

# The socio-genetics of a complex society: female gelada relatedness patterns mirror association patterns in a multilevel society

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## Abstract

Multilevel societies with fission–fusion dynamics—arguably the most complex animal societies—are defined by two or more nested levels of organization. The core of these societies are modular social units that regularly fission and fuse with one another. Despite convergent evolution in disparate taxa, we know strikingly little about how such societies form and how fitness benefits operate. Understanding the kinship structure of complex societies could inform us about the origins of the social structure as well as about the potential for individuals in these societies to accrue indirect fitness benefits. Here, we combined genetic and behavioural data on geladas (*Theropithecus gelada*), an Old World Monkey, to complete the most comprehensive socio-genetic analysis of a multilevel society to date. In geladas, individuals in the core social ‘units’, associate at different frequencies to form ‘teams’, ‘bands’ and, the largest aggregations, ‘communities’. Units were composed of closely related females, and females remained with their close kin during permanent fissions of units. Interestingly, female–female relatedness also significantly predicted between-unit, between-team and between-band association patterns, while male–male relatedness did not. Thus, it is likely that the socio-genetic structure of gelada society results from females maintaining associations with their female relatives during successive unit fissions—possibly in an attempt to balance the direct and indirect fitness benefits of group living. Overall, the persistence of associations among related females across generations appears to drive the formation of higher levels of gelada society, suggesting that females seek kin for inclusive fitness benefits at multiple levels of gelada society.

*Keywords:* fission, gelada, genetic structure, multilevel society

*Received 21 August 2014; revision received 18 October 2014; accepted 27 October 2014*

## Introduction

Multilevel societies with fission–fusion dynamics are arguably one of the most complex animal societies. They are defined by two or more nested levels of organization composed of nuclear, modular social units that fission and fuse with one another across years, days and even hours (Grüter *et al.* 2012). Because of their social

complexity and their convergent evolution in disparate taxa, multilevel societies are drawing increasing attention from those interested in social and cognitive evolution (Aureli *et al.* 2008). Understanding the kinship structure of complex societies could tell us both about the origins of the social structure (e.g. sex-biases and distances of dispersal) as well as the potential for individuals to increase indirect fitness-derived benefits by preferentially supporting kin (Hamilton 1964). However, we know strikingly little about how these societies form and about the role of kinship in multilevel societies.

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When populations are subdivided into stable social groups, such as in the more common, single-level societies, group boundaries often correspond to familial boundaries (Di Fiore 2012). This suggests simple dispersal patterns and indicates a strong potential for individuals to increase their indirect fitness benefits by helping kin in or near their group (Hamilton 1964; Langergraber 2012). Indeed, numerous studies have found a fine-scale genetic structure wherein individuals of the more philopatric sex are more closely related (e.g. white-tailed deer, *Odocoileus virginianus*: Robinson *et al.* 2012; red deer, *Cervus elaphus*: Nussey *et al.* 2005; yellow baboons, *Papio cynocephalus*: Altmann *et al.* 1996; raccoons, *Procyon lotor*: Ratnayeke *et al.* 2002). Such a relatedness structure provides increased opportunities to interact and possibly cooperate with close relatives, potentially maximizing indirect fitness benefits (Hamilton 1964; Alexander 1974; West Eberhard 1975). For example, in species that exhibit limited or no female dispersal, most female–female interactions are highly nepotistic and mutually beneficial (e.g. house mice, *Mus domesticus*: Sutherland *et al.* 2005; grey seals, *Halichoerus grypus*: Pomeroy *et al.* 2001; alpine marmots, *Marmota marmota*: Hackländer *et al.* 2003; baboons, *Papio* spp.: Silk *et al.* 2003, 2009, 2010). These kin-biased association patterns and behaviours also extend to the more complex fission–fusion societies (e.g. bottlenose dolphins *Tursiops* spp.: Connor *et al.* 2000; Krützen *et al.* 2003; Krützen *et al.* 2004; Möller & Beheregaray 2004; Frère *et al.* 2010; chimpanzees *Pan troglodytes*: Langergraber *et al.* 2007a,b, 2009; bonobos, *Pan paniscus*: Eriksson *et al.* 2006). Thus, given this propensity for animals to preferentially associate with kin in both single-level and fission–fusion societies, it is likely that some of the association patterns in multilevel societies also result from individuals maintaining ties with close relatives.

Yet, we know strikingly little about the fine-scale, cryptic genetic structure that underlies the tiered nature of multilevel societies, despite the fact that they have evolved in multiple taxa (e.g. zebra, *Equus burchelli*: Rubenstein & Hack 2004; bats, *Myotis bechsteinii*: Kerth *et al.* 2011; bee-eaters, *Merops bullockoides*: Hegner *et al.* 1982; bell miners, *Manorina melanophrys*: Painter *et al.* 2000; elephants, *Loxodonta africana*: Wittemyer *et al.* 2005; sperm whales, *Physeter macrocephalus*: Whitehead *et al.* 2012). To date, the most detailed data on the underlying kinship structure of multilevel societies come from two studies of African elephants, which showed that small, cohesive groups of related females formed the core of elephants' multilevel society. However, this relatedness structure was only present in the core groups of females, and there was no strong genetic signal among females with weaker association patterns (Archie *et al.* 2006, 2008; Wittemyer *et al.* 2009). Further, as both studies

were conducted on elephants, we do not know whether close association among related females represents a general pattern across convergent multilevel societies. Multilevel societies have also evolved in multiple species within the primate lineage (Grüter *et al.* 2012). For the best-known primate example, hamadryas baboons (*Papio hamadryas*), it is hypothesized that strong bonds among male relatives, as opposed to females, form the core of their multilevel society (Sigg *et al.* 1982; Colmenares 1992; Schreier & Swedell 2009). However, the cryptic patterns of genetic relatedness in this and other primate multilevel societies have not been described. Thus, fine-scaled genetic analyses of nonelephant multilevel societies are essential to improve our understanding of the evolution and maintenance of complex societies.

Here, we conducted a comprehensive, fine-scale socio-genetic analysis of the fluid, multilevel society of an Old World Monkey, the gelada (*Theropithecus gelada*). Gelada society is composed of core social groups (reproductive 'units') that associate at different frequencies to form, in increasing size, 'teams', 'bands' and, the largest aggregations, 'communities' (Snyder-Mackler *et al.* 2012). Genetic analyses of geladas have been conducted both in cross-population analyses (Shotake & Nozawa 1984; Belay & Shotake 1998; Belay & Mori 2006) and in a fine-scale study within the units (Tinsley Johnson *et al.* 2014). However, we still do not know how kinship is structured across the multiple levels of social organization. Thus, we asked two questions about the multilevel society of geladas:

- 1 What can kinship patterns tell us about the formation of core social groups, which appear to correspond to reproductive units – the groupings in which all reproductive activity takes place?
- 2 What can kinship patterns tell us about the formation of the higher levels of social organization, which consist of teams, bands and communities?

First, we set out to corroborate behavioural findings (Dunbar & Dunbar 1975; Ohsawa 1979; Dunbar 1983; Le Roux *et al.* 2011) that gelada females remain in their natal units, while males disperse—the typical mammalian pattern (Greenwood 1980). We predicted that female geladas within units were more closely related than both males within units and females from different units. Furthermore, gelada units are small compared to other cercopithecine social groups. The small size is maintained by 'fissions' of units, in which large units permanently split into two or more independent 'daughter' units (Dunbar 1984, 1989, 1993; Le Roux *et al.* 2011). It is currently unknown whether kinship influences how individuals choose their postfission units. Fissions could arise primarily because of male–male

competition for females. Alternatively, females may attempt to maximize their postfission dominance rank by entering a daughter unit other than the one containing their immediate superior from the original unit (Ron *et al.* 1994). In these scenarios, we would not expect fissions to occur along lines of female kinship, particularly because avoiding animals close in rank would mean avoiding close kin: rank is maternally inherited and closely ranked females tend to also be close kin (Le Roux *et al.* 2011). However, our previous observations indicate that kinship structures social interactions among females within units, suggesting that kin relationships are important to females (Le Roux *et al.* 2011; Tinsley Johnson *et al.* 2014). Thus, if unit fissions are based on females maintaining ties with close kin (but not based on rank acquisition), we would expect females to actively seek kin during these events.

Second, units preferentially associate with some units more units than others, forming 'teams' and 'bands' (Kawai *et al.* 1983; Snyder-Mackler *et al.* 2012). We addressed two alternative pathways leading to these higher levels. First, we looked at historical fissions as a source of higher structure. In most other taxa, subgroups cease to associate after a permanent group fission (Koyama 1970, 2003; Cords & Rowell 1986; Armitage 1987; Robinson 1988; Hohmann 1989; Holekamp *et al.* 1993; Ron *et al.* 1994; Li *et al.* 1996; Armitage & Schwartz 2000; Okamoto & Matsumura 2001; Lefebvre *et al.* 2003; Widdig *et al.* 2006; Van Horn *et al.* 2007). In contrast, gelada daughter units continue to share the same home range and associate (but do not groom) significantly more frequently with each other than with other units in their band (Snyder-Mackler *et al.* 2012). Thus, higher levels of gelada society may result from repeated fissions of units. If this were the case, we would expect a correlation between female relatedness and unit association patterns because both relatedness and association pattern should weaken across generations following fissions. Second, male-male relatedness could underlie the higher level associations—as has been suggested in hamadryas baboons (Sigg *et al.* 1982; Colmenares 1992; Schreier & Swedell 2009). If this were the case then we would expect that units with more closely related leader males would associate more often than units with less closely related males.

## Materials and methods

### *Gelada society*

Geladas are a large-bodied, terrestrial Old World primate endemic to the highlands of Ethiopia. The main food source of geladas is grass, and the apparent lack of contest competition over grass may allow geladas to

form extremely large and variable aggregations, which can range in size from 13 to 1000 individuals on any given day (Snyder-Mackler *et al.* 2012). Gelada aggregation, or 'herd', size and composition vary on a daily and even hourly basis as bands fission and fuse with one another—creating a complex pattern of associations and interactions (Kawai *et al.* 1983; Dunbar 1986; Snyder-Mackler *et al.* 2012). Gelada society is composed of four hierarchical levels (i) the *unit*—composed of one dominant, 'leader', male, one to 12 adult females, and anywhere from 0 to 5 subordinate, 'follower', males; (ii) the *team*—an aggregation of two or more units that associate with each other at least 90% of the time (the team is not an obligatory level of gelada society as only ~1/3 of units are members of a team); (iii) the *band*—a collection of units that spend between 50% and 90% of their time together; and (iv) the *community*—the set of units with overlapping home ranges that are found together <50% of the time (Snyder-Mackler *et al.* 2012). Note that our known members of neighbouring bands are found together in the same herd an average of 27% of the time (Snyder-Mackler *et al.* 2012). Additionally, unattached males form all-male bachelor groups that are loosely associated with bands (Dunbar 1984).

We studied a population of wild geladas living in the Sankaber area of the Simien Mountains National Park, Ethiopia. Data were collected over a 64-month period from January 2006 to April 2011 as part of the University of Michigan Gelada Research Project. Subjects included 49 unit males (leaders and followers), 35 bachelors in five all-male groups, and 114 females in 19 units.

### *Observational methods*

A team of four observers conducted a weekly census of all known study individuals (~300 of ~1200 individuals in the community), identified all unit males and females, and noted all births of new infants. We assessed spatial association among all study individuals and units using previously described methods (Snyder-Mackler *et al.* 2012). Briefly, this association index (AI) was calculated from the proportion of time units or males were found together after they ascended from the sleeping cliffs in the morning. Units that ascend the cliff together in the morning were assumed to have spent the night together and were typically found together through part, or all, of the next day. AI was averaged over the entire study period.

### *Genotyping*

We collected at least one and up to four faecal samples from all study individuals, as well as 18 samples from

unknown geladas from three separate populations each at least 15 km from our study population. These 18 samples were used as an out-group for our relatedness analysis. All samples were collected using methods described in Alberts *et al.* (2006), with the exception that our samples were collected in RNAlater (Applied Biosystems/Ambion, Austin, TX, USA) instead of ethanol. We extracted DNA from the faecal samples using the QIAamp DNA Stool Mini Kit (QIAGEN, Valencia, CA, USA), with slight modifications as described in Buchan *et al.* (2003).

We genotyped samples using polymerase chain reactions (PCR) at 23 human derived MapPairs microsatellite loci (described in Tinsley Johnson *et al.* 2014), which were found to be variable in this gelada population (average number of alleles/locus = 5.91). We performed PCR using QIAGEN multiplex PCR kits with 3–6 loci multiplexed in a single PCR (multiplex combinations and PCR conditions available upon request). PCR products were separated via capillary electrophoresis on an ABI 3730 automated DNA Analyzer at the Duke Institute for Genome Sciences & Policy DNA Sequencing Facility Core and analysed using GENEMAPPER 3.5 (Applied Biosystems, Carlsbad, CA, USA). Individuals were genotyped at an average of 95% of the 23 loci; the minimum number of loci typed per individual was 12 ( $N = 1$  individuals) and the maximum was 23 ( $N = 90$  individuals).

#### mtDNA sequencing

To further examine the extent of female philopatry in geladas, we sequenced 409 base pairs of the first hypervariable region of the mitochondrial (mtDNA) D-loop—a maternally inherited marker. We amplified the region using two previously published primers with a slight modification to one (H15840; CCGAGCGGGAT ATTGGT) to successfully amplify this region in geladas (Hapke *et al.* 2001). We used the PCR protocol described in Hapke *et al.* with the modification that we prepared our samples for cycle sequencing by incubating each successfully amplified sample with ExoSAP-IT (Affymetrix Inc., Santa Clara, CA, USA). Sequences were aligned using SEQUENCHER v5.0 (Gene Codes Corporation, Ann Arbor, MI, USA) and analysed using ARLEQUIN v3.5 (Excoffier & Lischer 2010). All samples produced only one haplotype, and all mother-offspring pairs shared the same haplotype. This effectively rules out the possibility that we amplified nuclear insertions of mtDNA (Bensasson *et al.* 2001).

We sequenced mtDNA from 98% of samples from our study population (114 of 114 females, 46 of 49 unit males, 35 of 35 bachelors) and 14 of 18 of the out-group individuals. In total, we found 43 polymorphic sites that defined 10 haplotypes in our study population. The

most common haplotype characterized 57% of our population. Less than half of the out-group individuals shared haplotypes with individuals in our study population (five of 14), while the other nine out-group individuals had a unique haplotype not shared with any members of the study population.

#### Relatedness estimates

The accuracy of the many different relatedness point estimates depends on the true underlying genetic structure of the study population (Van De Castele *et al.* 2001; Wang 2011). For example, the Queller & Goodnight (1989) and Wang (2002) estimators perform best when samples contain many related dyads (Wang 2011), as is likely to be the case in this study. We therefore assessed the suitability of six relatedness estimators by carrying out Monte Carlo simulations with the analysis program COANCESTRY v1.0 (Wang 2011), which simulated genotypes from observed allele frequencies (Van De Castele *et al.* 2001). The simulations revealed that Wang's estimator produced the strongest correlation ( $r = 0.84$ ,  $P < 0.001$ ) between the relatedness estimates of simulated dyads and the expected relatedness value of that dyad (i.e. parent-offspring relatedness = 0.5, half-sibling relatedness = 0.25). Therefore, we used this estimator (hereafter  $r_w$ ) for all dyadic relatedness estimations.

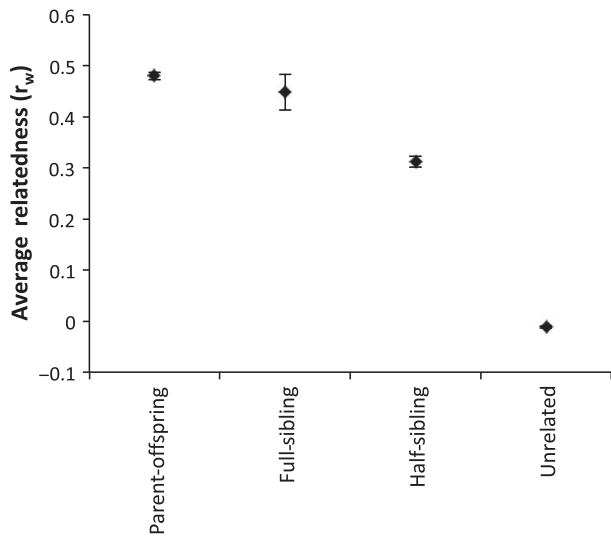
#### Accuracy of relatedness estimators

We first compared the  $r_w$  of known relatives (parent-offspring, half-sibling and full-sibling) in our population to their expected relatedness values. Females from different bands were assumed to be unrelated ( $N = 4596$  dyads). We found a significant correlation between  $r_w$  and the expected relatedness ( $r = 0.55$ ,  $P < 0.0001$ ; Fig. 1), suggesting that  $r_w$  was an accurate, unbiased and appropriate estimator for our population.

#### Relatedness within units

To test our first hypothesis that gelada females are philopatric while males disperse, we first examined the relatedness of all study individuals within three types of dyads (male–male, female–female and male–female) in which the members belonged to the same unit. To do so, we used 10 000 bootstrap iterations in the 'Pops Mean' function in GENALEX v6.41 (Peakall & Smouse 2012) to determine whether the observed average relatedness of individuals within units was significantly higher than the average relatedness of individuals randomly assigned to units (i.e. the average relatedness expected by chance).





**Fig. 1**  $r_w$  value of dyads of known relationship (black dot = average  $\pm$  SE). Parent-offspring ( $N = 246$  dyads), full-sibling ( $N = 12$  dyads), half-sibling ( $N = 195$  dyads), unrelated ( $N = 4596$  dyads).

#### Effect of fissions on within-unit relatedness

To test the hypothesis that females maintain ties with close relatives during fissions, we drew on data from three permanent unit fissions that occurred during the study period (hereafter B-unit, C-unit and H-unit fissions). Each of the three unit fissions occurred after an immigrant male entered the unit, becoming the new leader male. We used a permutation test to examine whether fissions of gelada social units occurred along familial lines or were random with respect to genetic relatedness. For each permutation, we randomly assigned individuals to daughter units and calculated an average within- and between-unit relatedness (cf. Lukas *et al.* 2005). After 10 000 permutations, we assessed significance by calculating the proportion of simulations that were greater than the observed within-unit relatedness between females in the new daughter units. The permutation analysis for each fission was run in two ways (i) by comparing the average  $r_w$  for all pairs within and between the daughter units to the same values from our permutations, and (ii) by comparing the number of mother–daughter pairs in the same unit after a fission to the number of such pairs randomly assigned to the same unit via permutation.

#### Kinship structure of higher levels

To test the hypothesis that female–female relatedness was a better predictor of spatial association patterns than male–male relatedness, we conducted two Mantel

tests (Mantel 1967) to assess the correlation between pairwise relatedness and AIs among all unit females ( $n = 114$  females; 6441 dyads) and among all unit males ( $n = 49$  males; 1035 dyads). We used PopTools (Hood 2010) to carry out all Mantel tests and determined significance using 10 000 permutations.

We then tested whether female–female relatedness also had a multilevel structure that mirrored the multilevel association patterns. To do so, we examined the relatedness structure within and between each level of gelada society using previously defined levels of gelada association (Snyder-Mackler *et al.* 2012). Each dyad was identified according to which level of gelada society it represented and belonged to only one of four mutually exclusive categories (i) within-unit dyads were pairs of individuals in which members belonged to the same unit, (ii) within team dyads were pairs of individuals in which the members belonged to the same team but different units, (iii) and within band dyads were pairs of individuals in which the members belonged to the same band but different teams, (iv) within community dyads were pairs in which the members belonged to the same community but different bands. We then compared the average pairwise relatedness of same-sex and male–female dyads at each level of gelada society. First, to test whether individuals within each level of society were more closely related than would be expected by chance, we again used the ‘Pops Mean’ function in GENALEX v6.41 (Peakall & Smouse 2012). Second, to determine whether there was a multilevel genetic structure that mirrored the spatial association patterns, we assessed the differences in average pairwise relatedness between the three sets of adjacent social levels (unit vs. team, team vs. band and band vs. community) by bootstrapping the individuals 10 000 times using the program COANCESTRY v1.0.

Previous research had found that our study population forms three bands (Snyder-Mackler *et al.* 2012), which may represent genetically identifiable subgroups. To test this possibility, we used the Bayesian model-based clustering method implemented in STRUCTURE 2.3 (Pritchard *et al.* 2000; Falush *et al.* 2003) to investigate the most likely number of  $K$ , genetic ‘clusters’, in our study population. We conducted 10 independent runs for each value of  $K$  between 1 and 15 using a model with admixture and correlated allele frequencies. Our exploratory STRUCTURE simulations showed that a burn-in period of  $10^6$  followed by  $10^6$  MCMC steps sufficiently converged on a stable value of  $L(K)$ . We then inferred the most likely number of subdivisions in our population by calculating  $\Delta K$  using the methods of Evanno *et al.* (2005). Briefly,  $\Delta K$  represents the rate of change in the log probability that the data have  $K$  clusters between successive  $K$  values (i.e. the rate of change

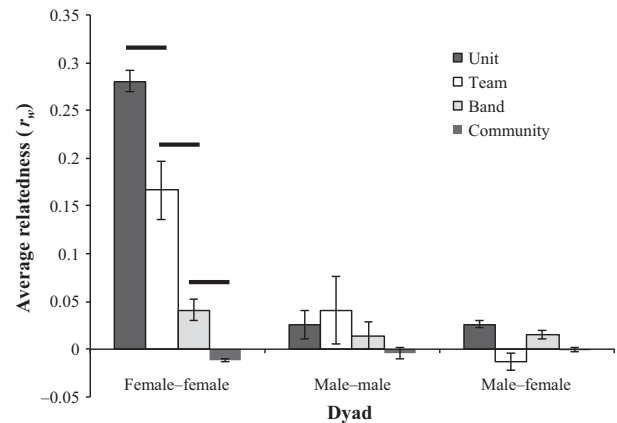
in the log probability of the data between  $K$  clusters and  $K + 1$  clusters). Essentially, the value of  $K$  with the largest  $\Delta K$  has the best evidence as the number of subgroups in the population. Furthermore, the values of  $\Delta K$  indicate the strength of population subdivision signal at that value of  $K$ . Some STRUCTURE analyses combine samples from both male and female genotypes (Coulon *et al.* 2006; Bergl & Vigilant 2007; Randall *et al.* 2009). However, because we were interested in the differences in genetic substructure between sexes, we ran one analysis that included only adult females and one that included only adult males (Guschanski *et al.* 2008). Lastly, we used the CLUMPP permutation program (Jakobsson & Rosenberg 2007) to average the fractional group membership,  $Q$  (i.e. the probability of an individual being part of one of the three genetic subgroups), of each female in our population across all 10 STRUCTURE runs. We also conducted a discriminant analysis of principal components (DAPC; Jombart *et al.* 2010) to complement the STRUCTURE analysis. DAPC analyses were conducted separately on females and unit males (i.e. leaders and followers) using the R package *adegenet* (v 1.3-6; Jombart 2008; Jombart & Ahmed 2011). We determined the optimal number of principal components using the 'optim.a.score' function; (Jombart 2008; Jombart & Ahmed 2011).

## Results

### Relatedness within units

As predicted, we found that patterns of relatedness within gelada units were consistent with a behavioural pattern of female philopatry and male dispersal. Specifically, within units, female–female dyads were significantly more related than would be expected by chance ( $P < 0.0001$ ; Fig. 2). Moreover, both male–male (i.e. between leaders and followers within a unit) and male–female pairs were not significantly more related than chance (both  $P > 0.1$ ; Fig. 2), suggesting that males dispersed from their natal units.

To further understand the variation in female–female relatedness between units, we next examined each unit independently. Females in 18 of 19 units were significantly more related than chance (all  $P < 0.03$ ; Fig. S1, Supporting information) and levels of female relatedness in the remaining unit approached significance ( $P = 0.051$ ). On average, females within units were related at the level of half-siblings ( $r_w = 0.28 \pm 0.01$ ;  $N = 325$  dyads). In the majority of units (16 of 19), all females in the unit shared the same mtDNA haplotype with other females in their unit. In three of 19 units, we found two distinct haplotypes among females in the same unit. In these units, one haplotype was found in



**Fig. 2** Relatedness across the four levels of gelada society in three classes of dyads. Female–female relatedness differed significantly across the four levels, while relatedness did not differ significantly in male–male or male–female dyads. We assessed significance using 10 000 bootstrap iterations in the program COANCESTRY v.1.0 (Wang 2011). Significant differences in relatedness are denoted by black solid lines.

~50% of the females in a unit while a different haplotype was found in the other 50% of females. In one of these units, the two haplotypes differed at one nucleotide, suggestive of a recent single nucleotide mutation passed from mother to daughter in one matriline. However, the other two units with two within-unit mtDNA haplotypes had much larger differences between the two haplotypes in each unit: in one unit, the two haplotypes differed at 11 nucleotides, while in the other unit the haplotypes differed at 24 nucleotides.

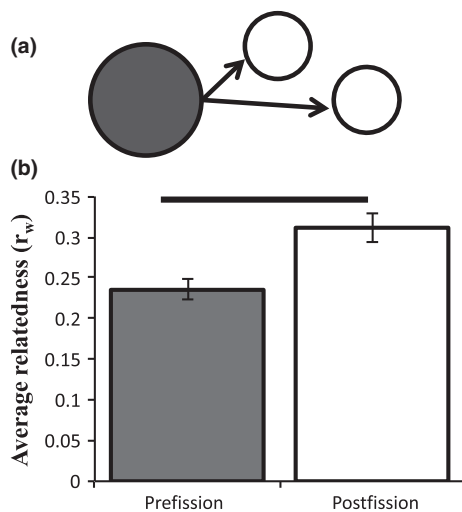
### Effect of fissions on female–female relatedness within units

All three units that fissioned had at least nine females prior to the fission and split into two or three 'daughter' units. Specifically, B-unit ( $N = 12$  females) fissioned into two daughter units of 8 and 4 females; C-unit ( $N = 9$  females) fissioned into three daughter units of 2, 2 and 5 females; and H-unit ( $N = 12$  females) fissioned into two daughter units of 3 and 9 females). Fissions occurred along familial lines such that all mothers and their adult daughters (14 of 14 mother–adult daughter pairs) joined the same postfission unit. Additionally, female–female relatedness within the newly formed units was significantly higher than relatedness within the unit prior to the fission event (B-unit fission,  $P < 0.002$ ; C-unit fission,  $P < 0.002$ ; H-unit fission,  $P < 0.02$ ; Fig. 3). Females were not significantly more related to males in their new, postfission unit ( $r_w = 0.019 \pm 0.027$ ) than to males in their prefission unit ( $r_w = 0.032 \pm 0.030$ ;  $P > 0.80$ ).

### Kinship structure of gelada society

In support of our prediction that groups of related females represent the core social groups in the gelada's multilevel society, we found a strong correlation between the AI value and pairwise genetic relatedness among all study females in the population (Spearman's  $\rho = 0.336$ ,  $P < 0.0001$ ; Fig. S2, Supporting information). In other words, female–female dyads that were found together more often had higher pairwise relatedness than females with lower AIs. Conversely, male–male relatedness and AI were not significantly correlated (Spearman's  $\rho = 0.012$ ,  $P = 0.37$ ; Fig. S3, Supporting information). Similarly, analysis of the maternally inherited mtDNA revealed that, on average, females that shared haplotypes had higher AIs than males that shared haplotypes ( $AI_{\text{females}} = 0.60 \pm 0.01$ ,  $AI_{\text{males}} = 0.49 \pm 0.01$ ,  $t = 7.218$ ,  $P < 0.001$ ; Table S1; Fig. S4, Supporting information). We found more mtDNA variation among the males in our study population than among the females (males = eight haplotypes, females = six haplotypes; Table S1, Supporting information), suggesting that some males had immigrated from bands outside of our study community. Further, we found more pairwise nucleotide differences within the males than within the females (male mean pairwise differences = 15.8, females = 10.4; Table S1, Supporting information).

Given the overall correlation between relatedness and spatial association in females, we expected to find differences in relatedness among the levels of gelada



**Fig. 3** (a) Schematic showing a fission event where a large unit (grey circle) fissioned into two or more 'daughter' units (white circles). (b) Relatedness within units after fissions (white bar) was significantly higher than relatedness within units prior to fissions (grey bar;  $P < 0.02$ ,  $N = 3$  fissions, within-unit  $N = 104$  dyads, between-unit  $N = 108$  dyads).

society (unit, team, band and community). We found a significant difference in female–female relatedness among all levels of gelada society (all  $P < 0.001$ ; Fig. 2). Specifically, pairs of females that lived in the same unit were the most closely related on average, females that lived in different units within the same team were the next most closely related pairs, females that lived in different teams within the same band were the third most closely related pairs, and females that lived in different bands but within the same community were unrelated on average. In strong contrast, male–male pairs and mixed-sex pairs all tended to have similarly low pairwise relatedness whether they were living in the same or different units, teams, bands or communities (all  $P > 0.1$ ; Fig. 2). Further, our bootstrap analysis revealed that, at the unit, team and band levels, female–female pairs were significantly more related than chance ( $P < 0.0001$ ; Fig. 2), but this was not true of male–male pairs or male–female pairs ( $P > 0.1$ ; Fig. 2).

Females within our three teams were, on average, less related than within-unit females, but were still slightly more closely related than cousins ( $r_w = 0.17 \pm 0.01$ ;  $N = 129$  dyads). Moreover, females in all teams shared the same mtDNA haplotype with their female 'teammates'. Thus, females in the same team descended from the same maternal lineage.

Graphical analysis of  $\Delta K$  from the STRUCTURE output revealed no optimal subdivision in the simulation including only males (Fig. S5, Supporting information). There was, however, strong evidence for genetic subdivision among females, in which the two most likely subdivisions were found at  $K = 3$  and  $K = 8$  (Fig. S6, Supporting information).  $\Delta K$  was three times as strong at  $K = 8$  than  $K = 3$ . However, STRUCTURE can overestimate the most likely value of clusters when the population contains many related individuals (Pritchard *et al.* 2000), as is the case with our population. It is therefore likely that there are three genetic subgroups in our population, corresponding to the three bands determined by association patterns (Snyder-Mackler *et al.* 2012). Our DAPC analysis corroborated the STRUCTURE results. Using only the genotypes, we were able to correctly assign 92% of females (105 of 114 females) to the band with which they were spatially associated (Snyder-Mackler *et al.* 2012), which was significantly more than would be expected by chance (Figs S7 and S8, Supporting information). Only 72% of the males were correctly assigned to their band, which was not significantly different from chance (Figs S7 and S8, Supporting information).

The CLUMPP permutation program (Jakobsson & Rosenberg 2007) assigned the majority of females (106 of 114) to one of the three genetic subgroups (clusters) with at least 50% probability (chance would be 33%

probability of being in one of the three clusters). We calculated the average  $Q$  value for females in each of the three bands (the largest level of structure in gelada populations below the community as a whole) and found that each band was characterized by a distinct cluster (Fig. 4). In other words, females in the same band occupied the same genotypic clusters defined by the unsupervised analysis (i.e. *STRUCTURE* did not take into account behavioural association patterns).

## Discussion

### *Females form the core of gelada multilevel society*

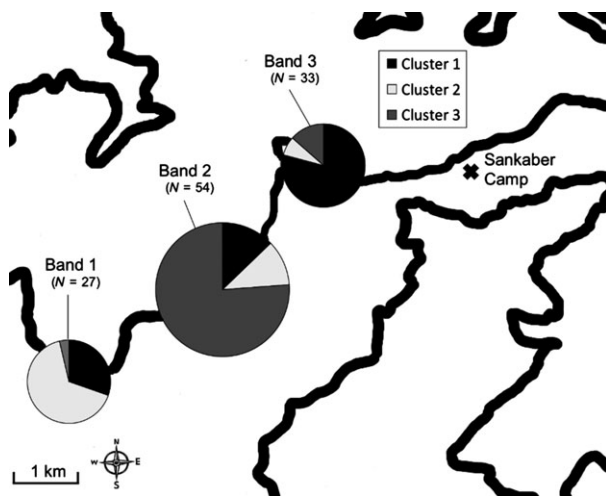
We found strong underlying genetic structure in the gelada multilevel society mediated by females' tendencies to associate with close kin. Multiple measures of female–female relatedness were positively correlated with association strength, while male–male associations did not predict genetic substructure. Intriguingly, female–female relatedness structure mirrored the multilevel association patterns of the multilevel society. That is, females within units were more closely related than females within teams, females in units that formed a team were more closely related than females in units that did not, and so on (Fig. 2). This tiered pattern of relatedness indicates that gelada society has a more

stratified genetic structure than the relatively continuous pattern created by isolation by distance observed in some nonsocial species (e.g. raccoons; Ratnayake *et al.* 2002). Furthermore, the multiple layers of relatedness indicated a more complex process of dispersal and association than the 'all or none' structure of single-level societies (e.g. red deer: Nussey *et al.* 2005). Sequencing of mtDNA corroborated our genetic findings from autosomal microsatellites. Namely, we found that as association increased (i.e. from community, to band, to team, to unit) females were more likely to share the same maternally inherited mtDNA haplotype. Moreover, the Bayesian *STRUCTURE* analyses revealed evidence for three genetic subgroups in our population, matching the previously reported number of bands (as measured by spatial association patterns) in this study population (Snyder-Mackler *et al.* 2012). This suggests that females within bands shared a more recent common ancestor with each other than did females between bands. Overall, we found strong support for our prediction that closely related females form the core of gelada society, while males mediate gene flow by dispersing from their natal units to other bands and, likely, communities.

### *Females fission along familial lines*

Unit fissions occurred along familial lines, with all mother–daughter pairs entering the same daughter unit after the fission event. This suggests that females choose their postfission unit membership based on patterns of kinship. Fissions induced by males would be expected to split females into daughter groups at random, irrespective of kinship, as is hypothesized to occur in hamadryas baboons (Sigg *et al.* 1982; Abegglen 1984; Swedell *et al.* 2011), but this was not seen in our study. In addition, the fact that mothers and daughters enter the same postfission unit and remain together, in spite of the fact that mothers and daughters tend to occupy adjacent rank positions (Le Roux *et al.* 2011), indicates that they are not abandoning their superiors in rank (as predicted by the 'abandon your superior' model; Ron *et al.* 1994). Overall, females in teams were still more significantly related than males in teams (Fig. 2), suggesting that closely related females, rather than the males, form the 'glue' keeping the daughter units together as a teams.

One possible mechanism for this fission process could be that females remain in groups with their primary social partners, which tend to be close kin (Tinsley Johnson *et al.* 2014). For example, mother–daughter dyads may join the same postfission units because they had a strong social bond prior to the fission event. Further research is needed to tease apart the different



**Fig. 4** *STRUCTURE* results showing average fractional group membership ( $Q$ ) of females in three study bands at each bands' modal sleeping site on a map of the study area. The solid line represents the 3000 m contour that corresponds to the escarpment where sleeping cliffs are located; Sankaber camp and the main study area are on an isthmus of grassland above the contour. The majority of females in each of the three bands were members of the same unique cluster, showing that females within bands were much more closely related than females living in different bands.



impacts of behaviour and kinship on unit fissions and subsequent group membership—however, this may be difficult due to the strong correlation between social behaviour and relatedness in female geladas (Tinsley Johnson *et al.* 2014).

Interestingly, we also found evidence suggestive of unit fusions (or alternatively of female immigration) in two of our study units. This corresponds to observations in elephants where fusions of female kin-groups are rare but detectable (Archie *et al.* 2008). The large within-unit mtDNA haplotypic differences that we observed in two units suggest one of two things: (i) that one or more unrelated females immigrated into the units in the recent past or (ii) that two units of unrelated females joined together to form a new unit in the recent past. Both scenarios indicate that there may be a selective disadvantage, such as inability to compete for food or mates, to residing in a very small unit (i.e. one or two females), which may cause small units to fuse together to form a larger unit that is composed of two unrelated matriline.

#### *Possible benefits to maintaining ties across units*

Given the above patterns, it is possible that the postfission association patterns of closely related females drive the multilevel socio-genetic structure of geladas. In other words, as fissions occur over multiple generations, teams, bands and eventually communities form. Female philopatry in a multilevel society allows geladas to increase their opportunities to maintain associations with both close and distant kin, creating the possibility that geladas accrue indirect fitness benefits by cooperating or grouping with kin across multiple levels of their society. For example, it is possible that female geladas benefit by sharing a home range with kin. In this sense, gelada unit fissions could be considered analogous to the limited, kin-based dispersal patterns seen in many vertebrates (e.g. 'budding'; Komdeur & Edelaar 2001). In these species, individuals either disperse with kin to new groups and/or disperse a short distance from their natal group, which decreases the costs of within-group competition while still allowing for the sharing of beneficial resources (e.g. Komdeur & Edelaar 2001; Bradley *et al.* 2007; Metheny *et al.* 2008). In geladas, it is also likely that the associations themselves are beneficial (e.g. through selfish herd effects; Hamilton 1971) and associations may happen along kin lines owing to mechanistic (as opposed to adaptive) reasons. For example, fissioned units may continue to associate simply because they have a shared home range not because they are seeking kin.

As in many other species (Quinn & Cresswell 2006; De Vos & O'Riain 2010), geladas form larger aggrega-

tions (i.e. more units) in areas with a higher predation risk (Dunbar 1986)—which may represent cooperation in group defence (Iwamoto *et al.* 1996) but may also lead to direct individual benefits through the dilution effect (Cresswell 1994). Similarly, unattached, bachelors pose a potential infanticidal threat to unit females who are pregnant (Roberts *et al.* 2012) or lactating (Mori *et al.* 1997; Beehner & Bergman 2008)—which represent the majority of females in the unit at any point in time. Therefore, females that can rapidly aggregate in response to the presence or proximity of bachelors may outcompete those that are unable to aggregate or 'clump' together (Pappano *et al.* 2012). Preferences for association with related individuals may facilitate these rapid aggregations. Additionally, bachelor males are a threat to unit males as every leader male will eventually lose reproductive access to 'his' females via a takeover from a bachelor male. Thus, males also benefit from the clumping of units in the presence of bachelors, yet gelada males do not (or are unable to) seek out kin during these aggregations.

If indirect fitness benefits are one of the driving forces underlying the social structure of geladas, the benefits must get weaker as relatedness drops towards zero at the community level. In fact, it is possible that there is a 'relatedness threshold' at which individuals no longer recognize kin and therefore cease to associate with them at high rates. Chapais *et al.* (1997, 2001) found just such a 'relatedness threshold' in Japanese macaques (*Macaca fuscata*), who consistently performed altruistic acts towards their closest kin ( $r > 0.25$ ), but less consistently to individuals who were more distantly related ( $0.25 > r > 0.125$ ). We observed a clear drop-off in strength of association between units within a team and units within a band, which corresponds to a 'relatedness threshold' that may occur after the level of the team. Interestingly, our genetic analysis show that this threshold is remarkably similar to the  $r = 0.125$  suggested by Chapais *et al.* (1997), as females in the same team are, on average, related at  $r_w \approx 0.15$ . It is therefore possible that kin selection may be driving the strong association between units in a team, but that other ecological (e.g. predation) or social (e.g. threat of bachelor males; Pappano *et al.* 2012) factors are the driving force behind the weaker ties among units in bands and communities.

#### **Conclusion**

Female philopatry, followed by an iterative process of kin-based group fission, gives rise to the multilevel societies of geladas. Female philopatry also forms the backbone of the multilevel society of elephants (Archie *et al.* 2006; Wittemyer *et al.* 2009), which suggests that similar

underlying evolutionary mechanisms may have led to the evolution of female-philopatric multilevel societies in some cases. Superficially, it seems that geladas also share a similar kin-structure with the fission–fusion society of bottlenose dolphins, in which female kin relations predict home-range overlap (Frère *et al.* 2010). However, it appears that male kinship patterns explain the core level ('first-order alliances') of the transient multilevel alliances formed by male bottlenose dolphins (Krützen *et al.* 2003). These differences suggest that the kin-structure of bottlenose dolphin society differs from that of geladas, perhaps because of differences in ecology. Female kin associations are also not present in the multilevel societies of the cooperatively breeding bell miners (Painter *et al.* 2000), suggesting that the multilevel societies of cooperatively breeding species may have evolved via different selective pressures than those of geladas and elephants. Interestingly, close associations between related females are unlikely to be the underlying mechanism for the multilevel society of hamadryas baboons (Sigg *et al.* 1982; Abegglen 1984; Kummer 1984; Colmenares 1992; Swedell *et al.* 2011). As such, two closely related species, geladas and hamadryas baboons, appear to have converged on superficially similar, but fundamentally different multilevel societies. The strong male–male bonds that characterize hamadryas baboons stand in stark contrast to the strong female-based association patterns that characterize gelada society. These differences, however, highlight the varied ways that multilevel societies can form. In geladas, the persistence of historical associations among females across generations appears to drive the formation of teams and bands. While the pattern creates the possibility that females actively seek kin for inclusive fitness benefits at multiple levels of gelada society, this is an area that needs further exploration.

### Acknowledgements

We thank the Ethiopian Wildlife Conservation Authority (EWCA) along with the wardens and staff of the Simien Mountains National Park for the opportunity to conduct research on geladas. This research could not have been conducted without the tireless dedication of the University of Michigan Gelada Research Project field team. We are also grateful to D. Cheney, R. Seyfarth, & J. Tung for insightful comments on earlier drafts of this manuscript as well as members of the Alberts' lab for their guidance with the genetics. This research was funded by the National Science Foundation (SMA-1306134, BCS-0715179, BCS-0962118 and the Graduate Research Fellowship Program), the Leakey Foundation, the National Geographic Society (#8100-06), the University of Pennsylvania and the University of Michigan. The University of Michigan UCUA (#09554) and the University of Pennsylvania IACUC (#802996) approved all methods.

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ples. S.C.A. provided supplies, equipment and support for all laboratory work. N.S.M. analysed the data. N.S.M. wrote the manuscript, with all authors contributing.

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### Data accessibility

All data necessary to re-create the analyses in this manuscript, including the microsatellite and mitochondrial genotypes, individual group membership and association data have been deposited in Dryad (doi: 10.5061/dryad.d8p5g).

### Supporting information

Additional supporting information may be found in the online version of this article.

**Table S1** Within bands, females are more likely to share the same haplotype than males.

**Fig. S1** Average relatedness among dyads with 95% confidence intervals (CI).

**Fig. S2** Female-female dyads that associated more closely had higher values of pairwise genetic relatedness.

**Fig. S3** Correlation between association and relatedness ( $r_w$ ) in female-female dyads (top panel) and male-male dyads (bottom panel).

**Fig. S4** Distribution of mtDNA haplotypes in the three study bands.

**Fig. S5** Delta  $K$  for STRUCTURE output using only male microsatellite genotypes.

**Fig. S6** Delta  $K$  for STRUCTURE output using only female microsatellite genotypes.

**Fig. S7** Bands are genetically distinct for females, but not males.

**Fig. S8** Scatterplot of the first two discriminant functions of the DAPC analysis.

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N.S.M. and T.J.B. conceived and designed the study. N.S.M. collected, extracted and genotyped all of the sam-