Published in final edited form as:

Am J Primatol. 2020 January ; 82(1): e23086. doi:10.1002/ajp.23086.

Sex differences in the impact of social status on hair cortisol concentrations in rhesus monkeys (*Macaca mulatta*)

Jessica J. Vandelee¹, Sasha L. Winkler^{1,2}, Brianne A. Beisner^{1,3}, Darcy L. Hannibal¹, Edward R. Atwill³, Brenda McCowan^{1,3}

¹California National Primate Research Center, University of California Davis

²Department of Anthropology, UCLA

³Department of Population Health and Reproduction, University of California Davis

Abstract

Social status impacts stress in primates, but the direction of the effect differs depending on species, social style, and group stability. This complicates our ability to identify broadly applicable principles for understanding of how social status impacts health and fitness. One reason for this is the fact that social status is often measured as linear dominance rank, yet social status is more complex than simply high or low rank. Additionally, most research on social status and health ignores the effects of sex and sex-specific relationships, despite known differences in disease risk, coping strategies, and opposite-sex dominance interactions between males and females in many species. We examine the influence of social status, sex, and opposite-sex interactions on hair cortisol concentrations in a well-studied species, rhesus macaques, where the literature predicts low ranking individuals would experience more chronic stress. Animals in three captive, semi-naturalistic social groups (N = 252, 71 male) were observed for 6 weeks to obtain metrics of social status (rank and dominance certainty (DC)). DC is a measure of one's fit within the hierarchy. Hair samples were collected from each subject and analyzed for hair cortisol concentrations (HCC). Generalized linear mixed models were used to examine 1) whether rank, DC, or sex predicted HCC, 2) whether same- or opposite-sex dominance relationships differentially impacted HCC, and 3) whether aggressive interactions initiated or received could explain any observed relationships. Results indicated that DC, not rank, predicted HCC in a sex-specific manner. For males, high HCC were predicted by receiving aggression from or having high DC with other males as well as having low DC with females. For females, only high DC with males predicted high HCC. These results likely relate to sex-specific life history pattern differences in inherited versus earned rank that are tied to female philopatry and male immigration.

Graphical Abstract

Correspondence: Jessica Vandelee, PhD, California National Primate Research Center, University of California, One Shields Ave, Davis, CA 95616, Phone: 1-530-752-1506, vandelee@ucdavis.edu.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

The authors declare there is no conflict of interest.

Keywords

Hair Cortisol; sex differences; dominance certainty; aggression; social status

INTRODUCTION

Social status is known to impact a variety of health outcomes in primates but the specifics of who (high or low status individuals) experiences the greatest health costs is difficult to predict. For example, lower status individuals have been shown to live shorter lives, have a greater risk for cardiovascular disease and exhibit reduced immune function (Marmot & Sapolsky, 2014; Sapolsky, 2004; Sapolsky & Share, 1994; Shively & Day, 2015; Snyder-Mackler et al., 2016). Complicating the picture, several studies have found no association between social status and stress or health (Abbott et al., 2003; Bercovitch & Clarke, 1995; Weingrill, Gray, Barrett, & Henzi, 2004), and there is evidence that high status individuals may experience greater parasite loads (Habig & Archie, 2015). These discrepancies have been attributed to species (e.g. social organization, dominance style) and environmental conditions (e.g. resource availability) (Creel, 2001; Sapolsky, 2005). One challenge in understanding the impact of social status on health in nonhuman primates is that a single metric, dominance rank, is often used to represent an individual's status. Yet we know that there is a great deal of complexity to social status and a greater understanding of this complexity is required to fully understand the impact of social status on health and fitness (Braveman et al., 2005). Finally, many diseases affected by status also display sex differences in their incidence (Anderson & Armstead, 1995; Kaplan et al., 1996; Mosca,

Barrett-Connor, & Kass Wenger, 2011) yet sex is rarely, if ever, included as a variable of interest in studies of social status and health in nonhuman primates.

One proposed mechanism for how social status impacts health is through differential experience of chronic stress, which can have consequences for health and fitness. Based on this hypothesis we would expect that measures of social status (e.g. dominance rank) would be associated with metrics of stress (e.g. cortisol), which are known to potentially have widespread impacts on health and fitness (Capitanio, Mendoza, Lerche, & Mason, 1998; Shively, Register, & Clarkson, 2009; Snyder-Mackler et al., 2016). Relatively consistent effects have been found in cooperative breeding species (e.g. marmosets) and lemurs where dominant animals tend to exhibit higher cortisol levels (Abbott et al., 2003; Cavigelli, Dubovick, Levash, Jolly, & Pitts, 2003; Sapolsky, 2005). In non-cooperatively breeding primate species, status-related stress was thought to be concentrated among low-status individuals as they experience reduced access to resources, reduced social support, and increased receipt of aggression from more dominant animals (Abbott et al., 2003; Sapolsky, 2004). However, support for this hypothesis is inconsistent, with studies examining the impact of social status on stress producing mixed results across and within-species (Dettmer, Novak, Meyer, & Suomi, 2014; Higham, Heistermann, & Maestripieri, 2013; Ostner, Heistermann, & Schulke, 2008; Sapolsky, 2005). Factors relating to species-typical social organization (e.g. dominance style, coping outlets, dominant avoidance, resource inequity) and the stability of the dominance hierarchy are key factors influencing these inconsistent findings (Sapolsky, 2005). For example, while high-ranking chimpanzees have been shown to have higher cortisol levels, it is low-ranking baboons that more commonly exhibit this pattern (Gesquiere et al., 2011). These species differences have been attributed to differences in dominance style. In chimpanzees rank is maintained through frequent aggression from dominant animals whereas in baboons rank is maintained more through intimidation (i.e. displacements and threats) (Muller & Wrangham, 2004; Sapolsky, 2005). Even within a species effects can vary; higher cortisol levels have been demonstrated in both high- and low-ranking squirrel monkeys (Abbott et al., 2003; Coe, Mendoza, & Levine, 1979; Manogue, Leshner, & Candland, 1975). It has been suggested, however, that given the social organization of a species and the stability of the social group under study, the individuals in the group that experience more physical or psychological stress (e.g. low social control and predictability, few coping outlets, frequent physical contests) (Goymann et al., 2001; Sapolsky, 2005) will have poorer health outcomes.

Complexity of social status

The majority of research on the relationship between status and stress in nonhuman primates focuses on one's position in a dominance hierarchy, often measured via one's dominance rank (either absolute or relative). However, social status is more complex than one's position in a dominance hierarchy. Hierarchies are an emergent property of social groups that arise from a set of dyadic dominance relationships that in turn are derived from a complex suite of interactions (e.g. aggression, submission, alliances (Hinde, 1976)). Dominance ranking methods generally uses a subset of these behaviors (e.g., dyadic aggression or status) to identify a linear ranking of individuals. Inconsistent findings from previous studies may be due to insufficient or incomplete characterization of individuals' social status. For example,

research suggests that social status is better defined by considering both the individual's rank in a dominance hierarchy and the stability of their social position (Vandeleest et al., 2016). For example, Sapolsky (1992) demonstrated that while the general pattern among male olive baboons is for subordinate animals to exhibit higher cortisol levels and poorer health, this effect was dependent on the stability of the dominance hierarchy. High ranking males that were about to lose their status exhibited higher cortisol levels than the males that were challenging them. In rhesus macaques, dominance certainty (an overall measure of the certainty of an individual's position in the hierarchy) has been shown to be a better predictor of health outcomes such as diarrhea than dominance rank (Vandeleest et al., 2016). Additionally, both rank and dominance certainty have been found to be important predictors of the inflammatory biomarkers IL-6, TNF- α , and CRP (Vandeleest et al., 2016) where dominance certainty modulated the effect of rank such that high-ranking animals with low dominance certainty had higher levels of inflammation than subordinates, but no effect was found for animals with high dominance certainty. Notably, these effects on inflammatory biomarkers were only found among males. Efforts to better characterize the true complexity of social status could provide critical information as to the specific components of status that are key to influencing health and fitness.

Sex differences in social status and health

Many of the studies on social status and health in nonhuman primates have focused on one sex or have lumped both males and females together, ignoring sex differences in physiology, social roles and environmental pressures. However, such sex differences have the potential to greatly influence stress and health. Human health studies have demonstrated important sex differences in the relationship between SES and health—for example, the risk of cardiovascular disease and coronary heart disease is correlated with SES, but the magnitude of the effect is significantly greater in women than men (Backholer et al., 2017). Additionally, the use of affiliation and social support to cope with stress is known to have sex differences in humans and other primates (Archie, Tung, Clark, Altmann, & Alberts, 2014; Belle, 1991; Silk et al., 2010). For example, the importance of affiliative social ties on longevity has been demonstrated in female, but not male, baboons (Silk et al., 2010). These sex differences in disease incidence, stress responses, and coping strategies suggest that the effects of social status could have differential impacts on the physiology and health of males and females.

To explore sex differences in the influence of social status, including both rank and dominance certainty, on stress-related diseases, we are using a rhesus macaque model. Rhesus macaques form strict hierarchies in which dominance is fairly stable across time and maintained through intimidation, suggesting that subordinates would exhibit higher cortisol levels (Sapolsky, 2005). In addition, due to sex differences in the life history patterns of males and females, we would predict sex differences in the impact of social status on health. Rhesus macaque females stay in their natal groups and generally assume a rank position similar to their mother's that is stable over time (Gachot-Neveu & Menard, 2004; Sade, 1969). In contrast, male macaques disperse at adolescence and must acquire their rank in new groups, often through physical contests or coalition building (Van Noordwijk & Van Schaik, 1985). Further, because females and males acquire rank in different ways (i.e.

inheritance vs. competition), we might expect the impact of the certainty of one's position in the hierarchy on physiology to depend on whether one is interacting with members of the same sex or the opposite sex. For example, since male rank is more labile and attained mainly through competition with other males, we predicted that male-male dominance certainty would have the greatest impact on male cortisol levels. However, research in capuchin and vervet monkeys (taxa that also exhibit female philopatry and male dispersal) suggests that females may play an important role in male rank attainment as they tend to preferentially affiliate with males prior to their rise in rank (McGuire, Raleigh, & Johnson, 1983; Perry, 1998; Raleigh & McGuire, 1989). What little research has been done on opposite-sex interactions has focused primarily on affiliative relationships and suggests that in rhesus macaques, male-female dyads maintain relationships outside the mating season (Hill, 1990). One proposed function for maintaining opposite-sex relationships is to reduce harassment of females by other males and potentially provide coalitionary support (Haunhorst, Heesen, Ostner, & Schülke, 2017). Due to the smaller relative body size of females and larger canines of males, frequent harassment and aggression from males to females may be more stressful than female-female aggression due to the increased risk of injury (Bernstein, Gordon, & Rose, 1974; Wang, Turnquist, & Kessler, 2016). Despite their potential impact on male rank acquisition and female harassment by males, the impact of opposite-sex dominance interactions as opposed to same-sex interactions in this species has not been explored.

The current study examined three primary questions relating to the impact of social status on chronic stress. First, we determined whether, similar to our previous work (Vandeleest et al., 2016), dominance certainty and/or rank are important predictors of a biomarker of chronic stress, hair cortisol concentrations (HCC). Second, we explored whether same-sex and opposite-sex dominance interactions differentially impact HCC. Finally, we determined whether any observed effects of social status on HCC could be explained simply by participation in aggressive interactions either as a result of metabolic costs of activity or the stress of being a target of aggression (Muller & Wrangham, 2004; Schrock, Leard, Lutz, Meyer, & Gazes, 2019).

METHODS

This research was conducted from March 2013 to October 2014 at the California National Primate Research Center (CNPRC) in Davis, California. Animal care and research protocols for this study were approved by the University of California, Davis Institutional Animal Care and Use Committee and were in accordance with United States federal regulations. Housing was in accordance with the National Research Council Guide for the Care and Use of Laboratory Animals, and all research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Subjects

Subjects were adult rhesus macaques (*Macaca mulatta*) living in three different social groups at the CNPRC (N = 252, Table 1). Subjects included all animals aged 3 to 29 years (mean = 7.7). Individuals under the age of 3 were excluded because they were unlikely to be well

integrated into the dominance hierarchy yet (Bernstein & Williams, 1983; de Waal & Luttrell, 1985). Social groups consisted of 125–185 animals of multiple ages and sex classes which were largely structured around multigenerational matriline (See table 1). All social were stable (i.e. no major outbreaks of aggression, changes in leadership, or animal introductions) for at least 1 year prior to the start of current study. Each social group was housed in a 0.2 hectare outdoor enclosure containing multiple benches, perches, and A-frame shelters. One social group (group C) contained specific pathogen free (SPF) animals. Subjects received Lab Diet 5038 chow twice daily and had ad libitum access to water. Scratch (a mix of seeds and grains) was provided daily and produce enrichment weekly.

Observation of aggression

Behavioral data was collected between the hours of 9a-12p and 1p-4p four days per week for 6 weeks on each social group. Event sampling was used to record aggressive interactions including initiator and recipient IDs and the specific behaviors displayed in the interaction. Aggressive behaviors included open mouth threat, vocal threat, head bobs, lunge, push, pull, grab, chase, pin, and bite. Submissive behaviors included freeze, turn away, run away, and crouch. These data were used to calculate the count of total aggression received and initiated for each subject and were further separated by the sex of the initiator and receiver.

Using all instances of dyadic aggression for each of the three social groups, dominance rank and dominance certainty were calculated for all subjects using the percolation and conductance method (*Perc* package in R) (Fujii et al., 2015; Fushing, McAssey, & McCowan, 2011; Vandeleest et al., 2016). A total of 4,526, 2,447, and 4,979 dyadic aggressive interactions were recorded for groups A, B, and C, respectively, resulting in an average of 47.4 interactions per animal (range: 2 – 201) across all three groups. Percolation and conductance is a network-based method for calculating rank that can handle missing data better than other ranking methods because it derives dominance information from *all* network paths, even for dyads that were never observed to directly interact. It incorporates information from both direct and indirect connections of each subject to calculate the probability of each individual outranking another. Information from indirect pathways in the aggression network are used to augment direct interaction data by counting the number of indirect, directed pathways that are identified between a dyad. The imputed information is data driven and weighted based on the indirect pathway length (shorter paths are given more weight) and the transitivity of the network (Vandeleest et al., 2016). For a more detailed description of the percolation and conductance method and how pathway information is tabulated please see Vandeleest et al., 2016.

This measure provides both information on the direction of a dominance relationship (dominant or subordinate) as well as the certainty of each dyadic relationship in a social group (values near 0.5 indicate an ambiguous relationship whereas values closer to 0 or 1 indicate more certainty). Using this information, we calculated 1) a linear dominance ranking and 2) a measure of overall certainty of an individual's position in the group hierarchy (i.e. dominance certainty). Rankings were obtained from the best ordering of the matrix of dominance probabilities. Due to differences in the number of animals in each group, rank is expressed as the percent of animals outranked. The certainty of one's position

is calculated by taking a dyad's dominance probability and rescaling it between 0.5–1 with values near 0.5 indicating a more ambiguous relationship and values near 1.0 indicating a very certain and settled relationship (regardless of who is dominant or subordinate). These values are then averaged over multiple dyads to create a metric we call dominance certainty (DC), which reflects whether an individual tends to have more ambiguous or certain dominance relationships with group members. Importantly, low dominance certainty is not a reflection of how often an individual participates in aggressive interactions; DC shows only a weak relationship with the frequency of dyadic aggressive interaction (Pearson correlation coefficient: $r = 0.38$). Rank and dominance certainty exhibit a U-shaped relationship with higher DC for both high and low ranked animals and lower DC for middle ranked animals although there is variation in DC across all ranks (Vandeleest et al., 2016). Finally, to allow for the investigation of sex differences, we also separate dominance certainty by sex. An individual's dominance certainty with males is the mean certainty between the subject and all males in the group, and dominance certainty with females is the mean certainty between the subject and all females in the group. This division will allow for the examination of how same-sex vs. opposite-sex dominance relationships impact cortisol levels.

Hair cortisol

Hair samples were collected during the fifth week of behavioral observations during routine, biannual physicals. Animals were anesthetized according to CNPRC standard operating procedures, given physicals by staff veterinarians, and hair samples were obtained by shaving a standard area at the nape of the neck and stored in aluminum foil. Samples were only collected once from these animals and reflected cortisol accumulation over the prior few months. Due to the stability of the observed social groups this provided a representative measure of their average cortisol levels in the existing social structure. Cortisol was extracted from the hair samples after they were washed and ground using established methods (Davenport, Tiefenbacher, Lutz, Novak, & Meyer, 2006; Vandeleest et al., 2019). Extracted samples were assayed in duplicate using an enzyme immunoassay (Salimetrics, State College, PA). The intra-assay CV was 2.29% and the inter-assay CV was 11.6%. HCC did not differ between males and females (Welch's t-test $t(107.74) = -0.84$, $p = 0.40$) or by SPF status (Vandeleest et al., 2019).

Data Analysis

A series of generalized linear models was run to determine whether social status-related variables predicted HCC. Models were run using a negative binomial distribution with a log link in SAS 9.4 software (proc glimmix). The first set of models (Question 1) examined the impact of rank, dominance certainty, sex, age, and season (fall or spring) on HCC. Season was included to control for any seasonal variation in cortisol levels (Romero, 2002; Vandeleest, Blozis, Mendoza, & Capitanio, 2013). The second set of models (Question 2) used the same set of predictors, but divided dominance certainty into DC with males and DC with females to determine if within- vs between- sex dominance interactions differentially impact HCC. Finally, a third set of models (Question 3) was run to determine if aggressive interactions (total, initiated or received) from males or females could explain the relationship between social status variables and HCC. Models were evaluated using an information theoretic approach in which AIC scores were used to select a candidate set of models for

each experimental question ($\Delta AIC = 5$), then models in the candidate set were evaluated for discussion using model likelihoods and model weights (Burnham & Anderson, 2002). Cage was tested in all models as a random effect but inclusion either did not change or increased AIC and therefore it was not included in any candidate set models. The goodness of fit of our models and the negative binomial distribution was evaluated using the Pearson chi-square statistic (SAS Institute Inc., 2009). Multicollinearity of predictors was evaluated using a combination of correlations, tolerance, stability of effect size and direction across models, and standard error size relative to β coefficients. The influence of outliers was examined using leverage and Cook's D and no cases exhibited undue influence using either metric. Candidate set models for all analyses are presented in Supplemental Table 1.

RESULTS

Question 1: Does social status predict HCC?

HCC were predicted by season and DC, although the effects of DC differed by sex ($\Delta AIC = 4.19$, model weight = 0.76). For males, having high DC was associated with lower HCC while the opposite was true for females (see Table 2). In addition, animals studied in fall had higher HCC than those studied in spring.

Question 2: Do same-sex and opposite-sex status relationships differentially impact HCC?

Sex differences in the impact of dominance certainty on HCC were evident ($\Delta AIC = 2.01$, model weight = 0.72). While high DC with males predicted higher HCC in all animals, low DC with females predicted high HCC for males only (see Table 2). Additionally, low rank predicted higher HCC for males and females. Finally, animals studied in fall had higher HCC than those studied in spring.

Question 3: Does participation in aggression explain the observed relationships?

In the best fit model, DC with males predicted HCC for both males and females while aggression received from males and DC with females predicted HCC for males only (model weight = 0.47). A second model with similar weight had similar effects with the only difference being the inclusion of a non-significant effect of rank ($\Delta AIC = 0.13$, model weight = 0.42). To facilitate discussion of effects of DC controlling for rank, we present the results from the model containing rank (see Table 2). These models also presented the lowest AIC score of all best fit models (See Table 3). As in our previous model, males that had low dominance certainty with females had higher HCC while little to no effect was seen for females (see Figure 1a). Similarly, more aggression received from males predicted higher HCC in males, but not females (see Figure 1b). Finally, high DC with males predicted higher HCC for both males and females (see Figure 2). Notably, other measures of involvement in aggression (total aggression initiated or received, or aggression received from females) did not predict HCC. Additionally, season and rank were not predictors of HCC in the best fit models.

DISCUSSION

We provide evidence that more complex representations of social status as well as accounting for sex differences may lead to new insights regarding its impacts on stress and health. We demonstrated that the certainty of an individual's position or "fit" in the dominance hierarchy, rather than their rank, plays an important role in status-related effects on physiology, but it does so in sex-specific ways. Initial models suggested that for males high HCC were associated with low DC whereas the opposite was true for females. Further analysis highlighted that the impact of DC depended on the sex of the subject *and* the interactant. For males, high HCC were primarily predicted by receiving aggression from other males, lower certainty with the females, and higher certainty with males of the group. For females, high HCC were predicted by high DC with males but not aggression received from males. Notably, female-female dominance relationships or aggressive interactions had little to no impact on female HCC.

While dominance rank is a commonly used metric to understand the impact of social status on health and fitness, our results provide additional evidence that there is more to social position than being subordinate or dominant. Previous research on the relationship between rank and cortisol levels suggests that in species where dominance is maintained largely through intimidation, we would see evidence of greater stress in subordinate animals. While rhesus macaques are a despotic species that largely follow this social organization, we find little to no effect of rank on glucocorticoid levels. In fact, the results from the literature for this species are mixed (Dominant > Subordinate: (Barrett, Shimizu, Bardi, Asaba, & Mori, 2002; Higham et al., 2013); Subordinate > Dominant: (Gust, Gordon, Hambright, & Wilson, 1993; Ostner et al., 2008), Subordinate = Dominant: (Bercovitch & Clarke, 1995; Dettmer et al., 2014; Hoffman, Ayala, Mas-Rivera, & Maestripieri, 2010)). This does not mean, however, that social status does not impact stress levels or health in this species. Our results suggest that rank provides an incomplete picture of social status, and that the certainty of one's status, even among a social group that has relatively stable social ranks, is important to include when trying to understand the health impacts of social status. Previous research into this area focused on relatively severe forms of instability (e.g., rank reversals, social collapse, new group formations (Golub, Sassenrath, & Goo, 1979; Higham et al., 2013; Sapolsky, 1992)). However, the recently developed percolation and conductance method allows us to obtain metrics of both dominance rank and the certainty of that rank, even among overall stable social groups and dominance hierarchies, by using a network approach (Fujii et al., 2015; Fushing et al., 2011).

Effects for males

Rhesus macaque males are the dispersing sex and therefore must obtain their social position after immigrating to new groups where they are unlikely to be related to any group members. Multiple factors have been shown to influence the success of male immigration, including the characteristics of resident males (age, sex, rank stability) and receptiveness and availability of resident females (Hill, 1990; Raleigh & McGuire, 1989; van Noordwijk & van Schaik, 2009). Once established in a group, dominance rank governs access to mating opportunities and food resources (Boccia, Laudenslager, & Reite, 1988; Cowlshaw &

Dunbar, 1991). Our results suggest that the biggest impacts on male HCC are derived from male-male aggressive competition and whether the males have a certain position with the females of the group. Aggression received from males has the potential to be severe and result in injury (Bernstein et al., 1974; Wang et al., 2016). Notably this impact is most strongly experienced by males, likely because male-male competition is a major determinant of male dominance rank whereas female rank is inherited rather than attained through agonistic competition (Sade, 1969; Van Noordwijk & Van Schaik, 1985). In addition to male-male aggression to establish and maintain dominance rank, immigrating males must gain acceptance from the females in order to fully integrate into the group and gain access to mating opportunities (Höner et al., 2007; van Noordwijk & van Schaik, 2009). As the philopatric sex, females can form aggressive coalitions with matrilineal kin against specific males to influence the whether males successfully immigrate and the rank they attain (Packer & Pusey, 1979; Raleigh & McGuire, 1989). Our results indicating that males with low DC with females had higher HCC supports the idea that when males are not well integrated with the females of the group, regardless of their rank, they may experience more stress. Finally, contrary to expectations, males that had high DC with other males experienced higher HCC, independent of the effects of rank or aggressive interactions. Overall, these results highlight that the certainty of one's position, even in a stable social group, is an important contributor to social status.

Effects for females

In contrast to males, female rhesus macaques generally inherit their family's rank position and aggressive encounters are therefore less influential in the maintenance of that position. Additionally, the presence of kin provides additional avenues for social support to buffer the effects of rank among philopatric females. Other recent work also suggests little to no effect of rank on inflammation in female baboons and rhesus monkeys (Lea et al., 2018; Vandeleest et al., 2016) living in wild or naturalistic social groups. Our results support the idea that aggressive interactions and female-female dominance relationships are not major contributors to female HCC levels. Instead, because females rely more on affiliative interactions to form alliances and cement their social positions we might expect that affiliative networks play a larger role in understanding the impact of female-female relationships on female health (Gust et al., 1993; Wooddell, Vandeleest, Nathman, Beisner, & McCowan, 2019). Male-female dominance relationships, however, seem to play a minor role in influencing female HCC levels. Unexpectedly, having high DC with males was associated with higher HCC in females. Notably, this effect was not explained by how much aggression females received from males suggesting it is not related to the stress of frequent harassment by males. While there is little research on opposite-sex dominance related interactions, previous research does suggest that there are enduring opposite-sex affiliative relationships that can impact agonistic encounters (Haunhorst et al., 2017). Although the implications of this finding are still unclear, the fact that DC with males was one of the predictors of HCC for females suggests that investigating dominance relationships between sexes is an important area for future research.

CONCLUSIONS

The potential impact of social status on health and fitness has been demonstrated within multiple species and contexts, yet a single common pattern has yet to be identified that applies broadly across species and different contexts. This failure to identify a common pattern highlights the complexity of social status and the need for multidimensional measures to better understand which particular features of status are more important for understanding health outcomes. Our results demonstrate that more complex conceptualizations of rank that include the stability or certainty of dominance status, even in a stable hierarchy, can help us better understand these relationships. Furthermore, we provide evidence that effects may differ by sex, and that taking the species' unique life history into account can help us to better understand how social status relationships differentially impact males and females.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

ACKNOWLEDGEMENTS

We would like to thank our dedicated team that collected the behavioral and physiological data (A. Barnard, T. Boussina, E. Cano, H. Caparella, C. Carminito, J. Greco, A. Maness, A. Nathman, S. Seil, N. Sharpe, A. Vitale). This research was funded by an NIH grant awarded to Brenda McCowan (R01-HD068335) and the California National Primate Research Center base grant (P51-OD01107-53).

REFERENCES

- Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, ... Sapolsky RM (2003). Are subordinates always stressed? a comparative analysis of rank differences in cortisol levels among primates. *Horm Behav*, 43(1), 67–82. 10.1016/s0018-506x(02)00037-5 [PubMed: 12614636]
- Anderson NB, & Armstead CA (1995). Toward Understanding the Association of Socioeconomic Status and Health. *Psychosomatic Medicine*, 57(3), 213–225. 10.1097/00006842-199505000-00003 [PubMed: 7652122]
- Archie EA, Tung J, Clark M, Altmann J, & Alberts SC (2014). Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc Biol Sci*, 281(1793). 10.1098/rspb.2014.1261
- Backholer K, Peters SAE, Bots SH, Peeters A, Huxley RR, & Woodward M (2017). Sex differences in the relationship between socioeconomic status and cardiovascular disease: a systematic review and meta-analysis. *J Epidemiol Community Health*, 71, 550–557. 10.1136/jech-2016-207890 [PubMed: 27974445]
- Barrett GM, Shimizu K, Bardi M, Asaba S, & Mori A (2002). Endocrine Correlates of Rank, Reproduction, and Female-Directed Aggression in Male Japanese Macaques (*Macaca fuscata*). *Horm Behav*, 42(1), 85–96. 10.1006/hbeh.2002.1804 [PubMed: 12191651]
- Belle D (1991). Gender differences in the social moderators of stress In Monat A & Lazarus RS (Eds.), *Stress and coping: An anthology* (pp. 258–274). New York, NY, US: Columbia University Press.
- Bercovitch FB, & Clarke AS (1995). Dominance rank, cortisol concentrations, and reproductive maturation in male rhesus macaques. *Physiology & Behavior*, 58(2), 215–221. 10.1016/0031-9384(95)00055-N [PubMed: 7568422]
- Bernstein IS, Gordon TP, & Rose RM (1974). Aggression and Social Controls in Rhesus Monkey (*Macaca mulatta*) Groups Revealed in Group Formation Studies. *Folia Primatologica*, 21(2), 81–107. 10.1159/000155607

- Bernstein IS, & Williams LE (1983). Ontogenetic changes and the stability of rhesus monkey dominance relationships. *Behavioural Processes*, 8(4), 379–392. 10.1016/0376-6357(83)90025-6 [PubMed: 24897682]
- Boccia ML, Laudenslager M, & Reite M (1988). Food distribution, dominance, and aggressive behaviors in bonnet macaques. *American Journal of Primatology*, 16(2), 123–130. 10.1002/ajp.1350160203
- Braveman PA, Cubbin C, Egerter S, Chideya S, Marchi KS, Metzler M, & Posner S (2005). Socioeconomic Status in Health Research: One Size Does Not Fit All. *JAMA*, 294(22), 2879–2888. 10.1001/jama.294.22.2879 [PubMed: 16352796]
- Capitanio JP, Mendoza SP, Lerche NW, & Mason WA (1998). Social stress results in altered glucocorticoid regulation and shorter survival in simian acquired immune deficiency syndrome. *Proceedings of the National Academy of Sciences*, 95(8), 4714–4719. 10.1073/pnas.95.8.4714
- Cavigelli SA, Dubovick T, Levash W, Jolly A, & Pitts A (2003). Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, 43(1), 166–179. 10.1016/S0018-506X(02)00031-4 [PubMed: 12614647]
- Coe CL, Mendoza SP, & Levine S (1979). Social status constrains the stress response in the squirrel monkey. *Physiology & Behavior*, 23(4), 633–638. 10.1016/0031-9384(79)90151-3 [PubMed: 116264]
- Cowlishaw G, & Dunbar RIM (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, 41(6), 1045–1056. 10.1016/S0003-3472(05)80642-6
- Creel S (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution*, 16(9), 491–497. 10.1016/S0169-5347(01)02227-3
- Davenport MD, Tiefenbacher S, Lutz CK, Novak MA, & Meyer JS (2006). Analysis of endogenous cortisol concentrations in the hair of rhesus macaques. *Gen Comp Endocrinol*, 147(3), 255–261. 10.1016/j.ygcen.2006.01.005 [PubMed: 16483573]
- de Waal FBM, & Luttrell LM (1985). The formal hierarchy of rhesus macaques: An investigation of the bared-teeth display. *American Journal of Primatology*, 9(2), 73–85. 10.1002/ajp.1350090202
- Dettmer AM, Novak MA, Meyer JS, & Suomi SJ (2014). Population density-dependent hair cortisol concentrations in rhesus monkeys (*Macaca mulatta*). *Psychoneuroendocrinology*, 42, 59–67. 10.1016/j.psyneuen.2014.01.002 [PubMed: 24636502]
- Fujii K, Jin J, Shev A, Beisner B, McCowan B, & Fushing H (2015). Perc: Using percolation and conductance to find information flow certainty in a direct network (R package version 0.1.0). R package version 0.1.0 <http://CRAN.R-project.org/package=Perc>.
- Fushing H, McAssey M, & McCowan B (2011). Computing a ranking network with confidence bounds from a graph-based Beta random field. *Proc R Soc*, 467(2136), 3590–3612. 10.1098/rspa.2011.0268.
- Gachot-Neveu H, & Menard N (2004). Gene flow, dispersal patterns, and social organization In Thierry B, Singh M, & Kaumanns W (Eds.), *Macaque societies: A model for the study of social organization*. Cambridge University Press.
- Gesquiere LR, Learn NH, Simao MCM, Onyango PO, Alberts SC, & Altmann J (2011). Life at the Top: Rank and Stress in Wild Male Baboons. *Science*, 333(6040), 357–360. 10.1126/science.1207120 [PubMed: 21764751]
- Golub MS, Sassenrath EN, & Goo GP (1979). Plasma cortisol levels and dominance in peer groups of rhesus monkey weanlings. *Hormones and Behavior*, 12(1), 50–59. 10.1016/0018-506X(79)90026-6 [PubMed: 113331]
- Goymann W, East ML, Wachter B, Höner OP, Möstl E, Van't Holf TJ, & Hofer H (2001). Social state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. *Proceedings of the Royal Society B*, 268, 2453–2459. 10.1098/rspb.2001.1828 [PubMed: 11747563]
- Gust DA, Gordon TP, Hambright MK, & Wilson ME (1993). Relationship between Social Factors and Pituitary-Adrenocortical Activity in Female Rhesus Monkeys (*Macaca mulatta*). *Hormones and Behavior*, 27(3), 318–331. 10.1006/hbeh.1993.1024 [PubMed: 8225256]

- Habig B, & Archie EA (2015). Social status, immune response and parasitism in males: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1669). 10.1098/rstb.2014.0109
- Haunhorst CB, Heesen M, Ostner J, & Schülke O (2017). Social bonds with males lower the costs of competition for wild female Assamese macaques. *Animal Behaviour*, 125, 51–60. 10.1016/j.anbehav.2017.01.008
- Higam JP, Heistermann M, & Maestripieri D (2013). The endocrinology of male rhesus macaque social and reproductive status: A test of the challenge and social stress hypotheses. *Behavioral Ecology and Sociobiology*, 67(1), 19–30. 10.1007/s00265-012-1420-6 [PubMed: 24634561]
- Hill DA (1990). Social relationships between adult male and female rhesus macaques: II. non-sexual affiliative behaviour. *Primates*, 31(1), 33–50. 10.1007/BF02381028
- Hinde RA (1976). Interactions, Relationships and Social-Structure. *Man*, 11(1), 1–17.
- Hoffman CL, Ayala JE, Mas-Rivera A, & Maestripieri D (2010). Effects of reproductive condition and dominance rank on cortisol responsiveness to stress in free-ranging female rhesus macaques. *American Journal of Primatology*, 72(7), 559–565. 10.1002/ajp.20793 [PubMed: 20039328]
- Höner OP, Wachter B, East ML, Streich WJ, Wilhelm K, Burke T, & Hofer H (2007). Female mate-choice drives the evolution of male-biased dispersal in a social mammal. *Nature*, 448(7155), 798–801. 10.1038/nature06040 [PubMed: 17700698]
- Kaplan JR, Adams MR, Clarkson TB, Manuck SB, Shively CA, & Williams JK (1996). Psychosocial Factors, Sex Differences, and Atherosclerosis. *Psychosomatic Medicine*, 58(6), 598–611. 10.1097/00006842-199611000-00008 [PubMed: 8948008]
- Lea AJ, Akinyi MY, Nyakundi R, Mareri P, Nyundo F, Kariuki T, ... Tung J (2018). Dominance rank-associated gene expression is widespread, sex-specific, and a precursor to high social status in wild male baboons. *Proceedings of the National Academy of Sciences*, 115(52), E12163–E12171. 10.1073/PNAS.1811967115
- Manogue KR, Leshner AI, & Candland DK (1975). Dominance status and adrenocortical reactivity to stress in squirrel monkeys (*Saimiri sciureus*). *Primates*, 16(4), 457–463. 10.1007/BF02382742
- Marmot M, & Sapolsky RM (2014). Of Baboons and Men: Social Circumstances, Biology, and the Social Gradient in Health In Weinstein M & Lane MA (Eds.), *Sociality, Hierarchy, Health: Comparative Biodemography: A collection of papers* (pp. 365–388). 10.17226/18822
- McGuire MT, Raleigh MJ, & Johnson C (1983). Social dominance in adult male vervet monkeys: General considerations. *Social Science Information*, 22(1), 89–123. 10.1177/053901883022001005
- Mosca L, Barrett-Connor E, & Kass Wenger N (2011). Sex/Gender Differences in Cardiovascular Disease Prevention. *Circulation*, 124(19), 2145–2154. 10.1161/CIRCULATIONAHA.110.968792 [PubMed: 22064958]
- Muller MN, & Wrangham RW (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY*, 55(4), 332–340. 10.1007/s00265-003-0713-1
- Ostner J, Heistermann M, & Schulke O (2008). Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). *Horm Behav*, 54(5), 613–619. 10.1016/j.yhbeh.2008.05.020 [PubMed: 18625235]
- Packer C, & Pusey AE (1979). Female Aggression and Male Membership in Troops of Japanese Macaques and Olive Baboons. *Folia Primatologica*, 31(3), 212–218. 10.1159/000155884
- Perry S (1998). A case report of a male rank reversal in a group of wild white-faced capuchins (*Cebus capucinus*). *Primates*, 39(1), 51–70. 10.1007/BF02557743
- Raleigh MJ, & McGuire MT (1989). Female influences on male dominance acquisition in captive vervet monkeys, *Cercopithecus aethiops sabaeus*. *Animal Behaviour*, 38(1), 59–67. 10.1016/S0003-3472(89)80065-X
- Romero L (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, 128(1), 1–24. 10.1016/S0016-6480(02)00064-3 [PubMed: 12270784]
- Sade DS (1969). An algorithm for dominance relations among rhesus monkeys: rules for adult females and sisters. *American Journal of Physical Anthropology*, 31(2), 261–. 10.1002/ajpa.1330310217

- Sapolsky RM (1992). Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology*, 17(6), 701–709. 10.1016/0306-4530(92)90029-7 [PubMed: 1287688]
- Sapolsky RM (2004). Social Status and Health in Humans and Other Animals. *Annual Review of Anthropology*, 33(1), 393–418. 10.1146/annurev.anthro.33.070203.144000
- Sapolsky RM (2005). The influence of social hierarchy on primate health. *Science*, 308(5722), 648–652. 10.1126/science.1106477 [PubMed: 15860617]
- Sapolsky RM, & Share LJ (1994). Rank-Related Differences in Cardiovascular Function among Wild Baboons - Role of Sensitivity to Glucocorticoids. *Am J Primatol*, 32(4), 261–275.
- SAS Institute Inc. (2009). *SAS/STAT® 9.2 User's Guide* (Second Edi). Cary, NC: SAS Institute Inc.
- Schrock AE, Leard C, Lutz MC, Meyer JS, & Gazes RP (2019). Aggression and social support predict long-term cortisol levels in captive tufted capuchin monkeys (*Cebus [Sapajus] apella*). *American Journal of Primatology*, e23001 10.1002/ajp.23001 [PubMed: 31180152]
- Shively CA, & Day SM (2015). Social inequalities in health in nonhuman primates. *Neurobiol Stress*, 1, 156–163. 10.1016/j.ynstr.2014.11.005 [PubMed: 27589665]
- Shively CA, Register TC, & Clarkson TB (2009). Social stress, visceral obesity, and coronary artery atherosclerosis: product of a primate adaptation. *American Journal of Primatology*, 71(9), 742–751. 10.1002/ajp.20706 [PubMed: 19452515]
- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, ... Cheney DL (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol*, 20(15), 1359–1361. 10.1016/j.cub.2010.05.067 [PubMed: 20598541]
- Snyder-Mackler N, Sanz J, Kohn JN, Brinkworth JF, Morrow S, Shaver AO, ... Tung J (2016). Social status alters immune regulation and response to infection in macaques. *Science*, 354(6315), 1041–1045. 10.1126/science.aah3580 [PubMed: 27885030]
- van Noordwijk MA, & van Schaik CP (2009). Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions In Kappeler PM & van Schaik CP (Eds.), *Sexual Selection in Primates* (pp. 208–229). 10.1017/cbo9780511542459.014
- Van Noordwijk MA, & Van Schaik CP (1985). Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). *Animal Behaviour*, 33(3), 849–861. 10.1016/S0003-3472(85)80019-1
- Vandeleest JJ, Beisner BA, Hannibal DL, Nathman AC, Capitanio JP, Hsieh F, ... McCowan B (2016). Decoupling social status and status certainty effects on health in macaques: a network approach. *PeerJ*. 10.7717/peerj.2394
- Vandeleest JJ, Blozis SAA, Mendoza SPP, & Capitanio JPP (2013). The effects of birth timing and ambient temperature on the hypothalamic-pituitary-adrenal axis in 3–4 month old rhesus monkeys. *Psychoneuroendocrinology*, 38(11), 2705–2712. 10.1016/j.psyneuen.2013.06.029 [PubMed: 23876853]
- Vandeleest JJ, Capitanio JP, Hamel A, Meyer J, Novak M, Mendoza SP, & McCowan B (2019). Social stability influences the association between adrenal responsiveness and hair cortisol concentrations in rhesus macaques. *Psychoneuroendocrinology*, 100, 164–171. 10.1016/j.psyneuen.2018.10.008 [PubMed: 30342315]
- Wang Q, Turnquist JE, & Kessler MJ (2016). Free-ranging Cayo Santiago rhesus monkeys (*Macaca mulatta*): III. Dental eruption patterns and dental pathology. *American Journal of Primatology*, 78(1), 127–142. 10.1002/ajp.22434 [PubMed: 26118545]
- Weingrill T, Gray DA, Barrett L, & Henzi SP (2004). Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior*, 45(4), 259–269. 10.1016/j.yhbeh.2003.12.004 [PubMed: 15053942]
- Wooddell L, Vandeleest J, Nathman A, Beisner B, & McCowan B (2019). Not all grooming is equal: differential effects of political vs affiliative grooming on cytokines and glucocorticoids in rhesus macaques. 10.7287/PEERJ.PREPRINTS.27961

Figure 1.
Question 3: Marginal predicted plots with 95% confidence intervals for the effects of A) dominance certainty with females and B) aggression received from males by sex.

Figure 2:

Question 3: Marginal predicted plot of the effect of dominance certainty with males (for both males and females) with 95% confidence interval.

Table 1:

Subject Demographics and Descriptive Statistics

Year (Season)	2013 (Spring)	2013 (Fall)	2014 (Fall)	
Cage	A	B	C	Total
N (male)	101 (27)	55 (16)	96 (28)	252 (71)
N of Matrilines (avg size)	13 (8.8)	6 (9.0)	13 (7.3)	
HCC at Baseline (SD) ¹	62.11 (24.84)	62.32 (18.34)	69.92 (33.91)	65.13 (27.70)
Age ² (range)	8.02 (3–29)	6.02 (3–11)	8.30 (3–21)	7.69 (3–29)

¹ pg/mg,² Age is in years

Table 2:Model Outputs: β coefficients with 95% confidence intervals

	Question 1	Question 2	Question 3
Intercept	3.04 (2.18 – 3.90)	2.8 (1.95 – 3.65)	3.58 (2.82 – 4.33)
Season (Fall)	0.12 (0.03 – 0.22)	0.1 (0.003 – 0.20)	-
Sex (Male)	2.08 (0.76 – 3.41)	1.81 (0.63 – 2.99)	0.99 (-0.16 – 2.13)
Rank	-	-0.31 (-0.50 – -0.13)	-0.14 (-0.33 – 0.06)
DC	1.26 (0.26 – 2.26)	-	-
DC * Sex	-2.46 (-4.06 – -0.86)	-	-
DCm	-	1.78 (0.84 – 2.71)	1.28 (0.33 – 2.23)
DCf	-	0.02 (-1.13 – 1.17)	-0.44 (-1.13 – 1.17)
DCf * Sex	-	-2.23 (-3.67 – -0.80)	-1.48 (-2.86 – -0.11)
AGRm	-	-	-0.0016 (-0.005 – 0.002)
AGRm*Sex	-	-	0.0077 (0.003 – 0.012)
Scale	0.1 (0.08 – 0.11)	0.09 (0.07 – 0.11)	0.084 (0.07 – 0.10)

DC = dominance certainty, DCm = dominance certainty with males, DCf = dominance certainty with females, AGRm = aggression received from males

Table 3:

Best Fit Model Weights and Likelihoods

Model	AICc	dAICc	Model likelihood	Model weight
Y = sex DCm DCf AGRm DCf*sex AGRm*sex	2232.16	0.00	1.00	0.53
Y = sex rank DCm DCf AGRm DCf*sex AGRm*sex	2232.41	0.25	0.88	0.47
Y = season sex rank DCm DCf sex*DCf	2244.83	12.67	0.00	0.00
Y = season sex DC sex*DC	2254.57	22.40	0.00	0.00

DC = dominance certainty, DCm = dominance certainty with males, DCf = dominance certainty with females, AGRm = aggression received from males