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Relationships between affiliative social behavior and hair cortisol concentrations in semi-free ranging rhesus monkeys

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Abstract

Sociality is a fundamental aspect of human behavior and health. One benefit of affiliative social relationships is reduced short-term levels of glucocorticoids (GCs), which are indicative of physiological stress. Less is known, however, about chronic GC production in relation to affiliative social behavior. To address this issue, we studied a semi-free ranging troop of rhesus macaques (*Macaca mulatta*) and collected hair samples to measure hair cortisol concentrations (HCCs), as a measure of chronic GC production, during routine biannual exams. We collected social behavior (both aggressive and affiliative) and hair samples for 32 adult female rhesus macaques over one year (Experiment 1). Our results indicated that adult females who initiated higher levels of social affiliation had significantly lower levels of HCCs. Neither the initiation nor the receipt of aggression were significantly related to HCCs in this study. In a second experiment we studied 28 mother-infant dyads for the first 90 days postpartum to examine mother-infant facial interactions (i.e. mutual gazing). We analyzed HCCs during weaning approximately one year later, which is a major transitional period. We found that infants that engaged in higher levels of mutual gazing in the first 90 days postpartum had significantly lower levels of HCCs during weaning. Finally, we studied 17 infant rhesus macaques (13 males) to examine whether social behavior (such as play) in the first five months of life correlated with infant HCCs over those months (Experiment 3). We found that infant males that engaged in more social play had significantly lower levels of HCCs. By relying on an animal model, our study shows that affiliative social traits are associated with

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lower long-term GC production. Future research should address the complex interactions between social behavior, chronic GC production, and mental and physical health.

Keywords

Macaca mulatta; HPA axis; play; grooming; face-to-face interactions

1. Introduction

Group living mammals have developed a complex system of social interactions that have evolved to create stable social bonds over time, which have reproductive and lifespan-extension benefits (Kappeler et al., 2015; Silk et al., 2010). For example, individuals with strong social bonds live longer (Silk et al., 2010; Yee et al., 2008), possibly because social support has been linked to lower disease risks (Seeman, 1996) and faster recovery (Kulik and Mahler, 1989). The health benefits of affiliative social relationships are also likely related to reduced levels of circulating glucocorticoids (GCs), hormones that participate in the physiological stress response, that result from affiliative social interactions (Heinrichs et al., 2003; Shutt et al., 2007). Indeed, chronic high levels of circulating GCs can result in cardiovascular impairments, reproductive inhibition, immunosuppression (Sapolsky, 2005), and neurobiological changes such as dendritic atrophy, which is a risk factor for depression (Qiao et al., 2016). Moreover, loneliness, or perceived social isolation, is a risk factor for mental and physical health issues (Hawkley and Cacioppo, 2013).

Studies examining sociality and endocrine measures of stress have relied on short-term samples of GCs, which are typically collected from urine, feces, saliva, and blood and are subject to a number of confounds including circadian rhythm, temporal restrictions, and environmental variability (Davenport et al., 2006; Meyer and Novak, 2012). Additionally, these samples relay little information about chronic hypothalamic-pituitary-adrenocortical (HPA) axis activity, unless numerous sequential samples are taken over time, which can pose various challenges (Davenport et al., 2006).

A recent tool to measure chronic HPA axis activity is the collection of hair to quantify hair cortisol concentrations (HCCs; Davenport et al., 2006; Meyer and Novak, 2012). Hair reflects chronic retrospective HPA axis activity over a period of weeks to months without the need for multiple samplings. HCCs have been increasingly relied upon in both animal and human biobehavioral research, and studies have revealed relationships between HCCs and mental disorders such as depression (Qin et al., 2015) and generalized anxiety disorder (Staufenbiel et al., 2013), as well as physical disorders such as cardiovascular disease (Manenschijs et al., 2013) and myocardial infarction (Pereg et al., 2011). In addition, HCCs may be a biomarker of major life stressors (Karlén et al., 2011) such as childhood abuse (Schreier et al., 2015) and chronic stress in dementia caregivers (Stalder et al., 2014). However, inconsistent results between self-reported stress and HCCs have been found in humans (associations: Gow et al., 2011; Kalra et al., 2007; Qi et al., 2014; no associations: O'Brien et al., 2013; Olstad et al., 2016; Stalder et al., 2010; 2017; Wells et al., 2014), with researchers hypothesizing that subjective measures do not capture experiences of stress in

the same way as physiological measures (Olstad et al., 2016). Indeed, studies utilizing more objective measures have established relationships with HCCs (Geng et al., 2016; Stalder et al., 2017). One objective measure may be overt social behavior, such as measured frequencies of aggression and affiliation. In this regard, several recent studies have begun examining the relationships between aggression and HCCs in mammals (Feng et al., 2016; Salas et al., 2016; Tennenhouse et al., 2016; Yamanashi et al., 2016). However, even though affiliation plays a fundamental role in social organization in humans and non-human primates, little research has examined the relationship between affiliation and chronic HPA axis activation.

One particular type of affiliative social behavior that has not been examined with respect to HCCs is the influence of maternal interactions. Previous research in animal models has suggested that mothers act as a buffering mechanism for stressors in infants, and infants who are deprived maternal care may lack the ability to regulate the HPA system (Dettmer et al., 2012; 2016a; Feng et al., 2011; Hennessy et al., 2009). However, less is known about how natural variations in maternal care, rather than the lack of maternal care *per se*, as well as other social behaviors such as play, relate to long-term HPA axis activity. Addressing this gap will elucidate the impacts that variable maternal care has on downstream infant HPA axis regulation and social development.

To address these literature gaps, we studied social behavior and HCCs in a troop of rhesus macaques (*Macaca mulatta*) living in a naturalistic, semi-free ranging environment. Rhesus macaques are an ideal animal model for these processes in humans because they have natural variations in the tendency of affiliation (Capitanio et al., 2014) and maternal behavior (McCormack et al., 2006), and they form strict dominance hierarchies characterized by frequent aggression. Aggression may be seen as a proxy for bullying in humans, which has also been related to GCs (Hansen et al., 2006.) In Experiment 1, we studied 32 adult female rhesus macaques over one year. We predicted that 1) high rates of received aggression would be associated with higher levels of HCCs, and 2) high rates of affiliation would conversely be associated with lower levels of HCCs. In Experiment 2, we studied 28 mother-infant dyads for the first 90 days postpartum to determine the relationship between early mother-infant face-to-face interactions (i.e. mutual gazing: Dettmer et al., 2016b; 2016c; Ferrari et al., 2009) and later offspring HCCs. Hair samples were obtained at routine semiannual health exams. We analyzed the hair samples taken at weaning age, which typically occurs after the birth of their next sibling, at an average of 12 months of age (Fooden, 2000). Because the transition from nursing to a weanling is a period of marked maternal-infant conflict (Trivers, 1974), we sought to explore whether variations in early maternal face-to-face interactions would relate to infant HPA axis regulation during this critical time of development. We therefore predicted that 3) higher frequencies of mutual gazing after birth would negatively correspond with HCCs during the time of weaning. In Experiment 3, we studied 17 infant rhesus macaques throughout the first five months of life to report on the relationship between infant social behavior and HCCs. We predicted that 4) infant social behavior, particularly social play (the most frequent peer-to-peer behavior at this age), would negatively relate to HCCs.

2. Methods

2.1 Subjects and housing

In Experiment 1, subjects were 32 adult female rhesus macaques (age range: 3 to 18 years; mean $\pm$ SD: 8.19 $\pm$ 3.34 years) observed from August 2014 to August 2015. The females represented all major lineages (i.e. matriline; N=3) in the troop (matriline 3: N=19; matriline 4: N=11, matriline 1: N=2). In Experiment 2, subjects were 28 mother-infant dyads (16 female infants; 12 males) studied in the first 90 days postpartum in 2013 and 2014. In Experiment 3, subjects were 17 infant rhesus macaques (13 males, 4 females) born between March and May 2015 and studied from birth through August 2015. All subjects were born and reared at the Laboratory of Comparative Ethology (LCE) field station at the NIH Animal Center in Poolesville, Maryland. The field station was a 5-acre (2.0ha) open-air enclosure with natural vegetation, a pond (0.9ha) with a centralized island (0.07ha), and climbing structures and enrichment. Three corncrib shelters (4.88 $\times$ 4.88 $\times$ 5.79 m) and three indoor climate controlled runs (2.74 $\times$ 5.79 $\times$ 4.27m) provided protection from inclement weather. Commercial lab diet (Purina Monkey Chow #5038, St. Louis, MO), natural vegetation, and water were available *ad libitum* and supplemented with fresh fruits and seeds/nuts twice a day. All procedures described below adhered to the NIH Guide for the Care and Use of Laboratory Animals and were approved by the NICHD Animal Care and Use Committee (ACUC).

2.2 Data collection

2.2.1 Experiment 1: Aggression—A total of 4,898 dominance interactions were recorded from August 2014 to August 2015 through both focal and *ad libitum* sampling (Altmann, 1974). Interactions included both aggressive (threat, chase, attack) and submissive interactions (fear grimace, displacement; see Wooddell et al., 2016). Dominance ranks were established via Elo-rating (Neumann et al., 2011; Wooddell et al., 2016).

2. 2. 2. Experiment 1 and 3: Adult and infant focal behavioral data—Adult behavioral data were collected via modified frequency sheets (Novak et al., 1998; Wooddell et al., 2016) by two primary observers (LJW and AMD; inter-rater reliability = 85%) from August 11, 2014 through August 10, 2015 using a 5-minute continuous focal animal sampling method (Altmann, 1974). Each 5-minute session was divided into 20, 15-second intervals. Any behavior that occurred within the 15-seconds was recorded in chronological order. The maximum frequency a behavior could occur therefore was 20 intervals per session. Each female (N=32) was coded for 1–2 sessions per week in both morning (900 to 1200) and afternoon sessions (1200 to 1700). A total of 1,833 adult observations (mean $\pm$ SEM: 57.28 $\pm$ 3.55 sessions per female) were collected during the study period, totaling 153 hours. Each infant born in 2015 received three weekly sessions following this coding scheme starting at approximately one month of age. A total of 446 infant focal observations (mean $\pm$ SEM: 26.23 $\pm$ 0.24 sessions per infant) were collected during the study period, totaling approximately 37 hours. Total focal data collection time (for both adults and infants) thus was approximately 190 hours.

Behaviors collected included nonsocial behaviors (locomotion, foraging, etc.) and social behaviors. For the purposes of this study, we only analyzed social behaviors including affiliative behaviors (contact, groom, grooming present, lipsmack, mount, play), aggressive behaviors (threat, chase, attack), and submissive behaviors (fear grimace, displacement).

2.2.3 Experiment 2: Maternal face-to-face interactions—Focal observations were conducted 3–5 times per week for the first 90 days postpartum for 28 mother-infant dyads in 2013 and 2014 by two primary observers (AMM and KJB: inter-rater reliability = 85%). The frequency of mutual gazing, which was defined as eye-to-eye contact between mother and infant lasting at least 3 seconds, in each 15-minute session (see Dettmer et al., 2016b, 2016c, for a more detailed description) was recorded. A total of 915 15-minute sessions were recorded (mean $\pm$ SEM: 32.68 ± 1.23 sessions per infant). Total data collection time for mother-infant interactions was thus 229 hours.

2.2.4 Hair cortisol concentrations (HCCs)—Routine biannual health exams were conducted every six months in February and August of every year. Beginning in 2012, during these health exams, hair samples were taken by shaving the back of the animals' necks for every individual in the population (infants, juveniles, and adults). Because these samples were taken every six months (always from the same location on the back of the neck following a shave-reshave procedure), the HCCs values reflected chronic retrospective activity over the past six months (since the last time it was shaved), during which cortisol was incorporated into the growing hair shaft.

In Experiment 1, hair samples were collected by shaving the back of the animals' necks during routine biannual health exams in February 2015 (reflecting activity from August 2014 to February 2015) and August 2015 (reflecting activity from February 2015 to August 2015) as part of a longitudinal study, reflecting the time period in which behavioral data were collected (August 2014 to August 2015). Samples were stored in a foil pouch at -80°C until shipment to the Hormone Assay Core Laboratory at the University of Massachusetts Amherst. Following Meyer et al. (2014), samples were weighed, washed twice with isopropanol and dried for 5–7 days under a fume hood. For all hair assays, we used the entire length of the shaved hair, as the founding study validating the hair cortisol assay in rhesus macaques found no significant difference in proximal versus distal hair segments when hair samples were divided in half (Davenport et al., 2006). After washing and drying, samples were then ground to a fine powder with a ball mill grinder (MM200; Retsch, Newtown, PA) and incubated in methanol for 24 hours to extract cortisol from the samples. Aliquots of the methanol extract were dried down and reconstituted with assay buffer, then analyzed via enzyme immunoassay (EIA) using a salivary cortisol kit (#1-3002; Salimetrics, Carlsbad, PA). Resulting values ($\mu\text{g/dL}$) were converted to pg/mg for analysis. Inter- and intra-assay coefficients of variation were $<10\%$ based on aliquots of the same extracted pooled hair sample analyzed repeatedly across assays.

In Experiment 1, two adult subjects had no hair sample taken at either time-point in February or August. Thus the total sample size for Experiment 1 was $n=30$.

In Experiment 2, hair samples were collected from infants born in 2013 and 2014 in August 2014 and August 2015 at the routine biannual health exams, depending on the cohort (infants born in 2013 had their weaning age hair sample taken in 2014, and infants born in 2014 had their weaning age hair sample taken in 2015). It is important to note that these subjects had hair samples taken every six months (every February and August) from birth onwards, so the hair samples reflected chronic retrospective activity over the past six months. However for the purposes of this study, we were interested in HCCs during weaning, as this is an important behavioral and developmental milestone, and we therefore included the samples from the weaning age. It is also important to note that the behavioral data were collected in the first few months of life, whereas the hair samples were taken during weaning approximately 1 year later. The selection of this approach was dictated by our desire to examine long-term relationships between early maternal affiliation and later HCCs in the offspring, rather than assess the possible relationship between neonatal behavior and contemporaneous cortisol levels. Four subjects were not available for hair sampling. Thus, the total sample size for Experiment 2 was $n=24$.

In Experiment 3, hair samples were taken in August 2015 at the health exams. The infants were born from March to May, thus the HCCs reflected activity over the first five months of life (during which the behavioral data were collected). Five of the infants born in 2015 in Experiment 3 were not available for hair sampling. The total sample size for Experiment 3 was $n=12$.

2.3 Statistical analyses

As instances of aggression were collected from all observed occurrences (focal + *ad libitum*) during other unrelated longitudinal projects, aggression for the present study was calculated as the proportion of aggressive interactions initiated and received by the individual divided by the total number of observed aggressive interactions. Therefore out of 108 attacks, an individual that initiated 5 attacks would have a proportion of $5/108$, meaning that this individual initiated a proportion of 0.046 (4.6%) of the attacks. This was done for each aggressive behavior (threat, chase, attack) and a composite aggression score.

All initiated and received affiliative social behaviors (contact, groom, grooming present, lipsmack, mount, play) per session were combined to create a total initiated and received sociality score. Average initiated and received sociality scores were then calculated to represent the average frequency an individual engaged in initiated or received social behaviors per 5-minute session. The maximum frequency was 20 intervals. Therefore an average frequency of 5 indicated that the individual initiated or received a social behavior in 25% of the intervals ($5/20$).

Average rates of mutual gazing per session between mother and infant were calculated for the first 90 days postpartum. The data did not follow a normal distribution, so the average frequency of mutual gazing was log transformed.

HCCs were log transformed prior to analysis to ensure normality. In Experiment 1, the two hair samples were averaged to represent the entire accumulation of HCCs that occurred over the course of a year for adult females.

In Experiment 1, linear regression tested whether social behaviors (affiliative and agonistic) predicted a significant proportion of the total variance in average HCCs over one year in adult female rhesus macaques. In Experiment 2, linear regression tested whether mutual gazing during the first 90 days postpartum (as well as age and sex) predicted a significant proportion of the total variance in HCCs at approximately the age of weaning (circa 1 year). In Experiment 3, Spearman correlations (due to the small sample size) were used to test the associations between infant social behavior and HCCs over the first five months of life. All alpha values were set at $P < 0.05$. SPSS 22 was used for all analyses.

3. Results

3.1 Experiment 1: General results for adult female rhesus macaque HCCs

Average adult female HCCs ranged from 28.99 to 68.92 pg/mg (mean $\pm$ SEM: 44.01 $\pm$ 1.58). There were no significant effects of age ($F(1,28)=0.04$, $P=0.84$, $R^2=0.002$, $\beta=-0.04$) or dominance rank ($F(1,28)=0.64$, $P=0.43$, $R^2=0.02$, $\beta=0.15$) on HCCs.

3.1.1 Experiment 1: Aggression and HCCs in adult female rhesus macaques—

Submissive interactions were the most common dominance interaction (43% of all interactions), followed by chases (27.56%) and threats (27.07%). Interactions that involved physical contact (attacks) were relatively infrequent, occurring in only 2.6% of all observed interactions.

Contrary to *prediction 1*, neither the amount of initiated nor received aggression was significantly related to adult female HCCs (initiated: $F(1,28)=0.25$, $P=0.62$, $R^2=0.09$, $\beta=0.09$; received: $F(1,28)=0.002$, $P=0.97$, $R^2=0.008$, $\beta=0.008$), even when segregated based on the intensity of aggression (threats, chases, attacks, in that order of intensity; all $P > 0.05$).

3.1.1 Experiment 1: Sociality and HCCs in adult female rhesus macaques—

Social contact was the most commonly initiated social behavior (65.48%), followed by grooming (32.18%). Adult females initiated grooming presents, (1.08%), play (0.57%), lipsmacks (0.38%), and mounts (0.3%) relatively infrequently. The average frequency of initiated social affiliation ranged from 4.28 intervals per 5-minute session (maximum intervals=20) to 11.96 intervals (mean $\pm$ SEM: 7.99 $\pm$ 0.34).

In support of *prediction 2*, linear regression revealed that the average frequency of initiated social affiliation (contact, groom, grooming present, lipsmack, mount, play) was negatively associated with adult female average HCCs over the course of a year ($F(1,28)=15.26$, $P < 0.001$, $R^2=0.35$, $\beta=-0.59$, see Figure 1a). In addition, when examining the two primary initiated social behaviors (contact and grooming) independently, both behaviors yielded significant results with average HCCs (contact: $F(1,28)=6.08$, $P=0.02$, $R^2=0.18$, $\beta=-0.42$; grooming: $F(1,28)=4.86$, $P=0.036$, $R^2=0.15$, $\beta=-0.39$). Surprisingly, received social affiliation did not significantly relate to average HCCs ($F(1,28)=1.83$, $P=0.16$, $R^2=0.06$, $\beta=-0.25$, Figure 1b), even when independently examining contact and grooming (received contact: $F(1,28)=1.94$, $P=0.17$, $R^2=0.07$, $\beta=-0.26$; received grooming: $F(1,28)=0.14$, $P=0.71$, $R^2=0.07$, $\beta=-0.07$).

The average frequency (maximum frequency of 20 intervals) of initiated affiliative social behavior per 5-minute session negatively corresponded to HCCs (pg/mg) in adult female rhesus macaques over a one year time period. No significant relationship was found for received social affiliation.

3.2 Experiment 2: Early maternal face-to-face interactions and HCCs

Average frequencies of mutual gazing ranged from 0 to 4 bouts per 15-minute session (mean $\pm$ SEM: 0.41 ± 0.15). Linear regression revealed sex as a main predictor of mutual gazing, with male infants engaging in higher rates of mutual gazing than females ($F(1,23)=5.69$, $P=0.03$, $R^2=0.19$, $\beta=-0.45$). We therefore examined sex effects in subsequent analyses. Because an age related decline has also been observed in HCCs in young primates (Fourie and Bernstein, 2011), we also examined age effects.

Weaning HCCs ranged from 27.47 pg/mg to 66.40 (mean $\pm$ SEM: 42.77 ± 1.79). Supporting *prediction 3*, linear regression revealed that the average frequency of mutual gazing 90 days postpartum negatively predicted HCCs during the weaning transition (mean $\pm$ SEM age at hair sampling: 476.57 ± 6.85 days; $F(1,19)=8.15$, $P=0.01$, $R^2=0.30$, $\beta=-0.55$, see Fig. 2). No age ($F(1,22)=2.39$, $P=0.14$, $R^2=0.10$, $\beta=-0.31$) or sex effects ($F(1,22)=0.005$, $P=0.94$, $R^2=0.00$, $\beta=-0.02$) on HCCs were revealed. Mother's dominance rank also did not predict any significant variation in HCCs during weaning ($F(1,22)=0.34$, $P=0.57$, $R^2=0.02$, $\beta=0.12$). Infants who engaged in higher frequencies of mutual gazing with their mothers per 15-minute session in the first 90 days postpartum also displayed lower levels of hair cortisol (pg/mg) during their transition to weaning approximately one year later.

3.3 Experiment 3: Infant social behavior and HCCs

Social contact was the most common social behavior (84.76% of social interactions) initiated by infants, followed by play (14.63%). Grooming (0.43%) and mounting (0.18%) were initiated relatively infrequently. Lipsmacking and grooming presents occurred negligibly. It is important to note that these interactions included all social partners (other infants, juveniles, and adults). Infant HCCs ranged from 40.45 pg/mg to 169.42 (mean $\pm$ SEM: 103.14 ± 11.34).

The average frequency of initiated and received social affiliation was not significantly related to infant HCCs (initiated: $r_s=-0.30$, $P=0.34$, $N=12$; received: $r_s=-0.37$, $P=0.24$, $N=12$), partially failing to support *prediction 4* for infants. However, *prediction 4* was partially supported by a significant negative relationship between initiated play and infant HCCs ($r_s=-0.58$, $P=0.048$, $N=12$). In contrast, no significant relationship was observed between infant HCCs and received social play ($r_s=-0.33$, $P=0.30$, $N=12$). However, there was a significant difference in the frequency of initiated play between males and females (Mann Whitney U test, $U=44$, $P=0.037$), with males exhibiting significantly more play (mean $\pm$ SEM: males: 1.55 ± 0.24 ; females: 0.55 ± 0.12). When examining sex differences, the correlation between initiated play and HCCs was only significant for males ($r_s=-0.70$, $P=0.036$, $N=9$, see Fig. 3), as there was not a large enough sample size of females for analyses ($N=3$). Mother's dominance rank ($r_s=-0.11$, $P=0.73$, $N=12$) and age ($r_s=-0.43$, $P=0.16$, $N=12$) did not significantly correlate with infant HCCs.

Male infants who initiated higher frequencies of social play per 5-minute session (maximum frequency of 20 intervals) displayed significantly lower hair cortisol (pg/mg) during the first five months of life. No significant relationship was found for received social play or other types of social affiliation.

4. Discussion

We sought to determine whether social behavior was associated with chronic HPA axis activity, reflected in HCCs, in semi-free ranging adult and infant rhesus macaques. For adults, we predicted that more agonistic social behavior (e.g. aggression) would be associated with higher levels of HCCs, and high rates of social affiliation (e.g. grooming) would be associated with lower levels of HCCs. In addition, we predicted that maternal face-to-face interactions would promote HPA axis regulation during a transitional period in life (e.g. weaning) and that affiliative social behavior would contribute to lower levels of HCCs in infants. Our results demonstrate that affiliative social interactions were associated with lower long-term HPA axis activity across development, although causation cannot yet be determined with the existing data.

Surprisingly, we found no significant association between levels of aggression and chronic HPA axis activity. At first this seems counterintuitive, as a number of studies have reported that frequent exposure to agonistic social behavior is associated with higher HCCs (Feng et al., 2016; Salas et al., 2016; Tennenhouse et al., 2016; Yamanashi et al., 2016). One possible explanation is that individuals who receive high rates of aggression, which is common in the despotic society of rhesus macaques, may often be able to predict aggression before it begins, and predictability has been associated with lower cortisol responses (Galhardo et al., 2011). This predictability may help offset the immediate stressors of agonistic behavior. This may also partially be supported by the finding that the most common type of dominance interaction was submission (moving away from or displaying a grimace to a dominant animal) rather than aggression, signaling that there may be some degree of predictability in dominance interactions (avoiding a dominant animal before aggression begins). In addition, individuals may reconcile following aggressive interactions (de Waal a Yoshihara, 1983), which may help mitigate the HPA axis response. Our results suggest that aggression alone may not be sufficient enough to explain significant proportions of the variance in chronic HPA axis activity, as individuals may be able to cope via other mechanisms. Thus further research is warranted, especially across a number of species, including humans, with various dominance styles ranging from tolerant to highly despotic (Thierry, 2007).

As predicted, we found that adult females who initiated more social affiliation also had significantly lower levels of HCCs over the course of a year, similar to studies using short-term measures of HPA axis activity (Shutt et al., 2007). These findings suggest either that females who were more social had subsequently lower levels of HCCs, or that females who had lower levels of HCCs (due to some trait-like aspect) were more likely to seek out social interactions, although our study cannot determine causation. Future experimental studies will be able to establish causal links between sociality and HPA axis activity. Perhaps the more interesting question is why there is no relationship between received social affiliation and HCCs. Similar to our results, Shutt et al. (2007) also found a significant relationship

with only initiated social grooming and fecal GCs, suggesting that the initiation of affiliative social behaviors may yield physiologically different results than receiving such behaviors. The social and biological benefits (coalitionary support, HPA axis activity, general health) and consequences (vigilance, foraging) of initiated and received social behaviors warrant further study. Future research should address the complex interactions between sociality, the HPA axis, and beneficial physiological outcomes. Moreover, Novak and Meyer (2017, unpublished data) found that in a large sample of 117 rhesus macaques, HCCs remained highly stable over time. Similarly, our results suggest that HCCs may reflect some trait-like aspect of the animal's behavior (such as social affiliation). However, this is not to say that social affiliation alone may relate to HCCs, as hair samples reflect a long period of time spanning cumulative months and events. Indeed, age (Fourie and Bernstein, 2011; Dettmer et al., 2014) genetics (Fourie and Bernstein, 2011), population density (Dettmer et al., 2014), early life adversity (Dettmer et al., 2012; 2016a; Feng et al., 2011) and dominance rank (Dettmer et al., 2016a; Feng et al., 2016) have all been shown to influence HCCs in monkeys (primarily rhesus macaques). Future research should address the significant predictors of monkey HCCs, much like a recent meta-analysis done in humans (Stalder et al., 2017). This will then allow us to investigate the role social affiliation has in HCCs, whether it be a main or a modulating effect.

We also provide evidence that early mother-infant face-to-face interactions (i.e. mutual gazing) in infancy negatively corresponded to HCCs during a highly transitional and stressful period in primate life: weaning. We previously found that early mother-infant face-to-face interactions were associated with more infant sociality later in development (Dettmer et al., 2016c). The present results indicate that early mother-infant affiliative bonds may also have downstream effects on offspring HPA axis activity, thus suggesting a potential mechanism for the Dettmer et al. (2016c) results. This promotion of social behavior may help regulate the HPA axis, especially during a major transitional period. It is therefore possible that the mediation of stress by maternal affiliation has long lasting influences, extending past the early months of life. Our results suggest that infant primates that engage in maternal-infant interactions more frequently may be better able to cope with the physiological and psychological stressor of weaning, possibly via enhanced social interactions. We do however acknowledge that the frequencies of mutual gazing were rare (ranging from 0 to 4 bouts per 15 minute session; mean $\pm$ SEM: 0.40 ± 0.15) and thus urge other researchers to replicate these findings. In addition, future studies should examine social behavior of the infants (both maternal and peer interactions) during the weaning period, as it is possible that the effects on chronic HPA axis activity of these early mother-infant interactions may extend to other social behaviors (i.e. grooming, play, etc.) during the transition to weaning. Moreover, future studies are necessary before we can be confident that more frequent face-to-face interactions between mothers and infants benefit the offspring in other socially and physiologically stressful times (e.g., emigration, transition to puberty, etc.).

Finally, we demonstrate that social play also negatively correlated with infant HCCs, but only for males. While we did not find any significant relationships with social affiliation overall, these results support the idea that social play may be an especially important social behavior for male infant macaques (Kulik et al., 2015), which is fundamentally different

than other forms of social affiliation (contact, grooming, etc.). This was additionally found in a recent study in nursery-reared rhesus macaques in which lip-smacking imitative ability in the first week of life predicted higher levels of social play (but not social grooming) in males at one year of age (Kaburu et al., 2016). As play occurs most frequently in young mammals, these results suggest there may be some inherent benefit of play during development, especially for males. Indeed, research with animal models has suggested that play is modulated by the brain's reward system (Manduca et al., 2016) and promotes brain and sensorimotor development (Pellis & Pellis, 2007). Furthermore, animals that are deprived of social play have impaired social interactions as adults (Hol et al., 1999) and altered dendritic morphology, which increases vulnerability to social stress (Burleson et al., 2016). Our results suggest that social play may additionally be related to the development of long-term HPA axis activity. However, as the results were correlational, it is difficult to interpret whether play behavior may have been an important coping mechanism thereby regulating HPA axis activity, or that males who were better able to cope with physiological stress were more able to allocate more time to social play. In addition, why some individuals engage in more social play than others may not only be a product of sex, but also previous maternal experience. In line with this, previous research has suggested that infant macaques that engage in higher frequencies of maternal mutual gazing during infancy have enhanced social interactions later (Dettmer et al., 2016c). We hypothesize that early maternal interactions may promote social behavior in infancy, and this enhanced sociality may help regulate the HPA axis. Further experimental studies will be able to identify the causal links between maternal behavior and play, which may provide valuable information on the downstream effects maternal behaviors have on the offspring, even into adulthood.

Several limitations of the present study warrant mention. One limitation is that adult behavioral data were only analyzed for females, and thus it is unclear whether these findings extend to males. Given that rhesus macaque society is female philopatric and males emigrate around the time of puberty, females develop strong social bonds and engage in more frequent social affiliation than males (Drickamer, 1976). While we did collect extensive behavioral observations on our adult males, the small sample size ($N=4$) made any analyses difficult to interpret. Therefore, an interesting opportunity exists for populations that have a larger number of males to study variations in social affiliation and chronic HPA axis activity. Another important limitation is that our findings do not address social behavior and HCCs during the juvenile period, which contains important behavioral, physiological, and developmental milestones for primates (Pereira & Fairbanks, 2002). Unfortunately during the time of this study, focal data on juveniles were not recorded due to limited researcher availability. Therefore, future studies should focus on the relationships between social behavior and chronic HPA axis activity in juveniles, which may have important implications for adult outcomes. For example, in mother-peer-reared but not nursery-reared rhesus macaques, the change in HPA axis activity during the juvenile period negatively predicted adult rank, suggesting that an ability to regulate the HPA system may promote later social competence and rank (Dettmer et al., 2016a). However the Dettmer et al. (2016a) study did not record affiliative social interactions, which may have also contributed to HPA axis regulation and subsequent adult social rank. Indeed, nursery-reared rhesus macaque infants have impaired social interactions (Andrews and Rosenblum 1994) and thus HPA axis

activity might not only be a product of rearing environment but also of impaired social interactions. Future work should address social behavior and HPA axis activity in juvenility in relation to adult outcomes.

Finally, although our longitudinal shave-reshave procedure was designed to assess adrenocortical activity over the six month period between shavings, it appeared that some monkeys had complete hair regrowth within the sampling area at the time of sample collection. For those subjects, therefore, the period of cortisol deposition may have been somewhat less than the full six months. Our methodology therefore does not allow us to determine the exact time course of hair cortisol accumulation in each individual monkey, and therefore parts of the behavioral measurements may not have been precisely contemporaneous with HCC accumulation. In the future, precise hair growth measurements are needed to account for individual variability in growth rates and to determine the specific time period of hormone incorporation for each subject. Examining the factors that promote varying degrees of hair growth in monkeys would also be invaluable in determining the biological and behavioral significance of hair cortisol. Finally, a longitudinal assessment of serially collected salivary cortisol in conjunction with HCCs would provide a robust validation into the temporal summation of cortisol into hair in monkeys, much like what has been observed in humans (Short et al., 2016).

5. Conclusion

Given that sociality relates to long-term HPA axis activity, and that long-term HPA axis activity can negatively affect health (Sapolsky, 2005), our results suggest that a potential mechanism for the link between sociality and health may be via mediation by the HPA axis. Because sociality is a fundamental aspect of both human behavior and human health, our study, conducted with a rhesus macaque animal model, warrants further investigations into complex interactions of sociality, HPA axis activity, and health outcomes. Further research should investigate immune function, reproduction, neurobiology, cardiovascular functions, and mental health in regards to social behavior and HCCs. This will help elucidate the downstream effects sociality has on health outcomes, possibly via the HPA axis.

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Highlights

- We studied sociality and hair cortisol (HCCs) in rhesus monkeys.
- Social affiliation was negatively associated with adult female HCCs.
- Mother-infant mutual gazing negatively related to offspring HCCs at weaning.
- Social play during infancy was negatively associated with infant male HCCs.
- Social affiliation is associated with lower long-term HPA axis activity.

Figure 1.
Relationship between affiliative social behaviors initiated (a) and received (b) and HCCs in adult female rhesus macaques

Figure 2.
Mutual gazing during the first 90 days of life and HCCs at weaning age