



Alpha male status and availability of conceptive females are associated with high glucocorticoid concentrations in high-ranking male rhesus macaques (*Macaca mulatta*) during the mating season



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ABSTRACT

The relationship between male mating opportunities, stress, and glucocorticoid concentrations is complicated by the fact that physiological stress and glucocorticoid concentrations can be influenced by dominance rank, group size, and the stability of the male dominance hierarchy, along with ecological factors. We studied the three highest-ranking males in nine different social groups within the same free-ranging population of rhesus macaques on Cayo Santiago, Puerto Rico, during the mating season, to examine variation in glucocorticoid concentrations in relation to number of females that conceived each month, alpha status, number of adult males in a group, and male rank hierarchy stability. We found that glucocorticoid concentrations were highest in the early mating season period when more females conceived in each group and declined linearly as the mating season progressed and the number of conceptive females decreased. Alpha males had significantly higher mean monthly glucocorticoid concentrations than other high-ranking males throughout the study period. Male age, number of adult males in a group, and hierarchy stability were not significantly associated with glucocorticoid concentrations. Our findings suggest that alpha males may experience significantly higher levels of physiological stress than their immediate subordinates and that this stress coincides with the period of the mating season when most conceptions occur.

1. Introduction

Male mammals often engage in intense competition for access to mates and can incur significant physical, physiological, and health-related costs (Corlatti et al., 2012; Emery Thompson and Georgiev, 2014; Kappeler and van Schaik, 2004; Kershaw and Hall, 2016; Key and Ross, 1999; Sands and Creel, 2004). These costs include physical injury (Arlet et al., 2009; Smuts, 1987), stress (Bergman et al., 2005; Corlatti et al., 2012; Higham et al., 2013; Sands and Creel, 2004; Setchell et al., 2010), reduced immune function (Corlatti et al., 2012; Prall and Muehlenbein, 2014), reduced energy balance (Georgiev, 2012), and a variety of health impairments (e.g. Nunn and Altizer, 2004). While it has often been assumed that the potential costs of male competition would be borne most heavily by the losers (i.e. males with low competitive success), a variety of evidence has accumulated to suggest that, at least

under some conditions, physiological stress can be skewed towards the highest ranking individuals (Abbott et al., 2003; Cavigelli and Caruso, 2015; Creel, 2001; Goymann and Wingfield, 2004).

Physiological stress can be assessed by measuring concentrations of glucocorticoids (GCs), a group of steroid hormones secreted from the adrenal glands that are involved in regulating metabolism and are important for mobilizing energy as part of the “fight-or-flight” response (Sapolsky, 1992; Sapolsky et al., 2000). GCs capture the generalized systemic response to a variety of stressors, both physical and psychological, which can, at chronically high levels, negatively affect health and survival (Mendoza et al., 2000). The relationship between glucocorticoids and male competition has received particular attention in studies of non-human primates, among which many species form stable, multi-male, multi-female groups. Among primates, there are some species in which subordinate males had elevated GC concentrations

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compared to dominant males, including squirrel monkeys (Coe et al., 1979; Manogue et al., 1975) and olive baboons (Sapolsky et al., 1997; Virgin and Sapolsky, 1997). High-ranking males had higher GC concentrations than low-ranking males in bearded capuchin monkeys (*Sapajus libidinosus*: Mendonca-Furtado et al., 2014), white-faced capuchin monkeys (*Cebus capucinus*: Schoof et al., 2016), chimpanzees (*Pan troglodytes*: Muller and Wrangham, 2004), and Japanese macaques (*Macaca fuscata*: Barrett et al., 2002). A number of explanations have been offered for the positive correlations between glucocorticoid concentrations and rank in male primates. Given that high-ranking males of most species have an advantage in securing mating opportunities, one hypothesis is that high glucocorticoid concentrations reflect the high physiological costs associated with mating effort, including mate guarding and direct aggressive competition for mates. In support of this, males in several seasonally breeding species have elevated GC concentrations during the mating season (e.g., *Cebus apella*: Lynch et al., 2002; *Eulemur fulvus*: Ostner et al., 2008b; *Brachyteles arachnoides*: Strier et al., 1999). In seasonally-breeding mandrills and in non-seasonally breeding bonobos, a positive association between rank and glucocorticoid concentrations was found only during mating periods (Setchell et al., 2010; Surbeck et al., 2012). However, in male Assamese macaques (*Macaca assamensis*), GC concentrations were higher in the mating season (Ostner et al., 2008a), but did not correlate with investment in mate-guarding (Schülke et al., 2014). Instead, GC concentrations were predicted by the amount of aggression received, resulting in higher concentrations for low-ranking males (Ostner et al., 2008a).

Alternatively, or additionally, high-ranking males may suffer increased physiological stress in their efforts to maintain high dominance rank against challenges from other males. These effects could contribute to the overall physiological costs of mating effort, but should also be expected to persist in non-mating periods when the dominance hierarchy is unstable. In male rhesus macaques and baboons, high-ranking males had higher GC concentrations than other males only during periods of social instability (Higham et al., 2013; Sapolsky, 1983, 1992). Other studies report higher GCs among males in larger groups (Goymann et al., 2003; Raouf et al., 2006). Under natural conditions, cliff swallows living in larger breeding colonies had higher GC concentrations (Raouf et al., 2006). Similarly, in male spotted hyenas, GC concentrations were unrelated to social status, but were highest for those males living in the largest social group (Goymann et al., 2003). Male spotted hyenas are similar to male rhesus macaques in that they queue for dominance (Goymann et al., 2003); thus, we can predict that rhesus macaques may show a similar pattern in which the number of adult males present in the group may be more influential in predicting GC concentrations than a male's individual dominance status.

For logistical reasons, most relevant studies of wild primates have examined variation in GCs within a single group of individuals. In such studies, inferences about causality from correlations between dominance rank and GCs are difficult to evaluate because dominance rank covaries with many behavioral factors. Furthermore, to the extent that many of these studies rely on the presence or absence of a significant correlation, they fail to reveal whether these relationships are driven by the proximate forces affecting high-ranking males or those affecting low-ranking males, which may be different. Factors that vary primarily between groups, such as number of other males or the overall availability of mating opportunities, may be expected to exert the biggest impact on the stress experienced by high-ranking individuals. Thus, in this study, we examined factors predicting GC variation among top-ranking males in nine different social groups of free-living rhesus macaques. We examined whether absolute rank (alpha vs. non-alpha top-ranking males), the number of females that conceived in each group during a given month, the number of males in each group, or male hierarchy stability influenced the absolute GC concentrations experienced by top-ranking males in different groups. Because the groups were all members of the

same provisioned population with low climatic variation over the course of this study, we could assume that the influence of ecological parameters (e.g. temperature and rainfall) on physiological stress was equivalent across all groups.

Rhesus macaques are highly social cercopithecine monkeys that usually range in south, southeast, and central Asia. They live in groups with matriarchal structure and linear dominance hierarchies for both males and females (Maestriperi, 2003; Manson, 1998; Missakian, 1972). Males disperse from their natal groups and join new groups at puberty. In the free-ranging rhesus macaque population on the island of Cayo Santiago, PR, migrating males generally enter a new group at the bottom of the hierarchy and gain dominance with seniority (Berard, 1999; Bercovitch, 1997; Manson, 1998). However, exceptions to this pattern, in which an immigrant adult male aggressively takes over the alpha position in a new group, have been reported (Georgiev et al., 2016). Rhesus macaques are seasonal breeders. On Cayo Santiago, mating occurs during the spring and summer and is followed by births during autumn and winter (Hernández-Pacheco et al., 2016). Female rhesus macaques on Cayo Santiago have a high degree of reproductive synchrony, such that the majority of females come into estrus at the same time and the number of pregnant females increases over the course of the mating season (Dubuc et al., 2011; Ostner et al., 2008c). Estrous females engage in consortships in which the males mate-guard the females (Dubuc et al., 2012). In the Cayo Santiago rhesus population, high-ranking males have a small reproductive advantage over low-ranking males (Berard et al., 1994; Dubuc et al., 2011; Widdig et al., 2004). A previous study showed that during the mating season, top-ranking males participated in more consortships with estrous females and had the highest levels of copulatory activity (Higham et al., 2011). Individual male copulation rates were negatively correlated with concentrations of urinary C-peptide of insulin (a validated biomarker of energy balance in rhesus macaques and other primates; Girard-Buttoz et al., 2011; Emery Thompson, 2017) and body fat, indicating that top-ranking males made the greatest mating effort and were in the worst energetic condition at the end of the mating season (Bercovitch, 1997; Higham et al., 2011). Associations between GC concentrations and rank in rhesus macaques have been inconsistent, with some studies finding no relationship between GC concentrations and dominance rank (Bercovitch and Clarke, 1995), while others reporting that high-ranking individuals have higher GC concentrations only during periods of instability (Higham et al., 2013; see also McFarland and MacLarnon, 2013).

In this study we analyzed data on GC concentrations of the alpha males and the two next highest-ranking males from each of nine social groups of free-ranging rhesus macaques on Cayo Santiago, during the mating season. Given that males in most rhesus macaque groups do not typically contest dominance rank, we hypothesized that male GC concentrations would be mainly driven by mating effort, operationalized here by the number of females that conceived in a given month and the number of males within each group that competed over those females. We tested the following four predictions:

- 1) GC concentrations vary in relation to the number of females that conceive within a group: If GC concentrations of top-ranking males are driven by the potential costs associated with mating effort, we expect that GC concentrations will be highest during the months when the most females conceive and to diminish with the number of mates available. The alternative to this prediction is that GC concentrations increase over the course of the mating season, indicating an accumulation of physiological stress and worsening physical condition, rather than being more closely linked to immediate investment in mating effort.
- 2) GC concentrations are higher in alpha males than among other top-ranking males: We predict that alpha males, in particular, will have significantly higher GC concentrations than other top-ranking males. Alpha males are predicted to have priority of mating access,

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