TITLE: Social status drives social relationships in groups of unrelated female rhesus macaques

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Strong affiliative relationships can confer important health and fitness-related benefits, including increased reproductive success and longer lifespans (reviewed in Silk, 2014). For example, wild female baboons that form strong affiliative relationships (often termed “social bonds”) have been shown to live longer and experience higher offspring survival than females that are more socially isolated (Archie et al., 2014; Silk et al., 2009, 2010; Silk, Alberts, & Altmann, 2003). Similar benefits of affiliative social relationships have been found in rats (*Rattus norvegicus*; Yee et al. 2008), guinea pigs (*Cavia porcellus*; Hennessy et al. 2008), rock hyraxes (*Procavia capensis*; Barocas et al. 2011), horses (*Equus caballus*; Cameron et al. 2009), dolphins (*Tursiops* spp.; Stanton & Mann 2012), and, most robustly, in humans. Indeed, a recent meta-analysis of 148 studies in humans estimated a 50% decreased mortality risk for socially integrated individuals of both sexes, across all adult ages (Holt-Lunstad et al. 2010). Understanding these substantial effects on fitness requires understanding how affiliative relationships arise. In addition, because patterns of social relationships help determine overall group structure (Hinde, 1976; Seyfarth, 1977), such analyses are important for understanding the evolution of group living.

Among species that exhibit female philopatry, in which females remain in their natal social groups after maturity, the most consistent predictors of social bond formation are kinship and dominance rank (De Waal, 1991; Langergraber, 2012; Range & Noë, 2002; Seyfarth, Silk, & Cheney, 2014; Seyfarth, 1980; Silk, 2007, 2009; Smith, Memenis, & Holekamp, 2006; Tiddi, Aureli, & Schino, 2012; Tinsley Johnson et al., 2014). Preferential bond formation with close kin, when available, likely arises because it maximizes the indirect genetic benefits of affiliative relationships (i.e., opportunity for

kin selection: Hamilton 1964; West Eberhard 1975). In turn, preferential bond formation with higher-ranking individuals could be favored if investing in these females increases levels of social tolerance or rates of social support. In support of this idea, a meta-analysis of 14 different non-human primate species found a significant positive relationship between grooming social support (Schino 2007; but see: Silk et al. 2004; Molesti & Majolo, 2015; Schino & Alessandrini, 2015), although the directionality of this relationship—grooming leading to social support or social support driving increased grooming—is often unclear (but see: Hemelrijk, 1994; Koyama, Caws, & Aureli, 2006).

Understanding the relative impact of dominance rank and kinship in social bond formation is important for two reasons. First, such an understanding would help to disentangle the degree to which rank effects and social bond effects on health and fitness outcomes are independent. Studies of the effects of social status in female primates have tended to produce mixed results (Abbott et al., 2003; Pusey, 2012), with the strongest relationships often identified in captive settings in which females are not housed with kin (Abbott et al., 2003; Gust et al., 1993; Michopoulos et al., 2012; Muller & Wrangham, 2004; Scott, 2001; Shen & Kern Reeve, 2010). These observations suggest that the absence of kin could exacerbate rank effects in these settings, especially if dominance rank becomes the primary determinant of social relationships. Second, rank effects on social bond formation may account for several emergent features of hierarchical societies. For example, in 1977, Seyfarth suggested a simple but highly influential model which showed how preference for higher-ranking individuals, combined with limited resources to invest in social relationships, could explain two common properties of social bonds in female philopatric primates: a correlation between

high rank and increased affiliative behavior, and the existence of strong bonds between adjacently ranked females. Seyfarth's model assumed that all females have the same objective: to invest their limited time budget in giving and receiving grooming by partnering with high-ranking females. However, because grooming is dyadic, and a female's rank may constrain her ability to express her preference, the grooming availability of the highest-ranking females is quickly exhausted. As a result, middle- and low-ranking individuals can only satisfy their preference for grooming higher-ranking individuals by targeting the remaining "available" females, who will tend to be close to them in the hierarchy (Seyfarth, 1977).

Empirical tests of rank effects on grooming relationships in female philopatric mammals are generally consistent with these arguments (De Waal, 1991; Schino, 2001; Silk, Altmann, & Alberts, 2006; Smith et al., 2006; Tiddi et al., 2012; Tinsley Johnson et al., 2014). However, data interpretation is complicated by the tight correlation between dominance rank and relatedness in female philopatric species. In all species investigated thus far, closely ranked females have also tended to be close relatives, making it difficult to untangle the relative impact of dominance rank versus kinship on social bond formation. Indeed, a 2001 meta-analysis found no significant signature of rank adjacency when kin were excluded from the sample (Schino, 2001)—an observation that is interesting but challenging to interpret, given that kin were still available in these groups as potential social partners.

Here, we aimed to investigate the effects of dominance rank on social partner choice in the absence of kin networks. To do so, we focused on behavioral data collected on 45 female rhesus macaques, housed in nine experimentally manipulated

social groups (five females per group) that were rearranged in a mid-study intervention to form nine new social groups. None of these groups, either pre- or post-intervention, contained close maternal or paternal relatives, and, prior to group formation, no members of the same group shared any prior social history. We were thus able to observe the emergence of completely novel social bonds in the context of stringently enforced dominance rank hierarchies, which are typical for this species and arise rapidly in newly formed groups (Bernstein & Gordon, 1974; Bernstein, Gordon, & Rose, 1974; Bernstein, 1976). We used this paradigm to investigate four questions: i) whether grooming was associated with social tolerance, suggesting that high-ranking females are more valuable social partners, ii) whether dominance rank therefore structured the establishment and maintenance of grooming relationships in the absence of kin networks, iii) what rules, including those suggested by Seyfarth (1977), best predicted observed rank-structured grooming patterns, and iv) whether an individual's tendency to engage in affiliative social behaviors was primarily determined by rank or by individual characteristics that remained stable across the mid-study intervention.

METHODS:

Study subjects

Study subjects were 45 adult female rhesus macaques (median age at the start of the study = 7.2 years, range = 3-20 years) housed in nine social groups of five females each at the Yerkes National Primate Research Center (YNPRC). Groups were initially formed in January – June 2013 using an established protocol (Jarrell et al., 2008; Tung et al., 2012). Briefly, females at the YNPRC Field Station with no shared

social history were sequentially introduced to indoor-outdoor run housing (25 m by 25 m for each area) over the course of 2 - 15 weeks, until all groups included five unrelated adult females (see Table S1 for information about individual study subjects). In this paradigm, earlier introduced females tend to occupy higher subsequent dominance ranks (Jarrell et al., 2008; Tung et al., 2012).

The current study was divided into two phases: Phase 1 (February 2013 - March 2014) and Phase 2 (April - December 2014). Starting dates for each group and phase were defined as occurring on the date of completion of group formation (after addition of the fifth female into each group: see Table S1). Phase 1 groups were formed as described above. Phase 2 groups consisted of the same 45 females included in Phase 1, but with females reorganized into new groups. Specifically, groups in Phase 2 consisted of females who all shared the same or similar dominance ranks in Phase 1 (maximum difference of 1 ordinal rank value: Table S1), a strategy that altered the dominance ranks of the majority of the females across the phases (Fig. S1). As in Phase 1, the Phase 2 groups contained unrelated females with no prior social history. In both phases order of introduction was strongly correlated with dominance rank (Phase 1: $r=-0.54$, $p=1.1\times10^{-4}$, $n=45$ females; Phase 2: $r=-0.68$, $p=3.4\times10^{-7}$, $n=45$ females)

Behavioral data collection

Behavioral data were collected during weekly focal observations (Altmann, 1974). During these observations, a trained observer recorded the behavioral activities of all females in the “focal” group, which was possible in our study population because of the small group sizes. Behavioral data were collected according to an established

ethogram (Jarrell et al., 2008). We collected a total of 345 hours of focal observations on the 18 groups (mean = 19.17 hrs, range = 8.5 – 27.5 hrs; 223.5 hours in Phase 1 and 121.5 hours in Phase 2). The data of primary relevance to this study were dominance interactions (e.g., visual and vocal threats, physical aggression, and submissive behaviors) and grooming, which is the currency through which social bonds are formed and maintained in rhesus macaques (Brent et al., 2013; Sade, 1989). To control for differences in observer effort, we report individual and dyadic grooming as either grooming minutes per hour observed or as a proportion of a female's total time spent grooming. Data for Phase 1 and Phase 2 were analyzed separately such that each female had a measure of each behavior (i.e., grooming given and grooming received) during Phase 1 and a separate measure during Phase 2. We only used behavioral data collected after a group's formation was complete (i.e., the fifth female was introduced into that group).

Dominance rank assignment

We assigned dominance ranks in each social group using two methods. For analyses that required ordinal ranks, we compiled all dominance interactions that occurred during each phase into a pairwise matrix. We then ordered females to minimize entries below the diagonal, which minimizes interactions in which a higher ranking female loses an interaction with a lower ranking individual. For analyses that did not require discrete rank values, we used the Elo rating method, in which higher scores correspond to higher status (Albers & de Vries, 2001; Elo, 1978; Neumann et al., 2011). The Elo method updates a female's rank after each dominance interaction in which she

is a participant based on the pre-interaction probability that she would win or lose the interaction. If a higher-ranking female defeated a lower-ranking female, the higher-ranking female's Elo rating would increase (and the lower-ranking female's will decrease) marginally because the result of the interaction was expected based on the relative Elo rating of the two participants. On the other hand, if a lower-ranking female defeated a higher-ranking female, each female's Elo rating would change substantially because this "surprising" result would indicate a need to update rank values to better reflect the observed rank dynamics. We chose to use Elo ratings where possible because they distinguish adjacently ranked individuals that are closely matched (e.g., Elo ratings of 2,000 versus 1,990) from those that are more clearly delineated (e.g., Elo ratings of 2,000 versus 1,500). Consistent with findings by others (Albers & de Vries, 2001; Neumann et al., 2011), Elo ratings were highly correlated with ordinal ranks ($r = -0.94$; $p < 10^{-15}$, $n = 90$, with each of $n = 45$ females represented once in each phase, Fig. S2: the correlation is negative because high Elo ratings signify high rank, whereas high numbers signify low ordinal rank).

We calculated Elo ratings using all dyadic dominance interactions that occurred after a group's formation was complete. Each female's initial Elo rating was set at 1000 and the baseline number of points a female gained or lost during a dominance interaction (k) was set at 100. This number was then weighted for each interaction by the expected probability of that individual winning or losing, based on a logistic function that was updated after each dominance interaction (Albers & de Vries, 2001). We calculated the rank disparity between two females in a dyad as the difference in their Elo ratings at the end of the study period (March 2014 for Phase 1 and December 2014

for Phase 2). Dominance hierarchies were rapidly established after group formation and were highly stable across the study period. Specifically, Elo ratings calculated at 8-11 weeks post-group formation were strongly and significantly correlated with Elo ratings at the end of each phase of study (25-56 weeks: $r = 0.88$, $p < 10^{-15}$, $n=90$, with each of $n=45$ females represented once in each phase).

Data analysis

Using the combined data on social bond patterns and dominance rank, we investigated four questions:

(i) Is grooming associated with social tolerance?

We investigated this question using two approaches. In the first approach, we used a binomial generalized linear mixed model to test whether the amount of grooming a groomer provided to her partner predicted whether that partner ever aggressed against her. We chose to use this outcome measure instead of rates of aggression because, for a large number of dyads, the groomee never exhibited aggression directed to the groomer ($n = 146$ dyads). In the majority of these dyads (140 of 146 dyads), the groomer was higher-ranking than the groomee. Fixed effect predictor variables in this model were: the rate of grooming given per hour by the groomer to the groomee; the difference between the Elo rating of the groomer and the groomee (note that this value differs from the absolute value of the difference between the two Elo ratings, which we call “rank disparity,” because it is directional); and the number of focal observations collected for the pair of females, to control for observer effort. We included the identities

of the groomer and the groomee nested within their group as random effects.

To evaluate the relationship between grooming rates and aggression rates (instead of presence/absence, as above), we analyzed the subset of our data that included only those dyads in which the groomee aggressed against the groomer at least once ($n = 214$ dyads; 59% of all dyads). Here, we used a linear mixed effects model (LMM) to model the rate of aggression per hour directed from the groomee to the groomer as a function of the rate of grooming given per hour by the groomer. We log-transformed hourly rates of aggression to approximate a normal distribution. The amount of grooming given per hour and the directional difference between the Elo rating of the groomer and the groomee were modeled as fixed effects, and the identities of the groomer and the groomee nested within their group were modeled as random effects. We also fit a parallel model replacing the effect of grooming given per hour with the effect of grooming received per hour. If grooming received from a partner was associated with reduced aggression received from that same partner, it would suggest that investment in the grooming relationship reduced aggression in general (as opposed to a purely transactional model in which grooming was directionally exchanged for reduced aggression).

Second, we tested whether grooming another female temporarily reduced the subsequent risk of aggression from that individual. To do so, we compared the aggression rate directed from the groomee to the groomer immediately after grooming, to the background rate of aggression directed from the groomee to the groomer across the entire study (i.e., the “background aggression rate”). For each 30-minute focal observation, we counted the number of aggressive behaviors a female received from

her grooming partner after the end of their last observed grooming bout until the end of the focal observation. We aggregated these counts across all of the observations for that dyad to calculate the rate of aggression directed from a groomee to a groomer after grooming events (i.e., “aggression received after grooming”; the denominator for this rate is the sum of all of the times from the end of the grooming bout to the end of the focal). Finally, we compared the rate of aggression received after grooming to the background aggression rate calculated for the same dyads ($n = 315$), using an LMM that included a binary predictor of the type of aggression rate (“background” vs. “post-grooming”) as a fixed effect, and identity of each individual nested within the group identity as random effects.

(ii) To what degree does dominance rank explain grooming behavior in the absence of kin networks?

To investigate this question, we calculated both individual-based and dyadic grooming measures. For individual-based measures, we calculated the total amount of grooming given and received per hour of observation, irrespective of partner, for each female in the study. For dyadic measures, we calculated the proportion of total grooming time that each female spent grooming each of her social partners (which we refer to as *pGroom*). Specifically, we calculated three measures: *pGroom_given*, *pGroom_received*, and *pGroom_total*. For *pGroom_given_{AB}*, the numerator includes only the amount of grooming directed from female A to female B, and the denominator is the total amount of grooming directed by A to all females. For *pGroom_received_{AB}*, the numerator includes only the amount of grooming A received from B, and the denominator is the total amount of grooming A received from all females. Finally, for

$pGroom_total_{AB}$, the numerator includes both the grooming directed from A to B *and* the grooming directed from B to A. Here, the denominator is the total time that female A spent grooming (given *or* received) irrespective of partner. Thus, $pGroom_total_{AB}$ and $pGroom_total_{BA}$ will not be identical because the denominators for each of these proportions will differ. We log-transformed all grooming measures to approximate a normal distribution and then modeled the resulting values using LMMs. All models included a random effect of individual identity nested within group identity to control for systematic inter-individual and inter-group differences in grooming behavior.

To test how dominance rank affected grooming behavior, we performed four related analyses. For all analyses, to ensure that all predictor variables were on the same scale, we mean-centered and scaled Elo ratings by dividing each value by the (mean-centered) standard deviation.

First, we tested whether dominance rank was a significant predictor of a female's individual grooming behavior (grooming minutes given per hour, grooming minutes received per hour, and the sum of the two) irrespective of her grooming partner. For these models, we included Elo rating as the only fixed effect in the models and individual identity as the only random effect (because each female was represented twice in this dataset, once for phase 1 and once for phase 2).

Second, we explored how changes in dominance rank from phase 1 to phase 2 (based on the difference in an individual's Elo scores, " Δ_{Elo} ") influenced changes in time spent grooming (hereafter, " $\Delta_{grooming}$ "). To so do, we modeled $\Delta_{grooming}$ as the response variable in an LMM, with Δ_{Elo} as a fixed effect and group identity in phase 1 and phase 2 as random effects.

Third, to determine if females preferred to groom with higher-ranking partners, we tested whether females exhibited a tendency to groom higher ranking individuals when faced with the possibility of grooming either an adjacently-ranked higher ranking female or an adjacently-ranked lower ranking female (i.e., a female either ranked one ordinal rank above them or one ordinal rank below them in the hierarchy). To do so, we focused on the females whose ordinal rank was 2nd, 3rd, or 4th in their groups, because the 1st and 5th ranking individuals did not have the opportunity to groom both lower and higher ranking females. We compared the rate of grooming (min/hr) that females directed towards higher-ranking females to the amount they directed towards lower ranking females, using a paired T-test.

Fourth, we tested whether females' preference for high-ranking social partners drove competition for access to high-ranking females, which would predict stronger grooming relationships between closely ranked high-ranking females than between closely ranked low-ranking females. To do so, we considered only the dyads that groomed at least once to test whether rank disparity (the absolute difference in Elo ratings between two females in a dyad), Elo rating, or a rank disparity x Elo rating interaction predicted the dyadic *pGroom* measures. This model is the basis for comparisons between the real data and our simulations (see below). In a complementary analysis, we also tested whether an alternative approach—modeling the dyadic *pGroom* measures as a function of Elo rating and the interaction between Elo ratings for grooming partners—corroborated our main results.

(iii) What rules govern the formation of social bonds?

We examined the extent to which patterns of social bond formation in our data

set could be explained by the simple rules of Seyfarth's model (1977), which has been difficult to test in previous studies due to the tight correlation between rank and kinship. To do so, we ran simulations based on the model and compared the results to our empirical data (hereafter "Simulation 1"). In each simulation we assumed that all females attempt to spend equal amounts of time grooming, although they may be constrained from doing so in practice. Thus, each female was allocated 100 units of time that they could spend grooming with other females. Each female was also assigned a target ratio of units devoted to grooming others versus units devoted to receiving grooming from others. These values reflect a female's "goal" for allocation of grooming resources, and again might not be achievable in practice. Targeted ratios for each female were randomly drawn (with replacement) from the realized ratios observed for alpha females in our data set, based on our assumption that the behavior of alpha females most closely achieved ideal ratios. Following Seyfarth, higher-ranking females were considered more attractive grooming partners than lower-ranking females. Each simulation had 3 steps:

- 1) Each female was assigned a random Elo rating from the observed Elo ratings (from table S1), producing a set of simulated group hierarchies (n = 18 groups, corresponding to the number of social groups we considered in the real data set across Phases 1 and 2 of the study).

- 2) Grooming behaviors were simulated starting with the highest ranking female and proceeding from high rank to low rank. The 1st ranking female (female A) allocated her grooming preferentially to the most desirable remaining partners in the group, starting with the 2nd ranking female (female B). If female A still had

remaining units of grooming to give after female B's allotment of grooming received was exhausted, she then moved on to grooming the 3rd ranking female (female C), and so on. When female A's allotment of grooming given was exhausted, female B was then allowed to distribute her grooming units. Once a female's allotment of grooming received was exhausted, she was no longer available for further grooming. Thus, low ranking females could end the simulation with units of grooming still to give or receive, but no potential partners (see Fig. S3).

3) We calculated *pGroom* measures for each female and her potential partners, for each simulation.

We used an LMM to model the log-transformed *pGroom* values from each simulation as a function of rank disparity, rank of the groomer, and the interaction between rank disparity and rank of the groomer, exactly paralleling the analysis we conducted on our observed data (see model description above). In total, we ran 1,000 simulations, each including 18 groups of females. We then compared the standardized effect statistics (the estimated effect statistic, β , divided by the standard error of the estimate, β_{se}) for each predictor variable in the simulations to the standardized effect statistic estimates in our real data. We calculated the proportion of simulations for which the true standardized effect statistic was equal to or more extreme than the standardized effect statistics observed in the simulations. This procedure generated, for each parameter, a p-value assessing the consistency of our observed data with the model outlined by Seyfarth (1977).

(iv) Is grooming behavior stable across changes in dominance rank?

Finally, we investigated the stability of grooming behavior across changes in dominance rank by measuring within-individual correlations between phase 1 and phase 2 of the study. We did so for the amount of grooming given per hour, the amount of grooming received per hour, and the total amount of grooming (given or received) per hour. We calculated these correlations based on the residuals of LMMs relating each variable to dominance rank, with dominance rank as the fixed effect and group as the a random effect, with data from phase 1 and phase 2 analyzed separately. These models thus allowed us to test the degree to which female grooming behavior remained stable between phases after controlling for the primary effect of rank.

We performed all statistical tests and simulations in R (R Development Core Team, 2015).

RESULTS

Grooming patterns in captive rhesus macaques

Grooming relationships were established quickly after group formation and remained stable throughout each phase of the study period. Dyadic grooming patterns within the first 8-11 weeks after group formation were strongly correlated with dyadic grooming patterns throughout the duration of the study ($r = 0.70$, $p < 10^{-15}$, $n = 360$ dyads). On average, females groomed for 8.50 min/hr (± 4.51 s.d.) and had a mean of 3.53 total grooming partners (range = 1 - 4). Grooming given was a significant predictor of grooming received both on an individual-specific level (LMM with individual identity and group identity as random effects; $\beta_{\text{groom_min/hr_given}} = 0.24$, $p = 0.021$, $n = 90$, with each of

n=45 females represented once in each phase, $T=2.35$, $df=88$) and, more strongly, on a dyadic level (LMM with identity of each individual in the dyad nested within group identity as random effects; $\beta_{\text{groom_min/hr_given}} = 0.39$, $p < 10^{-14}$, $n=360$ dyads, $T=8.15$, $df=347.6$).

Grooming relationships are associated with social tolerance

The amount of grooming a female provided to a particular partner did not predict whether she was ever likely to be aggressed by that partner ($\beta_{\text{groom_min/hr_given}} = 0.14$, $p = 0.63$, $n = 360$ dyads, $Z=0.48$). However, among dyads in which the groomee aggressed against the groomer at least once, we found that females who groomed their partner more frequently were targeted at a lower rate by that partner ($\beta_{\text{groom_min/hr_given}} = -0.17$, $p = 0.045$, $n=214$ dyads, $T=-2.02$, $df=178.8$). Lower rates of aggression were also correlated with increased rates of grooming directed from the aggressor to her target, reflecting the relatively equitable nature of social relationships in our study ($\beta_{\text{groom_min/hr_received}} = -0.20$, $p = 0.037$, $n=214$ dyads, $T=-2.10$, $df=177.4$).

These results are consistent with two scenarios: grooming as a driver of social tolerance or aggression as a disincentive for grooming. To differentiate these possibilities, we compared the amount of aggression a female received from a social partner immediately after grooming with that partner to the background rate of aggression a female received from the same partner. We found that a female was significantly less likely to be targeted by another female after grooming her, compared to the background rate (mean rate of aggression received after grooming = 1.30 aggression/hr; mean background rate of aggression received = 2.42 aggression/hr;

$\beta_{aggression_post_grooming} = -1.17$, $p = 2.1 \times 10^{-10}$; $T = -6.48$, $n = 360$ dyads, $df = 523.8$, Fig. 1). This result suggests that grooming promotes social tolerance, at least on a short-term basis. Note that we could not assess whether grooming also increases the likelihood of social support, as coalition formation was rarely observed in our study groups: solicitations of social support occurred only 92 times in the 345 hours of observation.

Dominance rank effects on grooming

Dominance rank was a strong predictor of grooming behavior in our study population. We found that rank was positively associated with both the amount of grooming received per hour ($\beta_{Elo_rating} = 0.72$, $p = 3.33 \times 10^{-7}$, $n = 45$ females, $T = 5.52$, $df = 88$; Fig. 2A) and the amount of grooming given per hour ($\beta_{Elo_rating} = 0.53$, $p = 3.27 \times 10^{-4}$, $n = 45$ females, $T = 3.74$, $df = 88$; Fig. 2B). In other words, higher-ranking females both groomed more and were groomed more often than low-ranking females. We also found that change in dominance rank between phase 1 and phase 2 (Δ_{Elo}) was significantly positively associated with change in total time engaged in grooming (min/hr) between the phases ($\Delta_{grooming}$; $\beta_{\Delta Elo} = 0.0043$; $p = 9.33 \times 10^{-8}$; $n = 45$ females, $T = 6.92$, $df = 31.0$, Fig. 2C). Specifically, an increase of an Elo rating of 485 between phase 1 and phase 2 (roughly corresponding to an ordinal rank change of 1 in our study) led to an increase in grooming of 2.1 min/hr – an approximately 25% increase over phase 1 rates. Consistent with these results, females who had the opportunity to groom females who were either one rank above or one rank below them directed their grooming efforts asymmetrically up the hierarchy (mean rate of grooming higher ranking females = 1.85 min/hr, mean rate of grooming lower ranking females = 1.21 min/hr;

$T_{\text{paired}} = 2.22$, $p = 0.031$, $df=53$; Fig. 2D). However, high-ranking females were generally equitable grooming partners: rank did not predict the $\log_2$ -ratio of grooming received to grooming given ($T_{\text{Elo_rating}} = 0.083$, $p = 0.57$, $n = 45$ females, $n=45$ females, $T=0.57$, $df=87.3$; Fig. S4).

Consistent with previous reports (Kapsalis & Berman, 1996; Schino, 2001; Seyfarth, 1980; Seyfarth, 1977; J. Silk, Alberts, & Altmann, 2006; Silk et al., 2006; Tiddi et al., 2012; Tinsley Johnson et al., 2014), we found that females who were adjacent in rank were more likely to groom together. This pattern was detectable whether we tested for a binary pattern (groomed at all versus never groomed: $\beta_{\text{rank_disparity}} = -1.53$, $p = 9.38 \times 10^{-7}$, $n = 360$ dyads, $Z=-4.94$), or whether we investigated the proportion of total grooming time that a female invested in a grooming partner, *pGroom total*, in those dyads that groomed at least once ($\beta_{\text{rank_disparity}} = -0.43$, 1.09×10^{-11} , $n = 318$ dyads, $T=-7.06$, $df=310.0$; Fig. 3). Familiarity (i.e., the amount of time two females had spent in the group together, measured as days separating their introductions into the group) did not account for this relationship, suggesting that rank itself, rather than the longer co-residency times, drove the patterns we observed ($\beta_{\text{familiarity}} = 0.0014$; $p = 0.72$). Further, dominance rank was a strong predictor of the magnitude of the relationship between rank disparity and *pGroom total*. Specifically, we observed a highly significant interaction effect between dominance rank and rank disparity on *pGroom total* ($\beta_{\text{rank*rank_disparity}} = -0.20$, $p = 3.11 \times 10^{-4}$, $n = 318$ dyads, $T=-3.65$, $df=288.0$; Fig. 3). This result indicates that social bonds involving high-ranking females tended to involve similarly ranked females more often than social bonds involving low-ranking females. In contrast, low ranking females distributed their proportional investment in grooming more

evenly across social partners of all ranks. Modeling an interaction effect between the dominance ranks of females within a dyad, as an alternative approach, supported the same interpretation. While all females preferred to groom with higher-ranking partners ($\beta_{rank_social_partner} = 0.25$, $p = 1.7 \times 10^{-4}$, $n = 318$ dyads, $T=3.87$, $df=140.1$), high-ranking females were better able to express this preference than low-ranking females ($\beta_{rank_focal_female*rank_social_partner} = 0.47$, $p = 2.32 \times 10^{-10}$, $n = 318$ dyads, $T=6.57$, $df=287.0$).

Simple simulation rules predict the direction but not the magnitude of rank effects on grooming patterns

Similar to the model in Seyfarth (1977), simulation 1 generated grooming patterns in which rank-adjacent females groomed significantly more often than females who were farther apart in rank ($p<0.05$): we observed this pattern in 929 of 1000 (92.9%) simulations. Further, and consistent with our empirical data, this pattern was stronger for higher-ranking females, resulting in a significant ($p<0.05$) interaction between rank disparity and dominance rank on $pGroom$ in 661 (66.1%) of simulations.

However, both the effect of rank disparity and the interaction effect between rank disparity and rank were significantly weaker in this simulation than they were in our observed data (Fig. 2). Specifically, females showed an even stronger tendency to apportion their grooming time to rank-adjacent females in the real data than expected based on the simulations ($p=0.006$; Figs. 4A and 4B). Similarly, the interaction between rank and rank disparity was significantly stronger in our observed data compared to the simulated results ($p=0.029$; Fig. 4C).

The difference between the results from simulation 1 and our empirical data could be explained if low-ranking females exhibited a weaker preference for the highest-ranking partners than predicted in the simulations. Indeed, we found that low ranking females were targeted for aggression at similar rates by all of the females that outranked them (Fig. S5). If a major role of grooming for low-ranking individuals is to increase social tolerance, as our data suggest (Fig. 1), then low-ranking females might be expected to distribute their grooming efforts more equitably among higher-ranking individuals than suggested by Seyfarth's model. To test this possibility, we modified our simulations such that females indiscriminately distributed their grooming to any available higher-ranking partner (rather than the highest-ranking partner available). This modification (hereafter "simulation 2") produced rank disparity effects that were stronger than in simulation 1 and that closely matched our observed data (Figs. 4D and 4E). However, the empirically estimated interaction effect between rank and rank disparity was still significantly stronger (i.e., more negative) than the effects estimated from this modified simulation ($p=0.023$; Fig. 4F). Low-ranking females in the real data still distributed their grooming more evenly across ranks (compared to high-ranking females) than expected from simulation 2.

Stability of grooming behavior is limited to grooming given

After controlling for dominance rank, we found that the amount of grooming a female provided to other females (min/hr) was significantly positively correlated across changes in dominance rank (i.e., between phase 1 and phase 2; $r = 0.32$, $p = 0.034$, $n=45$ females). However, we found no evidence of equivalent stability for either total

amount of grooming ($r = 0.21$, $p = 0.16$, $n=45$ females) or the amount of grooming a female received ($r = 0.074$, $p = 0.63$, $n=45$ females).

DISCUSSION

Our results show that dominance rank exerts substantial influence on the establishment of social bonds, even (and perhaps particularly) in the absence of kin networks. Specifically, we found that high dominance rank strongly predicted increased grooming activity and that rank disparity strongly predicted the likelihood that two females would form grooming relationships with each other, even though closely ranked females were not kin. Notably, the strength of the relationship between rank disparity and grooming was strongest among high-ranking individuals and weakest among low-ranking individuals, suggesting that high-ranking females may be better able to exert their preference for grooming with other high-ranking partners. The results from our first simulation suggest that these two patterns can be explained, in part, by the combination of limited time to invest in grooming and attraction to higher-ranking partners, as predicted by Seyfarth's model (Seyfarth, 1977). However, we identified a stronger effect of rank disparity than predicted by a simple model of restricted access of low-ranking females to high-ranking partners (Figs. 4A and 5A). Specifically, in the empirical data, females exhibited an even stronger tendency to groom rank-adjacent females than expected.

The difference between the observed and simulated data is probably not a result of heightened competition for high-ranking partners in the real world, as we simulated very strong competition for high-ranking partners (in simulation 1, all females have the

same goal: to groom the highest ranking females in each group). Instead, we believe our data are consistent with an alternative explanation: that, in contrast to Seyfarth's assumptions, the desirability of a social partner does not linearly covary with dominance rank. If all higher-ranking females are equally desirable partners, low-ranking individuals should groom them indiscriminately. Indeed, when we modified the simulations to allocate grooming randomly across higher-ranking females, as opposed to maximizing grooming time with the highest ranking available female ("simulation 2"), rank disparity effects in the simulations closely recapitulated our empirical results (Figs. 4D and 4E). However, we still found that the lowest ranking females distributed their grooming efforts more evenly across all ranks than expected (Figs. 4C and 4F). This result may be due to the strict time constraints on grooming imposed in both simulations, which often meant that low-ranking females had only one or a few remaining available partners and did not exhaust their allocated grooming time (Figs. S3 and S6). In reality, females may not be as tightly constrained (Majolo et al., 2008; Grueter et al., 2013). Further, the meaning and value of a social interaction may be contingent on past social history (Arnold & Aureli, 2007; Crockford et al., 2013; Crockford et al., 2008; Gust et al., 1994; Weidt, Hofmann, & König, 2008; Wittig et al., 2008). The social relationships formed in our study arguably satisfy the definition of a "social bond" (*cf* Silk 2012: they were equitable, stable for the duration of our study period, and associated with reduced aggression). Once such bonds were established, females may have preferentially chosen to service these relationships even when other, higher-ranking partners were available.

In addition, we found that while dominance rank had a pervasive effect on social

affiliation patterns, the role of individual characteristics was much more muted. Specifically, the only consistent grooming pattern across phases of the study was for grooming given, and this was detectable only after controlling for the main effect of dominance rank. In contrast, neither the amount of grooming received nor the total amount of grooming that females engaged in were stable across phases, indicating the central importance of social milieu (rather than stable individual characteristics or behavioral syndromes: e.g., Sih, Bell & Johnson 2004; Sih et al. 2004; Bell 2007) in shaping animal behavior. Importantly, our results provide interpretative clarity to previously reported correlations between rank and grooming (e.g., Schino 2001). While some of these results could be interpreted as the product of individual characteristics that drive both rank and attractiveness as a grooming partner (although maternal inheritance is the general pattern in female cercopithecines, it is not absolute: Lea et al. 2014), our experimental paradigm suggests that rank itself is the more important measure.

Our study represents the first to investigate dominance rank effects on grooming patterns and social bond formation in the absence of kin in social mammals. The remarkably strong effects of dominance rank on an individual's total grooming time (Fig. 2A and 2B) suggest that the presence of kin may make the effects of rank less tangible in naturally constituted social groups. Specifically, female relatives provide opportunities for social support motivated by kin selection as well as in exchange for grooming. Consistent with this idea, dominance rank does not predict overall levels of female social connectedness to other females in wild baboons, while the presence of female kin does (Archie et al. 2014). However, dominance rank does predict female social

connectedness to adult males, a relationship type in which the availability of kin is much less likely to play a role: adult female and adult male baboons are generally unrelated because of obligate male dispersal in this species (Archie et al., 2014). In combination with our results, this observation suggests that dominance rank influences the ability of females to access the most desirable social partners. In our study, these individuals were likely to be high-ranking females, but in the wild could include potential mates or physically powerful allies.

Finally, dominance rank in nonhuman primates is often used as a model for understanding the effects of social adversity on health (reviewed in: Sapolsky 2004; Sapolsky 2005; Marmot & Sapolsky 2014). In wild primates, however, the effect of dominance rank on stress physiology has generally been found to be weaker than in studies of captive primates, especially compared to experimentally formed social groups such as those investigated here (Abbott et al., 2003; Gust et al., 1993; Michopoulos et al., 2012; Michopoulos et al., 2012; Muller & Wrangham, 2004; Scott, 2001; Shen & Kern Reeve, 2010). Our findings suggest that experimental manipulations of dominance rank in captivity not only affect rank, but also alter the opportunities for females to invest in affiliative social relationships and concentrate on their most important social partners. If so, rank effects on physiology and health may, in these settings, capture the dual effects of both low social status and relative social isolation. Our results thus emphasize the importance of jointly considering the effects of social relationships and social status – two axes of social adversity that are both connected to health and fitness (Altmann et al., 1996; Archie et al., 2014; Brent et al., 2013; Cameron et al., 2009; Clutton-Brock, Albon, & Guinness, 1984; Creel et al., 1997; Holekamp, Smale, & Szykman, 1996; Holt-

550 Lunstad et al., 2010; A. Pusey, Williams, & Goodall, 1997; Silk et al., 2003, 2010;
551 Stanton & Mann, 2012; Yee et al., 2008), but which are rarely jointly tested (but see:
552 Silk et al. 2009; Silk et al. 2010; Archie et al. 2014). Indeed, the observation that social
553 status predicts social affiliation patterns in our study system, but not in wild female
554 primates (Archie et al., 2014), suggests the key importance of kin networks in disrupting
555 this correlation. Together, our findings indicate the need to develop a more nuanced,
556 comparative understanding of how the effects of social status are shaped by the context
557 in which they are measured.

FIGURE CAPTIONS

Figure 1. Grooming promotes social tolerance on a short-term basis. In the majority of dyads (80%: blue lines) females received less aggression from a social partner after grooming with them compared to the background rate of aggression received from the same partner. Pink lines show the minority of dyads (20%) in which females received more aggression from a social partner after grooming with them.

Figure 2. Relationships between grooming and dominance rank. Higher-ranking females both received (A) and provided (B) more grooming than lower ranking females. (C) Δ_{Elo} between phase 1 and phase 2 significantly predicted Δ_{grooming} ($\beta_{\Delta\text{Elo}}=0.0043$; $p=9.33 \times 10^{-8}$). (D) Females who had the opportunity to groom females who were either one rank above (blue boxplot) or one rank below them (red boxplot) groomed the higher-ranking female more often (57% of cases).

Figure 3. The effects of rank disparity on the proportion of grooming time a female invested in a given partner ($p\text{Groom total}$). High-ranking females tended to groom with adjacently ranked females more often than low-ranking females. Lines show the fit from a linear model.

Figure 4. Simulation results. (A) The effects of rank disparity on the proportion of grooming time a female invested in a given partner ($p\text{Groom total}$) in simulation 1. As in the observed data, high-ranking females tended to groom adjacently ranked females more often than low-ranking females. (B, C) Histograms showing the distribution of

581 standardized effect statistics from 1000 iterations of simulation 1 for rank disparity (B)
582 and the rank x rank disparity interaction (C). Dotted lines show the observed effect
583 statistics in the empirical data. (D, E, F) depict parallel results for simulation 2. Unlike
584 simulation 1, simulation 2 accurately recapitulates the rank disparity effect observed in
585 the empirical data. However the interaction between rank and rank disparity is
586 significantly stronger in the observed data than in both simulations (C and F; both
587 $p < 0.05$).

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809

Figure 1

Figure 2

Figure 3

Figure 4