

Not all grooming is equal: differential effects of political vs affiliative grooming on cytokines and glucocorticoids in rhesus macaques

Lauren J Wooddell^{Equal first author, 1}, Jessica J Vandelee^{Corresp., Equal first author, 1}, Amy C Nathman¹, Brianne A Beisner^{1, 2}, Brenda McCowan^{1, 2}

¹ California National Primate Research Center, University of California, Davis, Davis, CA, United States

² Department of Population Health and Reproduction, University of California, Davis, Davis, CA, United States

Corresponding Author: Jessica J Vandelee
Email address: vandelee@ucdavis.edu

Positive social relationships in humans are known to have health promoting effects while negative social relationships have detrimental effects. Features of the broader social network, including indirect connections, also impact health. However, complicating our ability to examine these features, human networks are diverse and difficult to fully quantify. Animal models where social networks can be fully characterized are useful in examining how structurally similar yet functionally different relationships can differentially relate to biomarkers of health. For example, in nonhuman primates, grooming serves two main functions, to maintain social bonds (family/friends networks) or gain access to resources/support (political networks). We examined whether an individual's position in these two network types was differentially related to biomarkers of inflammation and physiological stress in female rhesus macaques (*Macaca mulatta*). Consistent with predictions, females with higher family/friends centrality had lower IL-6/TNF- α levels, while females with high political centrality showed elevated levels. Middle-ranking females with high political centrality showed elevated hair cortisol yet little to no benefit of family/friend centrality. These results indicate that while grooming interactions are structurally similar, they may be functionally distinct and therefore have very different, even opposite, effects on health. Affiliative interactions occurring within the context of an established relationship (i.e., family/friends) can provide opportunities for social buffering. In contrast, interactions among individuals without established relationships, even friendly interactions, may ultimately be physiologically costly. Ultimately, these results indicate that while social relationships may appear similar, the underlying functionality can have fundamentally diverse physiological outcomes.

Not all grooming is equal: differential effects of political vs affiliative grooming on cytokines and glucocorticoid biomarkers of health in rhesus macaques

Lauren J. Wooddell^{1*}, Jessica Vandeleest^{1*Ψ}, Amy C. Nathman¹, Brianne A. Beisner^{1,2}, Brenda McCowan^{1,2*}

¹Neuroscience & Behavior Unit, California National Primate Research Center, University of California, Davis, California, United States

²Department of Population Health & Reproduction, University of California, Davis, California, United States

*Equal Contributions

ΨCorresponding author details: Jessica Vandeleest, PhD

Email: vandeleest@ucdavis.edu

18 Abstract

19 Positive social relationships in humans are known to have health promoting effects while
20 negative social relationships have detrimental effects. Features of the broader social network,
21 including indirect connections, also impact health. However, complicating our ability to examine
22 these features, human networks are diverse and difficult to fully quantify. Animal models where
23 social networks can be fully characterized are useful in examining how structurally similar yet
24 functionally different relationships can differentially relate to biomarkers of health. For example,
25 in nonhuman primates, grooming serves two main functions, to maintain social bonds
26 (family/friends networks) or gain access to resources/support (political networks). We examined
27 whether an individual's position in these two network types was differentially related to
28 biomarkers of inflammation and physiological stress in female rhesus macaques (*Macaca*
29 *mulatta*). Consistent with predictions, females with higher family/friends centrality had lower IL-
30 6/TNF- α levels, while females with high political centrality showed elevated levels. Middle-
31 ranking females with high political centrality showed elevated hair cortisol yet little to no benefit
32 of family/friend centrality. These results indicate that while grooming interactions are
33 structurally similar, they may be functionally distinct and therefore have very different, even
34 opposite, effects on health. Affiliative interactions occurring within the context of an established
35 relationship (i.e., family/friends) can provide opportunities for social buffering. In contrast,
36 interactions among individuals without established relationships, even friendly interactions, may
37 ultimately be physiologically costly. Ultimately, these results indicate that while social
38 relationships may appear similar, the underlying functionality can have fundamentally diverse
39 physiological outcomes.

40 Keywords: Grooming, *Macaca mulatta*, glucocorticoids, cytokines, health

41 Introduction

42 Decades of research has established that social relationships are a critical factor affecting
43 an individual's health (Uchino, Cacioppo, & Kiecolt-Glaser, 1996; Cacioppo & Hawkley, 2003;
44 Uchino, 2006; Kappeler, Cremer, & Nunn, 2015). While social conflict can lead to stress (e.g.,
45 Sapolsky, 2005), it is generally thought that affiliative social relationships promote good health.
46 For example, previous research in both human and nonhuman animals has revealed that
47 individuals that have a greater number and/or strength of social relationships have reduced
48 glucocorticoid (GC) concentrations (barbary macaques, *Macaca sylvanus*: Shutt et al., 2007;
49 rhesus macaques, *Macaca mulatta*: Wooddell et al., 2017), with higher levels of GCs known to
50 influence a wide variety of other physiological systems (e.g., Sapolsky, 2005). Socially
51 integrated individuals also generally have greater reproductive success (e.g., horses, *Equus ferus*:
52 Cameron, Setsaas, & Linklater, 2009; barbary macaques: Schülke et al., 2010; baboons, *Papio*
53 *spp.*: Silk, Alberts, & Altmann, 2003; humans: Collins et al., 1993), greater immune function
54 (e.g., cynomolgus monkeys, *Macaca fascicularis*: Cohen et al., 1992; bonnett macaques,
55 *Macaca radiata*: Boccia et al., 1997; humans: Kiecolt-Glaser et al., 2005; Lutgendorf et al.,
56 2005), greater recovery after illness (humans: Kulik & Mahler, 1989; Seeman, 1996; Cohen et
57 al., 1997; Corrigan & Phelan, 2004), and greater longevity (e.g., bottlenose dolphins, *Tursiops*
58 *truncatus*: Stanton & Mann, 2012; rhesus macaques: Brent, Ruiz-Lambides, & Platt, 2017a;
59 baboons: Silk et al., 2010; Archie et al., 2014; Alberts, 2019; humans: Holt-Lunstad, Smith, &
60 Layton, 2010; Sprague dawley rats: Yee et al., 2008). Although it is unclear whether the positive
61 health benefits of social affiliation/integration are the proximate or ultimate mechanisms driving

such behaviors (e.g., Brent et al.,2014), the health benefits nonetheless emphasize the sheer importance of social relationships on the quality and quantity of life.

However, humans have a notoriously complex system of social interactions, which can include family, spouses, friends, work colleagues, church members, etc. Social relationships in humans have been analyzed as perceptions of social integration and support, the complexity and variety of social relationships (e.g., a social network-based approach), the frequencies of social behaviors, the quality of relationships, or presence/absence of certain social relationships (i.e., spousal relationships or living socially/alone; see Berkman et al., 2000 for a review). Given the complexity of human social behavior and the various methods utilized to capture human sociality, generalizations and direct comparisons between studies examining sociality and health is difficult. For example, questionnaires that focus on binary outcomes (presence/absence of a spouse; living alone/with others) may not accurately capture the entirety of that individual's social life, as social integration may be manifested elsewhere outside of these specific relationships (Holt-Lunstad et al., 2010). Furthermore, human self-reports (or perceptions) of social integration or loneliness (i.e., subjective experiences) can be independently associated with health outcomes (Melchior et al.,2003; Rico-Uribe et al., 2016) yet they often are weakly related to objective experiences (e.g., face-to-face interactions; received support; Haber et al.,2007; Dias et al.,2018). Social network analysis may therefore be an advantageous way to capture sociality, as it can be used to quantify the multiscale complex web of social interactions and relationships that make up social life. Whereas traditional methods rely solely on direct social interactions, social network analysis measures both direct (interactions between two individuals) and indirect (the interactions among other individuals that one interacts with) connections (Brent, 2015; Farine & Whitehead, 2015; McCowan et al., 2016). Given that social

networks can be incredibly large in human societies, determining the boundaries of a network to allow for measurement of indirect ties is difficult, but these indirect ties have been shown to be highly important in animal models of health and survival, where the entirety of an animal's social network can be quantified (rhesus macaques: Brent, 2015; Balasubramaniam et al., 2016; bottlenose dolphins: Stanton & Mann, 2012).

Furthermore, it is possible that not all social relationships, even those thought to reflect strong affiliative bonds, have comparable effects on health, and limited research has supported this notion. For example, the quality of relationships with family members was found to be inversely associated with psychosomatic symptoms in low-income mothers, whereas the quality of intimate relationships (e.g., husband/boyfriend) was not (Hall, Schaefer, & Greenberg, 1987). Family (i.e., genetic relatives excluding children) and friend network variables predicted disability and recovery risks among adults 65 years and older, but network variables relating to children and partners did not (Mendes de Leon et al., 1999). Similarly, research with nonhuman primates has indicated that females shrink and focus their networks on a few preferred social partners (mainly close kin) during times of stress (Crockford et al., 2008; Wittig et al., 2008), indicating that not all social relationships are equally important, and that a strong network of a few individuals can have a meaningful impact on infant and adult survival (Silk et al., 2003; 2010; although see McFarland et al., 2017 for the importance of weak social bonds). Further, in Assamese macaques (*Macaca assamensis*), strong social bonds with males or females predicts lower GC levels, depending on the season, indicating that the effects of strong social bonds are context-dependent (Fürtbauer et al., 2014). These results, although limited, indicate that while social relationships generally are a major factor affecting fitness in both human and animals, certain social relationships appear to be especially salient.

In primates, grooming is a primary social affiliative behavior that is accompanied with physiological responses in both the initiator and receiver, evidenced by lowered heart rates (Boccia, Reite, & Laudenslager, 1989; Aureli, Preston, & de Waal, 1999) and lowered cortisol concentrations (Gust et al., 1993; Shutt et al., 2007; Wooddell et al., 2017). Although the hypotheses for the function of grooming range from parasite reduction (Barton, 1985; Akinyi et al., 2013), to thermoregulation (McFarland et al., 2015; 2016), one of the most highly considered functions of grooming is for social purposes. Grooming may be used to maintain social bonds (Dunbar 1991) and social cohesion (Lehmann, Korstjens, & Dunbar, 2007) and possibly for tolerance and exchange for agonistic support (Schino, 2007; Borgeaud & Bhsary, 2015, although this remains debated). Given this, grooming can serve two primary social functions: 1) to perform among close kin and close ‘friends’ to solidify bonds and 2) to serve political or economic functions and be performed ‘up the hierarchy’ from low-ranking individuals to high-ranking individuals (Seyfarth, 1977; 1980) that promote tolerance and/or solicit support in agonistic interactions (Schino, 2007; Borgeaud & Bhsary, 2015). Therefore, although grooming is the same physical behavior, it may serve two fundamentally different functions based on the dyadic identities of the individuals involved. However, to date, studies examining social grooming have typically combined all forms of social grooming into a single category. Therefore, whether differential effects on health exist in primates based on the type of grooming relationship are unknown.

To better understand the physiological consequences of different types of “affiliative” interactions, we used rhesus macaques as a model species. Animal models provide greater ability to collect detailed information about the impact of complex and varied social networks on health (Karelina & deVries, 2010) for two primary reasons. First, data used to generate animal

social networks are collected by direct observation, rather than self-reports, which is common in human studies and can be prone to recall error and bias (Van de Mortel, 2008). Second, the entirety of an animal's social network can be quantified, including all present or absent relationships, as every individual in the network can be observed. Specifically, we examined whether centrality in two different grooming social networks predicted two biomarkers of inflammation (e.g., interleukin-6 [IL-6] and tumor necrosis factor-alpha [TNF- α]), and hair cortisol concentrations (HCCs) in female rhesus macaques. The first network (termed "family/friends") consisted of dyads for which the individuals have both a grooming and huddling relationship, as this indicates that individuals were comfortable enough to be in physical contact with one another in the absence of an overt behavior (such as grooming). The second network (termed "political") was comprised of dyads for which there was only ever grooming recorded between the dyad, inferring that there may not be a comfortable enough relationship in the dyad for close proximity to occur without an appeasement behavior. We assayed two biomarkers of inflammation (IL-6; Scheller et al., 2011) and TNF- α), which are risk factors for a variety of diseases and mortality (Bruunsgaard et al., 2003) and have previously been reported to be associated with social variables in humans (e.g., IL-6: Friedman et al., 2005; TNF- α : Marucha et al., 2005) and rhesus macaques (IL-6, TNF- α : Vandeleest et al., 2016). We additionally analyzed HCCs as a biomarker of hypothalamic-pituitary-adrenocortical activity. HCCs are non-invasive and long-term (e.g., weeks to months) measures of cortisol secretion and are less susceptible to circadian and temporal fluctuations (Davenport et al., 2006; Meyer & Novak 2012). Given that rhesus macaques are nepotistic (i.e., direct most of their social interactions towards close kin) and despotic (forming a strong linear hierarchy with little social tolerance), we predicted that family/friends network measures would be reflective of supportive

affiliative relationships and be associated with reduced levels of these biomarkers, whereas political grooming network measures would likely be more economic in nature and therefore be associated with elevated levels.

Materials and Methods

Subjects and housing

Subjects were 222 adult (3 years and older) female rhesus macaques (*Macaca mulatta*) born and reared at the California National Primate Research Center in Davis, California. Notably, we only used female subjects for this study, as although male social bonds have important fitness outcomes (e.g., barbary macaques: Schülke et al., 2010; bottlenose dolphins: Stanton & Mann, 2012), male rhesus macaques engage in social affiliation far less frequently (Drickamer, 1976) and tend to be more socially isolated than females (Brent, Ruiz-Lambides, & Platt, 2017b). Furthermore, given that male rhesus macaque dominance rank is not inherited, as it is in females, but is rather achieved by group tenure (Manson, 1998), our previous research has indicated that markers of social status are better indicators of health in males than females (Vandeleest et al., 2016; 2018). Subjects lived in one of four large, multigenerational and matrilineal social groups containing 100-200 mixed-sex individuals (Group A: 132 individuals, 15 matrilineal groups ranging in size from 1-20 individuals; Group B: 204 individuals, 37 matrilineal groups ranging in size from 1-15 individuals; Group C: 125 individuals, 7 matrilineal groups ranging in size from 1-36 individuals; Group D: 185 individuals, 14 matrilineal groups ranging in size from 1-24 individuals). Each group lived in a 0.2 hectare outdoor enclosure, which was equipped with A-frames, hanging barrels, and perches. Subjects were fed commercial monkey chow twice a day and received scattered foraging enrichment (nuts, oats, or seeds) once a day. Colony produce

176 enrichment (fruits or vegetables) was provided once per week. All procedures and protocols were
177 approved by UC Davis Animal Care and Use Committee.

178 Behavioral data collection

179 Four groups were studied as part of an ongoing study regarding the associations between
180 social networks and health. Groups A and B were studied for six continuous weeks from March
181 to April 2013 and 2014, respectively. Groups C and D were studied for six continuous weeks
182 from September to October 2013 and 2014, respectively. Rhesus macaques are seasonal breeders
183 (Vandenbergh & Vessey, 1968), with the breeding season occurring primarily from August-
184 February, and the birthing season taking place from March-June, thus both distinct seasons are
185 represented in the dataset.

186 Behavioral data were collected six hours per day, four days per week from 0900-1200
187 and 1300-1700 each day by one of three observers (inter-rater reliability, Krippendorff's alpha
188 ≥ 0.85). Affiliative behavior was collected via instantaneous scan sampling every 20-minutes
189 (totaling 18 scans per day), where identities of all adult female dyads (3 years and older)
190 affiliating were recorded. During scan samples, we focused on two affiliative behaviors:
191 grooming and huddling. Grooming was defined as picking apart the fur, possibly licking the fur,
192 and removal of debris. Huddling was defined as physical contact with another individual in the
193 absence of grooming, i.e., the individuals were touching one another. Grooming and huddling
194 behaviors were mutually exclusive for the dyad (an individual grooming another was also not
195 huddling that individual), but individuals could be huddling with other individuals that they were
196 not grooming. Aggression data (threats, chases, bites) were also collected via an event sampling
197 protocol for six hours per day, four days per week by two other observers. Dyadic aggression

data was used to calculate dominance ranks via the R package *Perc* (Fujii et al., 2015; Vandeleest et al., 2016).

Social network analysis

Political and family/friends grooming networks (see Fig. 1) were considered as weighted and undirected networks, with the exception of degree metrics which were both directed and undirected. Centrality and cohesion measures for each individual were calculated for each grooming network in Cytoscape 3.7.1 using two plug-ins, NetscapeAnalyzer and CytoNCA (Shannon et al., 2003; Tang et al., 2014). Table 1 presents the network measures utilized in this study. Centrality measures included weighted and unweighted overall degree, indegree, and outdegree, weighted and unweighted eigenvector, weighted and unweighted betweenness, weighted and unweighted information, and weighted and unweighted closeness (see Fig. 2). Cohesion was measured using clustering coefficient. Links in the family/friends grooming network were largely driven by familial relationships whereas links in the political grooming tended to go up the dominance hierarchy (Fig. 1). Dominance rank was calculated for all subjects using data from dyadic aggression via the percolation and conductance method (*Perc* package in R; Fushing et al., 2011; Fujii et al., 2015). Two rank related variables were constructed; 1) percentile dominance rank which reflected the percent of animals in the cage outranked and 2) rank categories of high (> 70%), middle (40-70%), and low (<40%).

-----Figure 1-----

-----Table 1-----

219 -----Figure 2-----

220 **Biological sample collection**

221 Samples (blood serum for cytokine assay, hair for cortisol assay) were taken during the
222 fifth week of each group's study period during routine, semi-annual health checks. On a single
223 morning, all animals were lightly sedated with ketamine (10 mg/kg) and given veterinary exams.
224 Then blood samples were obtained from the femoral vein and serum was aliquoted and stored at
225 -80°C for later assay. Finally, hair samples were taken by shaving the back of the animals'
226 necks and stored in an aluminum pouch at room temperature until further processing. The order
227 in which animals were processed and samples were collected during the morning was recorded to
228 control for any potential impacts of time of collection on the physiological variables examined.

229 **Cytokine assay**

230 Serum levels of IL-6 and TNF- α were measured using commercially available, species
231 specific Milliplex multi-analyte profiling (MAP) reagents purchased from EMD/Millipore
232 (Billerica, MA, USA), and utilizing Luminex Xmap technology (Luminex, Austin, TX, USA).
233 Color coded polystyrene microbeads coated with specific antibodies for IL-6 and TNF- α were
234 incubated with the serum samples, washed, and then were further reacted with biotinylated
235 detector antibodies followed by Streptavidin-PE to label the immune complexes on the beads.
236 After a final washing to remove all unbound material, the beads were interrogated in a BioPlex
237 dual laser (BioRad, Hercules, CA, USA). The median fluorescent index for each sample was
238 compared to a standard curve to calculate the concentration. Samples were tested in duplicate

and had an intra-assay coefficient of variability of 15.3%. Samples falling below the threshold sensitivity of the assay (1.6 pg/mL) were assigned a value of one.

Hair cortisol concentrations (HCCs)

Cortisol was extracted from the hair using established methods (Davenport et al., 2006; Vandeleest et al., 2019). There was insufficient hair available for collection and cortisol analysis for eight subjects. Briefly, samples were washed with isopropanol and dried before being ground to a fine powder using a ball-mill grinder (Retsch MM400). Cortisol was extracted from powdered hair using methanol overnight. Finally, methanol supernatant was removed and dried under a stream of air and samples were reconstituted using assay buffer and stored at -80°C until assay. Samples were assayed in duplicate with an enzyme immunoassay (Salimetrics, State College, PA). Resulting values were converted to pg/mg for analysis. Inter and intra- coefficients of variation for the assay were 11.6% and 2.33%, respectively.

Statistical analysis

Generalized linear models using a negative binomial distribution were run using STATA 15.1 (StataCorp., 2017) to examine the impact of grooming network variables on each biomarker separately. A random effect indicating the cage of origin was included in all models. For each outcome (i.e., IL-6, TNF- α , HCCs), variables relating to demographics (age, rank), network position in the family/friends grooming network (e.g., weighted closeness centrality), and network position in the political grooming network (e.g., weighted eigenvector centrality) were entered and AIC values and Wald's statistics were examined. Both continuous dominance rank and rank categories were entered to determine if non-linear rank effects were present. Highly

correlated network variables (e.g. weighted and unweighted eigenvector centrality or betweenness and information centrality) were never run in the same model. Using an information theoretic approach, we identified a candidate set of models ($dAIC < 2$ and significant Wald's statistic) which were further compared using model likelihoods and model weights (Burnham and Anderson, 2002). We present the candidate set of models but one model for each outcome was selected for interpretation of effects.

Results

IL-6

Models indicated that weighted eigenvector centrality in the political grooming network, weighted closeness centrality in the family/friends grooming network, and age predicted baseline levels of IL-6 (see Table 2). Specifically, individuals with greater centrality (weighted eigenvector) in the political grooming network exhibited *higher* levels of the pro-inflammatory cytokine IL-6 (Table 3; Fig. 3A) while more central individuals (i.e. high weighted closeness centrality) in the family/friends network showed *lower* levels of IL-6 (see Table 3; Fig. 2B). Finally, older animals tended to have higher levels of IL-6.

-----Table 2-----

-----Table 3-----

-----Figure 3-----

279 TNF- α

280 Baseline levels of TNF- α also were predicted by weighted eigenvector centrality in the
 281 political grooming network and weighted closeness centrality in the family/friends grooming
 282 network in the best fit models (see Table 2). As with IL-6, higher connectivity in the political
 283 grooming network (Fig. 4A) and lower connectivity in the family/friends grooming network
 284 were associated with higher levels of TNF- α (Fig. 4B; see Table 3) While included in the
 285 models, the effects of age and sampling order were not significant predictors of levels of TNF- α .

286 -----Figure 4-----

287 HCCs

288 Best fit models predicting HCCs indicated that information weight centrality in the
 289 political grooming network, weighted closeness centrality in the family/friends network, rank,
 290 and their interactions were important (see Table 2). Plotting of the interaction effects indicated
 291 that more central females in the political grooming network exhibited higher HCCs, but only if
 292 they were middle-ranking (see Table 3, Fig. 5A). More central females in the family/friends
 293 grooming network had lower HCCs if they were low- or high-ranking but no effect was seen for
 294 middle-ranking females (Fig. 5B). Finally, animals whose samples were collected earlier in the
 295 morning exhibited lower HCCs than those collected later in the morning.

296 -----Figure 5-----

297 Discussion

Humans and rhesus macaques are characterized by a plethora of social relationships ranging from affiliation among close family and friends, to political relationships with individuals in power, and to agonistic encounters. Generally, research has indicated that affiliative social interactions promote health. However, our findings indicate that not all relationships that appear affiliative on the surface are of the same type and quality and have similar effects on health. Specifically, we found that females that were more socially connected in family/friends grooming networks had lower levels of biomarkers of inflammation (IL-6 and TNF- α), whereas females that were more socially connected in political grooming networks (i.e., those that may be associated with economical purposes or dominance rank) had higher levels of biomarkers of inflammation. Furthermore, while middle-ranking females with higher levels of social centrality in the political grooming network displayed higher levels of HCCs, these females did not reap the same benefits of lowered HCCs as low- and high-ranking females in the family/friends grooming networks.

Unsurprisingly, females with greater centrality in the family/friends grooming networks exhibited lower levels of biomarkers of inflammation, indicating social affiliation (i.e., grooming) among close kin and friends can impact health (Yang, Schorpp, & Harris, 2014). This is consistent with a variety of research suggesting that strong affiliative bonds can buffer individuals from stress and promote health (Boccia et al., 1997; Shutt et al., 2007; Archie et al., 2014). We defined family/friends relationships as those in which there is both a huddling and a grooming relationship, suggesting a functionally strong relationship, rather than inferring strong bonds based on genetic or familial ties alone. We used huddling behavior because coming into close proximity with another individual (with or without the occurrence of grooming) can result in aggression (Schino & Alessandrini, 2015), and therefore animals will likely only engage in

this type of contact with others with whom they have a clearly defined relationship. Although kinship commonly drives social affiliation in many animal species (Brent et al., 2014), not all kin exhibit close bonds (Beisner et al., 2011), and close bonds can be exhibited by non-kin (i.e., friends) as well (Fig.1; Brent et al., 2014; horses: Cameron et al., 2009). Therefore, our behavioral definition of family/friends networks requires that there is a degree of comfortability in the dyad (as exhibited by close physical contact in the absence of grooming behaviors), which may indicate an underlying strong, established bond. Indeed, in both human and nonhuman primates, physical contact, or embracing, can predict the strength of a dyad's social bond (Suvilehto et al., 2015; Pallante et al., 2019). This indicates that strong bonds are likely exhibited by both a huddling (physical touch) and grooming relationship, which has also been found in Barbary macaques where dyads that spend more time grooming each other also were more likely to huddle (Campbell et al., 2018). While our study cannot determine causality (did social centrality in the family/friends network reduce biomarkers of inflammation or did reduced biomarkers induce centrality in the family/friends network), Brent et al., (2017a) similarly found that family network size (i.e., the number of adult female kin) predicted survival in prime-aged (i.e., 6-17 years) female rhesus macaques. While their study did not directly examine social networks (constructed through behavioral data) as a predictor of survival, our study hints at an intriguing possible mechanism underlying these effects: affiliative behavior among close kin and friends may result in lower susceptibility to many disease states, as found in a recent study in which close social relationships were found to buffer pathogen transmission (likely via reduced inflammatory responses) under stable social conditions (Balasubramaniam et al., 2016). Likewise, Yang et al. (2014) found in humans that support from family and friends protected against risks of inflammation, whereas social strain in these relationships had even greater

negative associations with biomarkers of inflammation. Given that familial (and to a lesser extent friend) relationships endure through various periods and can persist decades (in both humans and nonhuman primates), these relationships likely have an important and long-lasting impact on health.

On the other hand, females with greater centrality in political grooming networks, i.e., networks governed more by social status, displayed higher levels of biomarkers of inflammation. Whereas the definition of family/friends networks required a dyad to exhibit both grooming and huddling relationships, females with political relationships exhibited no observed physical contact behaviors (i.e., huddling) during a 6-week period. The absence of close physical contact may suggest that these individuals do not have clearly established relationships or that their established relationship is one in which agonism is possible. Therefore, these social interactions can be unpredictable, resulting in a degree of risk, uncertainty, and anxiety. These interactions, rather than reflecting an existing affiliative relationship, may be transactional in nature, reflecting a desire to maintain peace/tolerance or used in a biological market exchange (Schino, 2007; Borgeaud & Bhsary, 2015). The health results associated with political grooming networks further indicate that they are likely a fundamentally different social network than affiliative networks (family/friends) and can even be associated with a physiological cost.

There are several hypotheses for which political relationships may be associated with increased (rather than decreased) physiological costs. Political relationships may be especially taxing on some individuals, as they may all be unidirectional in nature. Given that female macaques typically groom up the hierarchy (Seyfarth, 1977; Schino, Ventura, & Troisi, 2005), political relationships are unlikely to be bidirectional, indicating that political relationships could

be a major time investment, with little reciprocation. An analogous example in humans is caregivers to the terminally ill, which invest significant time and often suffer increased stress loads and poorer health outcomes themselves as well (Schulz & Beach, 1999; Son et al., 2007). Furthermore, the engagement in political grooming may be governed by force, which can have detrimental health outcomes. For example, individuals grooming family/friends may be choosing to do so, at their own will, due to an established, comfortable relationship. Individuals grooming others for rank-related purposes may be delegated by a social contract, as aggression may result if grooming is not given. Indeed, Schino et al. (2005) found that in Japanese macaques (*Macaca fuscata*; a species with a similar social system to rhesus macaques), females directed their grooming to higher-ranking females that directed the most aggression to them. In this case, grooming may be given by means of the threat of force, deemed the “extortion hypothesis” (Silk, 1982). While speculative, this scenario is analogous to forced friendly human interactions, such as work-boss encounters or other scenarios in which there is little choice for (un)involvement. Accordingly, Yang et al. (2014) concluded that strain in familial networks have the greatest adverse effect on biomarkers of inflammation, likely because these relationships are long-term and less governed by choice. Therefore, it could be possible that negative health outcomes could be associated with social relationships in which there is little active choice (which may be possibly seen in political grooming). Indeed, control and predictability of the environment (which may include choice) are often associated with lower levels of GCs in both animals and humans (Weiss, 1970; Miller, 1979; Evans, Wener, & Phillips, 2002), which could lead to systemic effects (e.g., inflammation; Sapolsky, 2005).

Given the dichotomy of health biomarkers associated with political compared to family/friends grooming networks, these results lead to an unusual conundrum: are all forms of

social grooming truly affiliative? While the overt behavior may *appear* to be the same, the *functionality*, may be fundamentally different. This is seen in other instances in primates, such as silent-bared teeth displays, in which the corners of the mouth are drawn back to display the teeth, resembling a human smile. Although overtly appearing identical, they can function differently depending on the social context and the dyad involved (Beisner & McCowan. 2014), either reflecting immediate submission in the context of an aggressive encounter or long-term subordination (i.e., in the absence of agonism) accompanied by an established social bond (Beisner & McCowan, 2014). A similar parallel can be found in humans in which the Duchenne smile (a spontaneous smile often accompanied by enjoyment) can appear similar as conscious smiling, although these have very different physiological processes and brain area activations and may signal different social communications (Ekman, Davidson, & Friesen, 1990; Frank & Ekman, 1993), similar to studies investigating the chemical composition of reflexive eye-protective tears and emotional tears. Although appearing similar, the chemical composition of tears resulting from emotions is fundamentally different than eye-protective tears (Frey II et al., 1981) and can serve communicative purposes to others (Gelstein et al., 2011). Thus, our research further brings into question whether similar overt behaviors reflect similar physiological processes and outcomes. Therefore, when analyzing sociality, the social behavior itself must not only be analyzed, but also the function and context in which it occurs.

Our results regarding HCCs are more complex. Whereas the previous results with cytokines revealed no main effects or interactions with dominance rank, the relationship with HCCs did. Specifically, whereas middle-ranking females with greater social centrality in the political grooming network had higher levels of HCCs, there was not a social buffering effect in their family/friends grooming network. In other words, while both low- and high- ranking

females with greater social centrality in the family/friends grooming network had lower HCCs, there was no effect for middle-ranking females. This suggests that while middle-ranking females have consequences of maintaining political bonds (e.g., higher HCCs), they reap very little benefit from strong close bonds. This poses an interesting scenario for middle-ranking females: why do they engage in political bonding when there is a physiological cost in doing so? And further, why are strong family/friend networks for middle-ranking females not associated with lowered HCCs? It is important to note that while there may be a *physiological cost* associated with political grooming that can be detrimental in the short-term (i.e., cytokines and inflammation), there may be a *social benefit* that can be advantageous in the long-term. Grooming can be used as a commodity to exchange for agonistic support, with females reciprocated grooming with coalitions and alliances (Schino, 2007). As female rhesus macaques rely on coalitionary support to maintain and reinforce the dominance hierarchy, long-term support may be given to females active in the political grooming network, which is necessary to maintain their dominance rank. Indeed, middle-ranking females are often the ones that have the highest levels of uncertainty in their social position (Vandeleest et al., 2016; Schrock et al., 2019) and thus may perform political grooming due to this uncertainty. It is also possible that because they are engaged in political grooming, the adverse biomarkers associated with greater political grooming may outweigh any potential benefits of family/friends grooming (e.g., Yang et al., 2014). Future research should examine coalitionary support in relation to political and family/friends grooming networks and the complex interconnections with health in both the short and long-term.

Our study is not without its limitations. First, we did not experimentally manipulate individuals, which did not allow us to make conclusions about the direction of relationships. For

example, Debray et al. (2019) experimentally manipulated dominance ranks of female rhesus macaques, which altered patterns of social affiliation, which in turn predicted mitochondrial DNA for immune cells. By experimentally manipulating patterns of social affiliation, future research will be able to compare the direct effects of social affiliation on both biomarkers and overt markers of health. Furthermore, our study also did not compare the time-budget of females engaged in social affiliation in either political or affiliative networks, and it is entirely possible that time constraints prevented inclusion in both networks equally.

Conclusion

Both humans and many species of nonhuman primates engage in a complex interconnected system of social interactions. Decades of research has established that affiliative social interactions can have a beneficial impact on health, however limited research has investigated which relationships are especially salient. By utilizing nonhuman primates as a model for the complexity of human sociality, we were able to tease apart two very physically similar, but fundamentally different social relationships and their effects on health. Our research has indicated that not all social relationships are equally associated with biomarkers of health, and even, can have opposite effects on health. This is important to consider for both human and nonhuman primate work. Our work has laid the groundwork for future studies in both humans and nonhuman primates examining the complexity of social relationships and its varying degrees of health implications.

Acknowledgements

455 JJV, ACN, BAB, and BM developed the research questions and study design. ACN
456 collected and supervised the data collection. LJW, JJV, and BM wrote the manuscript. BM and
457 JJV analyzed the data and prepared the graphs. The authors have no conflicts of interest to
458 declare. We thank the data collection team: A. Barnard, T. Boussina, E. Cano, H. Caparella, C.
459 Carminito, J. Greco, A. Maness, A. Nathman, S. Seil, N. Sharpe, A. Vitale, & S. Winkler.

460

461

462 References

463 Akinyi, M.Y., Tung, J., Jeneby, M., Patel, N.B., Altmann, J., & Alberts, C. (2013). Role of
464 grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behavior*
465 85, 559–568. <https://doi.org/10.1016/j.anbehav.2012.12.012>

466 Alberts, S.C. (2019). Social influences on survival and reproduction: Insights from a long-term
467 study of wild baboons. *Journal of Animal Ecology*, 88, 47–66.
468 <https://doi.org/10.1111/1365-2656.12887>

469 Archie, E.A., Tung, J., Clark, M., Altmann, J., & Alberts, S.C. (2014). Social affiliation matters:
470 both same-sex and opposite-sex relationships predict survival in wild female baboons.
471 *Proceedings of the Royal Society of Britain*, 281(1793).
472 <https://doi.org/10.1098/rspb.2014.1261>

473 Aureli, F., Preston, S.D., & de Waal, F.B. (1999). Heart rate responses to social interactions in
474 free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *J Comp Psychol* 113(1),
475 59–65. <http://dx.doi.org/10.1037/0735-7036.113.1.59>

476 Balasubramaniam, K., Beisner, B., Vandeleest, J., Atwill, E., & McCowan, B. (2016). Social
477 buffering and contact transmission: network connections have beneficial and detrimental
478 effects on *Shigella* infection risk among captive rhesus macaques. *PeerJ*:
479 e2630. <https://doi.org/10.7717/peerj.2630>

- 480 Barton, R. (1985). Grooming site preferences in primates and their functional implications.
481 *International Journal of Primatology*. 6, 519–532. <https://doi.org/10.1007/BF02735574>
- 482 Beisner, B.A., Jackson, M.E., Cameron, A.N., & McCowan, B. (2011). Detecting Instability in
483 Animal Social Networks: Genetic Fragmentation Is Associated with Social Instability in
484 Rhesus Macaques. *PLoS ONE* 6(1), e16365.
485 <https://doi.org/10.1371/journal.pone.0016365>
- 486 Beisner, B.A., & McCowan, M. (2014). Signaling context modulates social function of silent
487 bared-teeth displays in rhesus macaques (*Macaca mulatta*). *American Journal of*
488 *Primatology*, 76(2), 111-121. <https://doi.org/10.1002/ajp.22214>
- 489 Berkman, L.F., Glass, T., Brissette, I., & Seeman, T.E. (2000). From social integration to health:
490 Durkheim in the new millennium. *Social Science & Medicine*, 51(6), 843-857.
491 [https://doi.org/10.1016/S0277-9536\(00\)00065-4](https://doi.org/10.1016/S0277-9536(00)00065-4)
- 492 Boccia, M.L., Reite, M., & Laudenslager, M. (1989). On the physiology of grooming in a pigtail
493 macaque. *Physiol. Behav.* 45, 667–670. doi:10.1016/0031-9384(89)90089-9.
- 494 Boccia, M.L., Scanlan, J.M., Laudenslager, M.L., Berger, C.L., Hijazi, A.S., & Reite, M.L.
495 (1997). Juvenile friends, behavior, and immune responses to separation in bonnet
496 macaque infants. *Physiology & Behavior*, 61(2), 191-198. [https://doi.org/10.1016/S0031-](https://doi.org/10.1016/S0031-9384(96)00370-8)
497 [9384\(96\)00370-8](https://doi.org/10.1016/S0031-9384(96)00370-8)

- 498 Borgeaud, C., & Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific
499 coalitionary support for grooming in experimentally induced conflicts. *Current Biology*,
500 25(22), 3011-3016. <https://doi.org/10.1016/j.cub.2015.10.016>
- 501 Brent, L.J.N. (2015). Friends of friends: are indirect connections in social networks important to
502 animal behaviour? *Animal Behaviour*, 103, 211-222.
503 <https://doi.org/10.1016/j.anbehav.2015.01.020>
- 504 Brent, L.J.N., Chang, S.W.C., Gariépy, J-F., & Platt, M.L. (2014). The neuroethology of
505 friendship, *Annals of the New York Academy of Science*, 1316(1), 1-17. doi:
506 10.1111/nyas.12315
- 507 Brent, L.J.N., Ruiz-Lambides, A., & Platt, M.L. (2017a). Family network size and survival
508 across the lifespan of female rhesus macaques. *Proceedings of the Royal Society of*
509 *Britain*, 284(1854). <https://doi.org/10.1098/rspb.2017.0515>
- 510 Brent, L. J. N., Ruiz-Lambides, A., & Platt, M. L. (2017b). Persistent social isolation reflects
511 identity and social context but not maternal effects or early environment. *Scientific*
512 *reports*, 7(1), 17791. <https://doi.org/10.1038/s41598-017-18104-4>
- 513 Bruunsgaard, H., Ladelund, S., Perdersen, A.N., Schroll, M., Jorgensen, T., & Pedersen, B.K.
514 (2003). Predicting death from tumour necrosis factor-alpha and interleukin-6 in 80-year
515 old people. *Clinical and Experimental Immunology*, 132(1), 24-31.
516 <https://doi.org/10.1046/j.1365-2249.2003.02137.x>

- 517 Burnham, K. P. & Anderson. (2002). Model selection and multimodel inference: a practical
518 information-theoretic approach. *Ecological Modelling. Springer Science & Business*
519 *Media, New York, New York, USA.*
- 520 Cacioppo, J.T., & Hawkley, L.C. (2003). Social isolation and health, with an emphasis on
521 underlying mechanisms. *Perspect. Biol. Med.* 46, S39–S52.
522 (doi:10.1353/pbm.2003.0049).
- 523 Cameron, E.Z., Setsaas, T.H., & Linklater, W.L. (2009). Social bonds between unrelated females
524 increase reproductive success in feral horses. *Proceedings of the National Academy of*
525 *Sciences*, 106(33), 13850-13853. <https://doi.org/10.1073/pnas.0900639106>
- 526 Campbell, L.A.D., Tkaczynski, P.J., Lehmann, J., Mouna, M., & Majolo, B. (2018). Social
527 thermoregulation as a potential mechanism linking sociality and fitness: Barbary
528 macaques with more social partners form larger huddles. *Scientific Reports*, 6074,
529 <https://doi.org/10.1038/s41598-018-24373-4>
- 530 Cohen, S., Doyle, W.J., Skoner, D.P., Rabin, B.S., & Gwaltney, J.M. Jr (1997). Social ties and
531 susceptibility to the common cold. *JAMA* 277, 1940–1944.
532 doi:10.1001/jama.1997.03540480040036
- 533 Cohen, S., Kaplan, J.R., Cunnick, J.E., Manuck, S.B., & Rabin, B.S. (1992). Chronic social
534 stress, affiliation, and cellular immune response in nonhuman primates. *Psychological*
535 *Science*, 3(5), 301-305. <https://doi.org/10.1111/j.1467-9280.1992.tb00677.x>

- 536 Collins, N.L., Dunkel-Schetter, C., Lobel, M., & Scrimshaw, S.C. (1993). Social support in
537 pregnancy: psychosocial correlates of birth outcomes and postpartum depression. *J Pers*
538 *Soc Psychol*, 65(6), 1243-1258.
- 539 Corrigan, P.W., & Phelan, S.M., (2004). Social support and recovery in people with serious
540 mental illnesses. *Community and Mental Health Journal*. 40(6), 513-523.
541 <https://doi.org/10.1007/s10597-004-6125-5>
- 542 Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M., & Cheney, D.L. (2008). Social
543 stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*).
544 *Hormones and Behavior*, 53(1), 254-265. <https://doi.org/10.1016/j.yhbeh.2007.10.007>
- 545 Davenport, M.D., Tiefenbacher, S., Lutz, C.K., Novak, M.A., Meyer, J.S. (2006). Analysis of
546 endogenous cortisol concentrations in the hair of rhesus macaques. *General and*
547 *Comparative Endocrinology*, 147(3), 255-261.
548 <https://doi.org/10.1016/j.ygcen.2006.01.005>
- 549 Debray, R., Snyder-Mackler, N., Kohn, J.N., Wilson, M.E., Barreiro, L.B., & Tung, J. (2019).
550 Social affiliation predicts mitochondrial DNA copy number in female rhesus macaques.
551 *Biology Letters*, 15(1). <https://doi.org/10.1098/rsbl.2018.0643>
- 552 Dias, A., Geard, N., Campbell, P.T., Warr, D., & McVernon, J. (2018). Quantity or quality?
553 Assessing relationships between perceived social connectedness and recorded encounters.
554 *PLoS ONE* 13(11), e0208083. <https://doi.org/10.1371/journal.pone.0208083>
- 555 Drickamer, L.C. (1976). Quantitative observations on grooming behavior in free-
556 ranging *Macaca mulatta*. *Primates*, 17, 323-335. <https://doi.org/10.1007/BF02382789>
- 557 Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. *Folia*
558 *Primatologica*, 57, 121-131. <https://doi.org/10.1159/000156574>

- 559 Ekman, P., Davidson, R. J., & Friesen, W. V. (1990). The Duchenne smile: Emotional
560 expression and brain physiology: II. *Journal of personality and social psychology*, 58(2),
561 342.
- 562 Evans, G.W., Wener, R.E., & Phillips, D. (2002). The morning rush hour: predictability and
563 commuter stress. *Environment and Behavior*, 34(4), 521-530.
564 <https://doi.org/10.1177/00116502034004007>
- 565 Farine, D.R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social
566 network analysis. *Journal of Animal Ecology*, 84(5), 1144-1163.
567 <https://doi.org/10.1111/1365-2656.12418>
- 568 Frank, M. G., & Ekman, P. (1993). Not all smiles are created equal: The differences between
569 enjoyment and nonenjoyment smiles. *Humor-International Journal of Humor Research*,
570 6(1), 9-26. <https://doi.org/10.1515/humr.1993.6.1.9>
- 571 Frey II, W. H., Desota-Johnson, D., Hoffman, C., & McCall, J. T. (1981). Effect of stimulus on
572 the chemical composition of human tears. *American Journal of Ophthalmology*, 92(4),
573 559-567. [https://doi.org/10.1016/0002-9394\(81\)90651-6](https://doi.org/10.1016/0002-9394(81)90651-6)
- 574 Friedman, E.M., Hayney, M.S., Love, G.D., Urry, H.L., Rosenkranz, M.A., Davidson, R.J.,
575 Singer, B.H., & Ryff, C.D. (2005). Social relationships, sleep quality, and interleukin-6 in
576 aging women. *PNAS*, 102(51), 18757-18762. <https://doi.org/10.1073/pnas.0509281102>
- 577 Fujii, K., Jin, J., Shev, A., Beisner, B.A., McCowan, B., & Fushing, H. (2015). Perc: Using
578 Percolation and Conductance to find information flow certainty in direct network. R
579 package version 0.1.3. <https://cran.r-project.org/web/packages/Perc/index.html>.
- 580 Fürtbauer, I., Heistermann, M., Schülke, O., & Ostner, J. (2014). Low female stress hormone
581 levels are predicted by same- or opposite-sex sociality depending on season in wild

- Assamese macaques. *Psychoneuroendocrinology*, 48, 19–28.
<https://doi.org/10.1016/j.psyneuen.2014.05.022>
- Fushing, H., McAssey, M.P., Beisner, B., McCowan, B. (2011). Ranking Network of a Captive Rhesus Macaque Society: A Sophisticated Corporative Kingdom. *PLoS ONE*, 6(3), e17817. <https://doi.org/10.1371/journal.pone.0017817>
- Gelstein, S., Yeshurun, Y., Rozenkrantz, L., Shushan, S., Frumin, I., Roth, Y., & Sobel, N. (2011). Human tears contain a chemosignal. *Science*, 331(6014), 226-230. DOI: 10.1126/science.1198331
- Gust, D.A., Gordon, T.P., Hambright, M.K., & Wilson, M.E. (1993). Relationship between social factors and pituitary: adrenocortical activity in female rhesus monkeys (*Macaca mulatta*). *Horm. Behav* 27, 318–331. doi:10.1006/hbeh.1993.1024.
- Haber, M.G., Cohen, J.L., Lucas, T., & Baltes, B.B. (2007). The relationship between self-reported received and perceived social support: a meta-analytic review. *American Journal of Community Psychology*, 39(1-2), 133-144. <https://doi.org/10.1007/s10464-007-9100-9>
- Hall, L.A., Schaefer, E.S., & Greenberg, R.S. (1987). Quality and quantity of social support as correlates of psychosomatic symptoms in mothers with young children. *Research in Nursing & Health*, 10(4), 287-298. <https://doi.org/10.1002/nur.4770100413>
- Holt-Lunstad, J., Smith, T.B., & Layton, J.B. (2010). Social relationships and mortality risk: a meta-analytic review. *PLoS Med.* 7, e1000316. (doi:10.1371/journal.pmed.1000316).
- Kappeler, P.M., Cremer, S., & Nunn, C.L. (2015). Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. *Phil. Trans. R. Soc. B* 370, 20140116. doi:10.1098/rstb.2014.0116

- 605 Karelina, K., & deVries, A.C. (2010). Modeling social influences on human health.
606 *Psychosomatic Medicine*, 73(1), 67-74. doi: 10.1097/PSY.0b013e3182002116
- 607 Kiecolt-Glaser, J.K., Loving, T.J., Stowell, J.R., Malarkey, W.B., Lemeshow, S. (2005). Hostile
608 marital interactions, proinflammatory cytokine production, and wound healing. *Arch Gen*
609 *Psychiatry*, 62, 1377–1384. doi:10.1001/archpsyc.62.12.1377
- 610 Kulik, J.A., & Mahler, H.I. (1989). Social support and recovery from surgery. *Health*
611 *Psychology*, 8(2), 221-238. <http://dx.doi.org/10.1037/0278-6133.8.2.221>
- 612 Lehmann, J., Korstjens, A.H., & Dunbar, R.I.M. (2007). Group size, grooming, and social
613 cohesion in primates. *Animal Behaviour*, 74(6), 1617-1629.
614 <https://doi.org/10.1016/j.anbehav.2006.10.025>
- 615 Lutgendorf, S.K., Sood, A.K., Anderson, B., McGinn, S., & Maiseri, H. (2005). Social support,
616 psychological distress, and natural killer cell activity in ovarian cancer. *J Clin Oncol* 23,
617 7105–7113. DOI: 10.1200/JCO.2005.10.015
- 618 Manson, J.H. (1998). Evolved psychology in a novel environment — male macaques and the
619 “seniority rule.” *Human Nature*, 9, 97-117. <https://doi.org/10.1007/s12110-998-1000-7>
- 620 Marucha, P.T., Crespín, T.R., Shelby, R.A., & Anderson, B.L. (2005). TNF- α levels in cancer
621 patients relate to social variables. *Brain, Behavior, and Immunity*, 19(6), 521-525.
622 <https://doi.org/10.1016/j.bbi.2005.03.014>
- 623 McCowan, B., Beisner, B., Bliss-Moreau, E., Vandeleeest, J., Jin, J., Hannibal, D., & Hsieh, F.
624 (2016). Connections Matter: Social Networks and Lifespan Health in Primate
625 Translational Models. *Front. Psychol.* 7:433. doi: 10.3389/fpsyg.2016.00433

- 626 McFarland, R., Fuller, A., Hetem, R.S., Mitchell, D., Maloney, S.K., Henzi, S.P., et al. (2015).
627 Social integration confers thermal benefits in a gregarious primate. *Journal of Animal*
628 *Ecology*, 84, 871-878. doi: 10.1111/1365-2656.12329
- 629 McFarland, R., Henzi, S.P., Barrett, L., Coetzee, A.W.E., Fuller, A., Hetem, R.S., Mitchell, D.,
630 & Maloney, S.K. (2016). Thermal consequences of increased pelt loft infer an additional
631 utilitarian function for grooming. *American Journal of Primatology*, 78(4), 456-461.
632 <https://doi.org/10.1002/ajp.22519>
- 633 McFarland, R., Murphy, D., Lusseau, D., Henzi, S.P., Parker, J.L., Pollet, T.V., & Barrett, L.
634 (2017). The 'strength of weak ties' among female baboons: fitness-related benefits of
635 social bonds. *Animal Behaviour*, 126, 101-106.
636 <https://doi.org/10.1016/j.anbehav.2017.02.002>
- 637 Melchior, M., Berkman, L.F., Niedhammer, I., Chea, M., & Goldberg, M. (2003). Social
638 relations and self-reported health: a prospective analysis of the French Gazel cohort.
639 *Social Science & Medicine*, 56(8), 1817-1830. [https://doi.org/10.1016/S0277-](https://doi.org/10.1016/S0277-9536(02)00181-8)
640 [9536\(02\)00181-8](https://doi.org/10.1016/S0277-9536(02)00181-8)
- 641 Mendes de Leon, C.F., Glass, T.A., Beckett, L.A., Seeman, T.E., Evans, D.A., & Berkman, L.F.
642 (1999). Social networks and disability transitions across eight intervals of yearly data in
643 the New Haven EPESE. *The Journals of Gerontology: Series B.*, 54B(3), S162-S172.
644 <https://doi.org/10.1093/geronb/54B.3.S162>
- 645 Meyer, J.S., & Novak, M.A. (2012). Minireview: hair cortisol: a novel biomarker of
646 hypothalamic-pituitary-adrenocortical activity. *Endocrinology*, 153(9), 4121-4127.
647 <https://doi.org/10.1210/en.2012-1226>

- 648 Miller, S.M. (1979). Controllability and human stress: method, evidence, and theory. *Behaviour*
649 *Research and Therapy*, 17(4), 287-304. [https://doi.org/10.1016/0005-7967\(79\)90001-9](https://doi.org/10.1016/0005-7967(79)90001-9)
- 650 Pallante, V., Ferrari, P.F., Gamba, M., & Palagi, E. (2019). Embracing in a female-bonded
651 monkey species (*Theropithecus gelada*). *Journal of Comparative Psychology*.
652 <http://dx.doi.org/10.1037/com0000173>
- 653 Rico-Uribe, L.A., Caballero, F.F., Olaya, B., Tobiasz-Adamczyk, B., Koskinen, S., Leonardi,
654 M., et al. (2016) Loneliness, Social Networks, and Health: A Cross-Sectional Study in
655 Three Countries. *PLoS ONE* 11(1), e0145264.
656 <https://doi.org/10.1371/journal.pone.0145264>
- 657 Sapolsky, R.M. (2005). The influence of social hierarchy on primate health. *Science*, 308(5722),
658 648-652. DOI: 10.1126/science.1106477
- 659 Scheller, J., Chalaris, A., Schmidt-Arras, D., & Rose-John, S. (2011). The pro-and anti-
660 inflammatory properties of the cytokine interleukin-6. *Biochimica et Biophysica Acta*
661 *Molecular Cell Research*, 1813(5), 878-888.
662 <https://doi.org/10.1016/j.bbamcr.2011.01.034>
- 663 Schino, G. (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal
664 altruism. *Behavioral Ecology*, 18(1), 115-120. <https://doi.org/10.1098/rsbl.2007.0506>
- 665 Schino, G., & Alessandrini, A. (2015). Short-term costs and benefits of grooming in Japanese
666 macaques. *Primates*, 56(3), 253-257. <https://doi.org/10.1007/s10329-015-0468-0>
- 667 Schino, G., Ventura, R., & Troisi, A. (2005). Grooming and aggression in captive Japanese
668 macaques. *Primates*, 46(3), 207-209. <https://doi.org/10.1007/s10329-004-0124-6>
- 669 Schrock, A.E., Leard, C., Lutz, M.C., Meyer, J.S., & Gazes, R.P. (2019). Aggression and social
670 support predict long-term cortisol levels in captive tufted capuchin monkeys (*Cebus*

- 671 [Sapajus] apella). *American Journal of Primatology*, e23001.
- 672 <https://doi.org/10.1002/ajp.23001>
- 673 Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance
- 674 reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210.
- 675 <https://doi.org/10.1016/j.cub.2010.10.058>
- 676 Schulz, R., & Beach, S.R. (1999). Caregiving as a risk factor for mortality: The Caregiver Health
- 677 Effects Study. *JAMA*, 282(23), 2215–2219. doi:10.1001/jama.282.23.2215
- 678 Seeman, T. E., 1996. Social ties and health: the benefits of social integration. *Ann.*
- 679 *Epidemiol.* 6, 442–451. doi: 10.1016/S1047-2797(96)00095-6
- 680 Seyfarth, R.M. (1977). A model of social grooming among adult female monkeys. *Journal of*
- 681 *Theoretical Biology*, 65, 671–698. [https://doi.org/10.1016/0022-5193\(77\)90015-7](https://doi.org/10.1016/0022-5193(77)90015-7)
- 682 Seyfarth, R.M. (1980). The distribution of grooming and related behaviours among adult female
- 683 vervet monkeys. *Animal Behaviour*, 28, 798–813. [https://doi.org/10.1016/S0003-](https://doi.org/10.1016/S0003-3472(80)80140-0)
- 684 [3472\(80\)80140-0](https://doi.org/10.1016/S0003-3472(80)80140-0)
- 685 Shannon, P., Markiel, A., Ozier, O., Baliga, N.S., Wang, J.T., Ramage, D., Amin,
- 686 N., Schwikowski, B., & Ideker, T. (2003). Cytoscape: a software environment for
- 687 integrated models of biomolecular interaction networks. *Genome Res.* 13(11), 2498–504.
- 688 DOI: 10.1101/gr.1239303
- 689 Shutt, K., MacLarnon, A., Heistermann, M., & Semple, S. (2007). Grooming in Barbary
- 690 macaques: Better to give than to receive? *Biology Letters*, 3(3), 231–233.
- 691 <https://doi.org/10.1098/rsbl.2007.0052>

- 692 Silk, J.B., (1982). Altruism among female *Macaca radiata*: explanations and analysis of patterns
693 of grooming and coalition formation. *Behaviour*, 79(2/4), 162-188.
694 <https://www.jstor.org/stable/4534159>
- 695 Silk, J.B., Alberts, S.C., & Altmann, J. (2003). Social bonds of female baboons enhance infant
696 survival. *Science*, 302(5648), 1231-1234. DOI: 10.1126/science.1088580
- 697 Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig,
698 R.M., Seyfarth, R.M., & Cheney, D.L. (2010). Strong and consistent social bonds
699 enhance the longevity of female baboons. *Current Biology*, 20(5), 1359-1361.
700 <https://doi.org/10.1016/j.cub.2010.05.067>
- 701 Son, J., Erno, A., Shea, D.G., Femia, E.E., Zarit, S.H., Parris Stephens, M.A. (2007). The
702 caregiver stress process and health outcomes. *Journal of Aging and Health*, 19(6), 871-
703 887. <https://doi.org/10.1177/0898264307308568>
- 704 Stanton, M.A.,& Mann, J. (2012). Early Social Networks Predict Survival in Wild Bottlenose
705 Dolphins. *PLoS ONE* 7(10), e47508. <https://doi.org/10.1371/journal.pone.0047508>
- 706 StataCorp. (2017). *Stata Statistical Software: Release 15*. College Station, TX: StataCorp LLC.
- 707 Suvilehto, J.T., Glerean, E., Dunbar, R.I.M., Hari, R., & Nummenmaa, L. (2015). Topography of
708 social touching depends on emotional bonds between humans. *Proceedings of the*
709 *National Academy of Sciences*, 112(45), 138811-13816.
710 <https://doi.org/10.1073/pnas.1519231112>
- 711 Tang, Y., Li, M., Wang, J., Pan, Y., Wu, F.X. (2014). CytoNCA: a cytoscape plugin for
712 centrality analysis and evaluation of biological networks. *BioSystems*, 127, 67-72. DOI:
713 10.1016/j.biosystems.2014.11.005.

- Uchino, B.N. (2006). Social support and health: a review of physiological processes potentially underlying links to disease outcomes. *J Behav Med* 29, 377–387.
<https://doi.org/10.1007/s10865-006-9056-5>
- Uchino, B.N., Cacioppo, J.T., & Kiecolt-Glaser, J.K. (1996). The relationship between social support and physiological processes: A review with emphasis on underlying mechanisms and implications for health. *Psychol Bull* 119, 488–531.
- Van de Mortel, T. F. (2008). Faking it: social desirability response bias in self-report research. *Australian Journal of Advanced Nursing*, 25(4), 40-48.
- Vandeleest, J.J., Beisner, B.A., Hannibal, D.L., Nathman, A.C., Capitanio, J.P., Hsieh, F., Atwill, E.R., & McCowan, B. (2016). Decoupling social status and status certainty effects on health in macaques: a network approach. *PeerJ*, 4, e2394.
<https://doi.org/10.7717/peerj.2394>
- Vandeleest, J. J., Capitanio, J. P., Hamel, A., Meyer, J., Novak, M., Mendoza, S. P., & Mccowan, B. (2019). Social stability influences the association between adrenal responsiveness and hair cortisol concentrations in rhesus macaques. *Psychoneuroendocrinology*, 100, 164-171.
<https://doi.org/10.1016/j.psyneuen.2018.10.008>
- Vandeleest, J. J., Winkler, S., Beisner, B., Hannibal, D., Atwill, R., & McCowan, B. (2018). Sex difference in the impact of dominance certainty and rank on hair cortisol concentrations in rhesus monkeys (*Macaca Mulatta*). *American Journal of Primatology* (80). 111 river St, Hoboken 07030-5774, NJ, USA: Wiley.

Vandenbergh, J. G., & Vessey, S. (1968). Seasonal breeding of free-ranging rhesus monkeys and related ecological factors. *Reproduction*, 15(1), 71-79.

<https://doi.org/10.1530/jrf.0.0150071>

Weiss, J.M. (1970). Somatic effects of predictable and unpredictable shock. *Psychosomatic Medicine*, 32(4), 397-408.

Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M., & Cheney, D.L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, 54(1), 170-177. <https://doi.org/10.1016/j.yhbeh.2008.02.009>

Wooddell, L.J., Hamel, A.F., Murphy, A.M., Byers, K.L., Kaburu, S.S.K., Meyer, J.S., Suomi, S.J., & Dettmer, A.M. (2017). Relationships between affiliative social behavior and hair cortisol concentrations in semi-free ranging rhesus monkeys. *Psychoneuroendocrinology*, 84, 109-115. <https://doi.org/10.1016/j.psyneuen.2017.06.018>

Yang, C., Schorpp, K., & Harris, K.M. (2014). Social support, social strain and inflammation: evidence from a national longitudinal study of U.S. adults. *Social Science & Medicine*, 107, 124-135. <https://doi.org/10.1016/j.socscimed.2014.02.013>

Yee, J.R., Cavigelli, S.A., Delgado, B., & McClintock, M.K. (2008). Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosom. Med.* 70, 1050–1059. (doi:10.1097/PSY.0b013e31818425fb).

Table 1 (on next page)

Network Measures

Metric	Description
Degree centrality	measures the number of direct connections for each node, as well as their direction as either incoming (indegree) or outgoing (outdegree)
Eigenvector centrality	measures degree centrality but weights more heavily neighbors who are also highly connected
Betweenness centrality	measures the number of times a node lies on the shortest path between other nodes
Information centrality	measures the number of times a node lies on any path between other nodes
Closeness centrality	measures how close each node is to all other nodes within the network
Clustering coefficient	measures the extent to which a node's neighbors are also connected to each other

1

2

Table 2 (on next page)

Best model results for IL6, TNF- α and hair cortisol analysis.

Model Parameters	AIC	Model Likelihood	Model Weight
IL-6			
Model 1: Political weighted eigenvector centrality (PolEW), Friends/family weighted closeness centrality (FFCW), Age	1349.9	1.00	0.35
Model 2: PolEW, FFCW, Age, Sampling order	1350.5	0.74	0.26
Model 3: PolEW, FFCW, Percentile dominance rank (PDR), Age, Sampling order	1350.8	0.65	0.23
Model 4: PolEW, FFCW, PDR, Age, Sampling order	1351.6	0.43	0.15
Model 5: Empty Model ^a	1363.1	0.00	
TNF-α			
Model 1: PolEW, FFCW, Sampling order	2346.38	1.00	0.31
Model 2: PolEW, FFCW, Age	2346.39	1.00	0.31
Model 3: PolEW, FFCW, PDR, Age	2346.70	0.85	0.27
Model 4: PolEW, FFCW, PDR, Age, Sampling order	2348.37	0.37	0.11
Model 5: Empty Model ^a	2356.49	0.01	
Hair cortisol			
Model 1: Political weighted information centrality (PolIW), FFCW, Rank, PolIW*Rank, FFCW*Rank, Sampling order	2064.9	1.00	0.47
Model 2: PolIW, FFCW, Rank, PolIW*Rank, Sampling order	2065.8	0.64	0.30
Model 3: PolIW, Rank, PolIW*Rank, Sampling order	2066.4	0.47	0.22
Model 4: Empty Model ^a	2103.9	0.00	

1 ^a Empty Model only includes the intercept and the random effect (Cage)

2

Table 3(on next page)

Best model results for IL6, TNF- α and hair cortisol analysis.

Model Parameters	β coefficient	p-value
IL-6		
Political weighted eigenvector centrality	3.84	0.003
Friends/Family weighted closeness centrality	-1.61	0.002
Age	0.042	0.161
Intercept	2.64	0.011
TNF-α		
Political weighted eigenvector centrality	4.06	0.016
Friends/Family weighted closeness centrality	-2.64	<0.0001
Sampling order	-0.03	0.569
Intercept	6.71	0.001
Hair cortisol		
Political weighted information centrality (PolIW)	0.008	0.930
Rank-low	0.418	0.291
Rank-mid	-1.068	0.003
PolIW*Rank-low	-0.142	0.227
PolIW*Rank-mid	0.271	0.012
Friends/family weighted closeness centrality (FFCW)	-0.624	0.023
FFCW*Rank-low	-0.021	0.953
FFCW*Rank-mid	0.580	0.052
Sampling order	0.053	<0.0001
Intercept	4.40	0.001

1

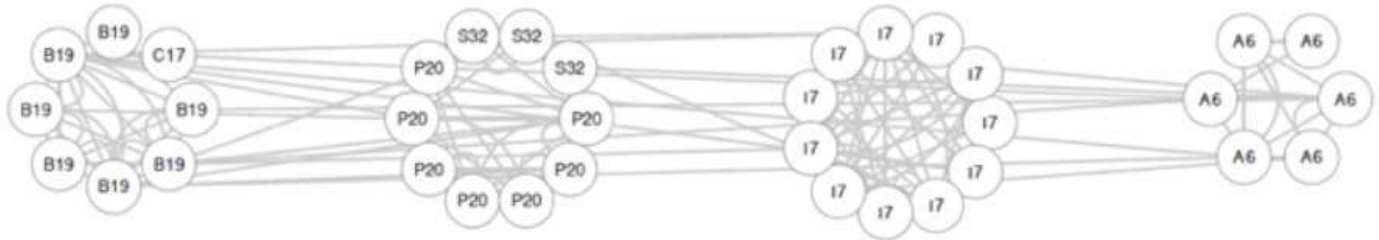
2

Figure 1

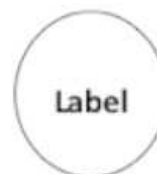
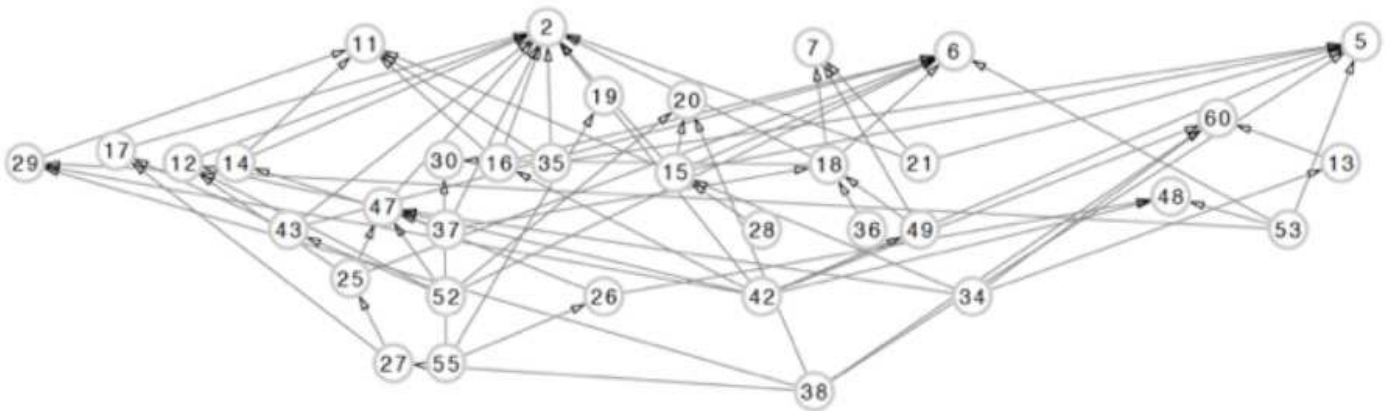
Example network graphs.

Example graphs of A. family/friends groom network and B. Political groom network from social group C.

A. Family/friends groom network



B. Political groom network



A. Matriline
B. Rank

Figure 2

Illustration of network metrics.

Example network illustrating nodes with the highest value for different types of centrality measures.

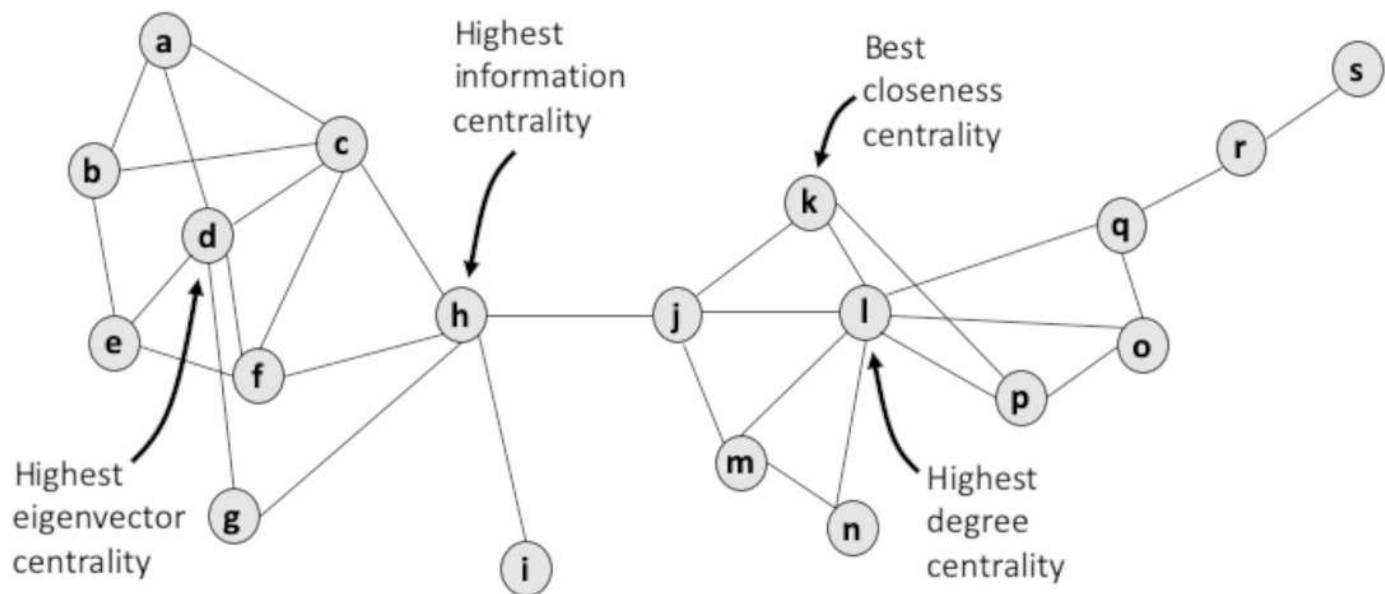


Figure 3

Effects of grooming centrality on IL-6.

Effects of political grooming centrality (A) and family/friend grooming centrality (B) on levels of IL6 with 95% confidence intervals.

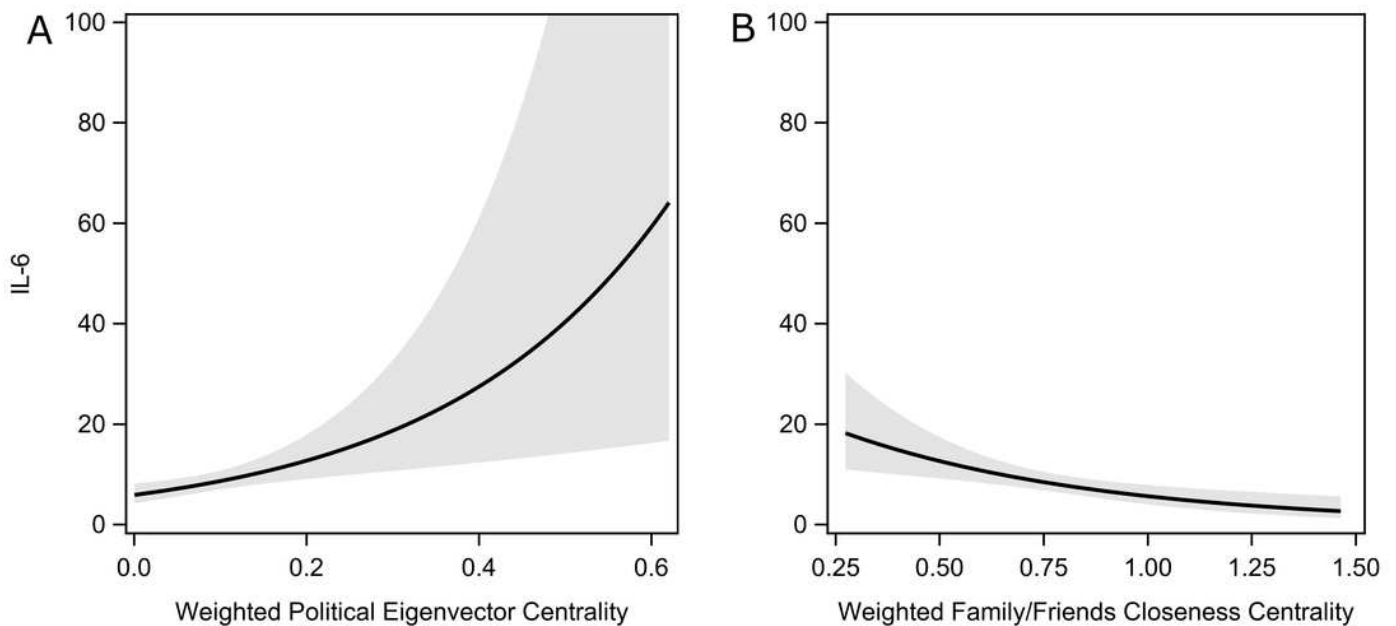


Figure 4

Effects of grooming centrality on TNF- α .

Effects of political grooming centrality (A) and family/friend grooming centrality (B) on levels of TNF α with 95% confidence intervals.

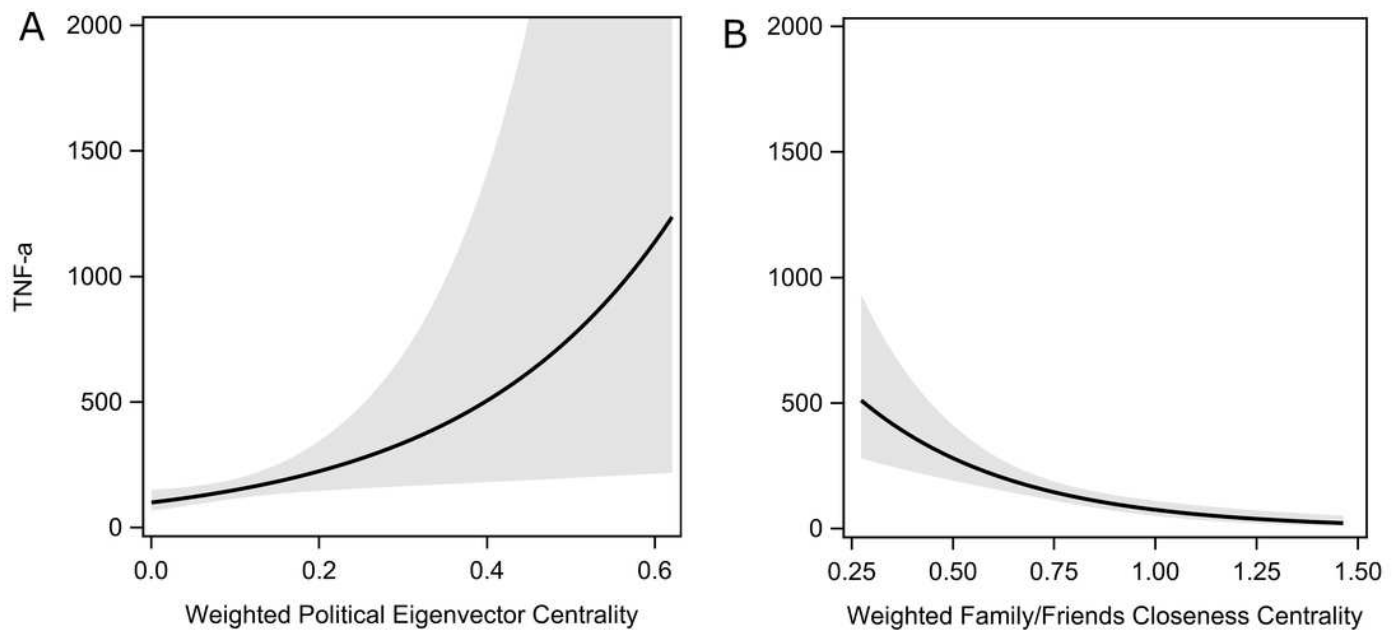


Figure 5

Effects of grooming centrality on hair cortisol concentrations.

Effects of political grooming centrality (A) and family/friend grooming centrality (B) by rank on hair cortisol concentrations.

