1   **Title**: Group size constraints may mask underlying similarities in social structure: a

2   comparison of female elephant societies

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4   **Short title**: Group size and social structure

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1   **Abstract**

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3   We report on female Asian elephant social structure in Nagarahole and Bandipur National

4   Parks (Kabini population), southern India, and examine the role of group size in affecting

5   the outcome of social structure analysis in female elephants, which show high fission-fusion

6   dynamics. Based on five years of data, we found the Kabini association network structured

7   into highly modular communities that we call clans. We then modified the dataset (to obtain

8   the Kabini 500-m dataset) to match sampling methods previously used in a study each of

9   Asian (Uda Walawe) and African savannah (Samburu) elephants, so that network and

10   association statistics could be compared across populations. Measures of association and

11   network structure previously used were more similar amongst the Asian elephant

12   populations compared to Samburu. The Samburu population formed a hierarchically-nested

13   multilevel society whereas the Asian populations did not. However, we found hierarchical

14   clustering levels in all three populations using Louvain community detection. Moreover, the

15   average community sizes obtained through the Louvain method were not significantly

16   different across populations, indicating basic similarities in social structure. Since fission-

17   fusion dynamics allow for community members to form groups of different sizes, we

18   examined the effect of average group size on association and network statistics. Higher

19   average association index and degree, and lower average path length in Samburu compared

20   to the Kabini 500-m dataset were explained by the larger average group size in Samburu.

21   Thus, underlying similarities in the social networks of species showing fission-fusion

22   dynamics may be obscured by differences in average group size.

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1   **Significance Statement**

2

3   Various measures of associations and social network analyses have been used to compare

4   social structures of different populations. We studied the social structure of female Asian

5   elephants in a southern Indian population and compared it with those of a Sri Lankan Asian

6   elephant population and an African savannah elephant population. We showed that, while

7   there were social differences between the Asian and African savannah elephant populations

8   using previous methods, there were basic similarities across all three populations using a

9   method of network community detection. This discrepancy across analyses partly stemmed

10   from differences in average group size between populations. Average group size in fission-

11   fusion societies variously affected different association and network statistics, which has

12   implications for inferences about social structure.

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14

1   **Introduction**

2

3   Social structure and organization, which include the patterning of relationships and the
4   system of interactions between individuals, may affect foraging, reproductive opportunities,
5   anti-predatory benefits, vulnerability to disease, and information transfer (e.g. 1-8), making
6   them important in the study of animal species. Social organization is thought to evolve in
7   response to resource-risk distributions (9-14), and one of the modal types of mammalian
8   social organization was called the fission-fusion society, in which groups fuse together or
9   split away in response to spatio-temporally varying resources, balancing the costs and
10 benefits of group-living (e.g. 13, 15-20). Distinct types of fission-fusion societies were
11 identified: multilevel societies that were either strictly hierarchically nested (e.g.
12 hamadryas) or flexibly nested (e.g. gelada baboons), and the classical or individual-based
13 fission-fusion society (e.g. chimpanzees and spider monkeys) (see 21). It has since been
14 recognized that fission-fusion societies form a continuum of different extents of fission-
15 fusion dynamics (see 22). Here, by analyzing social structure in female elephants, we show
16 how group size may bridge modal fission-fusion societies. Group size is the number of
17 individuals sighted together in the field and may often be smaller than the size of the most-
18 inclusive, socially-meaningful community in species showing fission-fusion dynamics.

19

20 Female elephants show high fission-fusion dynamics (see 22), and previous studies have
21 suggested a multitiered (hierarchically-nested multileveled) social structure in African
22 savannah elephants (19, 23) and non-nested, multileveled social structure in an Asian
23 elephant population (24). The differences between these social structures may arise from
24 group size limitation in the Asian elephant, preventing hierarchical structure from being
25 apparent, but this has not been examined previously, as only one detailed study of Asian
26 elephant social structure (25) was available. Since observed social structure may reflect
27 evolved patterns, as well as plastic responses to the current environment (see 26, 27), studies
28 of multiple populations are required to understand the social structure of a species. Here, we
29 examine the role of group size in affecting social structure by collecting the first large-scale
30 quantitative data on Asian elephant social structure from India, from the Nagarahole-
31 Bandipur (Kabini) population, and by comparing this with data from the Uda Walawe Asian
32 elephant population in Sri Lanka, and the Amboseli and Samburu African savannah
33 elephant populations, for which published data on female social structure are available (19,
34 23-25, 28-29).

4

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2   The Asian elephant (*Elephas maximus*) is an endangered species, whose social organization

3   may have been impacted to varying extents across its range by prolonged, historic

4   manipulation by humans. Therefore, there have been calls for detailed studies from multiple

5   populations in order to understand the drivers of their social organization (24-25, 30-31).

6   Asian and African savannah elephants form matriarchal societies, with females and their

7   dependent offspring living together in groups, and adolescent males dispersing from the

8   groups and leading largely solitary lives thereafter (23, 31-34). However, based on previous

9   studies, there seemed to be differences in social structure within and between elephant

10 species, possibly from different sampling methods and ecology (see below).

11

12 The African savannah elephant exhibits a multitiered female society (19, 23, 32), with

13 mother-offspring units being the basic units, and "family group" referring to one to a few

14 closely related mother-offspring units (35). In Amboseli, family groups identified at the

15 beginning of the study were later called core groups, and associations of family or core

16 groups were termed bond groups (23, 28). Family groups that shared dry-season home

17 ranges were called clans (23). Social tiers in Samburu were identified statistically through

18 cluster analysis and included, hierarchically, second-tier units (family groups), third-tier

19 units (kinship groups of Douglas-Hamilton (32) or bond groups of Moss and Poole (23)),

20 and fourth-tier units (19). Groups themselves were differently identified in the field, with

21 individuals of core groups having to be within 100 m of one another in order to qualify as

22 being associated in Amboseli (28), and individuals within a 500-m radius of an aggregation

23 centre being classified as a group in Samburu (19). Amboseli and Samburu have also

24 experienced different extents of poaching (36-37), but the association network in Samburu

25 was found to be resilient to the elevated levels of poaching (38). Samburu and Amboseli are

26 similar in elephant density and ecology (39) and social tiers are similar in the two

27 populations (Table 1). Therefore, differences between the female social networks of the two

28 populations, with the Samburu network being much more interconnected than the Amboseli

29 network (Fig. 1), are likely to stem from differences in sampling methods.

30

31 Studies on female Asian elephant social organization had suggested a matriarchal society

32 with fission-fusion dynamics, inferred from female social groups of varying sizes (33-34).

33 However, the precise nature of social organization was ambiguous, with studies from Sri

34 Lanka largely not describing multitiered societies but those from southern India implying

1 them (see below). McKay (33), in southeastern Sri Lanka, described the most inclusive

2 female social group as a "herd" (of 15-40 individuals), which could contain subunits that

3 showed fusion and fission, but which did not associate with other "herds" that shared their

4 home range. Fernando and Lande (30) found smaller group sizes subsequently (see Table 1),

5 but these groups too did not associate with other groups that shared their home range, and

6 were referred to as family groups. A study in southern India (34) suggested the existence of

7 a multitiered society, with "family groups" (single adult female and her dependent

8 offspring), "joint-family groups" (two or more adult females and their offspring), "bond

9 groups", and "clans" (50-200 individuals). Baskaran *et al*. (40), in southern India, referred

10 to social associations of females that showed coordinated movement and were presumably

11 related as a "clan" (of up to 65 individuals), but did not demarcate social tiers within clans.

12 The first large, quantitative study of Asian elephant social organization, carried out in Uda

13 Walawe, Sri Lanka, found female social organization with long-term associates, and larger

14 social units than typically seen associating at any time in the field (25), which was also the

15 case with the previous, less quantitative studies (and indeed expected in fission-fusion

16 societies in general). However, unlike the previous studies, the larger social units ("herds"

17 or "family groups" or "clans" as the term might be) were connected to one another in a

18 social network at the level of the entire population (24-25). In a comparative analysis,

19 female groups in Uda Walawe were smaller, showed weaker associations, and were less

20 connected at the population level than those in the Samburu African savannah elephant

21 population (24-25). The Uda Walawe population thus showed a non-nested, multilevel

22 society, with individuals associating differently with two types of social affiliates, in

23 contrast to a multitiered society in Samburu with nested social tiers (24). Although some of

24 the initial confusion relating to female Asian elephant social organization seems to have

25 stemmed from an attempt to equate social levels in the Asian elephant with those described

26 in the better-studied African savannah elephant, there was also the possibility of female

27 Asian elephant social organization being different between Sri Lanka and the mainland

28 because of extensive historical disturbance to elephants in Sri Lanka compared to southern

29 India (pp. 68-69 in 41, 42).

30

31 We used data from the Nagarahole-Bandipur (Kabini) population in southern India to find

32 out whether female social structure in this population was similar to that in Sri Lanka, and,

33 if so, whether the difference in social structure from that of the African savannah elephant

34 could be explained by a constraint on group size. We also wanted to find out whether the

1   wider social network in Uda Walawe compared to associations found in previous studies in

2   Sri Lanka could have resulted from differences in methods. A 100-m distance cutoff had

3   been traditionally used to delineate Asian elephant groups (30, <150m in 33), while a 500-m

4   cutoff, similar to the one in Samburu, had been used in Uda Walawe (25). We expected that

5   there might be lower levels of connectedness in the Uda Walawe population compared to

6   the Kabini population because of extensive historical disturbance in the former. However,

7   on the whole, we expected greater similarity between Kabini and Uda Walawe, with smaller

8   group sizes and lower network connectivity in the Asian elephant populations than in the

9   African savannah elephant because of ecological differences. We further attempted to find

10 out how group sizes would affect network statistics in general, given these fission-fusion

11 societies.

12

13 **Results**

14

15 The dataset used to examine female associations comprised 3893 sightings of female

16 groups, sighted between 2009-2014, in which all the females that were ten years old or older

17 (referred to simply as females in the rest of the paper) could be identified. These 3893

18 sightings constituted 87% of all the female group sightings during the study period, and

19 comprised 9551 individual female sightings, including repeat sightings of the same

20 individuals. A group was an aggregation of female elephants that showed coordinated

21 movement and/or behaviours, and were usually within 50-100 m of one another. Members

22 of a group were said to be associating with one another. The number of uniquely identified

23 females from this dataset was 330. Since we wanted to compare our data with the Uda

24 Walawe and Samburu populations in which a 500-m distance cutoff had been used to

25 identify associations, we created an additional dataset (the Kabini 500-m dataset) in which

26 we grouped together females that were within 500 m of one another.

27

28 *Association network and AI in the Kabini population based on the original dataset*

29 Data on female group sightings were used to calculate an Association Index (AI, see

30 Methods) between each pair of females. AIs were used to construct association networks.

31 The association network based on the original Kabini dataset showed clearly demarcated

32 communities (Fig. 2), with associations between females being highly non-random

33 compared to Poisson expectation (*G*-test for goodness of fit, $G=1514.46$, *df*=23, *P*<0.001)

34 and based on permutation tests (Table S3). The overall network modularity, which is a

1   measure of the extent to which a community is partitioned, was high (0.936). Community

2   structure within networks was identified using the Louvain method (43, see Methods). We

3   refer to the final communities obtained as clans, in keeping with previous terminology used

4   to refer to the most inclusive female social grouping of elephants in southern India. The

5   largest clan in our study consisted of 32 females (83 individuals, including their offspring).

6   We did not find female associations across clans during over five years, except on seven

7   occasions (Fig. 1). Upon executing the Louvain algorithm (and excluding the 30 single

8   females that were rarely seen), we found 60, 40, and 39 (which corresponded to the eventual

9   39 clans) communities after the first, second, and third rounds (passes) of hierarchical

10   community detection, respectively. Thirteen of the 39 clans showed two levels (i.e., changed

11   in composition from the first to the second pass) and one clan showed three levels of social

12   organization (changed from the first to the second, and from the second to the third passes),

13   whereas the remaining clans showed a single social level (did not change across passes).

14   The clans that showed more than one social level were significantly larger (average=14.4,

15   SD=7.57, N=14) than those that had a single social level (average, SD, N of clan size: 3.9,

16   2.74, 25; Mann-Whitney U test: U=20.0, Z_{adj}=-4.598, P<0.001, Fig. S4). Based on clans that

17   were sighted over 150 times, we found that 95% of the clan members were sighted on

18   average within the first 40 sightings of the clan (and 92% within the first 30 sightings).

19   Since under-sampling could lead to incomplete clans, we additionally analyzed only clans

20   sighted >40 times and found that they were also significantly larger when they were

21   composed of more than one social level (average=17.0, SD=7.29, N=10) compared to a

22   single level (average=7.2, SD=3.66, N=6; Mann-Whitney U test: U=6.0, Z_{adj}=-2.609,

23   P=0.009, Fig. S4).

24

25   In keeping with clearly defined clans with few associations between them, the overall AI

26   distribution was highly skewed (Fig. 3), with only 2.5% of the AI values being non-zero

27   (average AI=0.004, SD=0.040, median=0) and 10.8% being non-zero when only individuals

28   that were seen at least 20 times were included (Table 2). The average degree (number of

29   associates of a female) and average distance-weighted reach (a measure of a female's reach

30   in the association network, see Methods) were low (Table 2) because of female associations

31   being restricted to clans. The average clustering coefficient (the probability that two

32   randomly chosen neighbours of a focal female are connected, see Methods) was high due to

33   the large number of connections within clans, and density, which measures connectedness

34   across the entire network, was low (Table 2).

8

1

2   *Comparison of association networks across populations*

3   The association network based on the original Kabini data was highly disconnected, unlike

4   female social networks in the previously studied African savannah elephant and Uda

5   Walawe Asian elephant populations (24, Fig. 1, first column), but more connected than the

6   network in the Lopé African forest elephant population (44). However, since different

7   criteria had been used for grouping females, we compared the Kabini 500-m network with

8   the Uda Walawe and Samburu networks, and the original Kabini network with the Amboseli

9   network (in which associations had been recorded somewhat similarly, see 28). The Kabini

10   500-m networks were intermediate in connectedness between the Samburu and Uda Walawe

11   networks (Fig. 1), with the average degree, average distance-weighted reach, and average

12   clustering coefficient in the Kabini 500-m network being significantly smaller than those in

13   Samburu (Welch's two-sample tests: average degree: $U=5.772$, $df=208.3$, $P<0.001$, average

14   distance-weighted reach: $U=6.216$, $df=207.9$, $P<0.001$, average clustering coefficient:

15   $U=10.636$, $df=195.3$, $P<0.001$), but significantly larger than those in Uda Walawe (average

16   degree: $U=23.862$, $df=179.3$, $P<0.001$, average distance-weighted reach: $U=25.687$,

17   $df=211.7$, $P<0.001$, average clustering coefficient: $U=13.068$, $df=140.2$, $P<0.001$; Table 2).

18   The average path length (the number of connections on the shortest path between two

19   females) in the Kabini 500-m network was also intermediate, being larger than that in

20   Samburu (Welch's two-sample test: $U=16.573$, $df=11452.6$, $P<0.001$) and smaller than that

21   in Uda Walawe ($U=64.999$, $df=9038.0$, $P<0.001$). Visually, the network based on our

22   original data was less connected than that of the Amboseli population when there was no AI

23   cutoff, but similar to Amboseli at AI cutoffs of 5% and 10% (Fig. 1).

24

25   The original Kabini network did not change substantially when an AI cutoff of 0.05 was

26   used, unlike networks from all the other datasets (Fig. 1). The Kabini 500-m network

27   changed dramatically at an AI cutoff of 0.05 like the Samburu network. However, network

28   structure curves, which illustrate the cohesiveness of social networks at different association

29   strengths (see 25, Methods), of the Kabini 500-m and the Uda Walawe datasets were

30   roughly similar in shape and differed from that of the Samburu population (Fig. 4, see 24).

31   The AI distribution based on the Kabini 500-m dataset (Fig. 3) bore a greater visual

32   similarity to that of Uda Walawe than to that of Samburu, as high AI values were absent

33   (see 24) and this similarity in AI distribution could have given rise to the similarity in

34   network structure curves. The average AI was, however, significantly smaller in Uda

9

1   Walawe (0.019) compared to that in Kabini 500-m dataset (0.034; Welch's two-sample test:

2   U=11.195, df=11295.3, P<0.001), which was in turn significantly smaller than that in

3   Samburu (0.049; Welch's two-sample test: U=8.209, df=9544.9, P<0.001). However, the

4   percentage of non-zero AI values was much higher in the Kabini 500-m dataset than in Uda

5   Walawe (Table 2). The kurtosis of the Kabini 500-m dataset was higher than those of both

6   Samburu and Uda Walawe (Table 2).

7

8   Louvain community detection on the Kabini 500-m dataset, and Uda Walawe and Samburu

9   datasets (from 24, kindly provided by the authors) showed up to two social levels in the

10   Kabini 500-m and Uda Walawe datasets, and up to three levels in the Samburu dataset

11   (although sometimes, Uda Walawe showed up to three levels and Samburu, up to two, see

12   SI 5). The numbers of communities after the first pass were 20, 16, and 24 in the Kabini

13   500-m, Uda Walawe, and Samburu, datasets, respectively, and the numbers of communities

14   after the second pass were 7, 9, and 9, respectively. Eight communities were detected after

15   the third pass in Samburu. In the Kabini 500-m dataset, five of the seven final communities

16   changed from the first to the second pass, while the other two remained compositionally the

17   same. The numbers of communities that changed in composition from the first to the second

18   pass were four out of nine in Uda Walawe, and seven out of nine in Samburu. As in the

19   original Kabini dataset, communities with two social levels were larger than those with a

20   single level, although this was not statistically significant in the Uda Walawe dataset

21   (Mann-Whitney U tests: Kabini 500-m: U=25.5, Z_{adj}=-2.480, P=0.013; Uda Walawe:

22   U=39.5, Z_{adj}=-1.856, P=0.063; Samburu: U=15.0, Z_{adj}=-3.808, P<0.001). Interestingly,

23   community sizes at a particular community detection round were not different across

24   populations (average±SD after the first pass: Kabini 500-m: 5.45±3.05, Uda Walawe:

25   6.56±4.87, Samburu: 4.58±2.34, Kruskal-Wallis test: $H_{2,69}$=0.380, P=0.827; average±SD

26   after the second pass: Kabini 500-m: 15.57±9.74, Uda Walawe: 11.67±7.47, Samburu:

27   12.22±7.60, Kruskal-Wallis test: $H_{2,25}$=0.594, P=0.743; Fig. 5A; Mann-Whitney U tests,

28   Kruskal-Wallis test, and test for homogeneity of slopes below carried out using Statistica 8,

29   (45)). There was a correlation between community sizes after the second pass and the

30   number of first-level communities within those second pass communities (Fig. 5B), and a

31   test for homogeneity of slopes showed no difference in slopes across the three populations

32   (Multiple R^2=0.765, P<0.001, Effect of population: F[2,19]=0.502, P=0.613; Effect of the

33   number of first level communities: F[1,19]=52.608, P<0.001).

34

1   *Cluster analysis and cumulative bifurcation curve*

2   We carried out average-linkage clustering of females based on AI and plotted the

3   cumulative number of bifurcations at different linkage distances in order to compare the

4   shapes of the curves across populations. The cumulative bifurcation curves were concave-up

5   in the Kabini and Kabini 500-m datasets (Fig. S6), indicating a smaller number of linkages

6   at small linkage distances (tight associations) than at large linkage distances (loose

7   associations). This was similar to the pattern seen in Uda Walawe and unlike that seen in

8   Samburu, in which the curve was convex (24).

9

10 *Observed group sizes and the effect of group size on AI and network statistics in random*

11 *networks*

12 The average group size in the Kabini population was small, with 2.38 females per group

13 (Table 2, median=2) and the group size distribution was skewed to the right (Fig. 3C). We

14 found Lopé to have a significantly smaller average group size than that in Kabini, the

15 Kabini 500-m dataset and Uda Walawe to have similar group sizes, and Samburu to have a

16 significantly larger group size than the Kabini 500-m and Uda Walawe datasets (Welch's

17 two-sample tests, Table 2). Since differences in group sizes are likely to affect AI and

18 network statistics, we examined the effect of group size on these statistics, to find out

19 whether differences across populations in these statistics could simply be a result of

20 differences in group size. This was done using random datasets with group size distributions

21 mimicking real distributions by adjusting beta distribution parameters (α=1, β=7, maximum

22 group size=19 for Uda Walawe, α=2, β=9, maximum group size=26 for Samburu, and α=1,

23 β=9.5, maximum group size=27 for Kabini 500-m dataset) (see Methods). Maximum group

24 size was altered to change the average group size. With the exception of some values at very

25 small group sizes, the three different beta distributions of group sizes did not significantly

26 change the expected value of the AI or network statistic considered under random

27 association (Fig. 6). Under all three beta distributions of group sizes, the average expected

28 AI increased linearly with increasing average group size, the average degree and average

29 clustering coefficient increased and plateaued with increasing average group size, and

30 average path length decreased with increasing average group size (Fig. 6).

31

32 For each observed statistic (calculated from field populations with an observed average

33 group size), we calculated an expected random value of the statistic, and obtained an

34 interval of [expected - lower 95% CI of observed]/expected and [expected - higher 95% CI

1 of observed]/expected values for each population. If these intervals overlapped across

2 populations, it indicated that the populations differed from the random expectations to the

3 same extent and, therefore, differences in the statistic could be explained by differences in

4 observed average group size (see Methods). The higher average AI in Samburu compared to

5 the Kabini 500-m dataset could be explained as an effect of group size, with the average AIs

6 being similar when average group sizes were taken into account. The observed average AI

7 in both Samburu and Kabini 500-m datasets were larger than the expected average AI for

8 the corresponding average group sizes to the same extent ($[E-O]/E$=-0.667, interval: -0.578

9 to -0.756 for Kabini 500-m, $[E-O]/E$=-0.626, interval: -0.522 to -0.730 for Samburu). The

10 smaller average degree in the Kabini 500-m dataset compared to Samburu could also be

11 explained as an effect of group size differences in the two populations, as the observed

12 average degrees in both these datasets were smaller than the expected average degrees for

13 the corresponding average group sizes to the same extent ($[E-O]/E$=0.111, interval: 0.154-

14 0.067 for Kabini 500-m, $[E-O]/E$=0.092, interval: 0.122-0.061 for Samburu). The higher

15 average path length in the Kabini 500-m network than in Samburu (Table 2) could also be

16 explained by differences in average group size (Table S7). We had previously found the

17 clustering coefficient in the Kabini 500-m network to be significantly smaller than that in

18 Samburu (see above), but the former was 5.5% smaller than expected for a random network

19 of the same average group size while the latter was 11% smaller than expected for its

20 average group size. Therefore, corrected for group size, the Kabini 500-m dataset would

21 have a significantly higher clustering coefficient than the Samburu population, although this

22 difference was small (Table S7). Whereas differences between Samburu and Kabini 500-m

23 datasets could largely be explained by differences in average group size, the higher average

24 AI and higher average degree in the Kabini 500-m data compared to those in Uda Walawe

25 (average AI: $[E-O]/E$=-0.014, interval: 0.085 to -0.113; average degree: $[E-O]/E$=0.722,

26 interval: 0.750-0.694) remained as average group sizes were not significantly different

27 between these two populations.

28

29 **Discussion**

30

31 *Social structure in the Kabini population*

32 Based on the first quantitative data on social structure of female Asian elephants from India,

33 we found highly non-random associations between females, with the association network

34 being clearly demarcated into communities that we call clans. That there were only seven

12

1   associations between clans over five years suggests that the clan is the most inclusive level

2   of meaningful social structure in the Kabini population. Using the Louvain method of

3   community detection, we found up to three hierarchical social levels within clans. However,

4   there was variability in clan structure, with 38% of the clans seen more than 40 times

5   showing a single social level, 56% showing two levels, and a single clan showing three

6   levels. The hierarchical levels did not show up in the form of a typical nested multitiered

7   organization (with clear 'joint-family groups', bond groups, and clans seen in the field,

8   which seem to have been inferred based on animals sharing a common area, see 34) because

9   of possible constraints on group size. It is not clear whether single social levels in some

10 clans arose from recent permanent fission, demographic factors (see *Implications for Asian*

11 *elephant social structure* section below), or from clans not being fully identified. While the

12 last is possible, it is not likely as we used a 40-sighting cutoff for clans (as we had found,

13 based on clans sighted over 150 times, that 95% of the clan members were sighted on

14 average within the first 40 sightings of the clan and 92% within the first 30 sightings). It

15 would be interesting to examine the attributes, other than clan size, of clans showing

16 different hierarchical levels in order to understand the differences in clan structure.

17

18 *Comparison of social structure across populations and the role of group size*

19 Asian and African savannah elephants were initially thought to share largely similar social

20 organizations (34, 46). Subsequently, they were found to differ in their social structure (24),

21 with larger groups and stronger associations within and across groups in the African

22 savannah elephant. The Kabini 500-m dataset showed intermediate average degree, average

23 distance-weighted reach, clustering coefficient, and path length, compared to those of

24 Samburu and Uda Walawe. The network structure curve, cumulative bifurcation curve, and

25 AI distribution from the Kabini 500-m dataset were more similar to those from Uda Walawe

26 rather than Samburu (see 24). However, contrary to previous finding that kurtosis was

27 higher in African savannah than in Asian elephants (24), we found that the kurtosis of the

28 Kabini 500-m dataset was higher than those of both Samburu and Uda Walawe populations

29 (Table 2). Since kurtosis measures the heaviness of the tail compared to the normal

30 distribution, this result reflects the difference between the average AI and AIs in the tail of

31 the distribution, and not the latter alone (which was highest in Samburu). Visual comparison

32 of the original Kabini dataset's network with the Amboseli network showed a more

33 connected network in the Amboseli population with no AI cutoff, but similar networks in

34 Kabini and Amboseli at AI cutoffs of 5% and 10% (Fig. 1). However, in the absence of

13

1   access to the Amboseli network data (29), we were not able to make any further

2   comparisons.

3

4   Despite the above differences between the Samburu African savannah elephant and Asian

5   elephant populations, we found through Louvain community detection that there was

6   hierarchical structuring within social networks in the Kabini 500-m dataset, Uda Walawe,

7   and Samburu populations. Since the cumulative bifurcation curve combines data from

8   across the clustering dendrogram, variation across social units in AIs and unequal tiers

9   across social units do not allow for hierarchical structure to be detected (also see 24), which

10 the Louvain algorithm can recover. The number of hierarchical communities found were

11 similar across populations. Although Samburu often showed a third round of clustering

12 (Uda Walawe sometimes showed a third round and Kabini did not), this only resulted in a

13 minor change, with nine communities grouping into eight after the third pass. Community

14 sizes were not significantly different across populations, both after the first and second pass

15 of community detection. There was also no difference across populations in the relationship

16 between second pass community sizes and the number of first-level communities within

17 second pass communities (Fig. 5B). Results from these analyses suggest basic similarities in

18 social structure across elephant species. We show that some of the differences in social

19 structure arose from differences in group sizes across populations. We found that the higher

20 average AI and higher average degree in Samburu compared to the Kabini 500-m dataset

21 arose from different average group sizes in the two populations. Average path length was

22 also similar when corrected for group size. The clustering coefficient in Samburu was

23 smaller than expected at the corresponding group size compared to that in the Kabini 500-m

24 dataset, but the extents to which they differed was small. We used 1.96 SE as the 95%

25 confidence intervals for comparisons of the observed and expected values. It is likely that

26 the errors and, therefore, the overlaps in statistics between populations would actually be

27 larger. Therefore, the tests are conservative, and it is plausible that group size differences

28 account for more of the social structure differences than we find.

29

30 Although there is a continuum of societies showing fission-fusion dynamics (22), if they

31 had to be compared to the modal multilevel organizations (see 21) based on AI, network

32 statistics, and cumulative bifurcation curves, the social structure of the African savannah

33 elephant would correspond to the flexible nested society (21; with the lower social level

34 stable and the higher level flexible) or lie between the strict nested and flexible nested

1   multilevel societies, while that of the Asian elephant would correspond to the classical

2   fission-fusion society (with the lower level flexible and the higher level stable) or lie

3   between the classical and flexible nested fission-fusion society. Nestedness does not seem to

4   be complete in the African savannah elephant since partial or whole core groups may

5   associate together to form a larger unit, and single females, although rare (47), have a choice

6   of associating or not with their family group members (29, 47). African forest elephant

7   social organization has been previously compared to the individual-based fission-fusion

8   society of chimpanzees (44). However, as mentioned above, we find underlying similarities

9   in network structure between the African savannah and Asian elephant populations and the

10   differences in network statistics seem to emanate from group size differences. Since the

11   average size of first-level Louvain communities is similar to the average group size in

12   Samburu, individuals of a first-level community can potentially be part of the same group,

13   resulting in high AI values, and easily detectable nestedness. This also results in lower-level

14   social units such as the family/bond group being stable units (see 19). On the other hand, the

15   average sizes of first-level communities are about twice the average group sizes in Uda

16   Walawe and Kabini (Kabini 500-m dataset). When group sizes are restricted, only subsets of

17   the first-level community can associate together, resulting in lower AIs, unstable lower-level

18   social units, and a less nested appearance. This would suggest that the multilevel social

19   structure observed in the Asian elephant is a derived condition due to restricted group size

20   (see 'Route A' of Aureli *et al.* (22)), compared to that observed in the African savannah

21   elephant. It is interesting that the average first- and second-level community sizes were not

22   different across elephant populations, indicating that there might be something fundamental

23   about these sizes. It is possible that demographic processes (e.g. 48) or cognitive factors

24   (e.g. 49) influence these community sizes.

25

26   The difference in group sizes between the Samburu population and the two Asian elephant

27   populations probably relate to differences in ecology, and more specifically to food resource

28   distribution. Asian elephants typically inhabit moister, more forested habitat than African

29   savannah elephants, and possibly face more challenges obtaining food. African forest

30   elephants, which inhabit wetter and denser habitats, with ephemeral and patchily distributed

31   resources (50), than the Asian elephant on average, show even smaller group sizes (44, 51,

32   see Table 2), a highly disconnected association network, and possibly an individual-based

33   fission-fusion society (44). Turkalo and Fay (52) suggested that, apart from the patchy

34   distribution of food, low predation by humans might explain the small group sizes of

15

1   African forest elephants compared to African savannah elephants that have faced high

2   poaching pressure. However, despite differences in predation between Sri Lanka (historic

3   human depredation, no current animal predator) and southern India (tigers can prey on

4   calves), there was no difference in the average group sizes in Kabini (Kabini 500-m dataset)

5   and Uda Walawe.

6

7   That group size and social structure are interlinked has been obvious (see 53). Grouping

8   patterns modulate interaction opportunities, thus resulting in the social structure seen (22,

9   27, 53-55). However, we show, for the first time, how social structures uncovered by AI and

10   network statistics in fission-fusion societies may differ primarily because of group size

11   differences. Thus group size differences may mask underlying similarities in the social

12   structures of related species showing fission-fusion dynamics, which can be uncovered by

13   hierarchical community detection.

14

15   *Implications for Asian elephant social structure*

16   Despite broad similarities, there were also some differences in Asian elephant social

17   structure based on the limited detailed comparison between one Sri Lankan (Uda Walawe)

18   and one southern Indian (Kabini 500-m dataset) populations. The average number of

19   associates, average association strength, and social network connectedness was greater in

20   the Kabini 500-m dataset compared to Uda Walawe, although average group sizes were not

21   different between the two populations (Table 2). It is possible that the lower levels of

22   cohesiveness in the Uda Walawe population arose from extensive historical disturbance in

23   Sri Lanka, with thousands of elephants having been hunted and captured during the 1800s

24   and early 1900s (see 33, 42), and the elephant population being decimated to only about

25   1500 individuals by the mid-1900s (see 33). By one estimate, at least 17,000 elephants were

26   hunted, exported, or died in captivity during the 19th century, changing the behaviour and

27   demographics of elephants on the island (see 42). Hunting and capture of elephants in

28   southern India appears to have occurred on a much smaller scale, with no decline in

29   population size (41, pp. 68-69). Moreover, the *kheddah* method used for capturing female

30   elephants in southern India (including in part of our study area, Nagarahole National Park)

31   was intended to capture entire groups rather than isolated individuals (41, pp. 70-73).

32   Therefore, female social organization in southern India is unlikely to have been as impacted

33   as that in Sri Lanka.

34

1   Although unrelated females from decimated surviving groups are known to associate
2   together in elephant populations subject to anthropogenic mortality (39, 56-58), breakdown
3   of social structure itself may or may not change group size. Smaller family groups were
4   found in highly poached African savannah elephant populations (see 56, 59), and heavy
5   poaching was also thought to have reduced associations and affected social network
6   structure in Lopé, Central Africa (44). Decimation of the population may increase group
7   size where the habitat allows it, but if there is a resource-based constraint on group size,
8   network cohesiveness is likely to decrease (because of associates being killed) while the
9   group size may not change. We think that this might be the likely scenario in Uda Walawe.
10   Recent anthropogenic disturbance appears to be similar in Kabini and Uda Walawe, with
11   dams built in the late 1960s-early 1970s, submerging forest land and creating reservoirs that
12   elephants now use.

13

14   As mentioned previously, associations in the Uda Walawe population had been defined
15   using a 500-m cutoff (24-25), which is why we used the Kabini 500-m dataset for an
16   appropriate comparison. If this was not used, as in our original network, the Uda Walawe
17   network would also presumably be even less cohesive and consist of small communities of
18   females. This might explain the observations of Fernando and Lande (30), who had used a
19   100-m cutoff to identify groups in southeastern Sri Lanka, and suggested that female social
20   organization was limited to the family level, based on family sizes of 10-20 individuals in
21   African savannah elephants mentioned by Wilson (60). We suggest that the most inclusive
22   level of female social structure, which is also the most stable level, in Asian elephants be
23   called clans. The numbers of females in the most inclusive level in the Kabini population
24   were similar to those in Samburu (Table 1). We also found structuring within some clans,
25   although this is not easy to discern because of groups being small. A common property of
26   clans in the Asian elephant seems to be the lack of association with other clans, despite
27   proximity ("herds" of McKay (33), "family groups" of Fernando and Lande (30), this
28   study). The extent to which the small number of observations resulted in smaller community
29   sizes in Ruhuna is not clear (herd sizes found by McKay (33): 15-40 individuals, by
30   Fernando and Lande (30): 7-24 individuals, by us: inter-quartile range: 17-40, maximum: 83
31   individuals). The smaller the group size, the longer is the study period required to observe
32   sufficient associations between individuals in order to interpret social structure in a species
33   showing fission-fusion dynamics. However, there were some small clans in Kabini too,
34   arising from deaths of females and/or a series of male offspring, who do not contribute to

17

1   clan size. Although most of the single females in Fig. 2 are from clans whose ranges are

2   probably at the periphery of our study area, such that we have not yet sighted other females

3   from those clans, there were a few clans that were sighted many times but continued to

4   show a small number of females. The most notable of them included only two females and

5   their dependant offspring, despite being sighted over 300 times. Although a clan of two

6   might as well be called a family group, we prefer to retain the term clan for the most

7   inclusive grouping because, in clans that show structuring, the clan and not the family group

8   seems to be the most stable unit.

9

10   **Methods**

11

12   *Field data collection*

13   The field study was carried out in Nagarahole National Park and Tiger Reserve

14   (Nagarahole; 11.85304°-12.26089° N, 76.00075°-76.27996° E, 644 km^2) and the adjacent

15   Bandipur National Park and Tiger Reserve (Bandipur; 11.59234°-11.94884° N, 76.20850°-

16   76.86904° E, 872 km^2), in the Nilgiris-Eastern Ghats landscape in Karnataka, southern India

17   (Fig. S1). The greater landscape holds the single largest population of over 8,500 (61) Asian

18   elephants in the world, of which about 2,600 (62) elephants probably use Nagarahole and

19   Bandipur. The area sampled was centred around the Kabini reservoir and extended into the

20   forests of Bandipur and Nagarahole, and we refer to the population as the Kabini population

21   (see 63).

22

23   Field data were collected from March 2009-July 2014, on a total of 878 field days.

24   Sampling during 2010 was limited because of field permit issues. We drove along pre-

25   selected routes from ~6:30 AM to 6:00-6:45 PM (depending on daylight hours and field

26   permits) and identified female elephant "groups" as aggregations of female elephants,

27   usually along with their young, that showed coordinated movement (especially towards or

28   away from a water source or salt lick), coordinated behaviours (such as bunching and facing

29   the same direction when perceiving a threat from other elephants or heterospecifics), or

30   affiliative behaviour, and were usually within 50-100 m of one another. During our original

31   data collection, we did not use a 500-m distance cutoff because it was clear from the

32   uncoordinated, and sometimes aggressive, interactions between different aggregations of

33   elephants within 500 m of one another that they did not belong to a single social group.

34   Sighting details of elephant groups, including group size, time of sighting, and GPS location

1   were recorded. Individuals were photographed and identified based on multiple natural

2   physical characteristics, and aged based on body size, skull size, and body characteristics,

3   using the Forest Department's semi-captive elephants of known ages in the area as a

4   reference (see 63). Although individuals older than 15 years have previously been referred

5   to as adults (34, 63), since we subsequently found that females were often sexually mature

6   at 10 years of age (as in other elephant populations, see 64-65), we analyzed associations for

7   females that were 10 years old or older (referred to simply as females in this paper).

8

9   *Association data*

10 We retained only sightings in which all the females could be identified. We considered

11 sightings of the same group to be independent if they were observed again after 2.5 hours

12 because this interval yielded roughly similar probabilities of groups either changing in

13 composition or not (Fig. S2). Changes in group composition within this time period were

14 not recorded as separate sightings. In the Kabini 500-m dataset, we grouped together

15 females that were within 500 m of one another, based on GPS data. In this dataset, sightings

16 sharing a common female during the day were merged together into a single sighting, after

17 the manner of de Silva *et al*. (25). Further, only females sighted at least 20 times were

18 retained in the dataset (n=109 females) as had been done in the Uda Walawe and Samburu

19 datasets. AI between pairs of females was calculated as the ratio of the number of times two

20 females A and B were seen together (N_{AB}) to the number of times either A or B was

21 observed (N-D, where N is the total number of sightings and D the number of times neither

22 A nor B was seen) (66). Unless otherwise mentioned, data manipulation and analyses were

23 carried out using MATLAB 7 (67).

24

25 *Social structure using networks*

26 We examined social structure using network and cluster analyses. Social networks were

27 constructed based on AI between individuals and visualized using Gephi 0.8.2 (68). The

28 following network statistics were calculated: *degree* (the number of connections or *edges*

29 arising from an individual or *node*), *clustering coefficient* (the proportion of all possible

30 edges between the immediate neighbours of a focal node that actually exist, and, therefore,

31 the probability that two randomly chosen neighbours of a focal individual are connected),

32 *path length* (the number of edges on the shortest path between two nodes), and *distance-*

33 *weighted reach* (the sum of the reciprocal of path lengths from a focal node to other nodes),

34 calculated for individual nodes, and *density* (the proportion of all possible connections in the

19

1   network that actually exist) and *modularity* (see below) calculated for the entire network

2   (69-71). In order to find out whether the observed network was different from a random

3   network, we compared the degree distribution of the observed network against Poisson

4   expectation that would arise from an Erdös-Rényi random network (72). We also tested for

5   preferred associations by randomly permuting the association data following Whitehead

6   (73; Table S3). Network statistics of the Kabini 500-m dataset were compared with

7   available statistics from previously studied populations. Since the mean and SD of these

8   statistics were generally available from other populations, but the distributions were likely

9   to be skewed and/or have different variances, we compared statistics across populations

10   using Welch's two-sample tests (74). It has been shown through simulations that the

11   Welch's test performs well under several scenarios involving the comparison of skewed

12   distributions with unequal variances and sample sizes (75). As a further precaution, we used

13   this test to compare statistics between the Uda Walawe and Samburu populations that had

14   earlier been analyzed using randomization tests (24), and found the same results in all eight

15   tests performed. Statistics from the Kabini 500-m dataset were used for comparison with the

16   Uda Walawe and Samburu populations (as shown in 24).

17

18   Community structure within networks, and hence *modularity* (a measure of the extent to

19   which a community is partitioned; this can be measured by comparing the fraction of edges

20   within communities to that between communities), was identified using the Louvain method

21   (43). The Louvain method identifies communities hierarchically and is known to be

22   accurate. It uses a weighted network (in which edge weights, which are AI values between

23   females, are incorporated rather than mere presence or absence of associations between

24   females) in which each node is initially considered a separate community. Changes in

25   modularity upon rearrangements of nodes are evaluated and rearrangements are stopped

26   when a local maxima of modularity is obtained. The communities detected at this point are

27   used as nodes for the next pass. Since the algorithm begins with rearrangements of single

28   nodes across communities, this method does not suffer from the problem of identifying

29   communities at a small scale. The algorithm is repeated iteratively until the maximum

30   modularity is obtained, resulting in hierarchical partitions of communities within

31   communities (43). This method allows for structure to be meaningfully examined at

32   different hierarchical levels because the intermediate partitions correspond to local

33   modularity maxima (43). This method, therefore, naturally lends itself to the investigation of

34   social organization, when one is interested in finding out whether there are hierarchies or

1   not. The Louvain method was implemented by calling the C++ codes made available by the

2   authors (https://sites.google.com/site/findcommunities/) from MATLAB. We carried out the

3   Louvain hierarchical community detection for the Uda Walawe and Samburu data also (data

4   from 24, kindly provided by the authors) for comparison with the Kabini (Kabini 500-m

5   dataset) population. We also constructed network structure curves following de Silva *et al*.

6   (25) for comparison across populations. Here, the number of clusters (based on the Louvain

7   method) with more than one female was plotted against AI threshold. The network structure

8   curve provides information on the cohesiveness of the social network at different

9   association strengths. Significant changes in the slope of the network structure curve were

10   detected by comparing the values of number of clusters to the left and right of each point

11   within a moving window of 0.3 using the Wilcoxon rank sum test (see 25).

12

13   *Effect of group size on AI and network statistics*

14   We created random datasets, each with 100 individuals in 1500 sightings, distributed in

15   group sizes following beta distributions with parameters that resulted in group size

16   distributions that mimicked known elephant group size distributions (α=1, β=7, maximum

17   group size=19 for Uda Walawe, α=2, β=9, maximum group size=26 for Samburu, and α=1,

18   β=9.5, maximum group size=27 for the Kabini 500-m dataset; Kabini group size

19   distribution from this study, Uda Walawe and Samburu group size distributions from 24).

20   The maximum group size was altered to change average group size. We calculated the

21   average, SD, and kurtosis of AI, and network statistics including average degree, average

22   clustering coefficient, and average path length for the random datasets. One hundred

23   random datasets were created for each beta distribution type with each maximum group

24   size. Therefore, average group size and the AI or network statistics were averaged across

25   these 100 replicates. We then plotted the statistic under consideration against average group

26   size based on the random dataset, for each of the three beta distributions of group sizes, to

27   visualize how the statistic changed with increasing average group size. For each observed

28   statistic (calculated from field populations with an observed average group size), we

29   calculated an expected random value of the statistic by interpolating the appropriate random

30   curve (with matching beta distribution). Interpolation was done using cubic spline in

31   CurveExpert version 1.37 (76). Using the 95% CI of the observed estimates, we calculated

32   an interval with (expected - lower 95% CI of observed)/expected and (expected - higher

33   95% CI of observed)/expected values for each population. If these intervals overlapped

34   across populations, it indicated that the populations differed from the random lines to the

21

1   same extent and, therefore, differences in the statistic between the populations could be

2   explained by differences in observed average group size. If the intervals of (E-O)/E did not

3   overlap, it indicated that differences in the statistic between populations were significant

4   beyond the effect of average group size. This was a conservative test because it was possible

5   that the intervals of (E-O)/E could actually be larger than what we calculated based on 95%

6   CIs.

7

8   *Cluster analysis and cumulative bifurcation curve using AI*

9   Although hierarchical cluster analysis based on AI may not be useful for detecting

10   hierarchical structure if social units at each tier of social structure show variability in AIs

11   (also see 24), we used this method simply to compare the shapes of cumulative bifurcation

12   curves across populations. We constructed dendrograms based on associations between

13   individuals and used the plot of the cumulative number of bifurcations in the dendrogram at

14   different linkage distances to identify knots (see 19). The average-linkage (UPGMA)

15   method was chosen for clustering because it yielded the maximum cophenetic correlation

16   coefficient value (CCC=0.976). Knots were identified by comparing the number of

17   bifurcations in 0.2 and 0.3 windows above and below each point in the cumulative

18   bifurcations plot, using a Wilcoxon rank sum test.

19

6

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1   **Figure Legends**

2

3   Fig. 1. Social networks in A) Kabini, original dataset, B) Kabini 500-m dataset, C) Uda

4   Walawe (Sri Lanka), D) Amboseli (Kenya), and E) Samburu (Kenya), based on all

5   associations (first column), associations with an AI cutoff of 5% (second column), and an

6   AI cutoff of 10% (third column). The networks in C and E are based on de Silva and

7   Wittemyer (24; data kindly provided by the authors) and those in D, from Archie and Chiyo

8   (29; reproduced with the permission of the publisher, John Wiley and Sons, license number

9   4025511083875). The dashed oval in D indicates a bond group. Only individuals sighted at

10   least 20 times are included in the Kabini networks, as was the case in the Uda Walawe and

11   Samburu networks.

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14   Fig. 2. Social network based on the entire dataset of 330 females drawn using the

15   Fruchterman Reingold layout (77) in Gephi. Each node here is a female and the edges

16   between the nodes indicate nonzero AI between females (edge thickness is proportional to

17   AI). Nodes are coloured based on modularity classes and we refer to nodes of the same

18   colour as a clan. The expected (Poisson) and observed degree distributions based on this

19   social network are shown. The average degree was 8.32 based on this network, which

20   includes individuals seen only once; when such individuals were removed, the average

21   degree was 9.55 (274 individuals). Most of the solitary nodes towards the centre are females

22   that were seen only once or a few times. The small number of connections across clans

23   arose from seven sightings during the five year study period. Four of these were due to

24   associations between a female with a newborn calf (that could not keep pace with the group)

25   with other clan females.

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27

28   Fig. 3. AI distributions based on A) the entire original Kabini dataset and B) the Kabini 500-

29   m dataset, and C) group size distributions based on the original Kabini dataset and Kabini

30   500-m dataset. The relatively high frequency of AI=1 in A) is because of small number of

31   sightings of some individuals, and this disappears if only females seen at least 20 times are

32   considered.

33

1   Fig. 4. Network structure curve (of females seen at least 20 times) for A) the original data

2   and B) data based on a 500-m distance cutoff, showing two points of slope change based on

3   window of 0.3 ($P<0.001$ for AI threshold of 0.32 and $P=0.006$ for AI threshold of 0.65,

4   points of slope change were 0.33 and 0.665 based on a window of 0.2; $P=0.001$ for AI

5   threshold of 0.38 and $P=0.012$ for AI threshold of 0.69, $P=0.082$ for the AI threshold of

6   0.69 based on the 0.2 window).

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9   Fig. 5. A) Community sizes after the first and second rounds of community detection using

10   the Louvain algorithm, based on the Kabini 500-m, Uda Walawe, and Samburu datasets.

11   Means and 95% CI (1.96 SE) are also shown. B) Sizes of communities after the second pass

12   of community detection, composed of varying numbers of first-level communities in the

13   Kabini 500-m, Uda Walawe, and Samburu datasets. Equations of the trendlines (in the same

14   colours as the data points of the respective populations) for the three populations are: Kabini

15   500-m: $y=5.227x+0.636$, $R^2=0.904$, Uda Walawe: $y=3.861x+4.803$, $R^2=0.453$, Samburu:

16   $y=3.521x+2.833$, $R^2=0.859$.

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19   Fig. 6. Observed average AI and network statistics from the Kabini 500-m, Uda Walawe,

20   and Samburu datasets, and expected values of these statistics at different average group

21   sizes, based on random datasets with different beta distributions ($\alpha=1$, $\beta=9.5$; $\alpha=1$, $\beta=7$;

22   $\alpha=2$, $\beta=9$, see Methods) of group sizes. A. average AI, B. average path length, C. average

23   degree, and D. average clustering coefficient. All the error bars are 1.96 SE.

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1 **Tables**

2

3 Table 1. Details of social tiers in previously studied elephant populations and from the
4 present study in Kabini. Clan sizes in Kabini are based on 16 clans seen at least 40 times
5 each. The other data come from Fernando and Lande (30) for Ruhuna National Park (Sri
6 Lanka), de Silva et al. (25) for Uda Walawe (Sri Lanka; the values were calculated using
7 Louvain community detection from data kindly provided by Shermin de Silva), Moss and
8 Poole (23), Lee (78), and Moss and Lee (47) for Amboseli (Kenya), and Wittemyer et al.
9 (19) and Goldenberg et al. (38) for Samburu (Kenya) (except for the cell marked ‡, whose
10 values were calculated using Louvain community detection from data in 24, kindly provided
11 by the authors).

12

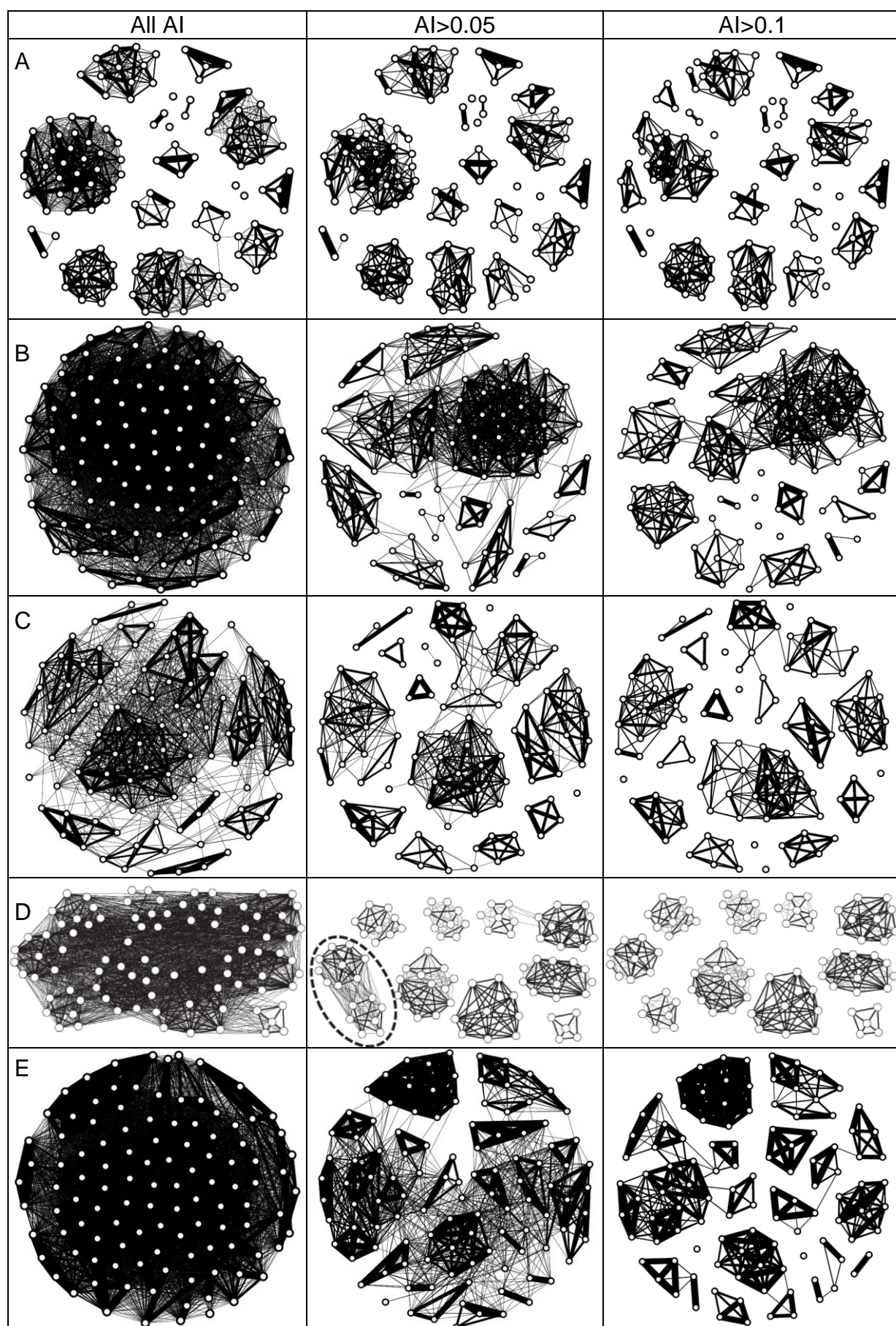| Population	Ave. no. of females in a family group (range)	Ave. no. of individuals in a family group (range)	Ave no. of females / family groups in a bond group	Ave. no. of individuals in a bond group (range)	No. of females in a clan / fourth-tier unit / most inclusive unit	No. of individuals in a clan / fourth-tier unit / most inclusive unit
Kabini	–	–	–	–	Mean: 13.31, SD: 7.78, Median: 11.5, IQR: 7.5-18.5, Max: 32	Mean: 29.19, SD: 19.76, Median: 21, IQR: 17-39.5, Max: 83
Kabini 500m, ≥20 sightings	–	–	–	–	Mean: 15.57, SD: 9.74, Median: 18, IQR: 9-19.5, Max: 31	–
Uda Walawe	–	–	–	–	Mean: 11.67, SD: 7.47, Median: 12, IQR: 5-17, Max: 23	–
Ruhuna	–	–	–	–	7.75 (4-11)[†]	14.75 (7-24)[†]
Amboseli	2.35 (1-9)*	7.22 (2-23)*	2-5 family groups	–	5-9 family groups	Range: 50-250
Samburu	2.2• (1-5)	7.64 (1-15)	2.0 family groups (4.4 females on ave., based on •)	16 (6-40)	‡Mean: 13.75, SD: 7.46, Median: 11, IQR: 8.8-16, Max: 28	Median: 33.5, IQR: 28.8-80.3; Median: 32, IQR: 23.5-38 during a subsequent period.

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2 *Family groups in Amboseli comprised, on average, 2.35 females and 7.22 total individuals

3 in 1976, while core groups (erstwhile family groups that had expanded) in 2002 comprised

4 an average of 7.08 females (47). The former are shown so that appropriate comparisons can

5 be made across populations. †These were described as family groups originally (because

6 families contained up to 10-20 females and their offspring according to Wilson (60)), but

7 Asian elephant populations are placed in the last two columns here as the most inclusive

8 social units. IQR: Inter-Quartile Range.

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1   Table 2. Average group size (number of females), AI statistics, and network statistics for

2   different elephant populations. Statistics for the Uda Walawe and Samburu populations are

3   reproduced from de Silva and Wittemyer (24) and the ones with asterisks were calculated

4   from network files (of 24) kindly provided by Shermin de Silva and George Wittemyer.

5   Statistics for the Lopé forest elephant population are reproduced from Schuttler *et al*. (44).

6   Statistics such as the degree and density might be underestimates in Lopé because the

7   number of times individuals were sighted was very small (network statistics based on

8   individuals sighted at least twice) and there was a significant correlation between the

9   number of sightings and the number of associates (44). The small average group size is,

10   however, in keeping with that found in forest elephants in Dzanga Bai (average female

11   group size including dependants: 2.7, SD=1.3) in a long-term study (51). The average group

12   size for Kabini ≥20 sightings is the average of group sizes of only those sightings in which

13   all the females were seen at least 20 times (this is shown for the sake of completeness).

14   Significant differences in metrics based on the Welch's two-sample test are shown using

15   superscripted alphabets (a<b<c), with α set to 0.0017 based on a flat Bonferroni correction

16   for 29 tests.

17

Population	Average group size (SD)	Percentage of non-zero AI values	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average distance weighted reach (SD)	Average path length (SD)	Modularity	Density
Kabini	2.38 (1.83)[b]	2.5	315.42	8.32 (8.15)	0.87 (0.165)	12.45 (9.14)	2.17 (1.433)	0.936	0.025
Kabini ≥20 sightings	2.35 (1.84)[b]	10.8	67.97	13.34 (9.95)	0.95 (0.082)	15.87 (9.85)	1.60 (1.160)	0.803	0.108
Kabini 500-m, ≥20 sightings	3.16 (3.14)[c]	69.4	37.71	74.95 (19.50)[b]	0.81 (0.056)[b]	92.46 (9.75)[b]	1.31 (0.463)[b]	0.398	0.694
Uda Walawe	3.07 (2.34)[c]	20.8	10.35	22.53 (11.85)[a]	0.63 (0.13)[a]	59.46 (9.04)[a]	* 2.07 (0.740)[c]	* 0.701	* 0.217
Samburu	5.03 (4.61)[d]	82.8	27.59	88.87 (16.00)[c]	0.88 (0.04)[c]	99.94 (7.96)[c]	* 1.18 (0.388)[a]	* 0.474	* 0.815
Lopé	1.48 (0.80)[a]	1.4	-	2.06	0.86	-	2.157	-	0.033

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1   **Figures: Fig. 1**

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1   **Fig. 2**

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1 **Fig. 4**

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1   **Fig. 5**

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Fig. 6