Responses to social and environmental stress are attenuated by strong male bonds in wild macaques

Christopher Young, Bonaventura Majolo, Michael Heistermann, Oliver Schülke, and Julia Ostner

In humans and obligatory social animals, individuals with weak social ties experience negative health and fitness consequences. The social buffering hypothesis conceptualizes one possible mediating mechanism: During stressful situations the presence of close social partners buffers against the adverse effects of increased physiological stress levels. We tested this hypothesis using data on social (rate of aggression received) and environmental (low temperatures) stressors in wild male Barbary macaques (Macaca sylvanus) in Morocco. These males form strong, enduring, and equitable affiliative relationships similar to human friendships. We tested the effect of the strength of a male’s top three social bonds on his folic glucocorticoid metabolite (fGCM) levels as a function of the stressors’ intensity. The attenuating effect of stronger social bonds on physiological stress increased both with increasing rates of aggression received and with decreasing minimum daily temperature. Ruling out thermoregulatory and immediate effects of social interactions on fGCM levels, our results indicate that male Barbary macaques employ a tend-and-befriend coping strategy in the face of increased environmental as well as social day-to-day stressors. This evidence of a stress-ameliorating effect of social bonding among males under natural conditions and beyond the mother–offspring, kin or pair bond broadens the generality of the social buffering hypothesis.

Strong affiliative social relationships exert powerful beneficial effects on an individual’s health and fitness in both humans and nonhuman animals (1–5). One well-studied mediating mechanism, conceptualized in the social buffering hypothesis, is that the presence of a close social partner attenuates the reactivity of the hypothalamic–pituitary–adrenal (HPA) axis (apart from other positive effects on physiological responses) and thus buffers against the potentially adverse effects of physiological stress (4, 6, 7). Evidence for the social buffering hypothesis rests primarily on experimental studies exposing subjects to stressful situations when a close social partner is present or absent (6–8). In that sense, previous studies on the social buffering effect captured an interaction effect of social bonding and a stressor, usually via exposure to a novel environment or, in humans, psychological stress on the stress response (4).

The individual functioning as a social buffer against stress is usually a pair-bonded partner (in humans and nonhuman animals (6, 8–11)) or mother (in infant nonhuman animals (11–13)). The “tend-and-befriend” stress-coping-mechanism (i.e., turning to close affiliates and kin), when under stress, has been linked to the attachment–caring system partly regulated by the oxytocinergic system (14–16). Possibly as a direct consequence of this, humans exhibit a strong sex difference in behavioral coping mechanisms to perceived stressful events; women are more likely to seek social support in stressful situations compared with men (17, but see ref. 18). Stress alleviation via social support has also been shown in nonhuman primates where females with stronger bonds or a tighter social network showed an attenuated response to stressors compared with those with weaker social ties (19, 20). For example, the death of a close female partner (catastrophic stressor), usually kin, in baboons led to increased physiological stress, and the bereaved partner attempted to alleviate this response by strengthening existing bonds (21). After a conflict event in chimpanzees (Pan troglodytes) and bonobos (Pan paniscus) closely bonded bystanders can actively console recipients of aggression, thereby reducing behavioral measures of stress (22–24). Many nonhuman primates females live in closely interwoven matrilineal networks of mutual affiliation and support (25–27) that generate strong fitness advantages in terms of increased reproductive rates and survival (1, 28, 29).

Because most males compete for opportunities to fertilize females (30) the focus of studies investigating correlates of male physiological stress have historically been on reproductive competition and hierarchical status (31–33). Nevertheless, recent and increasing evidence has shown that males of some vertebrate species also form strong social bonds that can enhance their fitness (refs. 34–38 and reviewed in ref. 39). However, to date social buffering effects on acute HPA responses in adult male vertebrates have been investigated predominantly in pair-living species (or pair-housed animals) in response to the female pair partner’s presence (reviewed in ref. 6). It remains to be shown whether the human sex difference in behavioral stress-coping mechanisms is exhibited by other mammals as well or whether males, like females, experience social buffering responses under stress when they have strong social ties to other same-sex individuals in their group.

Significance

Male macaques form social bonds similar to human friendships that buffer them against day-to-day stressors. If male primates live in multimale groups they usually fight fiercely over access to females, but males can develop friendly relationships with a few group mates. The strength of these “friendships” has now been shown to buffer against the negative effects of social and environmental stressors, a phenomenon that was previously only described for females and pair-living animals. Long-term glucocorticoid (stress hormone) elevation can increase susceptibility to disease and mortality. This study shows that variation in everyday stressors such as the amount of aggression received or cold stress can cause such long-term elevated glucocorticoid levels but that keeping a few close male associates will avoid that.

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Similar to philopatric female baboons and male chimpanzees (38, 40, 41) macaque males of some species, including Barbary macaques (Macaca sylvanus), form strong social relationships with a few male partners (35, 36, 39, 42) that are stable over consecutive years and characterized by equitability in exchanges of affiliation (37). The mechanisms guiding partner selection for the formation of social bonds in male macaques are currently unknown. Parallel dispersal has been observed (43), and in large provisioned groups maternal relatedness partly drives agonistic support (44), but the strength of male social bonds is not decreased in maternally unrelated males in the wild (35). Males vary in the number and strength of social bonds they form (37), which may partly be guided by age (36, 45) and may additionally be affected by personality (46, 47).

Barbary macaque males frequently experience noncatastrophic stressful situations in their daily lives that may be social or environmental. Within-group conflicts resulting in aggression represent a social stressor that is positively correlated to glucocorticoid levels (a measure of physiological stress) across many primates (19, 48–51). Within-group aggressive conflicts also vary between individuals (50, 52) and between seasons, with peaks during the mating season (36). An annually recurring environmental stressor in the study population of Barbary macaques is cold stress during the winter months. Winter survival probability was found to be predicted by the number of affiliative relationships an individual formed (53). In baboons temperature stress is associated with increased glucocorticoid levels (54, 55).

Here we took advantage of this macaque system of strong male bonding and the occurrence of several stressors in an individual’s daily life to test the social buffering hypothesis in a natural situation and within the male sex. As the buffering hypothesis proposes that social support or bonding is related to well-being only during stressful situations (4), we predicted an interaction effect: As stressor intensity increases (i.e., rate of aggression received increases or minimum temperature declines), the attenuating effect of an individual’s social bond strength on faecal glucocorticoid metabolite (fGCM) levels becomes stronger. We also controlled for an alternative, not mutually exclusive, hypothesis, the “immediate effects hypothesis,” stating that affiliative social behavior directly alleviates physiological stress irrespective of the social relationship the partner(s) has to an individual (20, 56, 57). For this, we tested the proximate effects of rates of grooming given and received by all group members, grooming with the top three male partners, or frequency of male–infant–male triadic interactions on fGCMs.

Results
Social bond strength was measured on a dyadic level via the composite sociality index (CSI) (Materials and Methods) comprising eight correlated measures of affiliative behavior. The male dyads with the highest 10% of CSI scores (n = 18) would, on average, be 12 times more likely to groom (0.12 vs. 0.00 interactions per hour) than dyads with the lowest 10% of CSI scores (n = 18); be twice as likely to sit in body contact (0.04 vs. 0.02 interactions per hour); be 20 times more likely to have male–infant–male triadic interactions (0.20 vs. 0.00 interactions per hour); and be 13 times more likely to be in social proximity (0.13 vs. 0.01 interactions per hour). To measure effects of the strength of a male’s social bonds instead of the effects of the number of affiliation partners we kept the number of partners constant and used the added CSI values of an individual’s top three relationships in our models. Stressor intensities varied widely from 0–13 bouts of aggression received per hour by an individual male and mean minimum daily temperature varied from −1 to +33 °C throughout the study across 10-d periods. Average individual fGCM levels increased with increasing stressor intensities for many individuals (Figs. S1 and S2). The rates of aggression received were variable for both males with strong and weak social bonds (the range of males’ summed top three CSI scores for the four quartile ranges of aggression received were as follows: low aggression, 0.5–11.1; low–mid aggression, 0.5–11.1; mid–high aggression, 0.5–12.9; and high aggression rate received, 0.7–12.9). Higher-ranked males did not necessarily have higher social bond strength; mean CSI score of a male’s top three social partners was not significantly correlated to a male’s mean dominance rank (Spearman’s rank correlation: r = −0.144, df = 12, P = 0.62).

Immediate Effects Hypothesis. We constructed a linear mixed model (LMM) (58) to examine both the immediate effects and social buffering hypotheses. We found no support for the immediate effects hypothesis because none of our independent behavioral variables (grooming given or received to all group members, grooming with the top three male partners, or frequency of male–infant–male triadic interactions) had an alleviating influence on fGCM levels (Table 1), even if models were run without the interaction terms of stressors and social bond strength (Table S1). We found that fGCM levels during the mating season (mean ± SD = 492.9 ± 207.8; range = 89.6–1,148.2 ng/g feces) were higher than during the nonmating season (mean ± SD = 344.1 ± 153.4; range = 71.5–1,043.1 ng/g feces) (Table 1; full vs. null model: χ² = 156.6, df = 13, P < 0.001, n = 437).

Social Buffering Hypothesis. We found the interaction between the number of aggressive bouts a male received and the strength of his top three social bonds to have a significant influence on fGCM levels (Table 1 and Fig. 1). At low levels of aggression, male social bond strength did not influence fGCM levels. However, as rates of aggression received increased, the weaker the social bond strength an individual had the higher his fGCM levels were, and this effect became stronger the higher the levels of aggression received. The interaction between mean minimum daily temperature (range of −1 to +33 °C) and the strength of a male’s bonds with his top three social partners also significantly influenced his fGCM levels (Table 1 and Fig. 2). Specifically, at the lowest mean minimum daily temperatures the weaker a male’s social bond strength was the higher his fGCM levels were. As mean minimum daily temperatures increased to mid-high levels the relationship between social bond strength and fGCM levels was much weaker. At highest mean minimum daily temperatures social bond strength seemed to have a very slight positive effect on fGCM levels; the stronger a male’s social bonds the marginally higher his fGCM levels were. Time spent in body contact was not a predictor of fGCM, indicating that the social bond strength–minimum temperature interaction effect on fGCMs was not a direct thermoregulatory consequence of more closely bonded males spending more time in body contact.

Discussion
This study tested predictions from the immediate effects and social buffering hypotheses in a nonhuman primate species characterized by strong male–male bonding by investigating the effects of different stressors on HPA axis activation. We show that the higher the rate of aggression received from group mates (social stressor) the stronger the attenuating effect of a male’s social bond strength on his fGCM levels. Male–male social bonds seem to provide a buffer against the negative effects of noncatastrophic daily stressors by reducing the physiological stress response. These social bonds can buffer against both social and environmental stressors, as emphasized by our finding that the lower the minimum mean ambient temperature, the stronger the negative effect of a male’s social bond strength on his fGCM levels became, providing further support for the social buffering hypothesis. This latter result was not explained by the beneficial effects of social thermoregulation via contact sitting that can characterize closely bonded dyads. From Fig. 2 it may be
concluded that at highest minimum temperatures social bond strength had a slightly positive effect on fGCM levels. Fig. 2 shows a plot of raw data uncorrected for random and fixed effects and is only an illustration of the statistical interaction effect that should not be interpreted without consideration of model outcomes. Future investigations that specifically target the warmest months, that coincide with the birth season, may elucidate whether the relationship between social bond strength and fGCMs is reversed, possibly as a consequence of increased rates of infant handling (42), which did not affect our overall model outcome. The immediate effects hypothesis was not supported because the frequency or duration of affiliative behaviors did not have a significant direct impact on physiological stress levels.

Chronically elevated glucocorticoid levels in response to aggression received from group mates is a major cost of group living for subordinates in many mammals (19, 49–51, 59). Several studies, however, failed to replicate the negative effect of aggression received on an individual’s physiological stress level (55, 60–63). Our results suggest that in these latter studies interaction effects were missed, possibly as a consequence of increased rates of infant handling (42), which did not affect our overall model outcome. The immediate effects hypothesis was not supported because the frequency or duration of affiliative behaviors did not have a significant direct impact on physiological stress levels.

Table 1. Results of an LMM with Gaussian error structure for the relationship between mean fGCM levels and social and environmental factors

<table>
<thead>
<tr>
<th>Factor</th>
<th>Estimate ± SEM</th>
<th>t value</th>
<th>pMCMC value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>−0.068 ± 0.027</td>
<td>−2.53</td>
<td>0.009</td>
</tr>
<tr>
<td>Interaction between CSI with top three partners and aggression received</td>
<td>−0.079 ± 0.032</td>
<td>−2.47</td>
<td>0.009</td>
</tr>
<tr>
<td>Aggression received</td>
<td>0.012 ± 0.023</td>
<td>0.52</td>
<td>0.588</td>
</tr>
<tr>
<td>Interaction between CSI with top 3 partners and mean minimum daily temperature</td>
<td>-0.032 ± 0.021</td>
<td>-1.67</td>
<td>0.102</td>
</tr>
<tr>
<td>Mating vs. nonmating season</td>
<td>0.424 ± 0.048</td>
<td>8.82</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body contact</td>
<td>0.035 ± 0.021</td>
<td>1.67</td>
<td>0.102</td>
</tr>
<tr>
<td>Grooming given</td>
<td>-0.014 ± 0.025</td>
<td>-0.56</td>
<td>0.564</td>
</tr>
<tr>
<td>Grooming received</td>
<td>0.013 ± 0.027</td>
<td>0.49</td>
<td>0.603</td>
</tr>
<tr>
<td>Grooming with top three partners</td>
<td>-0.009 ± 0.026</td>
<td>-0.36</td>
<td>0.677</td>
</tr>
<tr>
<td>Rank</td>
<td>-0.011 ± 0.051</td>
<td>-0.22</td>
<td>0.706</td>
</tr>
<tr>
<td>Male-infant–male triadic interaction</td>
<td>0.016 ± 0.026</td>
<td>0.59</td>
<td>0.561</td>
</tr>
<tr>
<td>Infant carrying</td>
<td>0.011 ± 0.026</td>
<td>0.42</td>
<td>0.663</td>
</tr>
</tbody>
</table>

fGCM levels are a mean across one to three samples per 10 d of observation. Social and environmental factors examined were: male ordinal rank, mating season or not, duration of grooming received from other group members, duration of grooming given to other group members, time spent carrying an infant, time spent in body contact, frequency of male–infant–male triadic interactions, time spent grooming (given and received) with a male’s top three partners, and the interactions between rate of aggressive bouts received and the sum of a male’s CsIs with his top three partners (a measure of strength of his social bonds), and the interaction between the mean minimum daily temperature and the sum of a male’s CsIs with his top three partners. Male identity and group were included as random factors. Those in bold type indicate significant predictors of fGCM levels. Factors included in significant interaction terms cannot be interpreted as independent variables (in italics and indented).

Primate social bonds are thought to be formed and maintained through a suite of affiliative behaviors including grooming or male–infant–male triadic interactions that individually have no effect on HPA axis activation (39, 65). This seems to suggest that the stress response of males with strong social bonds is buffered by the combined direct effects of these behaviors. It is important to realize, though, that not all grooming is equal. Peripheral urinary oxytocin levels measured after a single grooming interaction suggest that individuals react to the same behavioral interaction (i.e., a grooming event) differently depending on the identity of their interaction partner. Oxytocin levels after grooming are much higher in strongly bonded partners compared with two individuals with overall low rates and durations of affiliation (66). Thus, it is not surprising that the independent effects of the behaviors that comprise the social bond measure did not affect fGCM levels. A male’s position in the dominance hierarchy also did not influence his physiological stress levels, which may be due to the relative stability of the hierarchies in our study groups. Dominance rank was not correlated to the strength of a male’s top three social bonds.

Our study extends the current literature; we found that dispersing primate males that form strong social bonds (37), seem to turn to close same-sex companions in stressful situations, indicative of a tend-and-befriend stress-coping mechanism that was previously thought to be characteristic of females (14–16). Mammalian females usually remain in their natal group (67) and their strongest social bonds are often with kin, particularly mothers and daughters, and as such females are expected to affiliate more frequently with these bonded partners under stressful situations (14–16). Because this phenomenon may be mediated by the oxytocinergic system (14–16) it is postulated to develop more easily in females than in males owing to the role of oxytocin in female care-giving toward, and attachment to, their own offspring in many mammalian species (14–16). Mammalian males, in general, use highly competitive reproductive strategies and therefore are proposed to use a “fight or flight” response to stressful situations (68), mediated by the androgenic system (14–16).

Conversely, we found in our study that primate males may employ a mechanism similar to the female “tend and befriend” (69).

Previous support for the social buffering hypothesis in males usually came from pair-living species, pair-housed animals, or experiments with preferred female partners where male physiological stress responses were alleviated in the presence of their female partner (reviewed in refs. 6, 7, and 59). Here we show that in the wild, and similar to females, the social bonds that males form with same-sex group members provide them with a buffer against both naturally occurring social and environmental stressors. Although rare among mammals, strong social
bonds between males can yield a number of adaptive benefits, including increased social status and mating and paternity success (34, 35, 37, 39, 70). Male macaques cooperate frequently with bonded male partners in agonistic coalitions (35, 37, 71, 72). Thus, as in humans and other mammals, individuals with strong social bonds may benefit from greater social support from other group members (4, 6, 7, 59). Conversely, individuals that form only weak social relationships may react to stressors more strongly, for example via impairing the regulatory function of the HPA axis (6, 7, 59). Dysregulation of the HPA axis increases susceptibility to disease (73, 74). Among captive rhesus macaques (Macaca mulatta) social stressors led to increased susceptibility to disease in individuals with a personality characterized by low sociability compared with individuals with high sociability (75). Together with the finding that in humans several negative health consequences and increased mortality are related to increased feelings of loneliness (76, 77), these results suggest that the effectiveness of sociality (formation of strong bonds) on responsiveness to stressors may be mediated by temperament. This is echoed in cercopithecine females where individuals with a loner personality (low rate of social interactions) had higher responsiveness to stressors. This visualization of raw data is not a substitute for the full statistical model results, which are presented in Table 1.

In humans, males and females frequently turn to close companions in times of high stress (14), and this is usually a core of three to five individuals (80, 81). Philopatric female nonhuman primates that lack these few strong bonds show increased mortality and reduced offspring survival (1, 28, 29), whereas those who established and maintained strong bonds to a few partners coped better with stressful situations (19–21) and lived a longer life. Our results contribute to these findings by showing that wild, nonphilopatric males also benefit from maintaining strong bonds to their top partners via attenuated responses to noncatastrophic daily stressful situations. Therefore, our study suggests that the ways in which social mammals affiliate, cooperate, and compete among each other is not fundamentally different in gregarious males and females (35, 39, 66, 82, 83). Thus, the attenuation of the stress response triggered by diverse sources is yet another adaptive benefit accruing from the establishment and maintenance of strong social bonds in either sex.

Materials and Methods
Subjects and Behavioral Observations. Data were collected from two wild groups (“green” (Gn) and “scarlet” (Sc) of Barbary macaques living in a deciduous cedar and oak forest in the Middle-Atlas Mountains of Morocco (84). The groups consisted of seven to nine adult males and eight adult females (Gn) and six males and eight females (Sc). Data were collected on the Gn group from October 2009–April 2011 and on the Sc group from July 2010–April 2011. This study adhered to the legal requirements of Morocco, Germany, and Great Britain.

Data of all social and agonistic behaviors were collected through 40-min focal sampling (85) of all males, giving a total of 2,033 h (1,676 h Gn and 358 h Sc) of behavioral data (Supporting Information, section 1). At the beginning of each focal follow, we recorded air temperature using a 3500 Kestrel Pocket Weather Station by placing the weather station in the shade at 1.5 m above the ground (84). Social behaviors recorded included grooming, infant carrying, male–infant–male triadic interactions (37), and time spent in body contact with other group members. Social relationship quality was measured...
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