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Low female stress hormone levels are predicted by same- or opposite-sex sociality depending on season in wild Assamese macaques

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Summary The social environment can have a powerful impact on an individual's stress response and thus affect health and biological fitness. Positive social interactions are particularly important for females of species living in complex societies, e.g. humans and non-human primates. Existing studies have mainly focussed on the effect of same-sex social interaction on the stress response, rather than both same- and opposite-sex social interaction simultaneously. However, consideration of both may be crucial since females may have different 'social needs' across different life-history stages. Applying the conceptual framework of allostasis, we tested the hypothesis that female allostatic load (measured through faecal glucocorticoid levels [fGCs]), of wild seasonally breeding Assamese macaques (*Macaca assamensis*), would increase if their social needs were not maintained in accordance with season. We found significant seasonal differences in same- and opposite-sex sociality which, depending on season, predicted female fGCs. In the mating season, females which spent more time close to males and more frequently groomed with them exhibited lower fGCs. In the non-mating season, when female—male interaction was infrequent, positive female—female sociality predicted lower fGCs. Our results support the hypothesis that same- and opposite-sex sociopositive interactions, specific to certain life-history stages, can mediate fGCs. We interpret this as a consequence of the positive

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direct and/or indirect effects of social contact in accordance with interactions pertaining to a given life-history stage, which are likely to impact positively upon fitness.

1. Introduction

The concepts of allostasis and allostatic load provide a framework for understanding better the demands of predictable and unpredictable social and environmental challenges (Creel et al., 2013; McEwen and Wingfield, 2003; Wingfield, 2005). Allostasis is the response of an individual to changes in the environment in order to maintain homeostasis for the current life-history stage, and allostatic load refers to the cumulative costs of allostasis and is reflected in glucocorticoid (GC) or ''stress hormone'' concentrations (McEwen and Wingfield, 2003). Whereas short-term elevations of GCs are adaptive, long-term exposure to increased GCs can have severe consequences, e.g. impairing immune, cognitive, and reproductive function (e.g. McEwen and Wingfield, 2003; Sapolsky, 1998, 2005).

Seasonal changes in allostatic load have been reported for many vertebrate species and have been primarily linked to increased energetic demands associated with reproduction (reviewed by Romero, 2002). Seasonal reproduction, however, also presents social challenges. The social environment, i.e. the frequency and type of interaction with conspecifics, as well as social status have been shown to significantly affect allostatic load (Creel et al., 2013). Many studies have investigated the effects of reproductive competition and social dominance (i.e. agonistic interactions) on GC secretion (reviewed by Creel et al., 2013); however, the patterning of affiliative interactions can also change seasonally. During the mating season, for instance, positive male—female interactions are essential for successful breeding. In other words, shifts in the frequency of sociopositive interactions might reflect different predictable 'social needs' across different life-history stages, and may have important fitness consequences. Applying the conceptual framework of allostasis, we hypothesise that any deviations in achieving these social needs contribute to increased allostatic load (together with increased energetic demands associated with reproduction).

Primates, many of which are seasonal breeders (Brockman and van Schaik, 2005), form complex societies which present multiple sources of social modulation of GC concentrations (Sapolsky, 1992, 1993, 2005; Creel, 2001; Abbott et al., 2003; Cavigelli et al., 2003; Goymann and Wingfield, 2004; Crockford et al., 2008; Cheney and Seyfarth, 2009). Females, in particular, engage in social interactions (i.e. grooming and close proximity) and form social relationships within and between sexes, both of which can provide important fitness benefits. For example, female—female sociality increases infant survival and longevity (Silk et al., 2003, 2009, 2010), and female—male sociality enhances offspring survival (Palombit, 2009) and female energy budgets (Huchard et al., 2013). If these social needs are unfulfilled, i.e. if females fail to engage in these positive social interactions, allostatic load may be increased. Female baboons, for instance, react to the loss of close kin, which usually is a close associate, with increases in GC levels (Engh et al., 2006a), and females with less close bonds (Wittig et al., 2008) react to the presence of an immigrant male with increases in GC levels. Furthermore, social interaction patterns are directly linked to GC levels and, as seen in Barbary macaques (*Macaca sylvanus*), both grooming frequencies and the number of grooming partners are important (Shutt et al., 2007).

Whilst the importance of affiliative female—female interactions for allostatic load is well documented (see above), much less is known about female—male interactions. This may reveal only half of the picture, given that females can gain fitness benefits from associating with males (e.g. Borries et al., 1999; Nguyen et al., 2009; Palombit, 2009); hence, positive female—male social interactions are likely to be reflected in female GC levels. In chacma baboons (*Papio hamadryas ursinus*), for example, lactating females that maintain a 'friendship' with a male show lower GC levels during an immigrant male take-over period compared to females without male friends (Beehner et al., 2005). To our knowledge, no study to date has investigated the effect of both same- and opposite-sex sociopositive interactions on allostatic load simultaneously.

Strictly seasonally breeding primate species living in multi-male, multi-female groups provide an ideal opportunity to study the effects of a predictably changing social environment (including both same- and opposite-sex interactions) on female allostatic load since: (1) They form stable social groups with affiliative bonds, mediated and maintained by social interactions, i.e. grooming and proximity (reviewed by Lehmann et al., 2007). (2) They are characterised by two distinct and predictable seasons, a mating and a non-mating season (Brockman and van Schaik, 2005).

We simultaneously investigate the effects of same- and opposite-sex interactions on faecal glucocorticoid levels (fGCs) in mating and non-mating seasons in wild female Assamese macaques (*Macaca assamensis*), whilst controlling for hormonally determined reproductive state (a major predictor of female GCs; Cheney and Seyfarth, 2009) as well as demographic and environmental factors. Given that female—female grooming and close spatial associations in macaques are usually year round and stable (e.g. Thierry et al., 2004), we predict that females with more frequent female—female social contact, i.e. grooming and proximity, will show lower fGCs in both mating and non-mating seasons (prediction 1). During the mating season, females are highly promiscuous, and also form sexual consortships with certain males (Fürtbauer et al., 2011a; Ostner et al., 2011). Furthermore, proximity to males affects mating frequencies which, in turn, determine male—infant interactions (Ostner et al., 2013). Because associating with males could have important fitness consequences for females (male—infant interactions may translate into paternal care; see e.g. Huchard et al., 2013), we predict that, during the mating season, females