RESEARCH ARTICLE

Rank-Dependent Grooming Patterns and Cortisol Alleviation in Barbary Macaques

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Flexibly adapting social behavior to social and environmental challenges helps to alleviate glucocorticoid (GC) levels, which may have positive fitness implications for an individual. For primates, the predominant social behavior is grooming. Giving grooming to others is particularly efficient in terms of GC mitigation. However, grooming is confined by certain limitations such as time constraints or restricted access to other group members. For instance, dominance hierarchies may impact grooming partner availability in primate societies. Consequently specific grooming patterns emerge. In despotic species focusing grooming activity on preferred social partners significantly ameliorates GC levels in females of all ranks. In this study we investigated grooming patterns and GC management in Barbary macaques, a comparably relaxed species. We monitored changes in grooming behavior and cortisol (C) for females of different ranks. Our results show that the C-amelioration associated with different grooming patterns had a gradual connection with dominance hierarchy: while higher-ranking individuals showed lowest urinary C measures when they focused their grooming on selected partners within their social network, lower-ranking individuals expressed lowest C levels when dispersing their grooming activity evenly across their social partners. We argue that the relatively relaxed social style of Barbary macaque societies allows individuals to flexibly adapt grooming patterns, which is associated with rank-specific GC management. *Am. J. Primatol.* 77:688–700, 2015. © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

A wide body of research has demonstrated that—especially for females—social behaviors can function as tools for physiological stress mitigation as reflected by glucocorticoid (GC) measures (for a review see [Cheney and Seyfarth, 2009]). However, as Cheney and Seyfarth [2009] point out: not sociality alone, but relationship quality (e.g. stability or strength of social bonds) between social partners is essential for coping with and managing GCs. For most social primate species, grooming represents one of the most important social behaviors [Hinde and Stevenson-Hinde, 1976; Kummer, 1978; Silk et al., 2010]. Grooming increases fitness [Kummer, 1978; Berghänel et al., 2011] in that it has positive effects on reproductive success [Silk et al., 2003] and is associated with longevity [Silk et al., 2010]. The variety of different grooming patterns, that is how individuals distribute grooming between group members, depends on various parameters such as

group size [Dunbar, 1991; Henzi et al., 1997], grade of cohesion, fission–fusion dynamics, sex ratio [Henzi et al., 1997; Lehmann et al., 2007], and social organization (egalitarian–despotic, for a review see [Thierry et al., 2004]), as well as on individual factors such as number of kin and rank [Schino, 2007]. As early as the 1970s Robert Seyfarth [1977] proposed a

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model for predicting grooming patterns among non-human primate females. Determining factors for grooming distributions were predicted to be (1) attraction to kin and (2) high-ranking individuals, as well as (3) competition over access to preferred grooming partners. A meta-analysis on different primate species (not including Barbary macaques, but other macaque species) verified the predictions of the model to a great extent and found an effect of rank on grooming distribution [Schino, 2001]. Female primates across species tend to groom up the dominance hierarchy (see [Small, 1990] for an example in Barbary macaques). Thus, high-ranking individuals can be viewed as preferred grooming partners and consequently competition over access to such partners should be expected [Seyfarth, 1977]. Furthermore, Seyfarth [1980] reasoned that high-ranking females should direct their grooming in relation to the grooming partner's rank position if competition is affecting grooming distributions, as dominant females would be least constrained in choosing whom to groom. Middle-ranking females on the other hand should have less flexibility in adapting their grooming behavior. For low-ranking females, no connection between rank and grooming direction was expected. Again, this pattern was confirmed with actual data on *cercopithecoidea* and *ceboidea* species [Schino, 2001]. Thus, certain social pressures seem to act on the expression of grooming patterns that can be observed in a given society of primates.

The more relaxed a species is in its social style (*in sensu* [Thierry et al., 2004]), the less impact hierarchies should have on access to grooming partners, and fewer constraints in grooming up the hierarchy would be expected [Butovskaya, 2004]. In hierarchical societies, there is evidence for low-ranking individuals attempting to groom higher-ranking individuals [Schino, 2001] and trading grooming for rank-related commodities such as agonistic support [Hemelrijk, 1994; Seyfarth and Cheney, 1984; Schino, 2007], tolerance at feeding sites [Richter et al., 2009; Ventura et al., 2006], and reduced aggression [Gumert and Ho, 2008]. In more tolerant societies, such as in Barbary macaques, Carne et al. [2011] found for females that the rank of the recipient was not a significant predictor for grooming given. Other studies showed that individuals gave more grooming to higher-ranking females than lower ranking ones and preferentially groomed their female kin, who are usually of similar rank [Paul and Kuester, 1987; Prud'Homme and Chapais, 1993a; Prud'Homme and Chapais, 1993b]. Grooming for rank-related benefits (agonistic support and tolerance around food) was limited.

When looking at the relation of rank hierarchies and GC measures (an endocrine hallmark for stress) studies on non-human primates have found no consistent relationship between the two parameters

[Sapolsky, 2005; Creel et al., 2013]. In general, subordinate females seem to be more likely to have higher GC measures than dominant females [Cavigelli and Chaudhry, 2012]. This is particularly true for females in socially despotic organizations [Cheney and Seyfarth, 2009]. Styles of dominance seem to modify patterns in GC physiology [Ray and Sapolsky, 1992]. Correlates to rank impact the interaction between dominance and GC largely: whether or not GC levels and rank are connected for a given species depends on various factors, such as the extent of social support available to low-ranking individuals [Abbott et al., 2003; Cheney and Seyfarth, 2009], differential access to resources, the stability of social hierarchy structures, and low-ranking individuals' coping strategies [Sapolsky, 2005]. In Barbary macaques, findings concerning rank and GC are inconsistent: middle rank is connected to highest and most variable GC measures according to Edwards et al. [2013], the most dominant individuals express highest GC levels in a study by Gustison and colleagues [2012], while no connection between the two parameters was found in a study by Shutt et al. [2007]. Behavioral proxies (scratching rates) for stress suggest that subordinate rank is associated with highest stress loads [Kaburu et al., 2012].

Although group life comes with many social stressors and potential for conflict social interactions have been found to constitute an effective tool for mitigating GC levels in various species (prairie voles: [DeVries et al., 2003]; baboons: [Crockford et al., 2008; Wittig et al., 2008]; chimpanzees: [Fraser et al., 2008b]; rhesus macaques: [Brent et al., 2011]). Although both giving and receiving grooming served as a tool for promoting GC-resistance, previous studies on primates demonstrated that grooming actively was more effective in terms of GC alleviation [Dunbar, 2010]. Studies on despotic species found that these primates seem to adapt their grooming patterns to social and environmental conditions. According to Crockford et al. [2008] female baboons, who concentrated their grooming activity on a small number of partners, had lower GC levels than those females who distributed those interactions more evenly among grooming partners. As the same group went through a period of social instability, GC levels initially increased for all females, but then decreased for individuals, who reduced their grooming network the most or already had had few predictable bonding-partners to begin with [Wittig et al., 2008]. Brent et al. [2011] found similar results for high-ranking female rhesus macaques, who had lower GC levels during periods with more focused proximity networks.

So far such detailed investigations on short-term changes in GC physiology and social behavior are not available for more relaxed species. A first indication for comparable mechanisms in rather tolerant species comes from a study in Barbary macaques,

which found that active—but not received—grooming as well as a high number of grooming partners were connected to reduced GC concentrations in females [Shutt et al., 2007]. This study pooled data over a whole observation period. Thus, potential changes in behavior and physiology within short time windows were not reflected in the data. Also, rates of given and received grooming as well as clique size were analyzed without a more detailed description of grooming patterns. Two main aspects discussed earlier make Barbary macaques a particularly interesting species to look at in more detail: (i) the very inconsistent findings regarding the influence of social rank on GC levels [Edwards et al., 2013; Gustison et al., 2012; Shutt et al., 2007], and (ii) the seemingly high behavioral flexibility associated to their social style [Carne et al., 2011; Gumert and Ho, 2008; Paul and Kuester, 1987; Prud'Homme and Chapais, 1993a; Prud'Homme and Chapais, 1993b]. We hypothesized that the rather relaxed social style (when compared to despotic species like baboons, Japanese macaques, or rhesus macaques) allows females of all rank groups to flexibly change their grooming behavior and that specific grooming styles associate to reduced GC measures. As time available for grooming and access to grooming partners differs for females of different dominance [Butovskaya, 2004; Paul and Kuester, 1987] we hypothesized that rank would impact which grooming patterns were connected to C-mitigation. Thus, the main aim of this study was to determine short-term grooming patterns expressed by female Barbary macaques and connect them to urinary cortisol (C) measures, while considering rank as a potential influencing parameter. We expected specific grooming patterns (that might be different for females of different rank) to be connected to C levels: females with a focused grooming network, high ratios of active grooming, and females, who modified their grooming focus according to changing conditions, were predicted to show lowest levels of urinary C. We analyzed grooming patterns with regard to grooming partner diversity, relative grooming activity, and grooming distribution among partners (grooming skew). Instead of pooling behavioral and physiological data from entire observational periods (e.g. [Shutt et al., 2007]), we followed the recent trend to focus on processes within smaller time windows to get a detailed picture of how grooming behavior and C management are interrelated.

METHODS

Ethical Standards

As the study consisted of behavioral observations and non-invasive hormonal sample collection there were no animal welfare implications. The Gibraltar Ornithological and Natural History Society

(GOHNS) of Gibraltar authorized non-invasive collection of behavioral and hormonal data in accordance with Gibraltar's legislative requirements for both observation periods. All research was conducted in accordance with Austrian legislation. The research adhered to the American Society of Primatologists principles for ethical treatment of primates.

Subjects and Study Site

The study was conducted on Gibraltar Barbary macaques (*Macaca sylvanus*) over two consecutive mating seasons (from November through February) in 2004, 2005, and 2006, respectively. Barbary macaque females are philopatric and female bonded [Wrangham, 1980], with females forming the core of the social group. Daughters inherit their ranks from their mother, resulting in adjacent rank positions for members of a matriline. Dominance hierarchies between matriline remain stable over generations. Previous research suggests that the most valuable social partners for adult females Barbary macaques are other adult females [McFarland and Majolo, 2011]. The groups "Apes Den (AD)" and "Prince Phillips Arch (PPA)" were chosen due to their good accessibility, the good view over the respective territories, and because group composition was similar. The population in AD consisted of 13 adult females, between three and nine adult males (immigration from neighboring groups took place during the study period), three subadult females, three subadult males, eight juveniles and five infants in the first season. In the second season, the group was composed of 14 adult females, nine adult males, four subadult females, five subadult males, five juveniles and seven infants. The PPA group consisted of 12 adult females, nine adult males, six subadult females, six subadult males, eight juveniles and seven infants. Age was classified after Burton [1972]. AD was observed over two consecutive reproductive seasons; PPA was included in the second observation period only. Tourist pressure, a potential cause for elevated stress levels [Maréchal et al., 2011], was similar at both sites as both territories are part of the standard sightseeing itinerary. Consequently, animals were well habituated to humans without being overrun, as the winter months are a lot quieter than the summertime. There are indications that the mating season in itself is more stressful than the non-mating season, at least for males (male squirrel monkeys: [Coe and Levine, 1995]; male Assamese macaques: [Ostner et al., 2008]). Although this may well have been the case for the females in our study groups as well, this general period of possibly higher anxiety was not unstable, as to our knowledge no catastrophic occurrences (e.g. storms, deaths, predator interactions) occurred during the observation periods. As background

information on the individuals was sparse and no rank order was available for either group at the onset of data collection, focal females (first season $n = 7$ for AD, second season $n = 6$ for AD as one female died between observational periods, and $n = 6$ for PPA) were selected to represent all age classes within the group of mature females (after analyzing agonistic interactions we found that females of all rank classes were represented in our list of focal females, ranging from high ranking females to the lowest ranking individual). While we acknowledge that the sample size of seven (1st season), respectively 12 (2nd season) individuals is relatively small, we focused on these females to grant sufficient hormonal and behavioral sample density. Information on kinship among the focal animals was not available. Only females without hormonal treatment were chosen as focal individuals. Hormonal samples and focal behavioral protocols were collected for these females only. All females (excluding the two females on contraceptives) were recorded in focal behavioral protocols as interaction partners only. *Ad lib* behavioral data were collected for all individuals of the groups. All females were cycling during the study periods. Some were lactating, as they were nursing offspring from the previous mating season. The Gibraltar Ornithological and Natural History Society (GONHS) provisioned both groups daily with fruit and vegetables, as the vegetation at the observation sites was nutritionally not sufficient for the number of animals present.

Hormonal and Behavioral Data Sampling

The collection of behavioral and physiological data took place during two seasons of roughly equal length (109 and 115 days, respectively). In the first season, data collection at AD took place on a daily basis from 08:00 to 17:00. Daily observations (also from 08:00 to 17:00) in the second season alternated between the two study groups (an observation day at AD was followed by data collection at PPA the following day).

In most mammals and all primates the main GC that is released in response to stressors is cortisol (C) [Bercovitch and Ziegler, 2002; Heistermann, 2010]. The analysis of free urinary C has proven to be a reliable method for stress monitoring (e.g. [Bahr et al., 2000; Crockett et al., 1993; Dittami et al., 2008]. Although potential confounding factors (circadian rhythms, female cycle, lactation or pregnancy) have to be considered in the analyses of urinary C excretion rates, urine samples offer one big advantage compared to fecal samples: while GC levels in feces represent an aggregate of several days (although see [Edwards et al., 2013]), urinary concentrations indicate physiological measures of shorter time periods.

Urinary C is subject to diurnal variation. Heistermann [2010] suggests collecting the first morning urine for optimal results. However, this was not feasible in our free-ranging study species, as roosting places were either unknown or inaccessible. Instead, we controlled for time of collection in our statistical models. An impact of the female ovarian cycle on C concentrations has been demonstrated. GC-increase is connected with an elevation of sex steroids [Bercovitch and Ziegler, 2002]. Also, pregnancy is associated with heightened C levels [Keller-Wood and Wood, 2001]. This may be due to the increased levels of estrogens, as they enhance sensitivity to adrenocorticotrophic hormones (ACTH) and thus affect the release of GC [Brunton et al., 2008]. Many studies [Brauch et al., 2007; Brauch et al., 2008; Grant et al., 2011] use the average gestation length of their study species to count back from the date of birth of the offspring to consider pregnancy stages in their data. Since we were looking at one-week time windows in our data, we considered individual variation in gestation length to be too high to apply this method. Instead, we analyzed urinary estrogen (E) levels that undergo fluctuations during pregnancy and ovarian cycles in order to control for effects of reproductive physiology on C measurements. We did not consider progesterone concentrations in our data, since progesterone is a precursor to C and discriminating between ovarian and adrenal progesterone would not have been possible [Wirth et al., 2007]. Lactation also affects GC levels, as has been demonstrated in various primate species (e.g. long-tailed macaques: [van Schaik et al., 1991]; rhesus macaques: [Hoffman et al., 2010]) and decreases the responsiveness to stressors, which may be due to low estrogen levels during lactation [Brunton et al., 2008]. Therefore we differentiated between nursing and non-nursing females and accounted for this information in our statistical models.

Urine Sample Collection

Urine samples were collected whenever possible on a daily basis between 08:00 and 17:00. Samples were only collected when a cross-contamination with urine of other individuals or fecal matter could be excluded, and the urinating female was reliably identified. Urine was soaked up on the excretion site using a cotton roll and stored at -20°C in salivettes (Sarstedt, Germany) until analysis. As the Gibraltar Barbary macaques were very habituated to humans, urine collection could take place immediately after excretion in proximity to the female (especially on slopes) or urine was soaked up as soon as the female moved. Samples were collected from rocks, soaked up from leaves, or from concrete around the feeding sites. The total number of samples in the first season was 165, giving an average of 2.06 samples a day. An

average of 24.1 samples per focal female were collected. In the second season, 226 samples were collected in total, averaging 1.96 samples per day. That is an average of 18.8 samples per focal female.

Cortisol and Estrogen Analysis

Before analysis, steroids were deconjugated with a glucuronidase/sulphatase after Palme and Möstl [1993]. All hormone concentrations were adjusted to urine dilution by analyzing creatinine concentration according to the standard Jaffe method [Slot, 1965]. Native C was measured (after [Dittami et al., 2008]) with an enzyme immunoassay (EIA) applying DADOO-biotinylated cortisol-3-CMO labels (1:250) and bovine serum albumin-coupled antibodies (1:20; raised in rabbits) against cortisol-3-CMO. Relevant cross-reactions with other steroids are described in [Palme and Möstl, 1997]. Main cross reactions were found with 4-pregnene-11 β ,17 α ,21-triol-3, 20-dione; 100%; 5 α -pregnane-11 β ,17 α ,21-triol-3,20dione 4.6%; 5 α -pregnane-3 α ,11 β ,17 α ,21-tetrol-20-one 0.8%; 5 β -pregnane-3 α ,11 β ,17 α ,21-tetrol-20-one 0.1%; all other steroids cross-reacted < 0.01%. The assay was previously used in several primate species, including macaques [Bahr et al., 2000]. Urinary concentrations were shown to correlate significantly with plasma levels of cortisol in baboons [French et al., 2004] and macaques [Crockett et al., 1993]. Intra-assay coefficient of variation (CV) was 9.86%, inter-assay CV was 14.65%.

Previous studies reported estrone, estriol, and estradiol to be dominantly excreted in the urine of macaques [Monfort et al., 1984; Shideler et al., 1993,2001] and baboons [Wasser et al., 1994]. Hence hydrolyzed urine samples were analyzed for estrogen concentrations with an antibody against total estrogens [Palme and Möstl, 1993]. Total estrogens were demonstrated an accurate measure for female macaque reproductive functions [Heistermann et al., 2001; Ostner and Heistermann, 2003]. Cross-reactions with relevant steroids were estrone 100%, estriol 129%, 1,3,5(10), 7-estratene-3-ol-17-one 87%, estradiol-17 β 70%, 1,3,5(10), 7-estratetraene-3,17 β -diol 20%, estradiol-17 α 19%, 1,3,5(10), 7-estrapentane-3-ol-17-one 1%. All other tested steroids had reactions below 1%. Intra-assay CV was 7.96% and inter-assay CV was 14.84%.

Behavioral Data Collection

In line with other studies [Brent et al., 2011; Crockford et al., 2008; Shutt et al., 2007; Wittig et al., 2008] we excluded males, juveniles, and subadult individuals from analyses and concentrated on female-female grooming interactions only.

Behavioral data were collected using continuous focal animal sampling according to Altmann [1974]. In addition dyadic agonistic interactions were noted

ad libitum, to gain a sufficiently large data set for establishing an unambiguous rank order. Individual protocols lasted 20 min in the first season and 15 min in the second. Both, affiliative and agonistic behavior was noted. Specifically, all grooming interactions (given and received), the identity of the grooming partners as well as the duration of the grooming bout was recorded. Agonistic interactions included threats, displacements, chases, attacks, and submissive behaviors. Females were observed in pseudo-random order, and no female was ever observed more than once on the same day. Morning, midday, and afternoon observations were balanced across focal females. Bad weather conditions or inaccessibility of specific areas on certain days limited behavioral observations. Individuals' behavioral data were corrected for total observation time.

A rank order was established by analyzing intra-sexual dyadic agonistic interactions [Deag, 1974] between all adult females of the group. Dominance rank was calculated using Mat Man 1.0 (Noldus, Wageningen, The Netherlands). The rank order was calculated separately for the two seasons. In order to be able to include rank information in our analyses, relative rank positions, controlled for the absolute amount of total rank places available, were established.

Data Analysis

Silk et al., [2013] published a summary on methods to study and describe social relationships. Hinde indices measure the symmetry or directionality of dyadic grooming interactions, while the Shannon Wiener Diversity index (SWDI) informs about the distribution of grooming across partners [Silk et al., 2013]. As these methods were previously used in studies comparable to ours [Brent et al., 2011; Crockford et al., 2008; Engh et al., 2006; Wittig et al., 2008], we applied these indices to describe grooming behavior of our subjects.

We calculated grooming indices to account for diversity and directionality in grooming behavior (see [Crockford and Boesch, 2005; Crockford et al., 2008; Hinde and Atkinson, 1970; Silk et al., 2013; Wilson and Bossert, 1971]). In all cases, only grooming interactions between adult females were included. The SWDI accounts for the spread and heterogeneity in grooming partners. This measure was then normalized (see [Silk et al., 1999]) by the number of total grooming partners, and standardized. Thus, this index does not reflect network size, but describes how an individual allocates grooming within its network. We termed this index "grooming distribution" (GD). The smaller the index, the more focused was the grooming behavior of an individual, and the higher the index the more dispersed an individual distributed grooming across all its interaction partners. Hinde indices account for activity in

relation to passivity in grooming behavior when looking at number of partners, grooming time, or grooming initiations (see supplementary material, Annex 1). The Hinde indices were found to have a high mutual correlation. Principle Component Analysis (PCA) can be used to reduce a set of correlated parameters and/or achieve non-collinear data [Fraser et al., 2008a; Osborne and Costello, 2004; Silk et al., 2013]. Therefore we extracted three orthogonal variables from the Hinde indices (through PCA, see supplementary material, Annex 1). These were (our interpretation in brackets):

(i) GGA (General Grooming Activity, Comp1, 93% of the variance explained): As this component increases as the Hinde indices increase, and these indices rise as the balance active versus received grooming (time, frequency, or number of partners) increases, GGA can be a good proxy for the amount of general active grooming the subject performs. As this component explained 93% of the variance in our data, we included GGA in further analyses.

(ii) GTA (Grooming Time Allocation, Comp2, 5%): This component increases as the active grooming time increases but drops whenever the number of active partners or active grooming frequency rises. Therefore, keeping in mind a naïve tradeoff between quantity and quality, this component can be interpreted as measuring how persistent subjects are in grooming. At one extreme, we have individuals with high GTA who groom rarely and have few active partners, but groom these partners for long periods. At the other extreme, we find subjects with low GTA, frequently grooming their many partners but only over short periods of time, while also having long periods of received grooming. However, as only a small percentage of variance was explained by this component, we did not include GTA measures in further analyses.

(iii) GBS (Grooming Bond Strength, Comp3, 2%): The last component is solely influenced by frequency and number of partners, with similar strength but opposite direction. A high GBS is achieved with many partners who are groomed infrequently. A low GBS characterizes a subject with few, frequent active grooming partners. Therefore this component can be seen as a proxy for network size and strength of social bonds. As only 3.2% of variance in the data is due to this component, we excluded it from further analyses.

Pooling all behavioral and hormonal data together and applying a test over an entire season may result in relevant information being overlooked [Brent et al., 2011]. In order to investigate the connection between variations in behavioral patterns and the corresponding fluctuations in C levels over time an analysis of changes in both parameters over short time windows is required. A day-by-day analysis would have required daily focal and hormonal sampling of each individual. As a compro-

mise, we calculated grooming measures (GD, GGA, grooming duration) and averaged our samples over a weekly moving time window. The dataset can thus be regarded as a multidimensional, cross-sectional time series. Ultimately our sample data consisted of the calculation of grooming indices (as described above) based on the behavioral records (frequency and duration of grooming interactions described above) of one week, and the averaged hormonal samples of the same time period. The dataset used for statistical analyses therefore featured one entry for each week and individual. As contraceptives were found to be connected to anxiety and aggressive behavior [Pazol et al., 2004] we performed our analyses with subsets of our data: excluding and including grooming partners on contraceptives (results did not differ; statistics for the data set including females on contraceptives are presented in the supplementary material only).

Finding relationships between physiological measures and either rank or grooming in primate societies is not straightforward [Brent et al., 2011]. Since both inter-individual differences and time-dependent intra-individual variation may play an important role in social dynamics, our statistical analysis consisted in mixed effects models on panel data (both longitudinal and cross-sectional). The latter can statistically explain variance due to individual heterogeneity, while the former deals with intra-individual variance over time (e.g. an individual's different C levels). Therefore, our method utilizes and combines in one model both, the explanatory power of individual differences and of time variation in behavior relative to C changes.

In order to take account for multicollinearity we either dropped or transformed some of the variables so regressors would not be correlated. Due to non-normality and non-linearity of the data, transformations (like those operated on C) were undertaken to achieve normally distributed data (standard scores). Independence and homoskedasticity were taken into account by the random effects approach and by modeling the residuals as an autoregressive process of order 2.

Our dependent variable was the natural logarithm of averaged (by week) cortisol (C). After log-transforming C, skewness and kurtosis tests for normality showed that our new variable did not significantly differ from a normal distribution (skewness: 0.51; kurtosis: 0.06; adjusted $\chi^2 = 4$, $P = 0.135$).

Additional parameters were considered as independent variables in our models. Fixed effect variables were (i) grooming distribution (GD), (ii) general grooming activity (GGA, as this first principal component explained 93% of the variance in the data, we excluded the other two principal components from our models), (iii) standardized rank, (iv) time of collection of hormonal samples, and (v) log-

transformed estrogen (E) values. As we hypothesized that rank might modulate the connection between grooming behavior and C, we also included the interactions of standardized rank and grooming measures in our models. Furthermore we included random effects: individual (with random slopes for E and lactation), group, season, and the number of samples collected.

The analysis included fitting several regressions using mixed (fixed, random and between) effects models. Fixed effects were included in the models as: (i) E and time of sample collection (null model), (ii) the null model and standardized rank, (iii) the null model and measures of grooming behavior, (iv) the null model and interactions between standardized rank and grooming measures, and (v) the null model and measures of grooming measures and their interaction with standardized rank. Independent variables were hierarchically nested in the models in that individuals were nested in group, nested in seasons. We estimated the fit of our model using Maximum Likelihood (ML) analysis. Model selection was based on Akaike Information Criterion (AIC), and weighted AIC (wAIC), respectively Bayesian Information Criterion (BIC) and weighted BIC (wBIC) scores [Burnham and Anderson, 2002]. Weighted scores indicate probabilities of how likely a given model is the best model of the set of available models.

RESULTS

First we fitted several regressions and compared these models against each other to find the model that explained C best (Table I). All models included the time of sample collection and standardized E, as well as individual (with random slopes for lactation and E) nested in group nested in season, and the number of C samples as random effects. In addition we included rank, measures of grooming behavior (grooming distribution (GD), the first principal component GGA, and grooming duration) as well as their interactions with rank into the diverse models.

The models (Table I) with the lowest AIC scores (grey background in the AIC column in Table I: models 1, 5, 6, 8, 9, and 12; scores between 165.27 and 173.09) all included the GD index. Models (model 2, 7, 10, 13, and 15) including the principal component 1 (GGA), but not the GD index clustered together with higher AIC scores (205.53 to 211.33). The highest scores (AIC from 429.25 to 436.07) were found for models (0, 3, 4, 11, and 14) containing rank only or grooming duration, but no grooming indices (the duration of grooming given ($z = -2.53$, $P = 0.011$, $n = 19$) and the interaction of grooming time given with rank ($z = 2.98$, $P = 0.003$, $n = 19$) were significant predictors of C(model 11)).

When models differ only marginally in their AIC and BIC scores (<10) they are to be treated as equivalent [Burnham and Anderson, 2002]. Consequently, models with fewer variables have to be preferred over models with many variables. Model 1 and 9 both contained the same (lowest) number of variables (that were E, time of sample collection, GD, and random effects in model 1; and E, time of sample collection, r*GD, and random effects in model 9) and did not differ substantially in their AIC or BIC scores. When looking at wAIC scores the model with the rank-GD interaction (wAIC=0.14) is much more probable than the model containing solely GD (wAIC=0.01). Calculating wAIC for these two models only showed that the rank-GD interaction model was more likely (wAIC=0.94) to predict C levels accurately. The r*GD model (model 9) also had lower BIC (188.32) and better wBIC (0.39) scores. This and the above make the model including the rank-GD interaction (model 9) our final model as it fits the data best.

In our final model (Table II) the interaction between rank and GD ($z = 2.70$, $P = 0.007$, $n = 17$) as well as E ($z = 6.65$, $P < 0.001$, $n = 17$) were significant predictors of C levels. Lowest levels of C were detected when higher-ranking individuals focused their grooming and when lower ranking females dispersed their grooming evenly among partners. High levels of C were associated with higher-ranking individuals grooming indiscriminately or lower ranking ones focusing grooming on few grooming partners (for the same results including female grooming partners, who were on contraceptives see supplementary material, Annex 2). In other words, once we controlled for rank in our model, GD had an effect on C. Analogously, after grooming behavior was accounted for, rank could statistically explain urinary C levels. Thus our results show that in female Barbary macaques GD and dominance as well as their reciprocal influence are associated with differences in C levels. (See Fig. 1 for a time series visualization and discussion of the relationship between C and grooming behavior over time in a high and a low ranking individual.)

DISCUSSION

In line with other studies, our results demonstrate that grooming behavior is associated with C alleviation. Looking at social patterns, we observed a gradual rank-dependence in the connection with specific grooming distributions and C measures. That is not to say that individual females did show specific grooming patterns that were stable over time. Individuals varied grooming behavior, but depending on their rank, certain grooming patterns were associated with alleviated C measures. Higher-ranking females, who focused grooming on a preferred partners within their grooming network

TABLE I. Model Comparison and Selection

model	measure	interactions	likelihood	AIC	BIC	wAIC	wBIC
0			-207.19	432.38	462.33	0.00	0.00
1	GD		-76.54	173.09	196.26	0.01	0.01
2	GGA		-92.94	205.87	231.2	0.00	0.00
3	rank		-207.03	436.07	472.67	0.00	0.00
4	duration active		-206.31	432.62	465.9	0.00	0.00
5	GD, GGA		-72.63	165.27	188.17	0.43	0.43
6	GD, rank		-75.77	171.54	194.71	0.02	0.02
7	GGA, rank		-92.36	206.72	234.58	0.00	0.00
8	GD, GGA, rank		-71.84	165.68	190.87	0.35	0.11
9		rank $\times$ GD	-74.73	167.46	188.32	0.14	0.39
10		rank $\times$ GGA	-96.67	211.33	234.13	0.00	0.00
11		rank $\times$ duration	-205.43	432.86	469.47	0.00	0.00
12	GD	rank $\times$ GD	-74.73	169.46	192.63	0.05	0.05
13	GGA	rank $\times$ GGA	-92.77	205.53	230.86	0.00	0.00
14	duration	rank $\times$ duration	-202.63	429.25	469.19	0.00	0.00
15	GGA, rank	rank $\times$ GGA	-92.16	208.33	238.72	0.00	0.00

All models included E and time of sample collection as fixed effects, and individual (with random slopes for E and lactation) nested in group, nested in season, and the number of samples collected as random effects. In addition, rank, grooming measures as well as interactions between grooming measures and rank were included in the various models. Grooming measures were grooming distribution (GD), general grooming activity (GGA, the first principal component), and grooming duration. Model selection was based on AIC and BIC scores, as well as on wAIC and wBIC values. The models with the lowest AIC and BIC scores that differed less than 10 units from each other are highlighted with gray background. Two models (model 1 and 9) in the set of models with lowest AIC scores contained fewest variables. wAIC and wBIC scores indicate that model 9 including the rank-GD interaction is the more probable of the two models. This model also has lower BIC scores.

(independent of network size) showed lower C levels. This association was less pronounced for females with intermediate dominance status. For lower-ranking females, C measures were predicted to be lower when they distributed their grooming evenly among their female grooming partners. Hence, whether focusing or dispersing grooming across social partners within a social network was associated with C mitigation depended on female dominance rank. This stands in partial contrast to other research demonstrating a general connection of focused social activity and low concentrations of GC hormones (baboons: [Crockford et al., 2008]), or showing GC-alleviating effects of focused social activity for high-ranking individuals only (rhesus macaques: [Brent et al., 2011]). These studies on despotic primate species [Brent et al., 2011; Crockford et al., 2008; Wittig et al., 2008] indicate that

focused social networks are beneficial in terms of GC mitigation, which begs the question, why do not all individuals in a rather tolerant society (such as Barbary macaques) have focused networks?

Barbary macaques are socially more relaxed than rhesus macaques and baboons (see [Thierry et al., 2004]). Therefore, we argue that low-ranking female Barbary macaques may have more behavioral flexibility and more social options to adapt their grooming to certain circumstances. In contrast to despotic species, low-ranking females of our study species are eventually able to gain access to more valuable higher-ranking females [McFarland and Majolo, 2011; Seyfarth, 1980] and gain advantages from grooming them. At the same time it is important to strengthen social bonds with more stable social partners [Henzi et al., 1997]. Thus subordinates profit from dispersing their grooming among all their

TABLE II. The Final Model

log-likelihood = -74.73			Wald χ^2 (3) = 51.96 $P < 0.001$			
	coefficient	St.Error	z	P	95% confidence interval	
rank $\times$ grooming distribution (GD)	0.205	0.758	2.7	0.007	0.056	0.353
log E	0.686	0.103	6.65	<0.001	0.483	0.888
time of sample collection	-1.261	0.849	-1.49	0.137	-2.924	0.402
constant	4.01	0.399	10.05	<0.001	3.228	4.792

The model that explained C best contained E, time of sample collection, rank, and the rank-grooming distribution (r $\times$ GD) interaction as fixed effects. Individual (with random slopes for E and lactation) nested in group, nested in season and number of samples were included as random effects. The r $\times$ GD interaction ($z = 2.7$, $P = 0.007$) and E ($z = 6.65$, $P < 0.001$) were significant predictors of C.

Fig. 1. (a) Time series of C and the rank - grooming distribution interaction ($r \times \text{GD}$) for a high-ranking individual over the first season. (b) Time series of C and grooming distribution (GD, dotted line) respectively $r \times \text{GD}$ (dashed line) for a low-ranking individual. For the dominant female, as her relative rank equals 1, GD and $r \times \text{GD}$ (equal in this case to $\text{GD} \times 1$) coincide, and both show an association with C. For the low-ranking female on the other hand there is no connection between C and GD. Only when the interaction between GD and rank is considered, does the association with C become apparent. (1a) shows the C and the rank-grooming distribution ($\text{rank} \times \text{GD}$) interaction for a high-ranking female over the first season. One might suspect that the GD, coinciding in this case with the time series of the interaction, would be a good candidate for mutual prediction with the C time series. However, the time series of a low-ranking female (1b) makes this hypothesis less likely. While the distribution of grooming activity (GD, dotted line) cannot predict C levels, its interaction with rank (dashed line) predicts C (unbroken line) more reliably. This is confirmed by the cross-correlation function (calculated up to a lag of 2), reaching maxima of +0.28 (high-ranking individual, Figure 1a) and +0.62 (low-ranking individual including the interaction, Figure 1b).

available partners evenly. In contrast, high-ranking females can benefit from focusing their grooming efforts on a selected partners. This reduces social bonding time and leaves more time for foraging and other important activities. McFarland and Majolo, [2011] predicted relationship asymmetry for Barbary macaques due to the importance of *resource holding potential*, which in turn implies that lower ranking females would need to groom more as a trade-off for social commodities. Another key aspect may be consistency [Silk et al., 2010] and security [McFarland and Majolo, 2011] of social partners. Even in a relatively tolerant society, dominant females represent long-term attractive partners, as they remain dominant for life. They most likely have the luxury of not only choosing but also keeping their friends a lot easier than subordinate animals.

Even in a tolerant society, a different time allocation may represent a good balance for animals of different ranks. Subordinate animals may need

more time to forage, as they do not have unrestricted access to prime food. They may also be considered less “valuable” as social partners and therefore need to compensate by offering more social investment time. In addition, they may need to use grooming as a social currency to barter for rank-related benefits (such as tolerance around food and agonistic support). Although these are surely key aspects in social patterns of macaque societies, factors such as frequency and duration of grooming, or the social network size did not show significant association with C levels in our study. This finding agrees with results by Edwards et al. [2013], whose data did not find a connection between daily rates of social behavior and associated fecal GC levels in Barbary macaques (grooming patterns were not analyzed in more detail). In contrast, Shutt et al. [2007] demonstrated that measures of ‘grooming per female’ and clique size was associated with GC levels in Barbary macaques: the more a female groomed, and the bigger her clique

size was, the lower her GC levels were. This difference to our study might be due to differences in study design: Shutt et al. [2007] pooled behavioral and hormonal data over a whole study period, while Edwards et al. [2013] and our data were analyzed for smaller time windows. Thus, our data allowed a more fine-grained analysis of short-term changes in behavioral and stress measures.

Tourism can impact behavior (scratching rates) and GC-physiology [Maréchal et al., 2011] in that it increases anxiety levels. As both our study groups were visited by tourists this might have had an influence on our results. However, exposure to tourists was comparable for all individuals and both groups. Consequently macaque-human interactions might be random noise in our data, but its impact should be similar for all our study subjects. Furthermore, tourist pressure was comparably low during the study periods (autumn and winter) as compared to summer months when tourists mainly visit the macaques. Aggressive interactions between macaques and humans were found to affect GC levels (in male macaques), but no other form of interaction was reflected in hormonal measurements Maréchal et al. [2011]. We did not observe such aggressive interactions within our observation periods, thus it is unlikely that we measured human disturbance in our hormonal samples. In the future data on tourist pressure and macaque-human interactions should be collected and accounted for in statistical analyses.

In a matrilineal society, it is challenging to distinguish between the influence of kinship and rank. Seyfarth [1977] proposed an effect of kin and high rank on grooming patterns and thus hypothesized that dominant matrilineal would be more cohesive than lower-ranking ones. As we had no information on kinship for our study population, we were not able to include kinship in our analyses. However, Schino [2001] did not confirm the prediction of Seyfarth's model and argued that high-ranking females did not show a kin preference since they could demand grooming from kin and non-kin. Also for baboons, no relationship between the number of close kin and GC levels was found [Crockford et al., 2008]. Although female baboons focus their grooming on kin [Silk, 2009; Silk et al., 1999, 2006, 2009] they compensate with non-kin social partners if related individuals are not available [Cheney and Seyfarth, 2009]. Furthermore, the identities and attributes of the grooming recipients were not a focus of this study, as we were mainly interested in finding a general overlaying grooming pattern expressed by our focal individuals. So far, key aspects of complex social behavior such as "reconciliation" in Barbary macaques showed high rates of affiliative behavior with non-kin [Thierry et al., 2008]. By definition, kin bias is less pronounced in relaxed species [Thierry et al., 2004]. This cannot exclude the possibility that matriline size influenced social network size and thus

played into our results. Nevertheless, it is unlikely that kinship was a decisive factor. Grooming focus within a network was independent of network size and number of relatives. Further studies on social networks in relaxed macaque societies with known kinship would be needed to resolve this issue.

Also, and not very surprisingly, our model revealed significant effects of E levels on C concentrations. Various other studies already demonstrated that the reproductive state of females has an impact on GC levels (e.g. [Brent et al., 2011; Cheney and Seyfarth, 2009; Pepe et al., 1982; Smith and Norman, 1987; Stavisky et al., 2003; Weingrill et al., 2004]). Our prediction of finding an effect of E concentrations on physiological stress measures in our study population was confirmed.

Past research demonstrated conclusively that close social bonds with other females are beneficial for female primates in matrilineal societies. Cheney and Seyfarth [2009] argue that focusing grooming on selected individuals has GC mitigating effects because these social bonds tend to be stable and predictable. Females with strong and consistent ties have lower GC levels [Seyfarth et al., 2012] and their longevity is enhanced [Silk et al., 2010], offspring survival and thus fitness is improved [Silk, 2009]. There appears to be an ideal size and strength for a social network, which varies with the circumstances and social standing of an individual. For instance, baboons extend their grooming network to as many individuals as time constraints allow [Henzi et al., 1997]. Within this network however they form particularly strong social bonds with a subset of these individuals (as reflected by their grooming distribution). When group size exceeds a level that allows individuals to have some social interaction with the majority of the group members, groups will split [Dunbar, 1992; Henzi et al., 1997]. In Barbary macaques dominant females express similar patterns: they concentrate their grooming activity on selected individuals within their network. Lower ranking females on the other hand might profit from dispersing their grooming activity across all their social partners.

According to Cheney and Seyfarth [2009], the degree to which rank plays a role in GC measures depends on the availability of support and the possibility of avoiding aggression. Our data suggest that female Barbary macaques, who live in relatively relaxed societies, are able to adapt their grooming patterns flexibly and have the behavioral options to potentially express rank-dependent grooming patterns that may be associated with efficient GC mitigation across all dominance ranks.

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REFERENCES

- Abbott DH, Keverne EB, Bercovitch FB, et al. 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior* 43: 67–82.
- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.
- Bahr NI, Palme R, Mohle U, Hodges JK, Heistermann M. 2000. Comparative aspects of the metabolism and excretion of cortisol in three individual nonhuman primates. *General and Comparative Endocrinology* 117: 427–438.
- Bercovitch FB, Ziegler TE. 2002. Current topics in primate socioendocrinology. p 45–67.
- Berghänel A, Ostner J, Schröder U, Schülke O. 2011. Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour* 81: 1109–1116.
- Brauch K, Hodges K, Engelhardt A, et al. 2008. Sex-specific reproductive behaviours and paternity in free-ranging Barbary macaques (*Macaca sylvanus*). *Behavioral Ecology and Sociobiology* 62:1453–1466.
- Brauch K, Pfefferle D, Hodges K, et al. 2007. Female sexual behavior and sexual swelling size as potential cues for males to discern the female fertile phase in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *Hormones and Behavior* 52: 375–383.
- Brent LJ, Semple S, Dubuc C, Heistermann M, MacLarnon A. 2011. Social capital and physiological stress levels in free-ranging adult female rhesus macaques. *Physiology & Behavior* 102: 76–83.
- Brunton PJ, Russell JA, Douglas AJ. 2008. Adaptive responses of the maternal hypothalamic-pituitary-adrenal axis during pregnancy and lactation. *Journal of Neuroendocrinology* 20:764–776.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York, Berlin, Heidelberg: Springer.
- Burton FD. 1972. The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar. In: Poirier FE, editor. Random House, NY. p 29–62.
- Butovskaya M. 2004. Social space and degrees of freedom. In: Thierry B, Singh M, Kaumanns W, editors. *Macaque societies A model for the study of social organization*. Cambridge: Cambridge University Press. p 182–185.
- Carne C, Wiper S, Semple S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology* 73:1127–1133.
- Cavigelli SA, Chaudhry HS. 2012. Social status, glucocorticoids, immune function, and health: can animal studies help us understand human socioeconomic-status-related health disparities? *Hormones and Behavior* 62:295–313.
- Cheney DL, Seyfarth RM. 2009. Stress and Coping Mechanisms in Female Primates. *Advances in the Study of Behavior* 39:1–44.
- Coe CL, Levine S. 1995. Diurnal and annual variation of adrenocortical activity in the squirrel monkey. *American Journal of Primatology* 35:283–292.
- Creel S, Dantzer B, Goymann W, Rubenstein DR, Boonstra R. 2013. The ecology of stress: effects of the social environment. *Functional Ecology* 27:66–80.
- Crockett CM, Bowers CL, Sackett GP, Bowden DM. 1993. Urinary cortisol responses of longtailed macaques to five cage sizes, tethering, sedation, and room change. *American Journal of Primatology* 30:55–74.
- Crockford C, Boesch C. 2005. Call combinations in wild chimpanzees. *Behaviour* 142: 397–421.
- Crockford C, Wittig RM, Whitten PL, Seyfarth RM, Cheney DL. 2008. Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior* 53: 254–265.
- Deag JM. 1974. A study of the social behavior and ecology of the wild Barbary macaque (*Macaca sylvanus*). In: The Barbary Macaque, JE Fa, ed. New York, Springer, pp. 3–15.
- DeVries AC, Glasper ER, Detillion CE. 2003. Social modulation of stress responses. Elsevier. p 399–407.
- Dittami J, Katina S, Mostl E, et al. 2008. Urinary androgens and cortisol metabolites in field-sampled bonobos (*Pan paniscus*). *General and Comparative Endocrinology* 155:552–557.
- Dunbar RI. 2010. The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews* 34:260–268.
- Dunbar RIM. 1991. Functional Significance of Social Grooming in Primates. *Folia Primatologica* 57:121–131.
- Dunbar RIM. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology* 31:35–49.
- Edwards KL, Walker SL, Bodenham RF, Ritchie H, Shultz S. 2013. Associations between social behaviour and adrenal activity in female Barbary macaques: consequences of study design. *General and Comparative Endocrinology* 186: 72–79.
- Engh AL, Beehner JC, Bergman TJ, et al. 2006. Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society B-Biological Sciences* 273:707–712.
- Fraser ON, Schino G, Aureli F. 2008a. Components of relationship quality in chimpanzees. *Ethology* 114:834–843.
- Fraser ON, Stahl D, Aureli F. 2008b. Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences* 105:8557–8562.
- French JA, Koban T, Rukstalis M, et al. 2004. Excretion of urinary steroids in pre- and postpartum female baboons. *General and Comparative Endocrinology* 137:69–77.
- Grant VJ, Konečná M, Sonnweber R-S, Irwin RJ, Wallner B. 2011. Macaque mothers' preconception testosterone levels relate to dominance and to sex of offspring. *Animal Behaviour* 82:893–899.
- Gumert MD, Ho MH. 2008. The trade balance of grooming and its coordination of reciprocation and tolerance in Indonesian long-tailed macaques (*Macaca fascicularis*). *Primates* 49:176–185.
- Gustison ML, MacLarnon A, Wiper S, Semple S. 2012. An experimental study of behavioural coping strategies in free-ranging female Barbary macaques (*Macaca sylvanus*). *Stress* 15:608–617.
- Heistermann M. 2010. Non-invasive monitoring of endocrine status in laboratory primates: methods, guidelines and applications. *Advances in Science and Research* 5: 1–9.
- Heistermann M, Ziegler T, van Schaik CP, et al. 2001. Loss of oestrus, concealed ovulation and paternity confusion in free-

- ranging Hanuman langurs. *Proceedings of the Royal Society B-Biological Sciences* 268:2445–2451.
- Hemelrijk CK. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour* 48:479–481.
- Henzi SP, Lycett JE, Weingrill T. 1997. Cohort size and the allocation of social effort by female mountain baboons. *Animal Behaviour* 54:1235–1243.
- Hinde R, Atkinson S. 1970. Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Animal Behaviour* 18: 169–176.
- Hinde RA, Stevenson-Hinde J. 1976. Towards Understanding Relationships: Dynamic Stability. p 451–480.
- 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* 72:559–565.
- Kaburu SSK, MacLarnon A, Majolo B, Qarro M, Semple S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology* 47: 74–79.
- Keller-Wood M, Wood CE. 2001. Pituitary-adrenal physiology during pregnancy. *The Endocrinologist* 11:159–170.
- Kummer H. 1978. On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information* 17:687–705.
- Lehmann J, Korstjens AH, Dunbar RIM. 2007. Group size, grooming and social cohesion in primates. Elsevier. p 1617–1629.
- Maréchal L, Semple S, Majolo B, et al. 2011. Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. *Biological Conservation* 144:2188–2193.
- McFarland R, Majolo B. 2011. Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). *PLoS ONE* 6: e28826.
- Monfort SL, Thompson MA, Czekala NM, et al. 1984. Identification of a non-steroidal estrogen, equol, in the urine of pregnant macaques: correlation with steroidal estrogen excretion. *The Journal of Steroid Biochemistry and Molecular Biology* 20:869–876.
- Osborne JW, Costello AB. 2004. Sample size and subject to item ratio in principal components analysis. *Practical Assessment* 9:8.
- Ostner J, Heistermann M. 2003. Endocrine characterization of female reproductive status in wild redfronted lemurs (*Eulemur fulvus rufus*). *General and Comparative Endocrinology* 131:274–283.
- Ostner J, Heistermann M, Schulke O. 2008. Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). *Horm Behav* 54:613–619.
- Palme R, Möstl E. 1993. Biotin-streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. *Advances of Steroid Analysis* 93: 111–117.
- Palme R, Möstl E. 1997. Measurement of cortisol metabolites in faeces of sheep as a parameter of cortisol concentration in blood. *International Journal of Mammalian Biology* 62: 192–197.
- Paul A, Kuester J. 1987. Dominance, kinship and reproductive value in female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Behavioral Ecology and Sociobiology* 21:323–331.
- Pazol K, Wilson ME, Wallen K. 2004. Medroxyprogesterone acetate antagonizes the effects of estrogen treatment on social and sexual behavior in female macaques. *Journal of Clinical Endocrinology and Metabolism* 89:2998–3006.
- Pepe GJ, Johnson DK, Albrecht ED. 1982. The effects of estrogen on cortisol metabolism in female baboons. *Steroids* 39:471–477.
- Prud'Homme J, Chapais B. 1993a. Aggressive interventions and matrilineal dominance relations in semifree-ranging barbary macaques (*Macaca sylvanus*). *Primates* 34:271–283.
- Prud'Homme J, Chapais B. 1993b. Rank relations among sisters in semi-free-ranging Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology* 14:405–420.
- Ray JC, Sapolsky RM. 1992. Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. *American Journal of Primatology* 28:231–250.
- Richter C, Mevis L, Malaivijitnond S, Schulke O, Ostner J. 2009. Social Relationships in Free-Ranging Male *Macaca arctoides*. *International Journal of Primatology* 30:625–642.
- Sapolsky RM. 2005. The influence of social hierarchy on primate health. *Science* 308:648–652.
- Schino G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour* 62:265–271.
- Schino G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology* 18:115–120.
- Seyfarth RM. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology* 65:671–698.
- Seyfarth RM. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour* 28:798–813.
- Seyfarth RM, Cheney DL. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308:541–543.
- Seyfarth RM, Silk JB, Cheney DL. 2012. Variation in personality and fitness in wild female baboons. *Proceedings of the National Academy of Sciences* 109:16980–16985.
- Shideler SE, Gee NA, Chen J, Lasley BL. 2001. Estrogen and progesterone metabolites and follicle-stimulating hormone in the aged macaque female. *Biology of Reproduction* 65:1718–1725.
- Shideler SE, Shackleton CH, Moran FM, et al. 1993. Enzyme immunoassays for ovarian steroid metabolites in the urine of *Macaca fascicularis*. *Journal of Medical Primatology* 22:301–312.
- Shutt K, MacLarnon A, Heistermann M, Semple S. 2007. Grooming in Barbary macaques: better to give than to receive? *Biology Letters* 3:231–233.
- Silk J, Cheney D, Seyfarth R. 2013. A Practical Guide to the Study of Social Relationships. *Evolutionary Anthropology* 22:213–225.
- Silk JB. 2009. Nepotistic cooperation in non-human primate groups. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 364:3243–3254.
- Silk JB, Alberts SC, Altmann J. 2003. Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234.
- Silk JB, Altmann J, Alberts SC. 2006. Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology* 61:183–195.
- Silk JB, Beehner JC, Bergman TJ, et al. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B-Biological Sciences* 276:3099–3104.
- Silk JB, Beehner JC, Bergman TJ, et al. 2010. Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology* 20:1359–1361.
- Silk JB, Seyfarth RM, Cheney DL. 1999. The structure of social relationships among female savanna baboons in Moremi reserve. *Botswana Behaviour* 136: 679–703.
- Slot C. 1965. Plasma creatinine determination. A new and specific Jaffe reaction method. *Scandinavian Journal of Clinical Laboratory Investigation* 17:381–387.
- Small MF. 1990. Social climber: independent rise in rank by a female Barbary macaque (*Macaca sylvanus*). *Folia Primatologica* 55:85–91.

- Smith CJ, Norman RL. 1987. Influence of the gonads on cortisol secretion in female rhesus macaques. *Endocrinology* 121: 2192–2198.
- Stavisky RC, Watson SL, Anthony MS, et al. 2003. Influence of estradiol on cortisol secretion in ovariectomized cynomolgus macaques (*Macaca fascicularis*). *American Journal of Primatology* 60:17–22.
- Thierry B, Aureli F, Nunn CL, et al. 2008. A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. *Animal Behaviour* 75:847–860.
- Thierry B, Singh M, Kaumanns W. 2004. Macaque societies. A model for the study of social organization. Cambridge University Press.
- van Schaik CP, van Noordwijk MA, van Bragt T, Blankenstein MA. 1991. A Pilot Study of the Social Correlates of Levels of Urinary Cortisol, Prolactin, and Testosterone in Wild Long-tailed Macaques (*Macaca fascicularis*). *Primates* 32:345–356.
- Ventura R, Majolo B, Koyama NF, Hardie S, Schino G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology* 68:1138–1149.
- Wasser SK, Monfort SL, Southers J, Wildt DE. 1994. Excretion rates and metabolites of oestradiol and progesterone in baboon (*Papio cynocephalus cynocephalus*) feces. *Journal of Reproduction and Fertility* 101:213–220.
- 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* 45:259–269.
- Wilson EO, Bossert WH. 1971. A primer of population biology. Sunderland: Sinauer Associates.
- Wirth MM, Meier EA, Fredrickson BL, Schultheiss OC. 2007. Relationship between salivary cortisol and progesterone levels in humans. *Biological Psychology* 74:104–107.
- Wittig RM, Crockford C, Lehmann J, et al. 2008. Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior* 54:170–177.
- Wrangham RW. 1980. An Ecological Model of Female-Bonded Primate Groups. *Behaviour* 75: 262–300.