  
21 species are generalist herbivores, however, the Asian population occupies a more productive and  
22 climatically stable environment relative to that of the African savannah population. We expected  
23 this would lower competition relative to the African taxon, relaxing the need for hierarchy. We  
24 tested: 1) whether observed dominance interactions among individuals were transitive 2) whether  
25 outcomes were structured either by age or social unit according to four independent ranking  
26 methods and 3) whether hierarchy steepness among classes was significant using David's Score.  
27 *E. maximus* displayed less than a third the number of dominance interactions as observed in *L.*  
28 *africana*, with statistically insignificant transitivity among individuals. There was weak but  
29 significant order as well as steepness among age-classes, but no clear order among social units.

30 *L. africana* showed significant transitivity among individuals, with significant order and  
31 steepness among age-classes and social units. *E. maximus* had a greater proportion of age-  
32 reversed dominance outcomes than *L. africana*. When dominance hierarchies are weak and  
33 nonlinear, signals of dominance may have other functions, such as maintaining social  
34 exclusivity. We propose that resource dynamics reinforce differences via influence on fission-  
35 fusion processes, which we term “ecological release.” We discuss implications of these findings  
36 for conservation and management when animals are spatially constrained.

37

38 Keywords: Hierarchies, ranking algorithms, socioecology, social dominance, triads, ecological  
39 release

40

## 41 **Background**

42

43 Competition for resources can lead to self-organizing mechanisms, such as the formation  
44 of dominance hierarchies, by which individuals minimize the costs and likelihood of conflicts,  
45 making foraging or mate searching more efficient (Sutherland 1996; Hemelrijk 1999; Chase et  
46 al. 2002; Bradbury & Vehrencamp 2014). While reproductive dominance (skew), concerns the  
47 distribution of reproduction (Vehrencamp, 1983), social dominance is a system for settling non-  
48 reproductive conflicts (Hand 1986; Drews 1993). While social dominance as well as  
49 reproductive skew among males may be largely governed by individuals' age- or size-related  
50 physical ability to monopolize resources or females (Emlen & Oring 1977; Boehm 1999;  
51 Clutton-Brock & Huchard 2013), other system-specific competitive factors are thought to shape  
52 female relationships (Kappeler & van Schaik, 2002; Payne et al. 2003). Here we focus on the  
53 structure of social rank hierarchies among females.

54

55 Socioecological models originally derived from studies of ungulates, and attempted to  
56 explain the ecological factors shaping social systems (Geist 1974; Jarman 2010). Subsequently,  
57 they have focused on the interaction of predation, intra-specific competition, and social pressures  
58 including infanticide in driving both female gregariousness as well as their dominance relations,  
59 particularly in primates (Broom et al. 2009; Isbell & Young, 2002; Koenig et al. 2013; Sterck &  
60 Watts, 1997; van Schaik & van Hooff, 1983; Wrangham, 1980). Strong hierarchies are expected  
61 where resources are monopolizable and there is strong competition within and between groups  
62 while egalitarian systems are expected when resources are non-monopolizeable and thus favor  
63 individual dispersal, when strong between-group competition favors philopatric resource

64 defense, or both (Koenig et al., 2013; Sterck & Watts, 1997). In this context, ‘despotic’ societies  
65 are those in which social hierarchies are strongly linear, whereas ‘egalitarian’ ones are those in  
66 which linearity is statistically insignificant (de Vries et al. 2006; Hand, 1986; Hemelrijk, 1999).  
67 However, linear hierarchies appear to be commonplace across diverse taxa (Shizuka &  
68 McDonald, 2012) irrespective of foraging ecology, suggesting other critical factors may be at  
69 play. For instance, water rather than forage can be a limiting resource for ungulates and thus a  
70 key determinant of movements (Rubenstein 1994; Wittemyer et al. 2008; Loarie et al. 2009a;  
71 Shrader et al. 2010; Rubenstein et al. 2015), whereas many nonhuman primates seldom need to  
72 drink. Gaps in our understanding of how ecological conditions relate to gregariousness and  
73 dominance therefore persist despite decades of effort, particularly with respect to the egalitarian  
74 end of the spectrum. Broader taxonomic perspective may provide more general insights into the  
75 factors that regulate hierarchy formation than clade-specific treatments (Silk 2007; Clutton-  
76 Brock & Janson 2012).

78 Proboscideans present an interesting clade for exploring socioecological models as they  
79 share similarities with both primates and ungulates. Gregariousness among African savannah  
80 elephants is favored in their relatively open environments due to the vulnerability of calves to  
81 large nonhuman predators and that of adult elephants to humans, which have co-evolved as their  
82 top predators (Power & Compion 2009; Ben-Dor et al. 2011). Asian elephants, which generally  
83 occupy more closed environments with historically few direct predators, generally favor  
84 crypticity and smaller, less conspicuous aggregations (de Silva & Wittemyer 2012). Females  
85 usually do not face harassment from males except during their oestrus periods, which are  
86 minimally spaced two years apart due to lengthy gestation and nursing periods (de Silva et al.

87 2013) and therefore favors a roving male strategy. Like female-bonded primates, female African  
88 savannah elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) maintain  
89 extensive networks of social relationships, typically, though not always, among related matriline  
90 (Fernando and Lande 2000; Wittemyer et al. 2005; Vidya and Sukumar 2005; Archie et al. 2006;  
91 Wittemyer et al. 2009; de Silva et al. 2011; de Silva and Wittemyer 2012). Both species are  
92 generalists capable of consuming a diverse diet alternating among graze, browse and fruit  
93 depending on season and geography (Loarie et al. 2009; Campos-Arceiz and Blake 2011). Like  
94 equids, elephants are hind gut fermenters and thus require a constant source of forage. But unlike  
95 many ungulates or primates, their dietary flexibility potentially allows greater behavioral  
96 flexibility. Although there is no discernible reproductive skew among females (de Silva et al.,  
97 2013; Moss & Poole 1983), African savannah elephants exhibit clear dominance hierarchies,  
98 which are age/size-based and weakly nepotistic in apparent contrast to expectations under  
99 socioecological models (Archie et al. 2006; Wittemyer & Getz 2007), indicating that within- and  
100 between-group competition is greater than gross foraging ecology would initially suggest. The  
101 nature of dominance relations among Asian elephants has not previously been described,  
102 presenting an opportunity for understanding what governs hierarchies among large-bodied, non-  
103 territorial, wide-ranging species. Here we compare social dominance behavior in female Asian  
104 and African elephants at the individual and population levels.

105  
106 *E. maximus* are physically and ecologically similar to *L. africana* as mega-herbivores,  
107 with an evolutionary divergence time of approximately six million years (Shoshani & Tassy  
108 1996). A naïve expectation based only on their generalist feeding habits and morphological  
109 similarities would be that hierarchies in Asian elephants should resemble those in African

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

131

## 132 **Methods**

133

134 *Study site*

135

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

149

150 *Data collection*

151

152 The study population consisted of 286 known adult or sub-adult females and their calves  
153 as well as periodic seasonal occupants. Identities of all known individuals within an observed  
154 group were recorded upon encounter. All individuals were assigned to 10 year estimated age  
155 classes (Table 1 & Figure 2 in de Silva et al. 2013). Analyses were based on 1923 hours of focal

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

171 We compared dominance interaction patterns among female Asian elephants to those of  
172 female African elephants at Samburu and Buffalo Springs National Reserves, Kenya, described  
173 by Wittemyer & Getz (2007). This savannah ecosystem receives on average 350 mm of rainfall  
174 and is situated along the Ewaso N'giro River. Dominance interactions were observed from 2001-  
175 2003, during 1161 hours of focal monitoring over 206 field days (5.5 hours per day on average).  
176 Sampling focused on between-group interactions and dominance interactions were also recorded  
177 *ad libitum* apart from focal observations. General behavioral classifications were analogous to



178 those described above but only agonistic interactions were used to determine dominance  
179 outcomes.

180

181 In the Asian dataset, both agonistic and submissive behavior included 75 interactions  
182 among 74 females aged 11 to 60< (six age classes), distributed among 28 social units. The  
183 African dataset contained 264 agonistic interactions among 66 females aged 12 to 55 (five age  
184 classes) and 34 social units. To control for the difference in number of observed interactions  
185 between the two systems, we repeated analyses with a randomly downsampled African dataset  
186 containing 75 interactions, which then included only 53 individuals. We did not match both the  
187 number of interactions and the number of individuals, as this would introduce artificial distortion  
188 to density of the *L. africana* network.

189

#### 190 *Data analysis*

191

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

199

200 Because sparsity in matrices distorts or precludes standard tests of linearity (de Vries et  
201 al. 2006; Shizuka & McDonald 2012; Wittemyer & Getz 2006), we tested dominance at the  
202 individual-level using network triad motifs (Shizuka & McDonald 2012; Wasserman & Faust,  
203 1994) (Figure 1B). Transitivity is a property of triads whereby  $A > B$ ,  $B > C$  and  $A > C$ . Cyclicity  
204 is a property of triads whereby  $A > B$ ,  $B > C$  and  $C > A$ . Multiple transitive relations that are  
205 consistent with one another yield an orderly linear hierarchy, whereas cycles disrupt linearity.  
206 Order and transitivity are related but not synonymous; all transitive systems are ordered but a  
207 system with consistent cycles, such as the rules governing the rock-paper-scissors game, can be  
208 ordered but not transitive. Shizuka & McDonald's (2012) technique examines the network  
209 context of dominance interactions, comparing the observed to the expected proportion of  
210 transitive vs. cyclic triads through randomization with the expectation that the greater the degree  
211 of transitivity, the greater the linearity within a system. We further extended this technique to  
212 incomplete triads. For incomplete, two-edge motifs, we assessed transitivity by comparing the  
213 proportion of motifs representative of transitive triads (double dominants or double subordinates)  
214 relative to those which could represent either cyclic or transitive triads (pass-along motifs). To  
215 generate the expected null distribution for each motif, the winner of each pairwise interaction  
216 was randomized such that each individual had equal (0.5) probability of winning. 10,000  
217 randomized datasets were generated and the frequencies of each type of motif in the observed  
218 and randomized datasets through triad census were assessed using the Statnet package in R  
219 v.3.03. Mutual edges (tied relationships) were not considered (Shizuka & McDonald, 2012). We  
220 rejected the null hypothesis that the observed frequencies of triad motifs could be obtained by  
221 chance if the Euclidean distance between the observed set of triad motifs and the centroid (mean)  
222 of randomized datasets was greater than or equal to the distance between the centroid and 95% of

223 randomized datasets. We used this rather than the simple Chi Square test for goodness of fit in  
224 order to avoid making assumptions about the underlying distribution. Tests were performed in R  
225 v.3.0.03 (R development core team, 2012).

226

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

242

243         We assessed hierarchy linearity among classes with  $h'$ , the modified version of Landau’s  
244  $h$  (de Vries 1995). We then tested rank differentiation among classes (age or social unit) by  
245 treating them statistically as individuals. We calculated David’s Score as a basis for evaluating

246 steepness, a measure of the degree of rank differentiation among classes (David 1987; David  
247 1988; de Vries et al. 2006). We tested the significance of hierarchy steepness through  
248 randomization (de Vries et al. 2006), using a binomial distribution of dyadic winning proportions  
249 together with a correction for chance (detailed in Appendix 2).

250

251 We further devised an alternative statistical test to determine whether there was  
252 significant ordering among classes. We reordered the collapsed matrices using four different  
253 ranking methods: the I&SI method (Schmid & de Vries, 2013), the Batchelder-Bershad-Simpson  
254 index (henceforth BBS, (Jameson et al. 1999)), Colley's Rating method (henceforth CRM,  
255 (Langville & Meyer, 2012)), and the Park-Newman Index (henceforth PNI, (Park & Newman,  
256 2005)). The four different algorithms were employed to ensure robustness of results. We then  
257 calculated the sum-of-reversals (SOR), i.e. the sum of entries which fall below the diagonal  
258 under a particular order (Figure S1). This quantity is the total number of directional interactions  
259 that are opposite the overall rank order. The more ordered a system, the fewer reversals it should  
260 have. We rejected the null hypothesis that a dataset is ordered by class if the observed SOR was  
261 less than the SOR obtained in randomized datasets with a one-sided significance threshold after  
262 Bonferroni correction for multiple testing set at 0.00625. Henceforth we shall refer to this test as  
263 the Sum-Of-Reversals test, or SOR test. For any particular collapsed dominance matrix –  
264 observed or randomized – these ranking methods might yield multiple equivalent orderings of  
265 classes. In such cases, we calculated the mean SOR from a sample of equivalent orders  
266 (Appendix 1). To test whether the dominance outcomes we observed were more orderly than  
267 expected by chance, we compared the observed SOR for a particular matrix with the SORs  
268 obtained through 10,000 randomized datasets, where the SOR values were calculated under each

269 of the four algorithms. Linearity, steepness and SOR tests were performed in Excel using an  
270 extended version of DomiCalc (Schmid & de Vries 2013), which is included in a supplementary  
271 file. All p-values are one-tailed.

272

## 273 **Results**

274

275 The distribution of age classes that participated in dominance interactions was  
276 significantly different between the two systems (Figure 2) with the *L. africana* dataset lacking  
277 individuals in the 60+ age class due to low survivorship in older age classes (Wittemyer, et al.  
278 2013). The direction of outcomes with respect to the age class of interacting individuals was  
279 significantly different between the two populations (Table 1), with the Asian population showing  
280 a higher proportion of age-reversed wins (Table 1, Figure 3).

281

### 282 *Ordering by individual*

283

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

291

292 *Ordering by class*

293

294 None of the datasets showed significant linearity either by age or social unit when  
295 assessed with  $h'$ . However, steepness (assessed using David's Score corrected for chance)  
296 collapsed by age as well as social unit for the Asian dataset were both significantly greater than  
297 expected (one-sided  $\alpha=0.025$ ;  $p_{\text{age}} < 0.005$ ,  $p_{\text{social}} < 0.01$ ; Table S1). The African datasets were  
298 likewise significantly steeper than expected by chance for age and social unit ( $p < 0.0001$ , Table  
299 S1). This also held true for the downsampled dataset ( $p_{\text{age}} < 0.0001$ ,  $p_{\text{social}} < 0.001$ ).

300

301 For the Asian dataset, there was agreement among all four ranking methods that  
302 dominance outcomes were significantly ordered by age ( $SOR_{\text{obs}} < SOR_{\text{exp}}$ ,  $p < 0.00625$   $\alpha$ -threshold  
303 after Bonferroni correction for multiple testing), while significant ordering by social unit was  
304 indicated by three of the four ranking methods employed (Figure 5, BBS and I&SI:  $p=0.0001$ ;  
305 PNI:  $p=0.0390$ ; CRM:  $p=0.0091$ ). In contrast, the full African dataset showed significant  
306 ordering both by age and by social unit across all ranking methods ( $p < 0.0001$ ; Figure 5). The  
307 downsampled African dataset was consistent with these results when ranked by age ( $p < 0.0001$ ),  
308 but only half the ranking methods showed significant order by social unit (BBS:  $p=0.0010$ ;  
309 CRM:  $p=0.0007$ ; PNI:  $p=0.0145$ ; I&SI:  $p=0.0218$ ).

310

## 311 **Discussion**

312

313 Many ungulates as well as primates do not readily conform to a simplistic  
314 socioecological model in which gross foraging ecology acts as a proxy for the degree of

315 competition individuals experience. Linear dominance hierarchies are commonly observed even  
316 among species feeding on seemingly uniform and widely-dispersed resources and do not have a  
317 clear relationship with levels of agonism, presenting a challenge for socioecological models  
318 (Wheeler et al. 2013; Clutton-Brock & Janson 2012; Koenig & Borries 2009; Thierry 2008).  
319 Despite their generalist diet, African savannah elephants exhibit strong linear dominance  
320 hierarchies within and between social groups where older, taller individuals are more dominant,  
321 likely because resource competition among individuals and groups is in fact salient (Archie et al.  
322 2006; Wittemyer & Getz 2007). However, because group living is inherently costly, one would  
323 expect the tendency to fission would be stronger under ecological conditions that make dispersal  
324 easier. In such situations, it would be difficult to exert and maintain strict hierarchies. We tested  
325 whether similar patterns hold for an Asian elephant population which shares analogous feeding  
326 habits but occupies an environment where forage, water availability and seasonal predictability  
327 of rainfall is greater and where large non-human predators are absent.

328  
329       The most striking quantitative and qualitative difference between the taxa at the  
330 individual level was the rarity of transitive motifs within the Asian population (Figure 4). Rather,  
331 they demonstrated a distribution of triadic motifs which could not be statistically distinguished  
332 from chance. In contrast, the African population exhibited triad motifs consistent with  
333 transitivity, as expected based on prior studies (Archie et al. 2006; Wittemyer & Getz 2007), a  
334 result robust to downsampling which matched sample sizes in the two datasets. This finding was  
335 driven by the disproportionately frequent occurrence of double-dominant motifs (which are  
336 inevitably transitive upon completion) and relatively infrequent occurrence of pass-along motifs  
337 (which could result either in cyclic or transitive triads) in the African population (table 2 and

338 figure 4). In contrast, the Asian population shows a disproportionately greater occurrence of  
339 pass-along motifs, highlighting the greater potential for cyclic relationships in the Asian system  
340 than in the African. Curiously, although double-subordinate motifs are analytically equivalent to  
341 double-dominant motifs since they also resolve only in transitive triads, they are not statistically  
342 overrepresented. A similar asymmetry between these motifs is observed in the dominance  
343 hierarchies of *Diacamma* worker ants (Shimoji et al. 2014), suggesting a widespread pattern in  
344 the way that hierarchy is behaviorally expressed that may merit further study.

345

346 We tested orderliness beyond the individual level by aggregating individuals into classes  
347 by age or social unit. The classical test of linearity,  $h'$ , was not significant in datasets collapsed  
348 by age or social unit for either species despite expectations to the contrary for the African  
349 system. However, outcomes were significantly steep both by age and social unit, in both taxa.  
350 We explored this further by devising the Sum Of Reversals test, which compares the number of  
351 reversals observed against the number of reversals expected by chance when wins and losses are  
352 arranged using ranking algorithms. Multiple ranking indices were in agreement that there is  
353 significant ordering by age in both populations, but there were a greater proportion of age-  
354 reversed wins in the Asian population (Table 1). Individuals in the oldest age class are missing in  
355 the African sample (Figure 1), unlike in the Asian. One might ask whether observed differences  
356 may be explained simply by the difference in the age structure of the populations, as weaker  
357 individuals in the oldest age classes could be dominated by younger females who are in better  
358 physical condition (Figure 3). Given the strong correlation between age and dominance in the  
359 African system (Wittemyer & Getz 2007), the presence of more older individuals should have  
360 reinforced a clearer hierarchy, the opposite of what is seen in the Asian population. In addition,



361 strict order by age was also found in the Amboseli National Park population of African  
362 elephants, which did contain individuals in the oldest age classes (Archie et al. 2006).

363  
364         Ordering by social unit was not well-evidenced in the Asian population in contrast to the  
365 African, even though more than half of all observed interactions occurred between individuals  
366 belonging to different social units. The artificially downsampled dataset for the African  
367 population shows similar results as the Asian, thus results are driven at least in part by the low  
368 overall rate of interaction. Archie et al. (2006) also found that at Amboseli National Park,  
369 hierarchies within families were ordered by age rather than matriline, making it a more important  
370 determinant of rank. Moreover, in the Asian system individuals from completely different social  
371 units seldom mingled into larger aggregations as they did in the African system, even when  
372 range use was highly overlapping (de Silva et al., 2011; de Silva & Wittemyer, 2012). On the  
373 majority of occasions when individuals from different social units passed by within detectable  
374 proximity of one another, they either ignored or avoided each other entirely. Therefore it is  
375 unlikely that null relations between social units could be resolved for truly biological rather than  
376 statistical reasons.

377  
378         While social dominance is typically assessed in terms of agonism (Francis 1988; Drews  
379 1993; Forkman and Haskell 2004), aggressive behavior need not accompany rank establishment  
380 or enforcement even where such exists (Drews, 1993; Francis, 1988; Hand, 1986), and  
381 conversely egalitarianism does not imply an absence of aggression (Strier et al. 2002; Strier,  
382 2007). The relationship between levels of agonism, hierarchical structure and foraging ecology  
383 is therefore not straightforward (Wheeler et al. 2013). Systems characterized as ‘tolerant’

384 manifest clear dominance hierarchies despite very low levels of aggression, as exemplified by  
385 equids (Rubenstein 1994). Among feral horses this is quantified as 0.1 aggressive interaction per  
386 hour of observation, which is still much greater than what was observed in the Asian elephants.  
387 The Asian dataset included all possible behavioral indicators of dominance or submissiveness,  
388 not merely aggression, and yet was far sparser than the African dataset, which was based solely  
389 on aggression. This was not due to a difference in total observation effort, as the Asian data  
390 comprised a greater number of observation hours. To obtain a similar number of interactions in  
391 the Asian population would require more than ten years of data collection (Figure S2), over  
392 which time some of the subjects will have died. Because association rates among social  
393 companions in Asian elephants are generally much lower than among African elephants, and  
394 interactions between individuals belonging to different social units are even less frequent, the  
395 lack of rank signaling among Asian elephants seems unlikely to conceal a strong latent  
396 hierarchy. The more mechanistically plausible and parsimonious interpretation of these  
397 observations is that rarity of dominance interactions reflects a much weaker hierarchy than that  
398 of African savannah elephants.

399

#### 400 *Social and ecological drivers*

401

402 The maintenance of dominance hierarchies is costly, having consequences for the health  
403 and fitness of individuals (Sapolsky 2005). Therefore one expects them to be favored in the face  
404 of competition when they obviate costly conflicts among individuals who repeatedly encounter  
405 one another. Where dominance hierarchies reduce overt conflicts, they are likely of greater  
406 importance among those who have the opportunity to interact more frequently. For instance, at

407 Amboseli National Park, Archie et al. (2006) found that agonistic interactions occurred more  
408 often among females with higher association indices. Conversely the ability to segregate  
409 spatially may remove or lessen the need for rigid hierarchies, whether among individuals in the  
410 same or different social groups (Hand 1986; Drews 1993). Spatial segregation reduces the ability  
411 to both to signal and appropriately respond to rank conflicts (Ang and Manica 2010). Scramble  
412 competition can occur where resource patches are inadequate to support stable aggregations of  
413 conspecifics, or when resources are plentiful in the absence of other factors favoring stable  
414 groups (such as predation or sexual harassment). If the former constitutes ecological  
415 ‘constraints’, the latter may be thought of as ecological ‘release’.

416  
417         On African savannahs, the dispersed and temporally dynamic nature of resource  
418 availability (e.g. fresh forage and water), as well as the presence of predators enhances the  
419 decision-making and resource acquisition value of older, experienced individuals, providing  
420 opportunities for exerting dominance as well as leadership (McComb et al. 2001; Foley et al.  
421 2008; Wittemyer et al. 2008; McComb et al. 2011). When errors are less costly, there is less need  
422 to rely on knowledgeable individuals, reducing the value of age. Since the protected Asian site  
423 has greater absolute rainfall with more predictable seasonality than the African site, no  
424 nonhuman predators that pose a serious threat to elephants, and very little poaching, the risks of  
425 movement and dispersal in the Asian site are likely lower relative to the African. Thus female  
426 Asian elephants in this population even with very young calves need not tolerate being socially  
427 subordinate and can afford to loosen maternal ties, resulting in the highly flexible contact  
428 patterns and low association rates observed. Indeed, solitary adult females were observed far  
429 more frequently than at the African site (de Silva & Wittemyer 2012). It follows that this Asian

430 population also lacks clear behavioral (as opposed to genetic) matriarchs, by definition the oldest  
431 and most dominant individuals (Archie et al. 2006; Wittemyer & Getz 2007), perhaps because  
432 matriarchal 'leadership/despotism' cannot be exerted. The general implications of these  
433 observations are that the evolution of strong centralized leadership is not favored under  
434 environmental conditions that enable spatio-temporal avoidance and dynamic group  
435 membership, reducing competition and impeding hierarchy formation, which we term ecological  
436 release.

437  
438         Encounters among unfamiliar individuals may nevertheless occur even in systems where  
439 scramble competition predominates. Among social foragers with non-territorial fission-fusion  
440 dynamics, dominance behaviors may be co-opted to enforce social group membership rather than  
441 social rank, excluding potential competitors from one's vicinity whenever direct conflicts arise.  
442 If such exclusion is not arbitrary but rather expressing preference for matrilineal kin (Fernando &  
443 Lande 2000; Vidya & Sukumar 2005), it is a form of nepotism (Wittemyer & Getz 2007), even if  
444 not embedded in a classical hierarchy (Sterck & Watts 1997). Dominance signals in Asian  
445 elephants (Figure 2A) may serve this secondary purpose. While Asian elephants show low rates  
446 of aggression among familiar individuals, conflicts including physical aggression can occur  
447 especially when individuals from two completely unfamiliar units intersect (video at  
448 <http://youtu.be/60KxqnVV424>). Although associations among non-relatives due to early  
449 socialization do occur in the Asian population (SdS, unpublished data), and likewise also in  
450 African savannah elephants under disturbed conditions (Goldenberg et al. 2016; Pinter-Wollman,  
451 Isbell, & Hart, 2009; Wittemyer et al., 2009), such cases likely represent substitute bonds where  
452 immediate kin are unavailable, rather than the norm. Aggregations of elephants are therefore

453 fluid, semi-permeable, but not amorphous entities, rendering ambiguous such concepts as  
454 'group' and 'group size', that have been so central to our understanding of social evolution  
455 (Robbins et al.1991; Silk 2007; Snaith & Chapman 2007). Asian elephants possibly share some  
456 similarities with human hunter-gatherer societies in which flexible band membership is also a  
457 hallmark (Aureli et al. 2008; Moffett 2013; Pennisi 2014), and is a factor thought to inhibit  
458 hierarchy formation (Turnbull 1965; Boehm 1999). This suggests that fission-fusion spatial and  
459 social dynamics (Aureli et al. 2008) may be key mechanisms behind the development and  
460 maintenance of non-hierarchical systems, beyond the absolute abundance or distribution of  
461 resources. Although the terms 'dominance' and 'hierarchy' are often linked together, dominance  
462 behavior need not manifest in linear hierarchies. The results of this study suggest dominance  
463 hierarchies may be viewed as falling along a gradient of strong to weak ordering, concurrent with  
464 the degree of fission-fusion expressed, rather than in terms of despotic/egalitarian or  
465 linear/nonlinear dichotomies. We propose that, in appropriately paired comparisons of sister taxa  
466 (or multiple subpopulations of the same species), one should expect to see that systems with  
467 greater levels of competition should also manifest greater levels of order than expected by  
468 chance, whether or not such order is statistically linear.

469

#### 470 *Conservation and management*

471

472 Because Asian elephants have substantial range requirements, occupy countries with  
473 some of the densest human populations, as well as some of the most threatened ecosystems, this  
474 species is extremely vulnerable to range constriction and fragmentation. They are consequently  
475 also the focus of intensive management and impacted by development activities. Typically,

476 behavioral considerations do not feature prominently in such decisions. These findings may  
477 nevertheless be important for interpreting results of prior management actions and forestalling  
478 negative impacts of future interventions.

479

480 In particular, practices altering the social organization of populations such as  
481 translocations, drives or roundups (used to move elephants into designated protected areas), may  
482 be detrimental (Lahiri-Choudhury 1993; Fernando et al. 2012). It has been assumed that social  
483 units consist of only those individuals observed together at any given time, and that capturing  
484 putative “matriarchs” will draw other family members, ensuring their capture or cooperation  
485 (Lahiri-Choudhury 1993). Our findings do not support such assumptions. Such displacements  
486 would not only disrupt long-term social bonds because social affiliates may not be close together  
487 at any given time, but could result in difficulties for the displaced individuals if habitats are  
488 already saturated with other elephants. Forced displacement could result in crowding and  
489 competition, with likely disproportionately negative impacts to the displaced individuals.  
490 Preserving remaining range and its connectivity should be the top priority; behavioral studies  
491 could be usefully integrated alongside such interventions and factored into management  
492 decisions. Likewise, allowing sufficient space for avoidance will be essential for reducing  
493 conflict among individuals confined to captivity.

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514

## 515 **Authors' contributions and statement of competing interests**

516

517 SdS conceived of the study, collected data, developed some statistical tools, conducted analyses  
518 and wrote the manuscript; VS developed some statistical tools, conducted analyses, and assisted  
519 in writing the manuscript; GW participated in designing the study, collected data, and edited the  
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521

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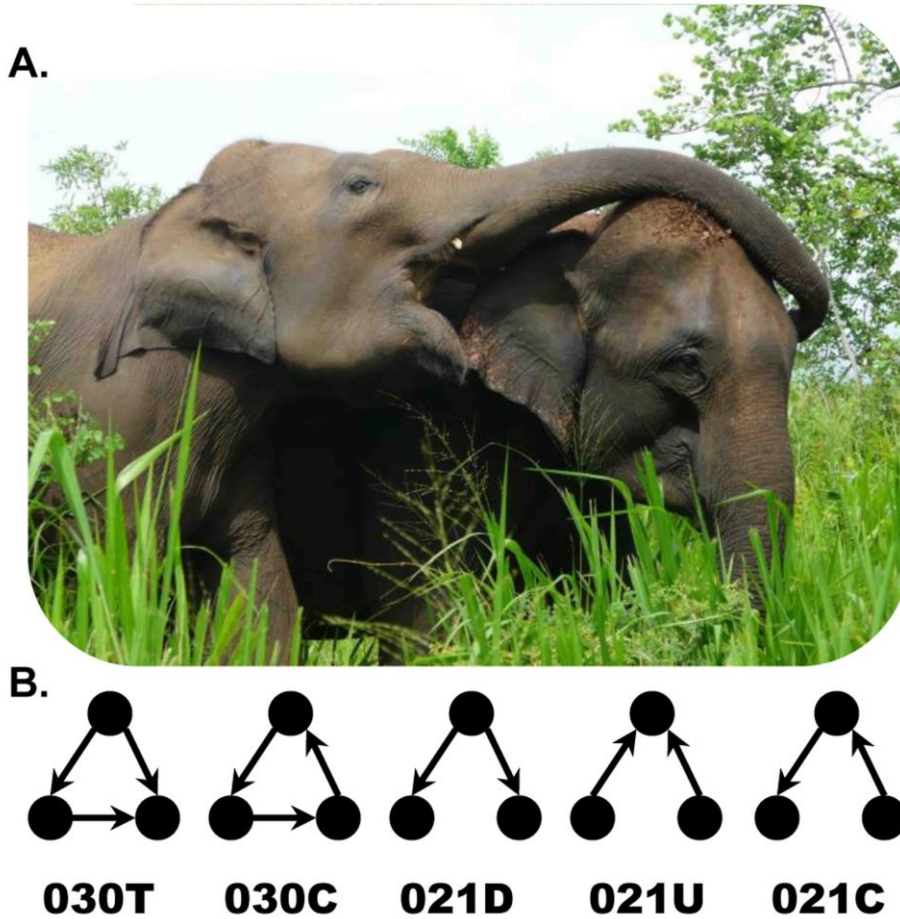
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725 **Figure 1 – Dominance behavior & triads**

726 **A. Trunk-over dominance gesture between two adult females.**

727 **B. Triad motifs, with MAN labelling scheme** (Wasserman & Faust 1994; Shizuka &

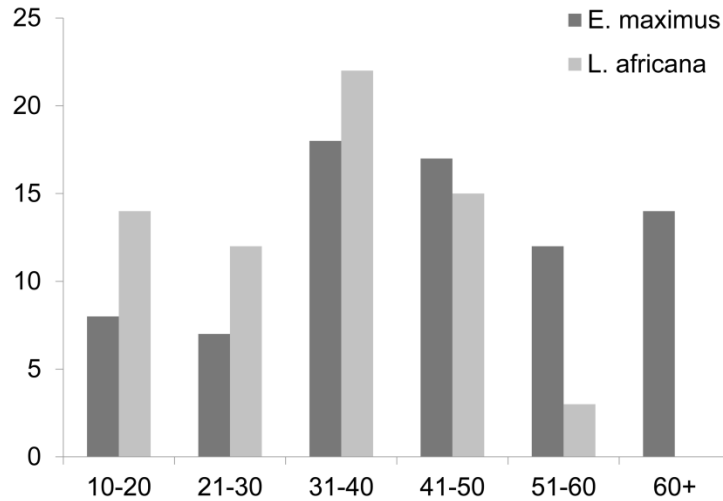
728 McDonald 2012). 030T is a transitive triad, whereas 030C is cyclic. Excluding

729 bidirectional outcomes, 021D (double-dominant), and 021U (double-subordinate) are

730 incomplete triads that would result in transitive triads no matter which way they are

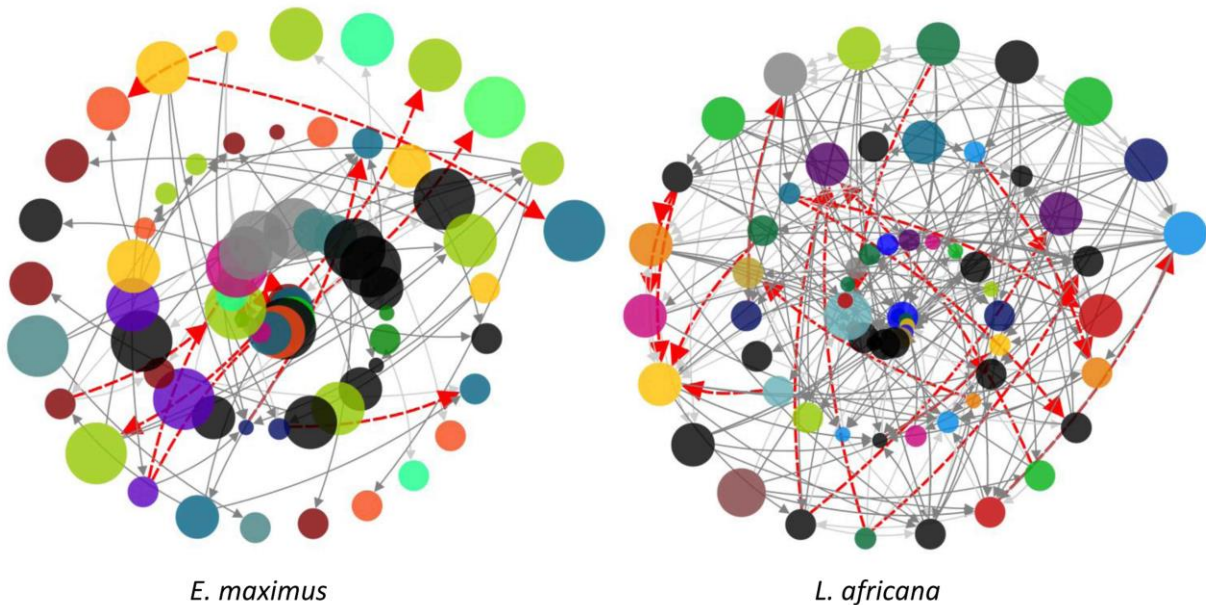
731 completed whereas 021C (pass-along) could result either in a transitive or cyclic triad

732 with equal probability.



733

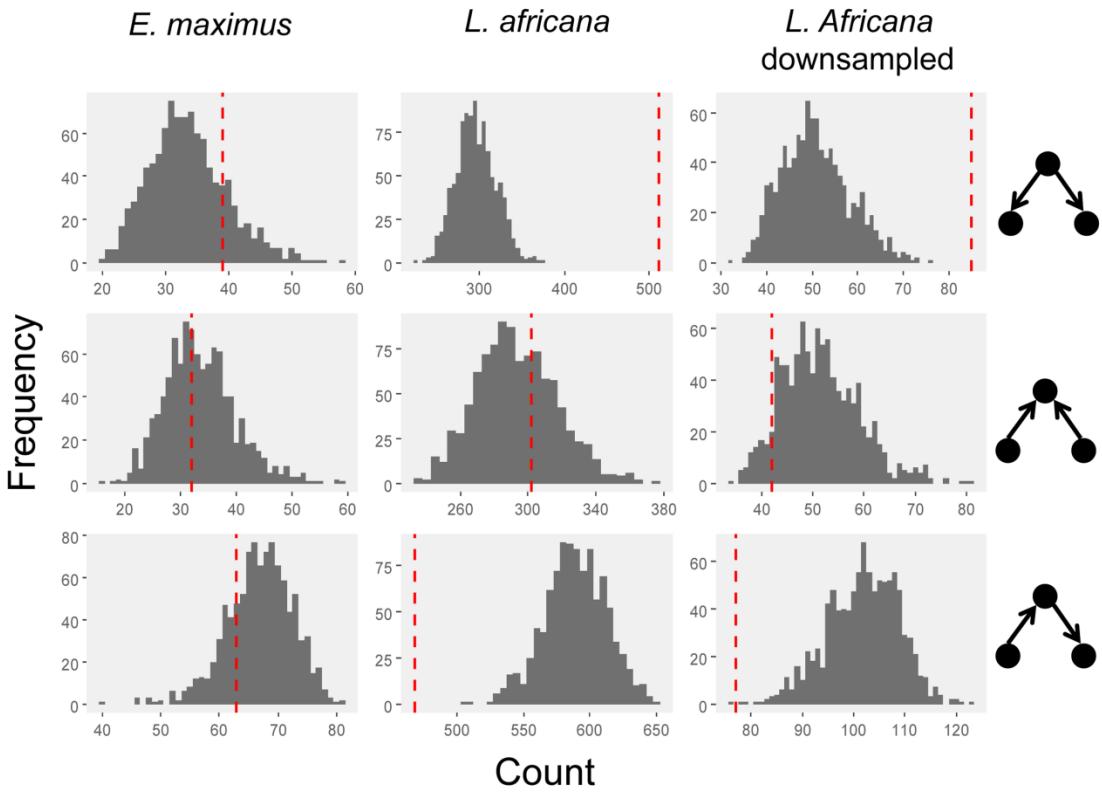
734 **Figure 2 – Distribution of age classes.** The distribution of ages among females who participated  
 735 in at least one dominance interaction in the two study populations (N=74 Asian, 66 African)  
 736 were significantly different ( $X^2=32.968$ , d.f.=5,  $p<<0.001$ ).



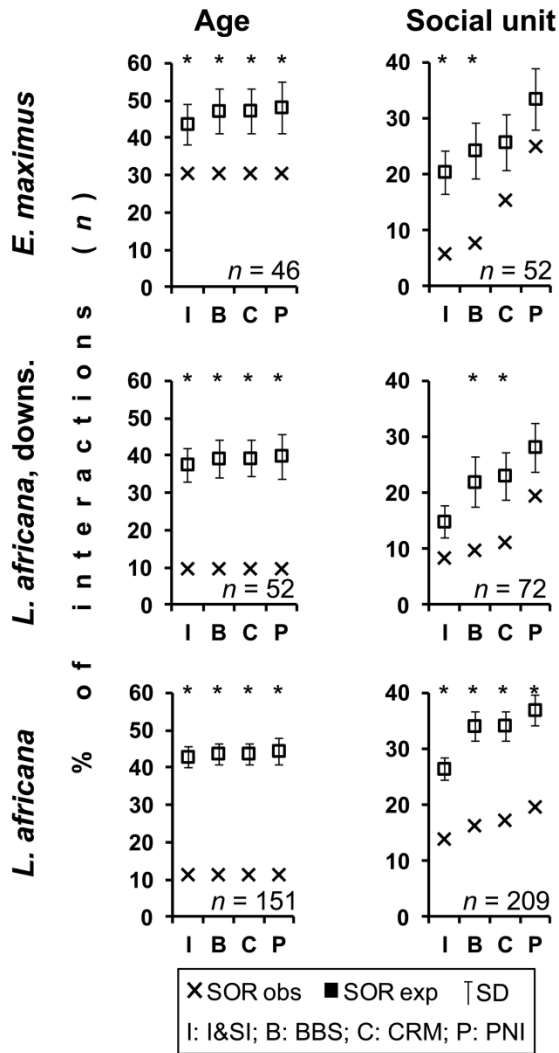
737

738 **Figure 3 – Dominance networks of *E. maximus* and *L. Africana*.** Nodes are sized by age class,  
 739 and colored by social unit (black nodes are singletons belonging to units from which no other  
 740 members were observed in a dominance interaction during the study). Graphs were generated on

741 NodeXL, where nodes spiral outwards in order of increasing out-degree (i.e. nodes with more  
 742 wins are more peripheral). Dark edges signify interactions in which the dominant was older, light  
 743 edges signify equal age, and dashed red edges signify reversals. Decreasing node size toward the  
 744 center in *L. Africana* indicates greater order by age relative to *E. maximus*. *E. maximus* exhibits a  
 745 sparser network with more age irregularities than *L. africana* despite a greater number of total  
 746 observation hours and an older age structure.



748  
 749 **Figure 4 – Frequency of triad motifs in observed vs. randomized datasets.** The ordinate is  
 750 the number of times the specified motif appears in a given dataset, the abscissa is the number of  
 751 randomized datasets in which that particular count occurs. The dashed line shows the actual  
 752 count for each motif observed in respective datasets (see Table 2). Complete triads were rare in  
 753 the observed data, and are therefore not presented.



755

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

762

763 **Table 1 – Direction of dominance by age.** The frequency of wins by older individuals vs.  
 764 younger individuals or those in the same age class (in 10-year bins, Figure 2) was significantly  
 765 different between the Asian and African datasets ( $X^2=13.652$ , d.f.=2,  $p<0.01$ ).

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

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768 **Table 2 – Triad census results for known females (N=74 Asian, 66 African).** Percentages  
 769 reflect proportion of each motif among these five motifs, disregarding others such as null triads  
 770 (no edges), singles, and motifs with mutual outcomes. Note that the number of transitive as well  
 771 as cyclic motifs are low simply because there are fewer complete triads than incomplete ones.  
 772 However, the number of pass-along and cyclic motifs together are disproportionately greater  
 773 relative to the other motifs in the Asian dataset in contrast to the African.

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	021D Double dominant	021U Double subordinate	021C Pass-along	030T Transitive	030C Cyclic
<i>E. maximus</i>	39 (28%)	32 (23%)	62 (45%)	5 (4%)	1 (<1%)
<i>L. 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

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