



## Regular article

## Costs of mate-guarding in wild male long-tailed macaques (*Macaca fascicularis*): Physiological stress and aggression



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## ABSTRACT

Mate-guarding is an important determinant of male reproductive success in a number of species. However, it is known to potentially incur costs. The aim of the present study was to assess the effect of mate-guarding on male physiological stress and aggression in long-tailed macaques, a species in which males mate-guard females to a lesser extent than predicted by the Priority of Access model (PoA). The study was carried out during two mating periods on three groups of wild long-tailed macaques in Indonesia by combining behavioral observations with non-invasive measurements of fecal glucocorticoid (fGC) levels. Mate-guarding was associated with a general rise in male stress hormone levels but, from a certain threshold of mate-guarding onwards, increased vigilance time was associated with a decrease in stress hormone output. Mate-guarding also increased male-male aggression rate and male vigilance time. Overall, alpha males were more physiologically stressed than other males independently of mating competition. Increased glucocorticoid levels during mate-guarding are most likely adaptive since it may help males to mobilize extra-energy required for mate-guarding and ultimately maintain a balanced energetic status. However, repeated exposure to high levels of stress over an extended period is potentially deleterious to the immune system and thus may carry costs. This potential physiological cost together with the cost of increased aggression mate-guarding male face may limit the male's ability to mate-guard females, explaining the deviance from the PoA model observed in long-tailed macaques. Comparing our results to previous findings we discuss how ecological factors, reproductive seasonality and rank achievement may modulate the extent to which costs of mate-guarding limit male monopolization abilities.

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## Introduction

Mate-guarding of females by males is a common strategy in a broad range of animal taxa (e.g. insects, Alcock, 1994; reptiles, Censky, 1995; Ancona et al., 2010; crustaceans, Sparkes et al., 1996; birds, Komdeur, 2001; Low, 2006 and mammals, Alberts et al., 1996; Matsubara, 2003; Willis and Dill, 2007). The main function of this behavior is to prevent competitor males from gaining access to reproductively active females (Andersson, 1994), thereby limiting the extent of sperm competition (Birkhead and Moller, 1998). As such, mate-guarding has been shown to significantly increase mating and/or reproductive success of males, in particular high-ranking individuals (Censky, 1995; del Castillo,

2003; Engelhardt et al., 2006; Setchell and Kappeler, 2003). Whereas the fitness benefit of mate-guarding is well established, there is a paucity of empirical data on the costs and limitations of this behavior. Such information is crucial to fully understand the variation in male reproductive skew observed within and across many species (Hager and Jones, 2009). In fact, one of the fundamental parameters in reproductive skew models is the degree of control top ranking males have over reproductive output within the group and thus on male reproductive skew (Clutton-Brock, 1998; Johnstone, 2000; Port and Kappeler, 2010).

In primates, the degree of male reproductive skew varies greatly across species living in multi-male multi-female groups (Kutsukake and Nunn, 2009). Recent studies have combined modeling and meta-analysis to better comprehend the factors driving this striking variation (Gogarten and Koenig, 2013; Kutsukake and Nunn, 2009; Ostner et al., 2008b; Port and Kappeler, 2010). Given that mate-guarding has been proven to significantly enhance mating and/or reproductive success in male primates (rhesus macaques, *Macaca mulatta*, Berard et al.,

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1994; Bercovitch, 1997, long-tailed macaques, *M. fascicularis*, de Ruiter et al., 1994; Engelhardt et al., 2006; Japanese macaques, *M. fuscata*, Matsubara, 2003; and mandrills, *Mandrillus sphinx*, Setchell et al., 2005), this behavior is also likely to be one of the determinants of male reproductive skew. Altmann (1962) developed a verbal model to explain the link between male reproductive skew and mate-guarding in primate species, the Priority of Access model (hereafter the PoA model). This model posits that female cycle synchrony and male rank position are the only limiting factors to female monopolization and hence fully determine male reproductive output. Yet in several primate species, reproductive output and/or mating frequencies are lower than predicted by the PoA model (savannah baboons, *Papio cynocephalus*, Alberts et al., 2003, rhesus macaques, Dubuc et al., 2011, long-tailed macaques, Engelhardt et al., 2006 and Barbary macaques, *M. sylvanus*, Young et al., 2013a). Additional factors other than female monopolisability, such as males' ability to assess the timing of female fertile phases and hence to adjust their mate-guarding activity accordingly (Engelhardt et al., 2006; Fürtbauer et al., 2011; Young et al., 2013b) and energetic and physiological costs (Alberts et al., 1996; Bergman et al., 2005) may further limit male mate-guarding activity and success. The ability of males to discern the female fertile phase has been tested in a number of primate species (chimpanzees, *Pan troglodytes*, Deschner et al., 2004; rhesus macaques, Dubuc et al., 2012; long-tailed macaques, Engelhardt et al., 2004; and Hanuman langurs, *Semnopithecus entellus*, Heistermann et al., 2001). In contrast, the costs of mate-guarding still remain largely unclear for primates and this parameter is still missing in primate reproductive skew models (Port and Kappeler, 2010).

Energetic costs of mate-guarding have been documented in various vertebrate and invertebrate taxa in the form of reduced feeding time and/or efficiency (Censky, 1995; Komdeur, 2001; Ancona et al., 2010; Smith et al., 2013) and body mass loss (Komdeur, 2001; Low, 2006; Schubert et al., 2009). In primates, evidence for these costs is equivocal. Feeding costs of mate-guarding have been documented in long-tailed and Japanese macaques (Matsubara, 2003; Girard-Buttoz et al., 2014), in yellow and chacma baboons (*P. cynocephalus* and *P. hamadryas*, Alberts et al., 1996; Weingrill et al., 2003) and in one study of olive baboons (*P. anubis*, Packer, 1979), but were not found in another study of olive baboons (Bercovitch, 1983) and were also absent in moustached tamarins (*Saguinus mystax*, Huck et al., 2004) and in Assamese macaques (*M. assamensis*, Schülke et al., 2014). Furthermore, reduction in feeding time as a consequence of mate-guarding does not necessarily lead to decreased energetic status as shown recently in long-tailed macaques (Girard-Buttoz et al., 2014). Yet energetic costs may not be the only factor limiting male mate-guarding ability. Physiological stress potentially associated with mate-guarding activity (e.g. Bergman et al., 2005), could also be a cost of this behavior. In fact, maintaining high levels of stress hormones (e.g. cortisol) for prolonged periods can carry high fitness costs in terms of suppression of the immune system (Grossman, 1985; Setchell et al., 2010), reduced sperm production (Hardy et al., 2005; Sapolsky, 1985) and general detrimental effects on an animal's health (Sapolsky, 2002).

In vertebrates, including primates, male-male competition for accessing fertile females is usually associated with a rise in stress hormone levels (glucocorticoids; GC) during the reproductive period (for a review see Romero, 2002, see also Barrett et al., 2002; Fichtel et al., 2007; Girard-Buttoz et al., 2009; Moore and Jessop, 2003; Mooring et al., 2006; Ostner et al., 2008a; Tokarz et al. 1998). In this highly energetically demanding context, cortisol plays a crucial role by stimulating gluconeogenesis and the mobilization of fatty acids from body stores (Sapolsky, 2002). This physiological process might be partly triggered by changes in males' activity budget during the reproductive period whereby males feed less time (see above) and, in some species, spend more time being vigilant (Li et al., 2012; Guillemain et al., 2003; Reboreda and Fernandez, 1997) in order to monitor other males as well as fertile females. This shift in energy budget might represent an energetic challenge since decreased feeding time might lead to reduced

energy intake and vigilance enhances energy expenditure (Warm et al., 2008). In addition to increased energetic needs during periods of strong competition, GC levels may also rise due to the emotional stress of increased aggression rates leading to increased risk of injuries and/or due to injuries themselves. In fact, in vertebrates, mate-guarding behavior is often associated with an increase in aggression rate and/or in time devoted to agonistic interactions (e.g. lemurs, Mass et al., 2009; lizards, Ancona et al., 2010; and birds Steele et al., 2007) and such interactions involve, by nature, a risk of physical injuries (Blanchard et al., 1988; Clutton-Brock et al., 1979; Drews, 1996).

Whereas males in general exhibit a seasonal and/or short term rise in GC levels associated to mating competition, important inter-individual differences in stress hormone levels can be found between males within the same group (Creel, 2001). In primates, these variations are often related to dominance rank, but the direction of the relationship between GC levels and rank can be negative or positive and may be mediated by several factors, e.g. hierarchy stability (Bergman et al., 2005; Higham, et al., 2012; Sapolsky, 1983) or opportunities for social support (reviewed in Abbott et al., 2003). Differences in GC levels between high- and low-ranking individuals may also derive from differential rank-related reproductive strategies. In fact, in many species, only high-ranking males mate-guard females intensively since they are the only ones able to efficiently exclude rival males from accessing the guarded females (Engelhardt et al., 2006; Higham et al., 2011; Setchell et al., 2010; Weingrill et al., 2000). In baboons, GC concentrations vary in accordance with mate-guarding duration and effort at both the inter- (alpha vs. beta males, Gesquiere et al., 2011) and the intra-individual levels (Bergman et al., 2005).

Although a number of studies have focused on the link between stress hormone concentrations, aggression rates and mate-guarding behaviors, these studies only analyzed the global effect of aggression over the whole reproductive period on average individual stress hormone levels. To date, little is known, about the proximate factors driving intra- and inter-individual differences in physiological stress levels accompanying male reproductive competition.

The aim of the current study was therefore to assess whether wild male long-tailed macaques (*Macaca fascicularis*) experience a rise in physiological stress during mate-guarding at the proximate level and, if so, what are the underlying behavioral factors potentially generating this rise. Long-tailed macaques live in multi-male multi-female groups and are non-strictly seasonal breeders (van Schaik and van Noordwijk, 1985). As several other non-strictly seasonal/capital breeder primates from south-east Asia (Brockman and van Schaik, 2005) female long-tailed macaques can conceive year round but conception peaks frequently occur during periods of high fruit availability (van Schaik and van Noordwijk, 1985). As can be expected for non-strictly seasonal breeders (Alberts, 2012), reproductive success is highly skewed towards the alpha male (de Ruiter et al., 1994; Engelhardt et al., 2006). Yet, although males are able to discern a female's fertile phase (Engelhardt et al., 2004), high-ranking males mate-guard females to a lower extent than predicted by the PoA model (Engelhardt et al., 2006). Interestingly, imperfect mate-guarding by dominant males does not seem to derive from any energetic limitations in this species since the energetic status of males is not significantly affected by mate-guarding (Girard-Buttoz et al., 2014). This suggests that other factors are more important in constraining mate-guarding activities in high-ranking males. In a previous study on the same population, we found that long-tailed macaque males exhibit a clear seasonal rise in fecal GC (fGC) levels associated with reproductive effort (Girard-Buttoz et al., 2009), which points to physiological stress levels playing an important role for male-male reproductive competition in this species. Which factors drive intra- and inter-individual differences in physiological stress levels on the proximate level in long-tailed macaques, remains, however, unknown.

In the present study, we used fGC measurements to assess whether mate-guarding effort is associated with an intra-individual rise in

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