Kinship and Dominance Rank Influence the Strength of Social Bonds in Female Geladas (*Theropithecus gelada*)

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Abstract In many primates, close social relationships are associated with lower stress, better health, and increased life span. However, individuals do not form bonds indiscriminately; rather, they focus on a few primary partners. This suggests that the identity of the partner may be as important as the bond itself. Although dominance and kinship have repeatedly emerged as salient predictors of female relationships, most of this research comes from species with multimale, multifemale groups and strict dominance hierarchies. Further, kinship was typically determined based on either behavior or on known mother–daughter relationships alone. To understand the generality of previous findings, we use behavioral and genetic sampling to examine whether dominance rank and/or genetic relatedness mediate female social bonds in geladas (*Theropithecus gelada*) living in the Simien Mountains National Park, Ethiopia. First, we found that, even though females in the same unit are closely related, female geladas still preferentially bond with the closest of these relatives. Second, females that were close kin formed the strongest bonds with females of similar rank to themselves. Finally, rank disparity predicted grooming rates but did not predict whether females were nearest

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neighbors. This suggests that, in contrast with data from other cercopithecines, spatial proximity among females may be less indicative of strong social bonds for geladas, a species that routinely exhibits a high degree of spatial overlap with extra-unit individuals. Together, these results highlight the importance of combining genetic data with detailed behavioral observations to help us understand how individuals choose and interact with social partners.

Introduction

Primates form highly differentiated social relationships with one another, which may be hostile, indifferent, or affiliative, depending on the individuals involved (Mitani *et al.* 2012). As we begin to uncover the many benefits associated with close affiliative relationships (Brent *et al.* 2011; Crockford *et al.* 2008; Schülke *et al.* 2010; Silk *et al.* 2009, 2010), it becomes increasingly important to identify the factors that determine why individuals form bonds with some group-mates but not others. For example, many female cercopithecines focus on one to three *primary*, or preferred relationships, spending any extra social time on *secondary* or "casual" relationships (Crockford *et al.* 2008; Dunbar and Dunbar 1988; Engh *et al.* 2006; Nakamichi and Shizawa 2003; Range and Noë 2002; Silk *et al.* 2012). Among female-philopatric species, the most consistent factors that characterize preferred social partners are 1) dominance rank (Range and Noë 2002; Seyfarth 1976, 1977), 2) kinship (Chapais *et al.* 2001; Silk *et al.* 1999, 2010), or 3) both (Bernstein and Ehardt 1985; Perry *et al.* 2008; Schino 2001; Schülke *et al.* 2013; Silk *et al.* 2006a,b).

First, socioecological theory predicts that female primates should form strict, linear, dominance hierarchies and differentiated social bonds when intragroup competition for resources is high and intergroup competition is low (Sterck *et al.* 1997; Wrangham 1980; van Schaik 1989). If dominant females are the most valuable allies during agonistic encounters, then competition for powerful partners should result in a consistent pattern: high-ranking females monopolize access to high-ranking partners, mid-ranking females monopolize access to mid-ranking partners, and the lowest-ranking females are left to form alliances with each other (Seyfarth 1977). Although this hypothesis specifically predicts that grooming is directed up the dominance hierarchy, the outcome is such that females end up grooming individuals that are adjacent in rank. In other words, the *rank disparity* between two females should predict the strength of the bond between them. Indeed, many studies have supported this hypothesis, demonstrating strong bonds among females with adjacent ranks, e.g., *Cercocebus torquatus* (Range and Noë 2002), *Macaca mulatta* (de Waal 1991), *M. radiata* (Silk 1982), *Papio cynocephalus* (Silk *et al.* 2006a), *P. ursinus* (Silk *et al.* 2010); reviewed in Kapsalis *et al.* (2004).

Second, inclusive fitness benefits may favor individuals that bias affiliative behavior toward close kin (Hamilton 1964). Therefore, kinship may represent an alternative (or additional) predictor of female social relationships. To date, researchers have focused mainly on the effects of *maternal* kinship on social bonds, which, unlike paternal kinship, can be identified through behavioral observations and long-term pedigrees. More importantly, the subjects themselves may be able to detect maternal relationships,

presumably through social overlap facilitated by a matriarch (Silk 2002). Indeed, maternal kinship is known to structure female social relationships in many primate species (*Cebus capucinus*: Perry *et al*. 2008; *Cercopithecus solatus*: Charpentier *et al*. 2008; *Macaca mulatta*: Schülke *et al*. 2013; *Papio cynocephalus*: Silk *et al*. 2006a; *P. ursinus*: Silk *et al*. 2010; reviewed in Chapais and Berman 2004). For example, female Japanese macaques (*Macaca fuscata*) preferentially form close relationships with females that fall within a threshold level of maternal relatedness, approximating a kinship "rule of thumb"; e.g., individuals should preferentially affiliate with individuals that are at least their half-sibling (Chapais *et al*. 1997). A handful of studies also suggest that paternal kinship may be important for female relationships. For example, in rhesus macaques (*Macaca mulatta*: Schülke *et al*. 2013; Widdig *et al*. 2002) and yellow baboons (*Papio cynocephalus*: Silk *et al*. 2006a; Smith *et al*. 2003) genetic data indicate that relatedness along both maternal and paternal lines predicts the degree of social affiliation. However, other studies suggest that paternal kinship has only a moderate effect (*Macaca mulatta*: Schülke *et al*. 2013; *Papio cynocephalus*: Silk *et al*. 2006a), or no effect at all, e.g., *Pan troglodytes* (Mitani 2009); *Cebus capucinus* (Perry *et al*. 2008), on social bond strength.

Despite widespread support for the effects of rank and kinship, the vast majority of these studies have been conducted on cercopithecines living in large, multimale, multifemale groups, making it difficult to extrapolate these findings to other primate species. Such large, mixed-sex groups typically include both related and unrelated females and exhibit despotic, linear, dominance hierarchies (Cords 2012). In one of the few studies of female bonds in a non-cercopithecine primate, white-faced capuchins (*Cebus capucinus*: Perry *et al*. 2008), both dominance rank and kinship were primary determinants of social relationships, yet, like most cercopithecines, female white-faced capuchins are matrilocal and their dominance hierarchies are matrilineal (Fedigan 1993; Jack and Fedigan 2004; Perry 1996; Perry *et al*. 2008). Not surprisingly, kinship plays a negligible role for female social bonds among species characterized by female dispersal, where few if any kin are available, e.g., chimpanzees (*Pan troglodytes*: Langergraber *et al*. 2009). What remains uncertain is the extent to which dominance and kinship influence female social relationships in matrilocal species that diverge from the typical cercopithecine social structure. Here, we explore whether dominance rank and kinship predict female social bonds in a wild population of geladas (*Theropithecus gelada*), a species that differs from other cercopithecines in that the individuals have 1) an unusual modular social system, 2) low food competition, and 3) extraordinarily high levels of social tolerance.

First, the modular social system of geladas is composed of small core units, i.e., *one-male units*, composed of closely related females, one dominant male, and zero to five subordinate males (Snyder-Mackler *et al*. 2012a). These units are socially "closed," meaning that grooming and other affiliative behaviors have never been observed between females of different units (with the rare exception of recently fissioned units; Bergman and Beehner, *unpubl. data*). In sharp contrast with the cercopithecine model, where females can associate with both kin and nonkin group members, gelada females have only kin from which to choose social partners (le Roux *et al*. 2011). In such a system we can therefore test if living in groups containing close relatives strengthens or weakens the importance of kin-biased behavior.

Second, although female geladas have a linear, stable, and maternally inherited dominance hierarchy, interactions among females are characterized by lower levels of

aggression and a less strict hierarchy than other cercopithecines (le Roux *et al.* 2011). These differences may reflect the characteristics of the gelada dietary staple —grass— a food resource that is not clumped, defensible, or in short supply (Dunbar 1977, 1992; Iwamoto 1979). Socioecological theory predicts that such a diet should result in a more egalitarian society with less emphasis on female competition (Sterck *et al.* 1997). Indeed, gelada hierarchies may be more tolerant than those reported for other cercopithecines (Dunbar and Bose 1991; Fashing *et al.* 2010). Consequently, dominance rank might not structure social relationships in geladas in quite the same way.

Third, geladas show unusually high levels of tolerance for extragroup individuals, including those they may not recognize (Bergman 2010). Gelada reproductive units join together to form large aggregations approaching 1200 individuals, but the specific units within any one aggregation can fluctuate across seasons and even throughout the day (Snyder-Mackler *et al.* 2012a). Further, at any given time, individuals from one unit can demonstrate a high degree of spatial overlap with individuals from other units (Snyder-Mackler *et al.* 2012a). Thus, although gelada reproductive units are socially closed, i.e., affiliative interactions are restricted to within the unit, they are by no means spatially closed, i.e., females are often in close proximity to extraunit individuals. Previous studies examining social bonds in primates have demonstrated that close proximity is a useful proxy for identifying a close relationship between two individuals. For example, in chacma baboons, females with strong social bonds frequently forage close together and individuals that co-feed have the strongest grooming relationships (King *et al.* 2011). However, this may not be the case for geladas, in which selection has favored larger aggregations than is typical among ceropithecines. Thus, even though closely bonded females are likely to be in close proximity, all females in close proximity may not necessarily be bonded.

Here, we examine whether the strength of the social bond between two females can be predicted by how close they are in dominance rank and/or relatedness. Although early field studies on geladas demonstrated that females preferred social partners that were both close kin and close in rank to themselves (Dunbar 1979, 1984), these studies relied on presumed lineal relationships, i.e., mother–daughter, for evidence of kinship rather than genetics. Further, the effects of dominance rank and kinship were not addressed separately. These two variables are likely to correlate highly, as female geladas, like most cercopithecines, inherit their position in the dominance hierarchy from their mothers (le Roux *et al.* 2011). In this study, we seek to contribute to and corroborate these early findings in the following ways: 1) We employ genetic analyses that allow us to examine relatedness overall, not just relatedness along maternal lines; 2) we use multivariate statistics to examine the effects of rank and kinship (and their interaction) on the formation of social bonds; and 3) finally, because proximity may be less indicative of close social bonds in geladas, we examine how grooming and proximity each contribute to female bonds.

Methods

Study Site and Subjects

Data for this study come from 22 reproductive units within a community of wild geladas living in the Sankaber area of the Simien Mountains National Park, Ethiopia.

The entire community of geladas has been under observation as part of the long-term University of Michigan Gelada Research Project since January 2006 and the geladas are fully habituated to human observers on foot. The mean number of adult females per unit in this population was 5.24 (± 0.09 SEM; range 1–11 females during this study). Adult males and females of the same unit are always found together, and because geladas are matrilocal, mothers and daughters are always in the same unit. Female geladas in this population spent, on average, 4.92 min/h grooming (mean ± 0.28 SEM; range: 0.36–21.43 min/h) and groomed with a mean of 3.6 adult female partners (± 0.15 SEM; range: 1–8 partners). This research was approved by the University Committee on Use and Care of Animals (UCUCA no. PRO00001011) at the University of Michigan and adhered to the laws and guidelines of Ethiopia.

Behavioral Data Collection

We studied all adult females in 22 units ($N = 124$ females). Relationships were assessed according to dyad, that is, by the frequency of interactions or proximity between any two females within the same unit. The 124 females correspond to 416 intraunit dyads (hereafter, *coresident dyads*: Silk *et al.* 2006a).

The data presented here represent a 4-yr subset of the long-term data set during a period when both genetic and behavioral data are available (January 2009–December 2012). Using 15-min focal animal samples (Altmann 1974), we recorded all social behaviors involving adult females, focusing on dominance interactions (i.e., visual threats, vocal threats, physical aggression, submission, and vocal submission), and grooming, for a total of 1653 h of focal observation. In addition, at 5-min intervals within each focal sample, we recorded the identity of the nearest intra-unit adult female and their distance (in meters) from our focal subject. Finally, because dominance interactions are relatively rare events (Dunbar and Bose 1991; Fashing *et al.* 2010), we supplemented data collection with additional *ad libitum* observations of dominance interactions, i.e., all approach–retreat interactions, both with and without aggression.

Dominance Ranks

We assigned dominance ranks to adult females within units using the Elo-rating system (Albers and de Vries 2001; Neumann *et al.* 2011), a system originally developed to rank chess players (Elo 1961, 1978). This system is thought to model the process by which dominance is generated within a group (Albers and de Vries 2001). Specifically, after each contest, the winner's rating increases (and the loser's rating decreases) based on the expected probability of that individual winning the interaction. For example, if a higher-ranking female, i.e., one with a higher Elo-rating, wins an interaction with a lower-ranking female, her Elo-rating will increase (and the lower-ranking female's will decrease) marginally. If, on the other hand, a lower-ranking female dominates a higher-ranking female, each female's Elo-rating will change to a greater extent. The Elo-rating system offers several advantages over other ranking methods because the rankings 1) are independent of the number of individuals (which varies across groups and through time), 2) easily accommodate the entry and exit of females across time (due to maturation and death), and 3) are particularly useful for our purposes because they distinguish between adjacently ranked individuals that are closely matched from those that are clearly delineated.

Elo-ratings were based on all dyadic dominance interactions between coresident females during the study period. We set the initial Elo-rating for each female, i.e., the ranking each female gets when she "enters" the unit, at 1000. The number of points an individual gains or loses during an encounter (k) was set at 100 and weighted for each interaction by the expected probability of that individual winning or losing. Because geladas have a relatively stable dominance hierarchy, altering these initial parameters did not change any of our results. Therefore each female's rank was calculated as her mean Elo-rating, i.e., rank, over the entire study period. Because the unit of analysis for this study is a female dyad, we subsequently calculated the difference in the Elo-ratings for the two females in the dyad (hereafter, *rank disparity*), which we then used in all subsequent analyses.

Strength of Social Bonds

To determine the strength of social bonds between females, we used a common method for calculating a composite sociality index (CSI: Silk *et al.* 2006a) that uses the frequencies of grooming behavior and time in proximity for each female in a dyad. We standardized by unit means rather than the study population average because the gelada unit is a closed social group, and other studies normalize their social measures to this level, e.g., standardize within each baboon troop rather than across the whole population (Silk *et al.* 2006a). Moreover, gelada females in different units have access to a different number of potential social partners owing to the wide variation in unit sizes. The CSI is the mean of the adjusted frequencies of grooming and proximity such that:

$$\mathrm{CSI} = \frac{\left(\dfrac{G_{ab}}{G_u}\right) + \left(\dfrac{P_{ab}}{P_u}\right)}{2}$$

where G_{ab} is the total time (in seconds) that each female in a dyad spent grooming with the other (ignoring directionality), controlled by total observation time; G_u is the mean grooming frequency for all dyads in the unit; P_{ab} is the proportion of point samples where each female in a dyad was each other's nearest neighbor and within 5 m of each other (as per Silk *et al.* 2006a), controlled by total observation time; and P_u is the mean proximity frequency for all dyads in the unit. High CSI values indicate dyads with strong bonds, i.e., stronger than the mean for the unit.

In addition, we calculated separate indexes for the individual components of the CSI (grooming and proximity) to examine whether each covaried, e.g., demonstrated the same pattern, according to rank disparity and relatedness. We used the following formula for the grooming index:

$$\mathrm{groogming\ index} = \frac{G_{ab}}{G_u}$$

Because our proximity data also included times when females were grooming, we subtracted the proportion of time a dyad spent grooming from the proportion of point samples when they were nearest neighbors to calculate a proximity index:

$$\mathrm{proximity\ index} = \frac{P_{ab} - G_{ab}}{P_u - G_u}$$

Genetics

We collected fecal samples from all females (one to four samples/female) and stored them in RNAlater for subsequent DNA extraction and genotyping (for methods of storage and extraction see Snyder-Mackler *et al.* 2012b). We genotyped samples using polymerase chain reactions (PCR) at 23 human derived MapPairs microsatellite loci (20 described in Snyder-Mackler *et al.* 2012b, as well as D4s243, D11s2002, D10s1432), which were found to be variable in this gelada population (average number of alleles/loci = 5.91). We successfully genotyped all individuals at the majority of all 23 loci (average percentage of loci typed per individual = 95%). Even with these genetic data, we could assign maternity and paternity to both females only in 10% (42/416) of the dyads because many of our subjects were born before the study began, meaning their parents were never sampled. Moreover, only 9% (39/416) of the dyads were known mother–daughter dyads. We therefore rely on pairwise estimates of relatedness for our analyses because the available pedigree information is sparse. Specifically, we used Wang's pairwise relatedness estimator (r_w: Wang 2002), because it provided the most accurate estimate of relatedness between individuals of known pedigree in our population (mean parent–offspring and full sibling r_w: 0.48 ± 0.095 SD).

Modeling with Relatedness Estimators

Recent studies have cautioned against the use of microsatellite-based relatedness estimators (Csilléry *et al.* 2006; Van Horn *et al.* 2008). Nevertheless, most primate studies, including our own, are limited in their knowledge of population pedigrees, owing to the long life spans and slow reproductive histories of primates. Where deep pedigrees are unavailable, noninvasive genetic data are the only way to address certain biological questions, such as how kinship contributes to social partner preference. Therefore, to help address concerns about the accuracy of our relatedness estimates, we carried out 10,000 simulations testing the robustness of our models to variation in our relatedness estimators, thus estimating the power of our models. Our approach was to simulate the possibility that our relatedness estimator could over- or underestimate the true dyadic relatedness by a set amount. We therefore introduced error to the relatedness estimates based on the maximum observed difference between the estimated relatedness (r_w) and the true relatedness ($r = 0.5$) of all 256 *known* parent–offspring and full sibling dyads in the study population, i.e., including males, juveniles, and infants that are not included in our behavioral analyses. The maximum error between our estimated dyadic relatedness and the known relatedness was 0.32. Note that we use only parent–offspring dyads and full siblings because they are the only dyads for which we know the true relatedness. We therefore used 0.32 to set the boundaries for a uniform distribution (ranging from –0.32 to 0.32) from which we drew a random amount of error in each case. We feel that this is a conservative approach, as 95% of the r_w values of known parent–offspring dyads were actually within 0.21 of their true relatedness. Specifically, each simulation consisted of three steps: 1) we added a random number drawn from a uniform distribution between –0.32 and 0.32 to the relatedness estimator for each of the 416 dyads; 2) we remodeled the simulated data for all three outcome variables (CSI, grooming, and proximity); 3) we determined the

number of simulations (out of 10,000 total) in which the relatedness estimator was not a significant predictor in the three models.

Data Analyses

First, to examine the relationship between social bonds, rank disparity, and relatedness, we used three linear mixed models (LMMs). Each model used a different outcome variable: the CSI, the grooming index, or the proximity index. We do not include female age or the separate contributions of maternal and paternal kinship because, at present, the majority of adult females in our population have unknown birthdates and unknown mothers and fathers. All outcome indexes were log-transformed to approximate a normal distribution (Fig. S1). Each model considered only the dyads with sociality measures >0, so the total number of dyads per model varied accordingly: CSI model ($N = 406$); grooming model ($N = 277$); proximity model ($N = 391$). Because a significant number of dyads were never observed to groom at all ($N = 129$), we also ran a binary generalized linear mixed model (GLMM; groomed vs. never groomed) to determine how relatedness and rank disparity predicted whether individuals groomed at all. We could not model proximity and CSI in this manner because very few intra-unit dyads were found in proximity to one another. As random effects for each model, we entered the unit and the identities of each female in the dyad. As fixed effects in each model, we entered the degree of relatedness and the rank disparity between the two females. We were able to include both rank disparity and relatedness as predictors in the models because the correlation between the two was low ($r = -0.10$, $P = 0.036$), suggesting that females that are closely related are not always close in rank (as measured by Elo). We compared the univariate models, i.e., only rank disparity or relatedness as a predictor, to the additive and interactive models using Akaike's Information Criterion (AIC) to find the model that best fit the data. All models were fit using the lmer function of the R package lme4 (Sarkar and Bates 2009; R package version 0.999999-2; R version 3.0.1, R Foundation for Statistical Computing, R Development Core Team 2013).

Second, we examined each individual female's primary and secondary social partners. Previous analyses have defined "preferred" partners as those that fall into the top 10% of the CSI distribution (Silk *et al.* 2006a). However, because we are comparing females from multiple groups that vary greatly in size and range of CSI scores, we labeled females as *primary social partners* if their dyadic CSI score was both the highest CSI score for one female and the first or second highest CSI score for the other female. By this definition, primary social partners do not necessarily reflect the highest dyadic CSI scores of the unit, but rather the highest scores for those individual females. We labeled females as *secondary social partners* if their dyadic CSI score was both the second highest CSI score for one female and the second or third highest CSI score for the other female. All other female dyads were labeled as *nonbonded*. We then compared these categorical levels of preferred partners across rank disparity and relatedness using a permutation test. In each simulation, we randomly assigned the category, i.e., primary, secondary, or nonbonded, for a dyad and calculated the average difference in relatedness and rank disparity between these categories in the permuted data, i.e., primary vs. secondary, secondary vs. nonbonded, and primary vs. nonbonded. We then counted the proportion of the 10,000 simulations in which the simulated difference in relatedness (or rank disparity) between each category was greater than the observed difference.

Results

Composite Sociality Index

In the CSI models, the best-fit model included rank disparity, relatedness, and an interaction between the two (ΔAIC >4.8; Table I). First, relatedness was a significant predictor of bond strength: CSIs were highest among dyads that were closely related ($t = 8.18$, $P < 0.0001$; Fig. 1). Second, the interaction between rank and relatedness was also significant: among females that were more closely related, the bonds were significantly stronger between females that were also closer in rank ($t = –2.61$, $P < 0.01$; Fig. 1). Finally, there was no significant effect of rank disparity on CSI in the interaction model ($t = –0.152$, $P > 0.8$; Fig. 1), although in the univariate models, rank disparity and relatedness each significantly predicted CSI scores.

CSI scores were highly variable, even among females with high relatedness and low rank disparity, e.g., the scatter in the points at the far right of Fig. 2a for relatedness and the left side of Fig. 2b for rank disparity. However, we found partner preference helped explain much of this variance. Indeed, there were significant differences in both rank disparity and relatedness among primary, secondary, and nonbonded social partners. Females that were primary social partners were more closely related ($r_w = 0.40 \pm 0.02$ SEM, i.e., approaching the relatedness between a mother and daughter) than females that were secondary social partners ($r_w = 0.25 \pm 0.02$ SEM, i.e., comparable to half-sisters; $P < 0.0001$) and nonbonded ($r_w = 0.19 \pm 0.01$ SEM; $P < 0.0001$). Further, secondary partners were more closely related than nonbonded partners ($P = 0.0027$; Fig. 2a). Finally, primary social partners were significantly closer in rank than both secondary ($P = 0.0016$) and nonbonded dyads ($P < 0.0001$), whereas secondary social partners were not significantly closer in rank than nonbonded partners ($P = 0.2677$; Fig. 2b).

Grooming and Proximity Indexes

In our analyses of the individual components of the CSI (grooming and proximity), we found that relatedness was the sole significant predictor of whether or not a dyad

Table I Effects ($\beta \pm$ SE) of rank disparity and relatedness on each of the three social metrics in the best-supported models, i.e., lowest AIC, for geladas living in the Simien Mountains National Park, Ethiopia (January 2009–December 2012)

Social index	Rank disparity	Relatedness	Rank disparity × relatedness
CSI	$-5 \times 10^{-5} \pm 3 \times 10^{-4}$	2.93 ± 0.36*	$-2.6 \times 10^{-3} \pm 9.8 \times 10^{-4}$*
Grooming	$-3 \times 10^{-4} \pm 6 \times 10^{-4}$	3.84 ± 0.72*	$-4.6 \times 10^{-3} \pm 1.9 \times 10^{-3}$*
Proximity	N/A[a]	2.75 ± 0.45*	N/A

Significant predictors at $P < 0.05$ are denoted with asterisks.

[a] Note that we do not report the effects of rank disparity and the interaction between rank disparity and relatedness for the proximity model because these two variables were not predictors in the model with the best support. Instead, the model with the best support for proximity was the univariate model with relatedness as the sole predictor.
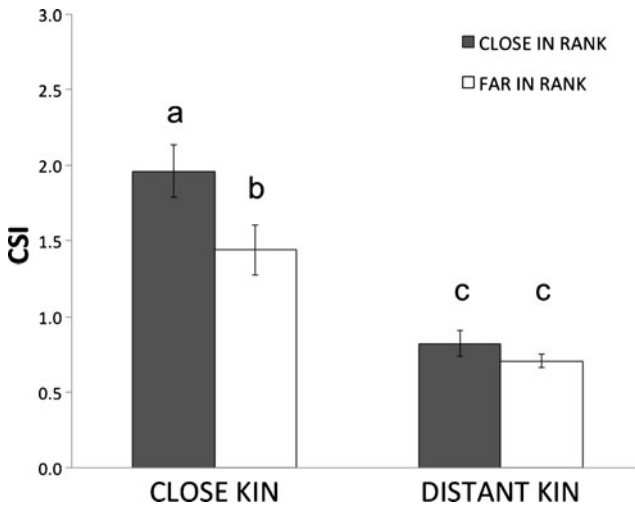
Fig. 1 The interaction between relatedness and rank disparity on the average composite sociality index (CSI) score for geladas living in the Simien Mountains National Park, Ethiopia (January 2009–December 2012). For visualization purposes only, we performed a median-split of rank disparity values, with values below the median labeled as *close in rank* and values above the median labeled as *far in rank*. Relatedness was also divided into two categories: where r_w was >0.25, females were labeled *close kin* and where r_w was <0.25, females were labeled as *distant kin*. Mean dyadic CSI scores for the following females are plotted: 1) close in rank and close kin (mean = 1.96 ± 0.17 SEM, N = 121); 2) far in rank and close kin (mean = 1.44 ± 0.16 SEM, N = 83); 3) close in rank and distant kin (mean = 0.82 ± 0.09 SEM, N = 87); 4) far in rank and distant kin (mean = 0.71 ± 0.05 SEM, N = 125). Means with different letters are significantly different.

groomed at all during the study period (β = 4.36, SE = 0.83, $P < 2 * 10^{-7}$). However, as in the CSI model, the best model for the grooming index included an interaction between rank disparity and relatedness (ΔAIC >3.96; Fig. 3a). Relatedness and the
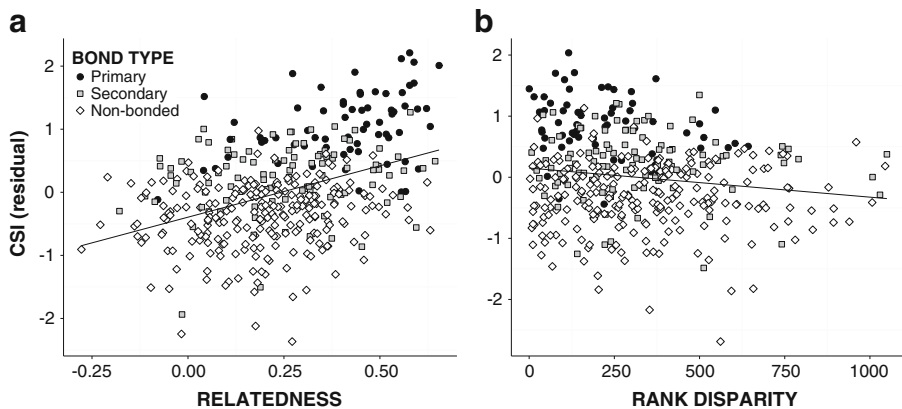

Fig. 2 Partial residual plots of the effects of (**a**) dyadic relatedness and (**b**) rank disparity on composite sociality index (CSI) for geladas living in the Simien Mountains National Park, Ethiopia (January 2009–December 2012). Dyads with high CSI scores have higher relatedness values and lower rank disparity. Furthermore, primary partners (black circles) are (**a**) more related and (**b**) closer in rank than secondary partners (gray squares) and nonbonded partners (white diamonds).

interaction between rank disparity and relatedness both significantly predicted the amount of grooming among dyads (Table I). In other words, closely related females groomed more in general ($t = 5.36$, $P < 0.0001$), but this effect was highest if these females were also close in rank ($t = -2.43$, $P < 0.02$).

When we examined the proximity index, we found that the univariate model with relatedness as the sole predictor was better at predicting which females were nearest neighbors than the additive or interactive models (ΔAIC = 0.63; Fig. 3b). Specifically, the females that were most often nearest neighbors were more closely related compared to females that were infrequently nearest neighbors ($t = 6.697$, $P < 0.0001$; Table I). Therefore, relatedness was a significant predictor for both grooming and proximity, but rank disparity was a significant predictor only for grooming, and not proximity. Although closely related females that were close in rank groomed the most, closely related females in general were often nearest neighbors, regardless of dominance rank.

Modeling with Relatedness Estimators

The simulations revealed that our models were extremely robust to these perturbations. For our CSI and proximity models, the effect of relatedness on the dependent variable was a significant predictor in all 10,000 simulations. The effect of relatedness on grooming failed to reach significance ($t > 1.66$; df = 111) in only 13 of 10,000 simulations. In other words, the power of our current test is >0.99, i.e., a <0.13% false negative rate, if we make the conservative assumption that our relatedness estimators are accurate to within 0.32. This suggests that, although researchers should exercise caution when using relatedness estimators in correlational analyses, they may still be meaningful and informative when both the effect of relatedness and sample sizes are large.
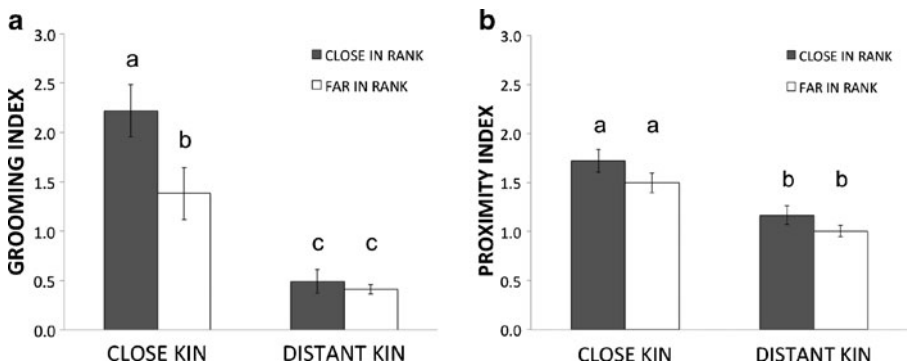

Fig. 3 The interaction between relatedness and rank disparity on (a) the average grooming index and (b) proximity index score for geladas living in the Simien Mountains National Park, Ethiopia (January 2009–December 2012). Categories were defined as in Fig. 1. Means with different letters are significantly different. (a) The mean dyadic grooming index is plotted for 1) close in rank and close kin (mean = 2.22 ± 0.26 SEM, N = 121); 2) far in rank and close kin (mean = 1.38 ± 0.26 SEM, N = 83); 3) close in rank and distant kin (mean = 0.49 ± 0.12 SEM, N = 87); 4) far in rank and distant kin (mean = 0.41 ± 0.05 SEM, N = 125). (b) The mean dyadic proximity index is plotted for 1) close in rank and close kin (mean = 1.72 ± 0.11 SEM, N = 121); 2) far in rank and close kin (mean = 1.49 ± 0.10 SEM, N = 83); 3) close in rank and distant kin (mean = 1.17 ± 0.10 SEM, N = 88); 4) far in rank and distant kin (mean = 1.00 ± 0.06 SEM, N = 127).

Discussion

Despite working with a relatively shallow pedigree, incorporating genetic data on overall relatedness corroborates earlier findings that the factors mediating social relationships for female geladas resemble those of other cercopithecines, where both kinship and rank disparity are important (Dunbar 1979, 1984). Females formed the strongest social bonds with females that were close kin and, among close kin, with females that were close in rank. Further, partner preference varied according to both dominance rank and kinship: primary partners were close kin and had lower rank disparity than both secondary partners and nonbonded dyads. Although secondary partners were not closer in rank than nonbonded social partners, they were more closely related than nonbonded dyads, which were the least related dyads in each unit.

Rank disparity had no predictive value for more distant kin. However, for close kin, females of similar rank were more closely bonded than females more distant in rank. Indeed, one interesting, and perhaps surprising, result of our analysis was the overall low correlation between relatedness and rank disparity, despite the fact that rank is maternally inherited. This is likely due to the fact that our relatedness estimator includes both maternal and paternal relatedness, whereas rank is inherited through the maternal line only. For geladas, male reproductive skew is relatively high, and therefore many females that are close in age will likely have the same father, i.e., be closely related (Snyder-Mackler *et al.* 2012b), but they may not necessarily be close in rank. In our analysis, such dyads, i.e., closely related but distantly ranked, exhibited higher levels of bonding than dyads that were distant kin, but were not as closely bonded as dyads that were both close kin and close in rank. Further, of all female dyads in the closely related but distantly ranked category ($N = 83$), we were able to assign paternity for both females in eight of them. Intriguingly, in all eight of these dyads, the females were paternal (and not maternal) kin, suggesting that paternal kinship is associated with detectable bonds in geladas. Alternatively, it is possible that some of the remaining dyads in the closely related but distantly ranked category are not as closely related as our relatedness estimator suggests (owing to overestimation error; Csillëry *et al.* 2006), which may contribute to their having reduced average levels of bonding. Certainly, a larger sample of pedigreed individuals will provide a better understanding of how maternal and paternal kinship as well as shared social history separately shape social bonds. However, the current data appear to add to the growing support that paternal kinship cannot altogether be ignored (Schülke *et al.* 2013; Silk *et al.* 2006a; Smith *et al.* 2003; Widdig *et al.* 2002).

Two primary goals for research on social bonds are to 1) standardize objective criteria by which researchers can quantify social relationships (and to find suitable operational indexes), and 2) identify functional outcomes. Although much debate centers on the definition and meaning of social bonds in nonhuman primates, there is a general consensus that the instrumental outcomes of the relationship, i.e., the phenomena we wish to explain using bonds, should not be confused with the behavioral proxies used to identify the relationship, i.e., the criteria by which we quantify bonds (Barrett and Henzi 2002; Dunbar and Shultz 2010). Some of the results presented here

have relevance for quantifying bonds. Although our results largely support the use of both social grooming and proximity as useful proxies for identifying female relationships in geladas, as in previous gelada research (Dunbar 1979, 1984; Dunbar and Dunbar 1977), grooming, and not proximity, varied according to both relatedness and rank disparity. This suggests that measures of proximity generally used to measure social bonding (Silk *et al.* 2006a, 2009) may need to be modified for use in geladas owing to their high level of spatial overlap. For example, although the dyads with the strongest grooming relationships were generally found in close proximity, it was also the case that dyads that exhibited weak grooming relationships were frequently found in close proximity. These results may reflect the unique demands of gelada social life, where direct competition over food is rare, and large foraging herds often consist of many intermingling one-male units. Regardless of why geladas exhibit such a high degree of social tolerance, our proximity measure may reflect an individual's social circle, e.g., its kin network, but not its closest social partners. Alternatively, it may be that geladas simply have a smaller threshold for discriminating neighbors, and if we were to define proximity differently, e.g., females within 1 m, we might find that proximity improves as a predictor of social bonds. Regardless, the behavioral proxies for identifying social bonds need to be considered carefully for each species, particularly if socioecological conditions select for larger or tighter aggregations of individuals (Dunbar and Shultz 2010; Silk 2002).

One potentially fruitful avenue for future research involves the identification and quantification of behavioral proxies for social bonds that may not require physical contact. For example, the exchange of vocalizations may be particularly relevant for geladas. Gelada females exchange vocalizations while foraging throughout the day, which Dunbar (1996) suggested might be akin to "vocal grooming," allowing females to maintain bonds with primary partners even while engaged in other activities. Indeed, unlike proximity, vocal contact is confined to members of the same unit (Dunbar 1996), suggesting that vocal exchanges may identify important aspects of gelada social relationships that may not emerge from grooming or proximity indexes. Overall, the challenge of identifying those behaviors that most closely reflect the phenomenon we seek to understand, e.g., the strength of a social bond, remains a relevant point of discussion.

With respect to the second goal, at present, we are unable to say whether a preference for closely related or closely ranked individuals might have functional consequences for gelada females. Studies that document direct and indirect fitness benefits associated with social bonds suggest that the formation and maintenance of relationships with specific individuals may confer fitness benefits. For example, Silk *et al.* (2009) demonstrated not only that female baboons preferentially affiliated with close maternal kin, but also that the strength of these kin bonds was associated with offspring survival. Rank-based associations, on the other hand, may reflect a different strategy, where females of adjacent rank are important allies in coalitions (Silk *et al.* 1999). Indeed, subtle differences exist in the quality and longevity of relationships between close kin and closely ranked females, with social bonds between kin emerging as more stable, less aggressive, and more equitable over the long-term than bonds between nonkin (Silk *et al.* 2010). Further analyses on female geladas that incorporate

measures of bond equality, diversity, and duration in combination with short- and long-term fitness outcomes will help complete the picture as to 1) whether, like baboons, gelada social bonds correlate with higher fitness, and 2) whether social bonds with some partners are associated with greater benefits than those with others.

In sum, this study demonstrates that genetic analyses of relatedness can reveal fundamental aspects of primate sociality. Even without knowledge of a deep pedigree, we were able to determine the effect of kinship on social bonds because relatedness had such a profound and strong effect on social bond strength. Indeed, with only limited pedigree information, a simple simulation demonstrated that the model was robust to the inherent variation that comes with using relatedness estimators. Thus, although researchers should exhibit caution when using relatedness estimators in correlational studies of biological phenomena (Csillery 2006; van Horn 2008), they nevertheless have their utility in field biology. There is great value in using relatedness estimators when deep pedigrees are absent, as is the case with new study populations. Our novel use of a simulation to test the robustness of our models to error in relatedness estimators is one way in which researchers can determine whether or not relatedness plays a significant role in answering biological questions. Further, we have begun to distinguish between two variables that are often highly correlated in female-bonded primate groups: kinship and rank. This study shows that, for gelada females, although both relatedness and dominance rank influence the strength of close social bonds, rank appears to be a secondary factor that comes into play only among close kin. We are now in the position to ask *why* kinship and rank structure gelada female social relationships.

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