

**Identifying Natural Grouping Structure in Gelada Baboons:
A Network Approach**

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Abstract

We use network analysis of co-herding and nearest neighbour data for harems from several study populations to examine the natural grouping patterns of gelada baboons, a molecular fission-fusion primate species. We show that the association patterns of the harems reflect grouping levels of ~2, ~4, ~7, and ~14 harems (equivalent to ~30, ~50, ~100 and ~200 individuals). These patterns are stable across both time and space. Analysis of the distribution of harem sizes across four study populations suggests that these grouping levels reflect the processes that influence harem fission, combined with a viscosity reflecting time since fission. We suggest that the natural social grouping for this species is a set of 2-3 harems that are the product of recent harem fission, in line with predictions from the social brain hypothesis, and that successive fission events over time cumulatively give rise to the other grouping layers. While the grouping of ~100 animals has previously been identified as the *band*, the ~50 layer was previously unidentified. We do not know what its function is, though it closely resembles typical *Papio* troops in size.

Key words: fission-fusion, hierarchical structuring, network analysis, social brain hypothesis, social organisation

Introduction

For most mammals, observers have little difficulty discerning social groups. Individuals forage and rest together, and, although animals may emigrate and immigrate from time to time, these movements occur relatively infrequently, and in consequence groups have a degree of demographic stability over at least the short term. In other cases, however, foraging groups are less stable, with individuals or subgroups joining and leaving with a frequency that can be on a scale of days or even hours (Sundaresan et al. 2007). In these cases, it is more difficult to discern the species' natural grouping pattern, or even whether there are stable relationships between individuals or groups of individuals. These species are typically characterised as having a fission-fusion social system, and examples include elephants, the herd-forming bovids, the cetaceans and, among the primates, chimpanzees (*Pan* spp.), spider monkeys (*Ateles* spp.), the gelada (*Theropithecus gelada*) and hamadryas (*Papio hamadryas*) baboons, as well as Guinea baboon (*Papio papio*) and the drills and mandrills (*Mandrillus* spp.), and perhaps the genus *Nasalis*.

It has become customary to differentiate two types of fission-fusion sociality: atomistic and molecular (Kappeler & van Schaik 2002). The first is defined by the fact that individuals join and leave foraging groups on their own, while the second refers to those cases where the fundamental unit of society is a small stable basal unit (usually a reproductive or family group) that joins and leaves unstable foraging herds as an integrated unit and is never further sub-divided. Examples of the latter kind include elephants (where the matriarch-led family unit forms a cohesive group: Moss et al. 2011) and the gelada and hamadryas baboons (where harems consisting of a breeding male, several females and their dependent offspring are the basal units of society: Dunbar & Dunbar 1975; Kummer 1965).

In molecular fission-fusion taxa, associations between basal social units in foraging herds can be highly unstable, with fission and fusion events occurring frequently (often on a daily basis). The home ranges of basal units overlap but aren't necessarily completely spatially co-terminus, and it is never entirely clear whether there are any consistencies in the patterning of relationships

between individual units. In cases such as the gelada and hamadryas, the fact that there is an identifiable basal social unit (the reproductive unit or harem) is uncontroversial, but it is difficult to be certain that there are higher order communities because grooming (the common basis for establishing relationships between individuals in primates) almost never occurs between members of different units. Nonetheless, most field workers have been persuaded that higher order groupings do exist (Dunbar 1984; Dunbar & Dunbar 1975; Kawai 1979; Kawai et al. 1983; Kummer 1968; Snyder-Mackler et al. 2012), albeit mainly on the basis of casual observation of the frequencies with which units forage together or share sleeping cliffs. For both species, several different grouping levels have been tentatively identified. In the case of hamadryas, these have been labelled harems, clans, bands and sleeping troops (with bands being thought to be the homology of conventional *Papio* troops) (Kummer 1968); in the case of the gelada, they are harems, teams, bands and, less certainly, communities (Dunbar 1984; Kawai et al. 1983; Snyder-Mackler et al. 2012). Although the evidence for this in the case of the gelada is based on the use of statistical clustering methods applied to different kinds of association data (Kawai et al. 1983; Snyder-Mackler et al. 2012), none of these analyses involved a comprehensive sample of all harems that use the same ranging area and, realistically, none did more than confirm the existence of bands. In addition, there remains some uncertainty both as to the natural grouping patterns for this species and whether the higher order groupings have a consistent numerical size. We here undertake a rigorous analysis of data for the gelada (*Theropithecus gelada*), using a network analysis approach to explore association patterns between individually known reproductive units (harems). Importantly, our main analysis focuses on all the harems that used a particular study area.

We use data of three different kinds. First, we use the frequencies with which gelada harems associated together in the same foraging herd (co-herding data set) to estimate network structure among the 51 identified units that foraged in a given locality (the Sankaber ridge in the Simen Mountains National Park, Ethiopia). This allows us to determine whether there is any consistent network structure among these units. This data set is necessarily coarse-grained, because any two

units that happen to spend at least part of a day in the same herd are counted as being associated, when in fact they may have spent the entire time on opposite sides of the herd and never actually come into direct contact (and might well have been antagonistic had they actually done so). A second, smaller data set (neighbourhood data set) overcomes this problem: it consists of nearest-neighbour data obtained from a subset of 21 of these harems, including all the harems of one band. These data allow a finer grained analysis of association patterns. The two data sets view the same spatial distribution of the harems in very different ways, providing, respectively, a coarse-grained top-down and a fine-grained bottom-up picture. In both cases, we use network analysis methods to determine natural clustering patterns within the data. Finally, we undertake an analysis of the distribution of harem sizes across four study populations to determine whether the patterns we observe might be explained by harem fission processes.

Methods

The main data sets used in the analyses of social networks were obtained in the Sankaber area of the Simen Mountains National Park, Ethiopia, between November 1974 and July 1975, inclusive. A detailed description of the study area and the animals can be found in Dunbar & Dunbar (1975). The data are based on a complete census of all the harems (reproductive units) that used the study area at the time. Individual harems were identified principally on the basis of recognised individuals. Combined with the obvious spatial integrity of the harems (although the adult members of a harem could become quite spaced out, neither the females nor their harem males were wholly tolerant of adult members of other units straying into their space: Dunbar 1983; Snyder-Mackler et al. 2012), these individually known animals allowed a large number of harems to be identified very quickly. All the adult members of around 15 of the 18 harems belonging to the main study band (in all, 224 individuals, plus associated all male groups) were known individually and could be identified anywhere, mainly because they were the subjects of regular focal individual sampling (Dunbar 1983, 1984). Most of the remaining harems were recognised either by specific

individually identifiable members or by their composition, but all were repeatedly censused to establish their size and composition. Daily records were maintained of the composition of each harem, tracking births, deaths and maturations, emigrations and immigrations. A complete list of harems and their sizes as of December 1974, together with their nominal band affiliations as identified at the time, is given in Table S1.

Each day that observers were in the field, the location and movement of all herds were recorded on scale maps of the study area, and the identities of all harems and all male groups present were noted. Whenever a herd was encountered for the first time on a given day, it was censused and its constituent harems and all male groups recorded. In most cases, the observer(s) stayed with the same herd for the whole day, but other herds might be encountered in passing and these would always be censused. If a herd fissioned, or two herds fused, during the course of a day, a new census was taken and counted as a separate sample. The data derive from 203 field days, during which 602 separate herds were encountered whose sizes ranged from 1-21 harems (mean = 4.6).

Although the 51 units in the study area were thought to belong to six different sub-communities (or bands) which had separate core ranging areas, the full ranging areas of all these bands overlapped and included the whole of the central study area (Dunbar & Dunbar 1975, Fig. 42); as a result, the various units from the different bands foraged together in the same herd on at least some occasions. On rare occasions, all the harems in the study area might be found in a single herd; more typically, however, herds that consisted of several bands contained only some of the harems of each band. Because herds fused and fissioned on an almost daily basis, co-presence in the same foraging herd provides an index of how closely individual units were associated with each other. We therefore adopted a gambit-of-the-group strategy (Whitehead & Dufault 1999) in which we assume that harems that occur in the same foraging herd have some kind of tie. In doing so, we make no assumptions about the band membership of individual harems, preferring to allow the data to tell us band membership.

The habitats occupied by gelada are extremely open, with visibility often unrestricted over many hundreds of metres. In addition, the animals were totally habituated (see Dunbar & Dunbar 1975, Fig. 2; Dunbar 1984, Fig. 1), allowing the observers to move through a herd without eliciting concern. Hence, if a harem was present in a herd, it would always have been identified. Absence from a herd can therefore unequivocally be interpreted as meaning that, on that particular day, the absent harem was not associated with the harems that were recorded as being present. Lists of units that occurred in the same time-stamped herd were extracted, and used to create an $N \times N$ matrix of dyadic harem associations by treating every pair of harems recorded as being in the same herd at the same time as having a tie on that day (a ‘gambit of the group’ network: Whitehead & Dufault 1999). A total of 51 identified harems (all the harems believed to belong to the six bands that used the study area) are included in the sample, between whom there were 688 dyadic ties.

The second data set (neighbourhood data set) recognises the fact that foraging together in the same herd does not necessarily mean that harems had equally strong affiliative relationships with each other. Even within a given band, individual harems did not all have equally harmonious relationships with each other: although some harems were very tolerant of each other, others ended up in conflict when their members came too close (Dunbar 1983, 1984). Although individuals from one harem sometimes became intermingled with those from neighbouring harems during foraging, it was not uncommon for conflict, initially between the females but with the males becoming involved if the conflict escalated, to result when the adults of neighbouring harems became intermingled during foraging (Dunbar 1983, Fig. 4). This tendency for harems to remain spatially discrete meant that they could easily be distinguished, especially once their members were individually known (see also Snyder-Mackler et al. 2012). To explore the fine-grained relationships between individual units, harem nearest neighbours were systematically sampled. Nearest-neighbour methods are typically used to examine association patterns between individuals (e.g. snub-nosed monkeys, *Rhinopithecus* sp.: Zhang et al. 2012; feral goats: Stanley & Dunbar 2013), but they are equally suitable for the study of association patterns between social units such as

harems.

The nearest neighbour harem to each of these 21 units was recorded on 50 occasions each over a period of two months, with 31 different harems appearing as neighbours. On any given occasion, a focal harem was selected at random from within the herd, and the identity of the harem that was spatially closest to it (defined by the centre of mass of the adult members) was identified. No more than five harems were sampled from any one herd over a period of an hour, and individual units were sampled at most only twice on the same day (and always after an interval of at least 3h during which there would have been considerable reshuffling of harems during foraging). Five of the 21 harems received only partial sampling (mean number of records for incompletely sampled units = 26.6, range 19-37). In order to permit direct comparison between all 21 units, the data for these partially sampled harems were rescaled to the equivalent of 50 samples each.

In addition, to provide support for these analyses we examine data from two other gelada study populations, the Sankaber population in 1971-72 (Dunbar & Dunbar 1975) and the population from the nearby Gich area of the Simen Mountains National Park in 1973 (Kawai et al. 1979). In both these cases, sampling was carried out in the same way as in the 1974-5 study. The 1972 Sankaber data set includes data on nearest neighbours (in this case, the frequency with which a set of 13 harems appeared among each other's three nearest neighbours: Dunbar & Dunbar 1975); nine harems were thought to belong to one band, two to another band, and one each to two other bands. The Gich data set includes data on the frequencies with which nine target harems (eight from one band and one from another) were recorded in the same foraging herd as each other (Kawai et al. 1979).

We also analyse the distribution of harem sizes for all three populations (based on data provided by Dunbar [1984], Dunbar & Dunbar [1975] and Kawai [1979]), plus that for the lower altitude Bole Valley population sampled in 1972 (Dunbar & Dunbar 1975). Harem sizes are based on individually identified reproductive units, whose identity and band membership, based on regular censusing, was broadly constant over a period of at least 6 months. For each study

population, the data represent a complete census of all harems that used each study area. For present purposes, harem size for each population was taken on a specific census day.

As the data derive from purely observational studies, there were no ethical issues. Data collection was carried out in compliance with the ASAB/ABS ethical guidelines.

Analysis

The number of harems in the network is given by N . For each data set, we provide a number of basic network indices. The mean degree $\langle k \rangle$ represents the number of neighbours a node has on average, while the mean weighted degree $\langle k_w \rangle$ gives the average number of associations that a harem has. The clustering coefficient C is an unweighted property providing information on how nodes (in this case, harems) cluster together (Watts & Strogatz, 1998). Other descriptive network indices are given in the *SI*.

Both unweighted and weighted networks are considered, with L denoting the number of unweighted interactions and L_w the number of weighted interactions. Unweighted networks consider only dichotomous association patterns (two units were observed at least once in association, however defined); weighted networks take account of the frequency of association between pairs of units to provide an index of the relative strength of the association. Franks et al. (2010) conclude that weighted networks yield more useful results than unweighted (dichotomous) networks. In the present case, the networks are highly connected and clustered, and hence the number of interactions between harems are important; hence, we place more emphasis on the weighted network properties than their unweighted counterparts. As part of this, we ran a k -core decomposition (Seidman, 1983) to identify the maximal connected subgraph within each data set as a way of determining whether there was a natural maximal grouping in the networks. A k -core is the maximal connected subgraph in which all nodes have a degree of at least k . This method has been generalised for weighted networks (Garas *et al.*, 2012).

The network indices described above tell us whether or not there is any significant

structuring in the networks. Given that there is, we first apply the Jenks natural breaks optimisation (often known as the goodness of variance fit: Coulson, 1987; Jenks, 1967) to the edge weights (i.e. association frequencies) to identify discontinuities in the cumulative plot of harem association frequencies. This starts by putting the data into n clusters and then moves values from the cluster which deviates most from the array mean to the cluster which deviates least until the goodness of fit approximates 1.0. Since a goodness of fit of 1.0 can only be attained when there is zero within-class variation, which will typically be the case when the number of clusters is the same as the sample size, we use a threshold where the goodness of fit first goes above 0.9 to identify the optimal number of clusters. We then identify which harems appear in the successive layers (clusters) identified by this algorithm.

We next take a bottom-up approach that treats each harem individually and groups their network neighbours into clusters based on the strength of their ties using a k -means clustering algorithm (MacQueen, 1967) in *SciPy* v.0.16.0. In order to choose the optimal number of clusters, we use the method given by Pham et al. (2005). We report the average cluster sizes and their standard deviations.

Finally, to determine whether there are any natural patterns in the harem size distribution that might illuminate the network data, we use k -means clustering applied to the observed distribution of harem sizes from the four study populations. We identify the optimal number of clusters by running the analysis with $k=2-6$ in *SPSS* v.22, using both the method of Pham et al. (2005) and the associated F -statistic as a measures of goodness-of-fit.

Results

Co-herding data set

The co-herding data set is based on a record of how often 51 individual harems appeared with each other in the same herd while foraging. Since the data derive from observations of the compositions of casually encountered herds, individual harems appear with different frequencies

that reflect the extent to which they were encountered foraging in the study area. For this reason, we considered the weighted tie values as reflecting actual frequencies of association: if a harem is not recorded as being present in a herd on a given occasion, it cannot have been associating with those harems that were recorded in that herd. The weighted tie values thus have real meaning.

The properties of the network and the degree distribution for this data set are given in the *SI* and Table S2, and the degree distribution for the network is shown in Fig. S1. The network has a high clustering coefficient $C = 0.85$, indicating that there are many closed triads. We also used a k -core decomposition to determine whether there was any natural maximal cluster in the network. For the unweighted network, this identified a cluster of 26 harems (317 animals) with a degree of at least $k = 25$, while for the weighted version it yielded a cluster of 14 harems with $k_w = 75$. Taken together, these two indices indicate that there is considerable structuring in the network.

Fig. 1 grows the network by connection weight (i.e. frequency of association): harems are added sequentially as a function of their weightings from highest (most frequently associated) to lowest (least frequently associated). The Jenks algorithm applied to the weights identifies 4 breaks at weights of 39, 57, 79 and 109 (identified by the dotted lines in Fig. 1). The number of harems (and total members) above each of these weights are 14 (199 animals), 11 (159 animals), 7 (103 animals) and 4 (62 animals), respectively. The constituent harems in these groupings are listed in the *SI (Co-herding Data set)*. The cluster of 14 harems are fully connected and were observed together more than 20 times during the observation period, suggesting a central core of harems. The 14 harems identified by this analysis are the same 14 harems identified in the k -core analysis of the weighted network. These harems were the ones whose core home range occupied the centre of the study area (the Sankaker ridge), and form the Main band (Table S1).

As a check, we also ran this analysis using the *half-weight association index* (Cairns & Schwager 1987) which compensates for differential visibility of harems. The results were identical to those described above, except for the absence of the 4-harem grouping level. All the other layers are identified, with the same constituent harems (for details, see *SI, Co-herding Data set*).

The properties of the network change over time, as can be seen from Fig. S2 which shows the number of connected harems for each observation day. We divided the data into three periods, defined by seasonal changes (November-December; January-April; May-July). The start of the series coincided with the end of the rainy season, and the first two months or so were a period when fresh graze was still relatively widely available and the harems congregated in medium-sized herds on patches of green grass (the species' preferred food source). From December onwards, there is little or no rain (Dunbar 1984) and, as the grass becomes increasingly desiccated, the gelada switch progressively to foraging on grass roots; as a result, harems are forced to disperse over a wider area, and smaller herds become more typical. The rainy season sets in again from May, and rapidly results in a dense sward of fresh green grass on which the harems reconvene, often in very large herds. These three periods thus correspond to very different ecological conditions for the gelada that dramatically affect the harems' propensity to form herds. A comparison of co-herding tendencies across these three periods provides a strong test of the robustness of the patterns that emerge from the preceding analyses since we might expect different patterns to emerge when the harems have radically different foraging strategies.

In each of these three periods, the same four harems identified above (N7, N12, N13 and N16) are fully connected and never seen together less than 18 times in a given period (Fig. S3). Similarly, at a lower frequency of association, the same set of seven harems identified above are also fully connected in each period, as are the 14 harems identified in the weighted k -core decomposition. Thus, despite significant ecological changes and associated variation in the harems' foraging and herding patterns, the grouping patterns remain consistent across the three periods, suggesting that these patterns are robust to ecologically-driven disturbances in harem ranging behaviour.

In summary, from the network approach, we find evidence for the following groupings of harems in this data set (with the total number of animals in each cluster in parentheses): 4 (62 animals), 7 (103 animals), 14 (199 animals) and 26 (317 animals).

The preceding analyses look at the gelada's world from above and, in essence, asks how harems are distributed in space. We now turn our attention to the individual harems and take a bottom-up approach using a k -means clustering algorithm. This allows us to ask whether individual harems' social networks have the same structure. We consider each harem in turn and ask how frequently it is associated with every other harem, and whether this distribution in each case forms a consistent pattern of layers or a simple undifferentiated linear pattern with no structure. We first use the Pham et al. (2005) algorithm to identify whether there is an optimal number of clusters in the association pattern for each harem, and then determine the number of harems in each cluster (or layer). For 34 of the 51 harems, the optimal number of clusters identified by the Pham criterion is $k = 4$, while for the remainder $k = 5$ is optimal. These break the co-herding associations of the harems into grouping layers that contain, on average, 3.9 ± 1.9 , 5.1 ± 2.4 , 5.9 ± 2.7 , 8.5 ± 5.0 and, for the 17 harems who are split into 5 clusters, an extra layer of 10.7 ± 6.9 harems. The cumulative cluster sizes are thus 3.9, 9.0, 14.9, 23.4 and 34.1 harems. The second group of 9 harems is between the 7 and 11 found from the top-down approach, but in general the two methods give closely comparable results. In effect, these layers form rings of decreasing association around each harem.

Neighbourhood data set

The neighbourhood data set is based on a balanced sample of the nearest harem neighbours of 21 focal harems, with 31 different harems appearing as neighbours on at least one occasion. As they map only the closest neighbour in each case, they represent the association patterns of the harems in much finer detail than the co-herding data set allows.

Standard network indices for this data set are given in the *SI*, and Table S2 summarises the network parameters. The network is highly clustered with a clustering coefficient $C = 0.77$, indicating significant structuring. Once again, we use a k -core decomposition to identify a maximal connected network, and this identifies a cluster of 20 harems that have a degree of at least $k = 12$ for the unweighted network, and a cluster of 21 with $k_w = 10$ for the weighted version. Fig. S3 shows

that the properties of the network stabilise once 19 harems have been added. These analyses thus suggest there is a grouping of approximately 20 harems within this data set, containing ~255 gelada.

The growth of the neighbourhood data set by adding edges above a successive connection weight thresholds is shown in Fig. 2. The Jenks optimization algorithm finds 6 breaks at connection weights of 15.0, 11.0, 8.0, 6.0, 4.3 and 2.4 (indicated by the dotted lines in Fig. 2). The number of harems (and animals) included in the successive clusters are: 4 (61 animals), 10 (133 animals), 20 (257 animals), 21 (264 animals), 26 (330 animals) and 30 harems (364 animals).

For high weights, the average degree of the network is very low. This is apparent from a comparison of network structure taking a cut-off at a weight of 11 connections (Fig. 3a). This network has no cycles (triads) and a clustering coefficient of zero (Fig. S5), with each harem being connected to only one or two other harems. This contrasts strikingly with the picture that emerges with even a very small shift in weight to 10 (Fig. 3b); here, the network is almost fully connected. The average degree is less than 4 until a weight of 8 is reached, suggesting that harems typically tended to be in groups of 2-3 harems. Thus a weight (or neighbourhood frequency) of 10-11 represents a point of rapid structural shift where the data switch precipitously from a pattern of small clusters of 2-3 harems to a single fully connected community.

Fig. 4 plots the network structure for the 31 harems recorded in the neighbourhood data set. The network structure suggests that, with a connection weight of 10, there is a central core of 13 harems that form a particularly tightly interconnected group (a “giant component”). (The network is too dense to detect communities if lower weights are used.) To examine the structure of this central core further, we apply a community detection algorithm. Many community detection algorithms have been developed, and here we choose the method known as *Infomap* (Rosvall & Bergstrom 2008) which has been found to yield among the most reliable results (Lancichinetti & Fortunato 2009). This yields 3 distinct sub-communities: two contain four harems (N12a, N17, N19, N28 [45 animals] and N5, N7, N8 and N21 [60 animals], respectively) and one contains five harems (N2, N13, N14, N16 and N17 [69 animals]), as shown in Fig. 4. The remaining units in the set are

isolates (recall that 10 of them appear in the data set only because they were recorded as occasional neighbours of the sampled harems). Once again, the 13 units in the three sub-communities are the same core units of Main band identified in all the previous analyses. Of the 21 harems sampled in this analysis, four (N11, N31, N34 and N45) did not belong to the Main band, and thus not surprisingly do not appear as regular neighbours of Main band harems.

In sum, from the network approach, we find grouping layers of 4 harems (58 animals), 10 harems (133 animals), 13 harems (174 animals) and 20 harems (255 animals) in this data set.

As before, we now use the *k*-means approach to examine the neighbours of each individual harem in turn. The optimal number of clusters here is 3 for each of the 21 focal harems. The mean cluster sizes and their standard deviations are 2.8 ± 1.7 , 4.7 ± 2.9 and 6.2 ± 3.4 harems. The cumulative groupings thus consist of 2.8, 7.5 and 13.7 harems. The first and last are identified in the network approach, but the 7.5 layer appears to be an amalgamation of the 4 and 10 harem clusters.

Association patterns in other populations

We also analysed two other smaller gelada association data sets, one from an earlier (1971-2) study of the Sankaber population and one from the nearby Gich area. The Sankaber data set (based on neighbourhood data for 13 harems) yields inner groupings of 3 or 4 harems with an average of 43 gelada, with a second layer of 7 harems (78 animals) (Figs. S4 and S5). The Gich data set (based on co-herding data for nine harems) has an inner group of 5 harems (62 animals) and larger one comprising the eight harems that make up the E-band (94 animals), with one isolate (a harem from the adjacent Cliff band) (Figs. S6 and S7). These results thus provide important independent confirmation of both the layered structure and, within the limits of the data, the respective sizes of some of these layers.

Distribution of harem sizes

Taken together, the network analyses in the preceding sections suggest a distinctive structure

to the relationships between harems: harems do not associate at random. Averaging across the two data sets, patterns of association exhibit a series of layers that involve, progressively, 4.0, 9.5, 14.0 and 21.7 harems, with a general scaling ratio between them of 1.8. This is close to the ratio of 2.0 that would result from the successive binary fissioning of units. In this section, we examine the distribution of harem sizes in order to see whether harem fission patterns might explain the clustering patterns we observed.

Fig. 5 plots the distribution of the sizes (including individuals of all ages and both sexes) of the 74 harems in the six bands at Sankaber in 1975 (Table S1). As there appear to be multiple peaks, we use *k*-means clustering to identify natural groupings. The number of clusters is optimised at four (Fig. S11: $F_{3,89}=323.6$, $p<0.0001$), whose mean values are shown by the vertical dashed lines in Fig. 5. These clusters are at harem sizes of approximately 7, 11, 15 and 22 individuals. Combining data on 132 harems from the two study periods at Sankaber with those from Gich and the Bole Valley yields clusters at 5, 8, 11, 15 and 22 (Fig. S10).

The largest ever observed harem in any population was 28 individuals (Fig. S10). Only 6.8% of harems were larger than 20 individuals, and only one (0.7%) was larger than 25. The mean values for the clusters can be interpreted as reflecting the natural pattern of harem fission. Harems grow endogenously until they reach a size of ~22 individuals (with harems increasingly likely to acquire one or more additional adult males as they grow, either as follower males or by being subjected to takeover by males from all male groups: Fig. 6); when fission occurs, harems split into a residual harem of 11-15 and a daughter harem of 5-8 (typically a young follower male with 1-2 adult females and their 3-4 immatures) (Dunbar & Dunbar 1975). This pattern would thus naturally explain the peaks at 7, 11-14 and 22. A simulation of harem lifehistories for the Sankaber population, parameterised by observed entry and fission rates, indicated that once harem size exceeds four breeding females, fission events became increasingly likely and result in a roughly constant average number of females per harem, and hence a relatively stable average harem size across the population as a whole (Dunbar 1984, p. 163).

Discussion

We used network analysis methods to investigate the association patterns of gelada with two different data sets from the same population, one relatively coarse-grained (co-herding data set) and the other very fine-grained (harem nearest neighbour data set). Both these data sets use the harem (or reproductive unit) as the basis for analysis. The first data set used the frequency with which any two harems appeared in a foraging herd as an index of association between them. This large data set comprised all the 51 harems that used the main study area at least some of the time. The second data set was smaller and focussed on a subset of 21 harems that were observed especially commonly in the central part of the study area. It used the frequency with which two harems appeared as each other's immediate neighbour in foraging herds as an index of association. Note that our nearest neighbour data differ from most (but not all) studies that use this technique: in most such cases, the individual is the basis for analysis, whereas in the present case we recorded the nearest harem neighbour to a set of focal harems. These analyses were supplemented by analyses of smaller data sets from two other study populations.

Perhaps the first, most important, conclusion is that the results quantitatively confirm the existence of the large scale grouping known as bands, which hitherto have been identified mainly on the basis of similarity in harem ranging patterns (Dunbar 1984, Fig. 2; Dunbar & Dunbar 1975; Kawai et al. 1979, Fig. 2; see also Snyder-Mackler et al. 2012). This is a grouping of about 100 individuals in about 7-10 harems (plus associated all male groups), though individual bands can reach double that size by the time they undergo fission (as the Main band had during the present study period).

Second, all the data sets also confirm the existence of structural layering in gelada social organisation, with a series of hierarchically inclusive groupings that form a regular sequence with a scaling ratio of ~ 2.0 . The analyses yield an inner cluster of ~ 4 harems, a second layer of ~ 7 harems, and a third grouping level of ~ 14 harems, with an outer layer of 20-25 harems that are more weakly

connected. Numerically, these layers correspond, respectively, to ~50, ~100, ~200 and 300+ individuals. (Note that these values do not include the all male bachelor groups that were habitually associated with each of the individual bands: Dunbar & Dunbar 1975; Kawai et al. 1979.) Importantly, we were able to confirm the existence of at least the two inner layers in two other data sets, suggesting that these generalise across populations and over time. In addition, from the much finer grain neighbourhood data set we identified an innermost layer of ~2.5 harems. With a mean harem size of 12.6 in the six bands in the study population (12.4 for Main band on its own, from which most of the data actually derive), this would be equivalent to a group of 33-34 animals, and seems to be equivalent to the unit identified by Kawai et al. (1983) and Snyder-Mackler et al. (2012) as a *team* (two, occasionally three, harems that were seen together especially frequently).

This pattern of hierarchically structured grouping layers is similar to that described for hamadryas baboons (Hill et al. 2008), as well as for humans (Zhou et al. 2005; Hamilton et al. 2007). Something similar has also been described for plains zebra, where individual harems (one male groups) exhibit “preferential associations....[that]... create temporally stable subgroups within the larger herd and indicate a type of non-randomness to herd formation and structure” (Rubenstein 1986). African elephants also seem to have a similar structure, with family groups associating preferentially in such a way as to create an intermediate level grouping known as a *bond* group (Moss et al. 2011). In both cases, the basal social unit (harems in the one case, family groups in the other) exhibit preferential association patterns that create a naturally hierarchical structure.

Kawai et al. (1979) used the correlation in harem ranging patterns and Snyder-Mackler et al. (2012) used co-herding frequencies to confirm the existence of bands, and hint at the likely existence of teams in their gelada populations. However, in both cases, they do so only with a modest sample of the harems that used a given ranging area. Our analyses confirm these conclusions using a much larger comprehensive sample that includes every harem known to use the central study area during a given year. In addition to confirming the existence of bands, our analyses go beyond this by confirming the existence of several additional clustering levels. While some of

these (the team) have previously been suspected, at least one (the grouping level of ~4 harems totalling some 50 or so animals) had not previously been recognised. This grouping layer was completely unexpected, even though it is extremely clear in all the association data sets. Numerically, a grouping of 50 individuals is close to the average size of *Papio* troops (54.5: Bettridge et al. 2010). One obvious interpretation of this grouping level would be that it consists of two teams, which themselves are the product of an earlier harem fission event whose recency is reflected in the two pairs of harems continuing to associate together, albeit at a lower frequency commensurate with the time lag since the original fission event. In contrast, the mean band size at Sankaber at the time of the study (98.6, excluding all male groups: Table 1) is significantly larger than the size typical for baboon troops, even though it was previously assumed to be functionally equivalent to a troop (Dunbar & Dunbar 1975; Dunbar 1983). In fact, it is virtually identical in size to the ~100 layer identified by the network analyses. At the time of the sample, the Main band in the Sankaber study area was considerably larger than all other bands in the area, with a total size of 224 (excluding all male groups) divided between 18 harems (Table S1). This likely corresponds to the largest grouping level of ~200 individuals identified by the network analyses, and to the size of some bands observed at Sankaber nearly four decades later when band sizes were 100, 179 and 179 (Snyder-Mackler et al. 2012).

As Fig. 2 suggests, the pattern of herd formation varies considerably through the year. This variation can be attributed entirely to the foraging conditions that the animals encountered across the seasons of the year. Large herds form when grazing conditions are good during the rains, but disperse when the grass becomes dessicated and too dry for gelada to process (Dunbar & Bose 1991), forcing the animals to search more widely for food patches. Such patterns are typical of grazing ungulates such as plains zebra (Rubenstein & Hack 2004) and elephants (Moss et al. 2011), both of whom are hindgut fermenters like the gelada: individual units congregate in large herds on lush grassy swards during the wet season when foraging conditions are at their best, but disperse during the dry season when foraging patches are small and scattered. In the present case, the

significance of these changes in herd formation is that they provide a natural experiment on the consistency of harem associations. Despite considerable differences in herd size and ranging patterns across the very different ecological conditions of the three seasons, the pattern of association between individual harems remained unchanged: the same grouping layers involving the same harems are observed in all three seasons. This suggests that the patterns we extracted from the data are very robust, at least at the within-population level. The comparisons between the different populations confirm that they are also robust at the between-population level, despite significant ecological differences between the three different habitats.

As with the social groups of all anthropoid primates, gelada bands grow endogenously as a result of births (and occasional immigrations by adult males from all male bachelor groups and the extremely rare immigration of young females); they eventually undergo fission when their size exceeds either the carrying capacity of the home range or the animals' ability to maintain coordination when travelling (Dunbar 1984; Iwamoto & Dunbar 1983). The estimated growth rate of harems in the Sankaber study area during the early 1970s, based on birth and death rates for individual harems, was very high (9.9-16.2% per annum: Ohsawa & Dunbar 1984), and would have resulted in the doubling of band size every 6.7 years (Dunbar 1984, p. 36). With a doubling time of roughly 6.5 years at the growth rates observed in the Sankaber area (representing optimal ecological conditions for the gelada: Dunbar 1992), the timeline between the formation of an independent harem and the band level community to which it eventually gives rise through successive harem fission events would be something in the order of 20 years (or close to the species' maximum longevity). In ecologically less ideal habitats at higher or lower altitudes (Dunbar 1992), this timeline will be proportionately longer, and that might in itself limit the ability to form the kinds of high level communities of 200-300 individuals seen at Sankaber if lack of familiarity results in more hostile relationships between distantly related harems.

The suggestion of a grouping level at ~34 individuals (2-3 harems) is particularly significant because it is very close to the estimated size of the previously identified units known as *teams* (2-3

harems that associated particularly closely with each other, mean=29.5 individuals: Dunbar 1995; Kawai et al. 1983; Snyder-Mackler et al. 2012), and likewise very close to the species' putative natural 'cognitive' social group size (28.6) predicted from the gelada's brain size by the social brain equation for monkeys (Dunbar 1995). This also coincides with the largest observed harem size, the largest ever recorded being 28 (Fig. 5 and Fig. S10).

Bergman (2010) reported that, in contrast to *Papio* males, gelada males do not seem to differentiate the calls of other males in their own band from those of males from other bands, and concluded from this that the natural social grouping within which males know each other is more likely to be the two to three harems that make up a team rather than the band as a whole (p. 3051). One likely reason for this is that harem males can originate in a different band to the one in which they hold a harem (Dunbar 1984; Dunbar & Dunbar 1975). Since males are only harem holders for, on average, 3.6 years (Dunbar 1984), it is likely that harem-holding males are not especially familiar with the voices of other males in their band (even though they may recognise them by sight: Dunbar 1984). A large gelada band like the Main band at Sankaber will typically contain 30-40 adult and subadult males (Dunbar & Dunbar 1975), compared to a mere 10-15 in the average *Papio* troop. Moreover, a gelada male's exposure to the voices of other males in his band is likely to be much less than that of *Papio* males because the harems of a band only spend about half their time foraging in the same herd. In contrast, it may be that females recognise a much wider range of individuals, since they remain within the same band for life (Kawai et al. 1983; Shotake 1980), and so are more likely to be familiar with many of the other females. This may point us towards a possible mechanism underpinning the hierarchical structure of harem relationships, namely long term familiarity between females that results in daughter harems continuing to forage near each other due to residual ties derivative of successive harem fissions over many years. Personal familiarity, based on frequency of contact and interaction, is likewise known to underpin the hierarchical structure of human social networks (Roberts & Dunbar 2011; Sutcliffe et al. 2012).

In summary, the network analyses we present here consistently identify several different

grouping layers in gelada society. One of these (the ~34 grouping) corresponds quite closely to the teams tentatively identified by earlier studies (Kawai et al. 1983) and to the ‘cognitive’ group size for the species (Dunbar 1995); a second (the ~100 grouping) corresponds to the mean band size (essentially, an ecological unit) and a third (~200 grouping) corresponds to the actual size of the Main band itself at the time of the study (and may correspond to the size that bands typically have to achieve before they can fission). The very large grouping of 250-300 animals identified in the co-herding data set probably reflects the fact that the main study band (Main band) formed combined herds especially often with units from one of the five bands whose ranges overlapped with theirs. In addition, however, analyses of both data sets also identified a hitherto unsuspected grouping layer of around 4-5 harems (50-60 animals), whose origin and function (if any) remain unknown, but may be analogous to the conventional *Papio* troop which it closely resembles in size.

These findings may provide us with a clue as to the origins of harem-based groupings in species like the gelada and hamadryas, and harem-like groupings in *Papio papio* (Dunbar & Nathan 1972; Goffe et al., in press) and, perhaps, drills and mandrills. In contrast to other species of *Papio*, all of these species are characterised by the formation of very large foraging or sleeping herds as a result of the habitats they typically occupy. Since increasing group size has an adverse effect on female fertility (Dunbar 1980, 1988; Smuts & Nicholson 1989) as well as dramatically increasing the risk of infanticide through the presence of large numbers of males (Opie et al. 2013), females may respond by forming protective female-based (e.g. matrilineal) coalitions that males then try to monopolise and harems or by attaching themselves to individual males as ‘hired gun’ protectors (Dunbar, 2010; Wilson & Mesnick 1997). While aspects of these social strategies may become hardwired through genetic adaptation in one or other sex (as is known to be the case in hamadryas: Bergman et al. 2007), these seemingly different forms of social organisation may simply be part of a natural range of behavioural variation for these cognitively advanced monkeys.

Acknowledgments

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Figures

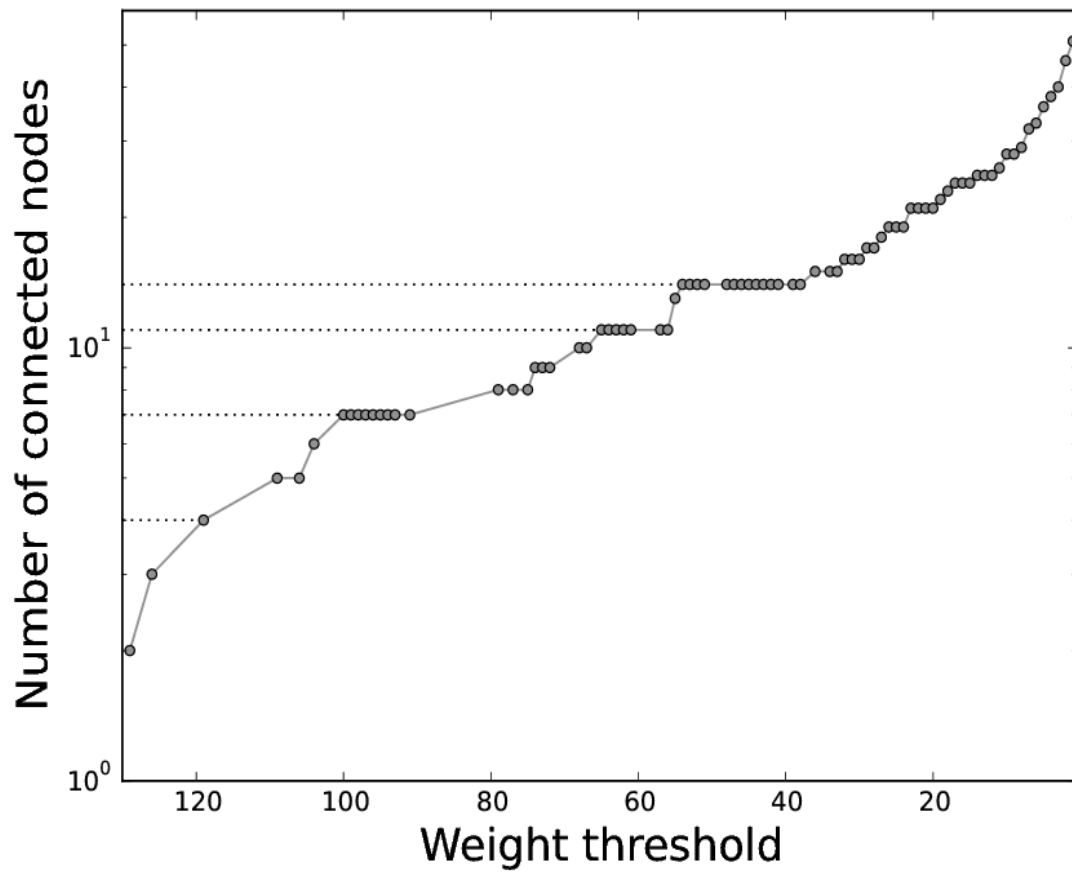


Fig. 1. The cumulative growth in the number of connected nodes (harems) in the co-herding network as the weight of interactions (connectedness) is lowered, plotted on a semi-log scale. The breaks found in the weight by the Jenks algorithm are identified by the dotted lines, and correspond to 4, 7, 11 and 14 harems.

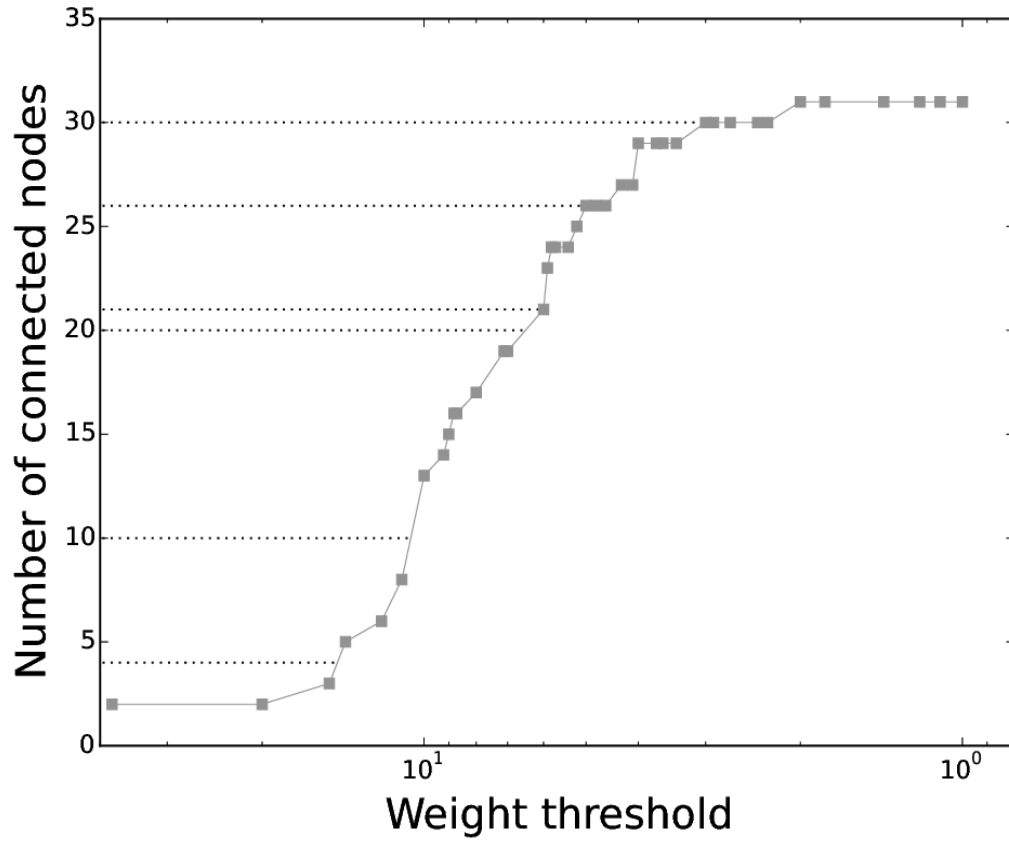
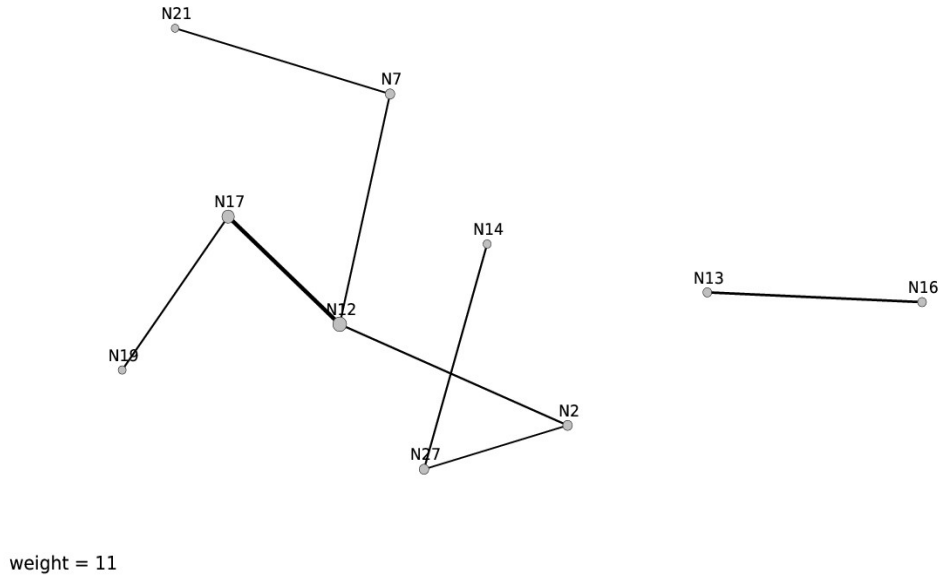


Fig. 2. The cumulative growth in the number of connected nodes (harems) in the neighbourhood network as the weight of interactions (connectedness) is lowered, plotted on a semi-log scale. The breaks found by the Jenks algorithm are at 4, 10, 20, 21, 26 and 30 harems, and are marked by the dotted lines. As this data set sampled only 21 harems, the larger groupings contain missing data.

(a)



(b)

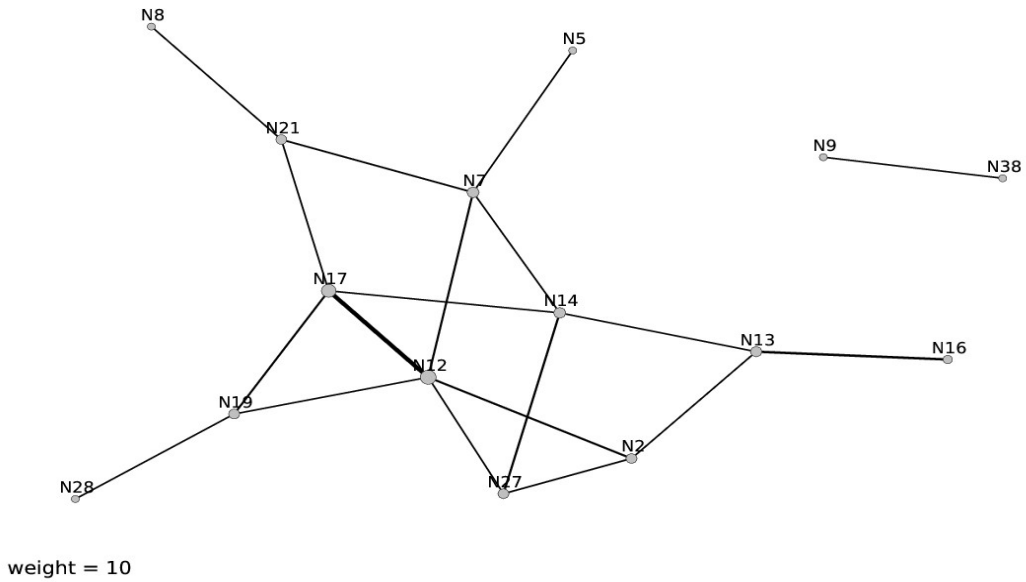


Fig. 3. Neighbourhood network, where each node represents a harem, using (a) a minimum weight of 11 and (b) a minimum weight of 10. In (a), the clustering coefficient is zero as there are no complete cycles (triads): harems interact most strongly with just one or two other harems.

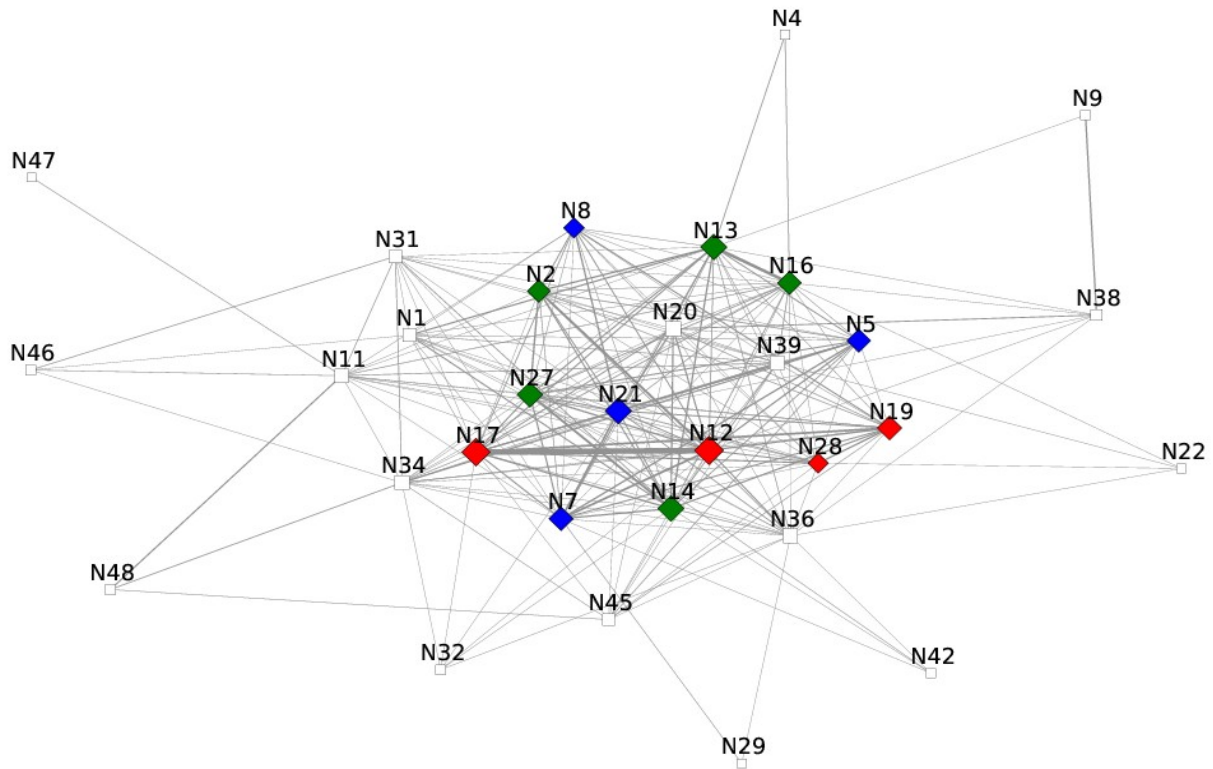


Fig. 4. The neighbourhood network, where each node represents a harem, showing the three sub-communities found by restricting the edge weight to 10 or higher. There are 13 central harems (all belonging to the Main band), which are broken into two groups of 4 and a group of 5 (colour coded), plus two isolates (N1 and N36). Harems N4, N9, N22, N29, N32, N38, N42, N46, N47 and N48 appear as neighbours, but were not themselves sampled. These, plus harems N11, N31, N34 and N45, do not belong to the Main band.

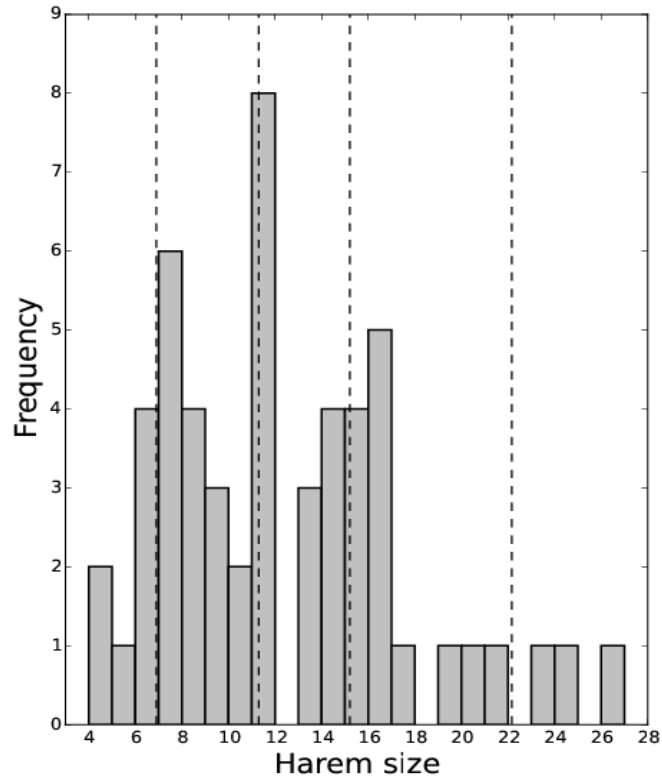


Fig. 5. Frequency distribution for harem sizes (including immatures) for the Sankaber 1974 gelada population (see Table S1). Vertical lines mark the mean values for the four clusters identified by a k -clusters analysis: the clusters are at 7, 11, 14 and 22 individuals.

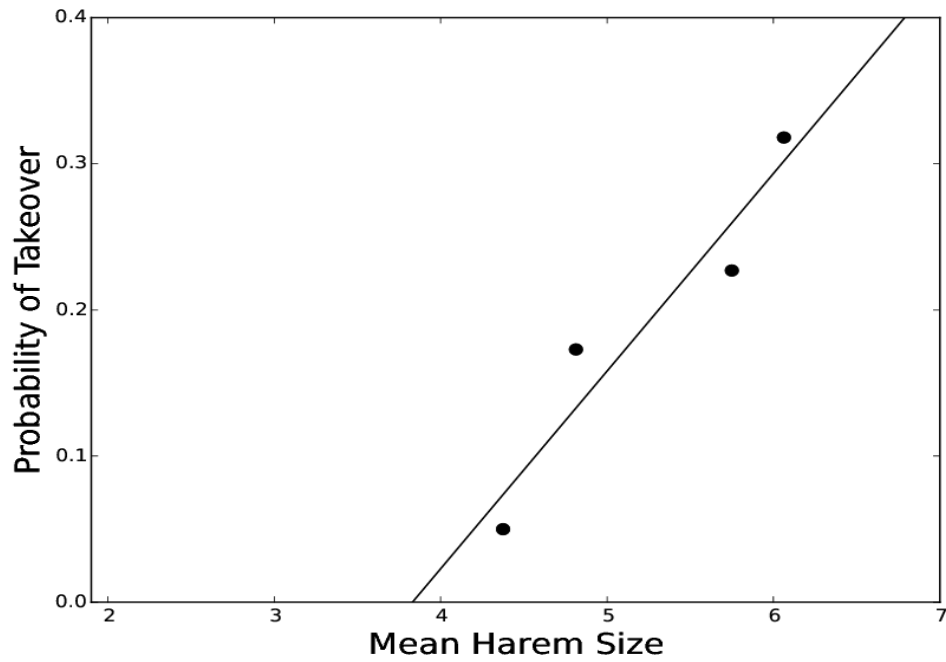


Fig. 6. Observed rates per unit per year with which adult males successfully entered harems in takeover challenges for four gelada bands (Main band 1971, Abyss band 1971 and Main band 1972 at Sankaber, E-band at Gich), as a function of mean harem size for each band. Source: Dunbar (1984).