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

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A B S T R A C T

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.

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.,

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 (*Saginus 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 interindividual 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

physiological stress levels. In this analysis we also tested for the influence on daily fGC levels of some behavioral parameters known to increase cortisol or fGC levels in human and/or non-human primates, i.e. vigilance, aggression, grooming and copulation rates (Arlet et al., 2009; Cheney and Seyfarth, 2009; Girard-Buttoz et al., 2009; Lynch et al., 2002; McFarland et al., 2013; Ostner et al., 2008a; Ray and Sapolsky, 1992; Surbeck et al., 2012; Warm et al., 2008). We also controlled for the number of males in proximity as an approximation of the degree of male-male competition. Secondly, we assessed the effect of mate-guarding on some behavioral parameters that are known to have an effect on fGC output (i.e. vigilance time and number of male in proximity) as well as on the likelihood of male-male aggression as a possible indicator of the risk of injury for the mate-guarding male. Thirdly, we investigated whether different reproductive tactics, i.e. high versus low investment into mate-guarding, result in inter-individual differences in male physiology by comparing fGC levels of males mate-guarding females extensively (i.e. high-ranking males) with fGC levels of non-mate-guarding males (i.e. low-ranking males). In order to ensure that a potentially detected effect of dominance rank on fGC derives from reproductive competition during mate-guarding and not from competition between males per se, we tested potential rank effects separately during and outside the mating period.

Methods

Animals and study site

The study was carried out on three groups of wild long-tailed macaques living in the primary lowland rainforest surrounding the Ketambe research Station (3°41'N, 97°39'E), Gunung Leuser National Park, North-Sumatra, Indonesia. The forest structure and phenological composition has been described in detail by Rijksen (1978) and van Schaik and Mirmanto (1985). The long-tailed macaques in the area have been studied since 1979 (de Ruiter et al., 1994; Engelhardt et al., 2004; van Schaik and van Noordwijk, 1985). For our study we collected data on three groups: Camp (C), Ketambe Bawa (KB) and Ketambe Atas (KA). For political reason we could not access the field station before January 2010 and after April 2011. Following a 2 month training period we therefore collected data between March 2010 and April 2011. Fecal samples were collected regularly during the entire study period and behavioral data during the two consecutive mating periods (see below). All adult individuals were individually known and well habituated to human observers. The total size of a social group varied from 22 to 58 individuals (see Table 1 for details on group compositions and spatial proximity between the groups). Between January and April 2011, four males migrated back and forth between the groups KA and KB and associated with one of the groups for periods between a few hours up to 3 weeks before migrating back to the other group. The study was conducted completely non-invasively and under the permission of the authorities of Indonesia. We adhered to the Guidelines of the Use of Animals in Research, the legal requirements of Indonesia and the guidelines of the involved institutes.

Behavioral data collection

Behavioral data were collected by C.G-B and six experienced Indonesian and international field assistants. All assistants were trained

by C.G-B for two months and inter-observer reliability was assessed repeatedly based on behavioral observations collected simultaneously by two observers on the same focal animal (measurement of agreement kappa > 0.8 for each assistant). The observations covered part of two mating periods. Each mating period was defined as the period between the first mate-guarding day and the last mate-guarding day ever observed during our study period, in any of the three groups, by any male. It is important to note that, since we could not collect systematic focal behavioral data before March 2010 and after April 2011 (see above), we do not know whether males mate-guarded females before March 2010 or after April 2011. The length and limit of the two mating periods are therefore defined as per our study period and limited by our ability to access the field site and are most likely shorter than the "true" mating periods during which males mate-guarded females. From March to July 2010, four observers followed groups C and KB every day and from December 2010 until April 2011, all three groups were generally followed every other day and frequency of observation increased to every day when alpha and/or beta males were observed mate-guarding.

Each day, groups were followed from dawn to dusk. We collected focal behavioral observations solely on alpha and beta males because they are known to mate-guard females most extensively (Engelhardt et al., 2006). All behavioral data were recorded using a handheld computer Psion Workabout Pro (Teklogix®). Every evening, the identity of the males to observe the next day was determined based on the mate-guarding activity of each male and on whether they were followed or not that day. Males were then followed half or full day depending on the number of observers available and on the number of males to follow (see Table 2 for details on observation time for each focal male). On each observation day, one observer was solely responsible for the entire focal protocol of one male.

The activity of the focal animal was recorded every minute using instantaneous sampling (Altmann, 1974) and comprised the following categories: resting, being vigilant, feeding, drinking, travelling, aggressing, affiliating, grooming and self-grooming (see Table 3 for the definition of the different activities). We recorded "vigilance" only when males were not feeding or grooming at the same time in order to 1) limit the degree of personal interpretation by the different observers by clearly defining mutually exclusive categories and 2) avoid recording "foraging vigilance" which often occurs during feeding when animals look around their surrounding environment to seek for food and not to monitor social partners. In addition, when the focal male was moving but paused more than once every minute to monitor his surrounding environment, and if the male was not feeding, the activity of the male recorded was "vigilance" and not "travelling". The mate-guarding behavior of the focal male and the distance between him and the mate-guarded female was also recorded every minute. Whether a male was mate-guarding or not a female on a given minute was coded

Table 1
Composition and neighboring groups of the study groups.

Group	N females	N males	N total	Neighboring groups
Camp	14-15	6-9	54-58	Ketambe Bawa
Ketambe Bawa	9-10	4-8	31-36	Camp and Ketambe Atas
Ketambe Atas	7	4-7	22-25	Ketambe Bawa

Table 2
Observation time, mate-guarding period length and number of females mate-guarded by the study males. MG refers to mate-guarding. MG days refers to days during which the males were mate-guarding female for more than 50% of observation time. The overall MG time is the percentage of observation time during which the male was mate-guarding females.

Group	Camp		Ketambe Atas		Ketambe Bawa	
Male rank	α	β	α	β	α	β
Number of mating periods	2	2	1	1	2	2
Focal observation time (hours)	668	455	185	111	388	323
Number of days of observation	147	114	68	48	122	85
Number of fecal samples	81	47	34	24	52	35
Number of females mate-guarded	5	3	3	2	8	5
Number of MG days	41	4	30	27	49	10
Mean MG period length (days)	3.9	1	4.9	9	3.7	1.5
Range of MG period length (days)	1-18	1-1	1-13	1-33	1-10	1-4
Overall MG time	27.4%	8.4%	40.2%	53.9%	36.9%	12.0%

Table 3
Definitions of the different type of activity recorded during the 1 minute focal scans.

Activity	Definition
Resting	Being still and while not looking into different directions and/or interacting socially with any other individual
Being vigilant	Monitoring the surrounding environment by looking in different directions, being either still or moving, and while not involved in feeding or social activity
Feeding	Handling or consuming food
Drinking	Ingesting water
Travelling	Continuous locomotion during at least one minute with no foraging activity and no social interactions
Aggressing	Being engaged in any type of agonistic interaction (i.e. threatening, chasing, hitting and biting)
Affiliating	Being engaged in any type of affiliative interaction (male-male mount, male–female copulation, lip-smacking, embrace)
Grooming	Grooming or being groomed by one or several other individuals
Self-grooming	Grooming itself

a posteriori. A male was considered as "mate-guarding" when he followed a sexually active female for more than 5 consecutive minutes and maintained a distance of less than or equal to 10 m between him and the female. A female was considered sexually active if she was observed copulating at least once on a given day. If the female moved away from the male and the male did not follow her for more than 2 minutes the mate-guarding activity was considered to have ended. Daily mate-guarding time was quantified as overall time spent mate-guarding any female regardless of whether the male mate-guarded the same female for the entire day or different females consecutively. In addition, all copulations and aggressions (including submissive expressions) between any adult individuals were recorded (all occurrence sampling for the focal male and ad libitum for all the other individuals). Aggressions comprised threatening, chasing, hitting and biting. Finally, the identities of all males within 10 m of the focal individual were recorded every 5 minutes.

Determination of fruit availability

The primary function of a rise in GC levels is to mobilize energy from fat storage to insure that vital energetic needs of individuals are fulfilled (Sapolsky, 2002). In periods of high fruit availability frugivorous primates (such as long-tailed macaques) have access to high quality food and hence have a high energy intake and are in a condition of positive energy balance. Under such condition, males do not need to mobilize energy from fat storage and their fGC levels are lower than in periods of low food availability (e.g. Muller and Wrangham, 2004). Given the effect of fruit availability on GC levels it was important to control for this parameter in our analysis and we monitored fruit trees to assess it. In each of the three studied groups, 40 locations, covering the entire home ranges, were randomly selected (120 locations in total over the three territories). To select these locations, we drew a grid of 25x25 m squares on the map of each territory. We then numbered each intersection of the grid lines within the territory. We randomly selected 40 of these intersects which constituted our 40 random locations. At each location, three trees were randomly selected from three different species among the tree species producing fruit eaten by *M. fascicularis* (Ungar, 1995). In total 360 trees, from 87 different species were selected (120 trees for each group's home range). Each tree was surveyed monthly, within the last 3 days of every month, by a field assistant experienced in phenology and fruit abundance was recorded using a logarithmic scale (**0**: absence, **1**: 1–10 items, **2**:11–100, **3**:101–1000, **4**:1001–10000, **5**: >10000). The average monthly score of fruit abundance in each territory was highly correlated with the percentage of trees fruiting. For the analyses, we therefore used percentage of trees fruiting as an index of fruit availability. This index was computed for

each study group separately using the 120 trees surveyed in each of their home ranges.

Fecal sample collection and hormone analysis

Fecal samples were generally collected from March 2010 until April 2011 once a week from four males in each group: alpha and beta males and two low-ranking males (rank 3 and below) as "controls" (males which usually do not mate-guard females extensively, Engelhardt et al., 2006). For low-ranking males we selected the two non-alpha non-beta males which were the ones most often present in the group during the 6 months preceding the data collection period. In addition, we collected fecal samples every third day from the mate-guarding male during each mate-guarding period and the two days following these periods (to account for the on average 36 h time-lag fGC excretion in long-tailed macaques; Heistermann et al., 2006). Right after defecation, samples were homogenized and 2–3 g of feces were collected and stored in a polypropylene vial and placed on ice in a thermos bottle. At the end of each fieldwork day, the samples were frozen at −20 °C in a freezer. In July 2011, all samples were transported, on ice, to the Hormone Laboratory of the Bogor Agricultural University (IPB) and then freeze-dried and pulverized before transportation to the Endocrinology Laboratory of the German Primate Centre for analysis.

For fGC analysis, an aliquot (50–70 mg) of the fecal powder was extracted within 3 ml of 80% methanol by vortexing for 10 min (Heistermann et al., 1995). Fecal extracts were analyzed for immunoreactive 3α,11ß-hydroxyetiocholanolone (3α,11ß-dihydroxy-CM), a group-specific measurement of 5-reduced 3α,11ß-dihydroxylated cortisol metabolites (Ganswindt et al., 2003; Möstl and Palme, 2002). The assay has been previously validated for assessing adrenocortical activity from feces in long-tailed macaques (Heistermann et al., 2006). Hormone measurements were carried out by microtiter plate enzymeimmunoassay according to methods previously described (Ganswindt et al., 2003; Girard-Buttoz et al., 2009). Intra- and inter-assay coefficients of variation of high- and low- value quality controls were 8.9% and 9.9% (high) and 6.3% and 14.3% (low), respectively.

Statistical analyses

For all analyses, we considered only days of observation for which at least 1 hour of focal data was recorded. The final data set thus comprised 2,088 hours of focal observations over 600 days (see Table 2 for detail about observation and mate-guarding time).

Influence of mate-guarding and other behaviors on male fGC levels

For each day, we calculated the percentage of observation time spent mate-guarding, grooming and being vigilant by each focal male. We also calculated, every day, the copulation rate (i.e. number of copulation between the focal male and any female per hour), the rate of male-male aggression (i.e. the number of aggression between the focal male and any other adult male per hour) and the number of males in proximity (defined as the average number of males within 10 m per 5 minute scan). For the calculation of aggression rates, both aggressions given and received were considered. We also calculated the number of sexually active females in each group on each observation day.

We tested whether, on a given day, males' stress hormone levels (as assessed by fGC measures) was influenced by 1) the percentage of time spent mate-guarding, 2) vigilance time 3) grooming time, 4) aggression rate and 5) copulation rate using a generalized linear mixed model (GLMM, Baayen, 2008) (model 1). Vigilance and grooming time were computed as percentage of observation time. Since the time-lag for excretion of glucocorticoid metabolites into the feces is on average 36 h in long-tailed macaques (Heistermann et al., 2006), we matched behavioral observations with fGCs levels measured in samples collected at either day +1 or day +2 after the observations. When samples were available

at both days, we used the mean fGCs levels of the two samples. The fGC level values were log-transformed to achieve a symmetric distribution and we used a Gaussian error structure in the model. To account for the degree of male-male competition for access to receptive females and the potential for male-male interaction we included, as control factors, the number of sexually active females and the number of males in proximity in this model. Since ecological conditions are likely to affect fGC levels in primates (Muller and Wrangham, 2004), we also included fruit availability as a control factor in model 1. Fruit availability on a given day was approximated using the fruit availability measured on the closest monthly record. For example, the percentage of tree fruiting recorded on the 31st of January was used as the fruit availability score for all the days between the 16th of January and the 15th of February. Finally, we included sample storage length (i.e. number of days between sample collection and sample lyophilisation) to account for any possible storage effect of fGC measures and focal observation time (in minutes) to account for the differences in the degree of accuracy in the estimation of daily behavioral parameters and mate-guarding time related to matched hormone samples.

Since mate-guarding may have an influence on the fGC levels only in a context of high male-male competition (high aggression rate, many number of males around and/or long time spent being vigilant), in model 1, we tested for the significance of the interactions between mate-guarding time and 1) aggression rate, 2) number of males in proximity and 3) time being vigilant. Only the latter was significant (likelihood ratio test, P < 0.05) and kept in the final model. Male ID and group were included in model 1 as nested random effects.

Influence of mate-guarding on vigilance, proximity of other males and likelihood of male-male aggression

In order to better understand the potential behavioral sources of physiological stress during mate-guarding we analyzed the effect of mate-guarding on the parameters which had a significant effect on fGC levels - i.e. vigilance time (although through an interaction with mate-guarding time) and number of males in proximity (see Table 4 and result section). In addition we also tested the effect of mate-guarding on the likelihood of male-male aggression as a possible indicator of the risk of injury. We used GLMMs to test whether the percentage of time spent mate-guarding on a given day affected the following parameters in the males: 1) vigilance time (model 2), 2) number of males in proximity (model 3), and 3) likelihood of aggression with other males (model 4). Similar to model 1 we included as control factors fruit availability and the number of sexually active females in all models and the number of males in proximity in models 2 and 4. Male ID and group were included in each model as nested random effects.

The rate of male-male aggressions in our study subjects was very low (0.22 ± 0.04 h^{-1}) and no aggression was recorded on most of the observation days (366 out of 600). Because the resulting distribution of daily aggression rate was thus highly zero inflated, we could not run a model with a Gaussian error structure. We thus first calculated daily male-male aggression rate as in model 1 and then coded each day with at least one aggression as an aggression day and other days as non-aggression day and used a model with a binomial error structure to test the influence of mate-guarding on the likelihood of aggression with other males on a given day (model 4). We considered both aggressions given and received by the focal animal. For the other models we used a Gaussian error structure since the response variable was symmetrically distributed. The likelihood of recording any male-male aggression on a given day being dependent on the observation time that day, we included observation time (in minutes) as a control factor in model 4.

Influence of mating period and dominance rank on male fGC levels

In long-tailed macaques, alpha and beta males are known to be the only ones using mate-guarding as their primary mating tactic (Engelhardt et al., 2006) while other males usually access females through sneaky copulations (de Ruiter et al., 1994). To test whether reproductive activity in general and male mating tactic in particular influence inter-individual variation in fGC levels, we analyzed the effect of dominance rank (as a proxy for primary mating tactic type) and of period (mating vs. non-mating periods) on fGC levels. We used a GLMM with Gaussian error structure (model 5) including fGC levels as response, male dominance rank (two categories: high-ranking for alpha and beta males, and low-ranking for two other males in the same group), period (mating, non-mating) and the interaction between the two as fixed factors, fruit availability and sample storage length as control fixed effects and animal ID and group as nested random factors. Dominance ranks between males were determined using the 'bared-teeth-face' display, a unidirectional submissive display (van Hooff, 1967). Bared-teeth-face giver and receiver were entered into a

Table 4
Results of the Likelihood-ratio-tests (LRT) run to compare full versus null models, an index of the percentage of variance explained by fixed and random factors for each model ($R^2_{GLMM\ (c)}$, for details see Nakagawa and Schielzeth 2013), estimates $\pm$ SE, t-value/Z-value and p-values for the different GLMMs run to test the influence of mate-guarding activity and other behavioral parameters on fGC levels and of mate-guarding on behavioral parameters. "MG" refers to mate-guarding, "N. males" to the number of males in proximity, "N. sex. act. fem." to the number of sexually active females and "AC term" to the autocorrelation term.

	Model 1			Model 2			Model 3			Model 4		
	fGC levels			Vigilance time			N. males			Aggression (Y/N)		
N. obs. days	273			600			600			600		
Null vs. full model	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P
	3	25.53	<**0.001**	1	15.17	<**0.001**	1	6.97	**0.008**	1	11.23	<**0.001**
$R^2_{GLMM\ (c)}$	0.515			0.079			0.196			0.319		
	Estimate $\pm$ SE	t	P_{MCMC}	Estimate $\pm$ SE	t	P_{MCMC}	Estimate $\pm$ SE	t	P_{MCMC}	Estimate $\pm$ SE	Z	P
Intercept	6.11 ± 0.08	71.94	<**0.001**	42.72 ± 0.83	51.46	**0.003**	0.50 ± 0.05	10.51	**0.004**	-0.54 ± 0.15	-3.56	<**0.001**
MG time	in an interaction in			1.87 ± 0.46	4.01	<**0.001**	0.02 ± 0.01	2.65	**0.009**	0.35 ± 0.10	3.45	<**0.001**
N. males	-0.06 ± 0.03	-2.23	**0.031**	-1.23 ± 0.45	-2.71	**0.016**				0.52 ± 0.10	5.05	<**0.001**
% tree fruiting	-0.25 ± 0.04	-6.52	<**0.001**	0.24 ± 0.52	0.45	0.521	-0.04 ± 0.01	-3.71	<**0.001**	-0.11 ± 0.12	-0.92	0.358
N. sex. act. fem.	0.08 ± 0.03	2.36	**0.017**	1.07 ± 0.48	2.23	**0.025**	0.04 ± 0.01	3.93	<**0.001**	0.15 ± 0.11	1.31	0.191
AC term	-0.04 ± 0.03	-1.489	0.152	2.90 ± 0.43	6.75	<**0.001**	0.03 ± 0.01	3.13	**0.003**			
Observation time	0.01 ± 0.03	0.39	0.711							0.85 ± 0.12	6.87	<**0.001**
Copulation rate	-0.01 ± 0.03	-0.33	0.761									
Aggression rate	0.03 ± 0.03	1.27	0.207									
Grooming time	0.02 ± 0.03	0.62	0.569									
Vigilance time	in an interaction											
Storage length	-0.08 ± 0.04	-1.98	**0.050**									
MG * Vigilance	-0.05 ± 0.03	-1.92	**0.037**									

sociometric matrix and dominance ranks were compiled with Matman 1.1.4 using the I&SI method (de Vries, 1998). All hierarchies were linear with a directional consistency index of 1 for the three groups and a Landau's linearity index varying between 0.6 and 1. In addition, to test whether being an alpha male is particularly stressful (Gesquiere et al., 2011), we ran another GLMM (model 6) using the same factors and error structure but the dominance rank categorization was modified as either alpha or other males. Since the interaction between dominance rank and period was not significant in both models (LRT, P > 0.4), we reran the models without the interaction.

Autocorrelation term and assumptions' checking

Each model was fitted in R 2.15.0 (R Development Core Team 2010) using the function lmer of the R-package lme4 (Bates and Maechler, 2010). The response variable in the different models with Gaussian error structure (models 1, 2, 3, 5 and 6) was likely to show temporal autocorrelation unexplained by the fixed effects included, potentially leading to violation of the assumption of independent residuals. Therefore, we included a temporal autocorrelation term into these models using an approach developed by Roger Mundry (see Fürtbauer et al., 2011).

In each model, we checked that the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. We checked for model stability by excluding data points one by one from the data and comparing the estimates derived with those obtained for the full model. Variance inflation factors (Field, 2005) were derived using the function vif of the R-package car (Fox and Weisberg, 2010) applied to a standard linear model excluding the random effects. VIF's which are less than 5 indicate that covariation between the predictors is not a problem (Bowerman and O'Connell, 1990; Myers, 1990). In all our models VIF's were less than 1.7. The other diagnostics also did not indicate obvious violation of the assumption.

For each model, we first determined the significance of the full model as compared to the corresponding null model using a likelihood ratio test (R function anova with argument test set to "Chisq"). For each model we also calculated the goodness of fit of the model to the data using a method recently developed by Nakagawa and Schielzeth (2013). We calculated the $R^2_{GLMM\ (c)}$ (c stands for conditional) which indicates the variance explained by both fixed and random factors (for details see Nakagawa and Schielzeth 2013). $R^2_{GLMM\ (c)}$ ranges from 0 to 1 where 1 represents a perfect fit of the model to the data. To achieve a more reliable P-value, we fitted the models using Maximum Likelihood rather than Restricted Maximum Likelihood (Bolker et al., 2009). Only if this likelihood ratio test revealed significance we considered the significance of the individual predictors. P-values for the individual effects were based on Markov Chain Monte Carlo sampling (Baayen, 2008) and derived using the functions pvals.fnc and aovlmer.fnc of the R package languageR (Baayen, 2010).

Results

Mate-guarding activity

In each of the three groups, the alpha male mate-guarded a higher number of females than the beta male (Table 2). Males mate-guarded each female on average 4 consecutive days (range 1–33, Table 2) and on average 29.8% (range 8.4 - 53.9%, Table 2) of their time was devoted to this behavior in general over the entire mating periods. A summary of the interrelationships between the variables tested in models 1–4 is presented in Fig. 1 (see below and Tables 4 and 5 for details on the statistical results).

Mate-guarding, male behavior and fGC levels

Overall, males had higher fGC levels when mate-guarding females than when not (model 1, Fig. 2). However, model 1 indicates that the effect of mate-guarding on fGC levels was significantly affected by the amount of time a male was vigilant during these days (N = 273 days, interaction between vigilance and mate-guarding time, P = 0.037, Table 4, Fig. 2). On days on which males did not mate-guard females, male fGC levels increased with the amount of time a male was vigilant. In contrast, on days on which males mate-guarded a female, increase in vigilance time was associated with a decrease in fGC levels and this effect was stronger the more time males spent mate-guarding females. Yet fGC levels while mate-guarding females were always above non-mate-guarding values.

Of the other variables tested in model 1, the number of sexually active females, the number of males in proximity and fruit availability also had a significant effect on fGC levels (all P < 0.05, Table 4) whereas
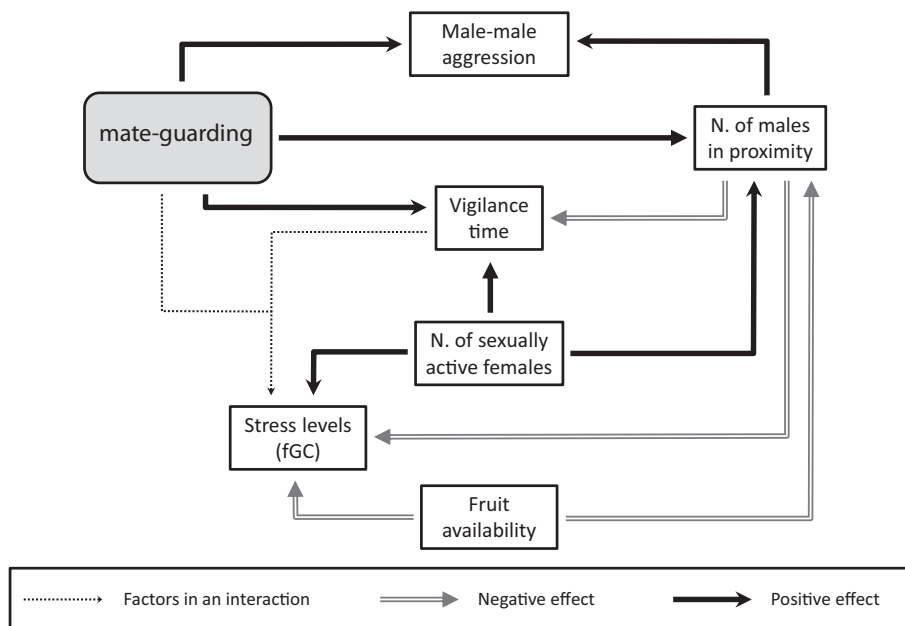
Fig. 1. Summary of the interrelationships between mate-guarding and the different behavioral, physiological, social and ecological parameters analyzed in models 1–4. For simplicity only the significant effects are presented. "N." indicates "number of".

Table 5

Results of the Likelihood-ratio-tests (LRT) run to compare full versus null models, R^2_{GLMM} (c) estimates ± SE, t-value and MCMC p-values for the two GLMMs run to test the influence of dominance rank and period (mating or non-mating) on fGC levels. In model 5 dominance rank is categorized as high (alpha + beta males) or low (other males) and in model 6 as alpha or other males. AC term refers to the autocorrelation term.

	Model 5			Model 6		
	fGC levels			fGClevels		
	Rank: High (α + β) vs. low (others)			Rank: Alpha vs. others		
Null vs.	df	χ^2	P	df	χ^2	P
full model	2	134.57	**<0.001**	2	137.79	**<0.001**
$R^2_{GLMM (c)}$	0.476			0.482		
	Estimate ± SE	t	P_{MCMC}	Estimate ± SE	t	P_{MCMC}
Intercept	5.79 ± 0.11	54.86	**<0.001**	5.97 ± 0.12	47.88	**<0.001**
Rank (others)	−0.09 ± 0.14	−0.69	0.443	−0.30 ± 0.14	−2.14	**0.035**
Period (mating)	0.41 ± 0.03	13.16	**<0.001**	0.41 ± 0.03	12.08	**<0.001**
% tree fruiting	−0.23 ± 0.02	−13.16	**<0.001**	−0.23 ± 0.02	−13.13	**<0.001**
Storage length	−0.06 ± 0.02	−3.31	**0.001**	−0.06 ± 0.02	−3.23	**0.001**
AC term	0.17 ± 0.01	11.38	**<0.001**	0.17 ± 0.01	11.42	**<0.001**

copulation rate, male–male aggression rate and grooming rate did not (all P > 0.2, Table 4). Male fGC levels increased with increasing numbers of sexually active females, with declining numbers of males in proximity and with diminishing fruit availability (Fig. 1).

Since we also found that mate-guarding itself enhances the likelihood of male–male aggression (see below); we wanted to ensure that the absence of a significant relationship between male–male aggression and fGC levels in our study males was not due to a covariation issue between the factors mate-guarding and male–male aggression rate in model 1 whereby the effect of mate-guarding would mask the effect of aggression. We built a new model (model 1b) including all the factors from model 1 except of "mate-guarding" and "vigilance" (vigilance could not be included as single factor in this new model since its effect on fGC levels is contingent on mate-guarding time). The null model comprised all factors from model 1b except of "male–male aggression rate". The full model was not significant from the null model (χ^2 = 1.37, df = 1, P = 0.242), confirming the absence of a significant effect of male–male aggression rates on fGC levels in our study males.

Mate-guarding, male behavior and proximity of other males

The amount of time a male spent mate-guarding had a significant positive effect on vigilance time (model 2, N = 600 observation days, P < 0.01, Table 4). In other words, the more time a male spent mate-guarding the more vigilant he was (Fig. 3a). Independent of whether
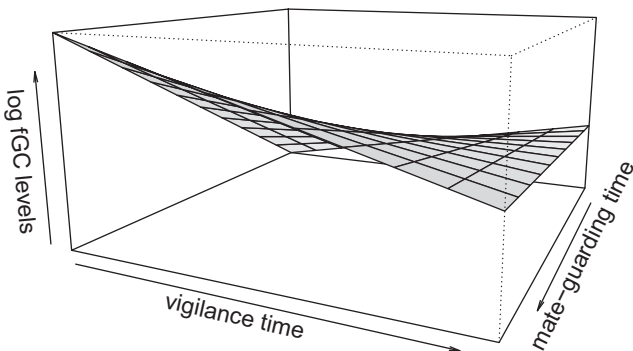
Fig. 2. Effect of mate-guarding time and vigilance time on fGC levels. The plane depicts values predicted by model 1.

and how much a male spent time on mate-guarding, increasing numbers of sexually active females also increased vigilance behavior in males (model 2, P = 0.025, Table 4, Fig. 1). Vigilance however decreased with increasing numbers of males in proximity (model 2, P = 0.016, Table 4, Fig. 1).

Mate-guarding also significantly increased the number of males in proximity and the likelihood of male–male aggression (models 3 and 4, both P < 0.01, Table 4, Fig. 3b and 3c). The latter may have been interdependent, because increasing numbers of males in proximity increased the likelihood of male–male aggression even independent of mate-guarding (model 4, P < 0.01, Table 4, Fig. 1).

Finally, the number of males in proximity was also significantly affected by the number of sexually active females (model 3, P < 0.01, Table 4). Males were more cohesive the more sexually active females were present in the group (Fig. 1).

Dominance rank, period, fruit availability and fGC levels

Males had significantly higher fGC levels during the mating than during the non-mating periods (models 5 and 6, N = 771 samples, P < 0.001, mean ± SE mating periods: 573.9 ± 44.4 ng/g feces, mean ± SE non-mating period: 412.5 ± 45.3 ng/g feces, Table 5, Fig. 4a). There was no significant difference between high-ranking (alpha and beta) and low-ranking (all others) males in fGC levels (model 5, P = 0.443, Table 5, Fig. 4b). However, alpha males alone had significantly higher fGC levels than other males, independent of period and fruit availability (model 6, P = 0.035, Table 5, Fig. 4c). Fruit availability in turn had a highly significant negative effect on fGC levels independent of period and male rank (models 5 and 6, P < 0.001, Table 5).

Discussion

Our results suggest that mate-guarding carries physiological costs in male long-tailed macaques that may limit mate-guarding stamina and lead to the observed imperfect pattern of mate-guarding by dominant males (see Engelhardt et al., 2006). In our study, males generally faced increased stress hormone (fGC) levels when mate-guarding females. Repeated exposure to high GC levels over an extended period may have deleterious impacts on male immunity and reproduction (Grossman, 1985; Hardy et al., 2005; Sapolsky, 1985; Sapolsky, 2002; Setchell et al., 2010, but see Boonstra, 2013) and may as such constitute a cost. The effect of mate-guarding on fGC levels however interacted with vigilance: from a certain degree of mate-guarding onwards an increase of vigilance time was associated with a reduction in stress hormone levels. Mate-guarding also increased the rate with which males were involved in aggressive interactions with other males. Although aggression did not significantly affect male fGC levels, increased aggression brings an extra risk of injury. Mate-guarding male long-tailed macaques may thus bear potential physical costs as well.

Altogether, male long-tailed macaques appear to be physiologically stressed during mate-guarding (as indicated by our measure of fGC levels), which confirms similar findings in chacma baboons (Bergman et al., 2005). Whereas in primates a rise in fGC levels often results from increased aggression and copulation rates (Arlet et al., 2009; Girard-Buttoz et al., 2009; Lynch et al., 2002; Ostner et al., 2008a; Ray and Sapolsky, 1992; Surbeck et al., 2012), two behaviors that generally accompany male mate-guarding activities, this was not the case in our study males. Given the limited sample size in our study (only six males) we cannot fully exclude that the absence of significant effects of copulation and male–male aggression on male fGC levels result from the lack of statistical power. Yet some other biological factors may explain the increased fGC levels during-mate-guarding in our study subjects.

For example, the increase in fGC observed may be triggered by the need for males to maintain a balanced energetic status (Girard-Buttoz
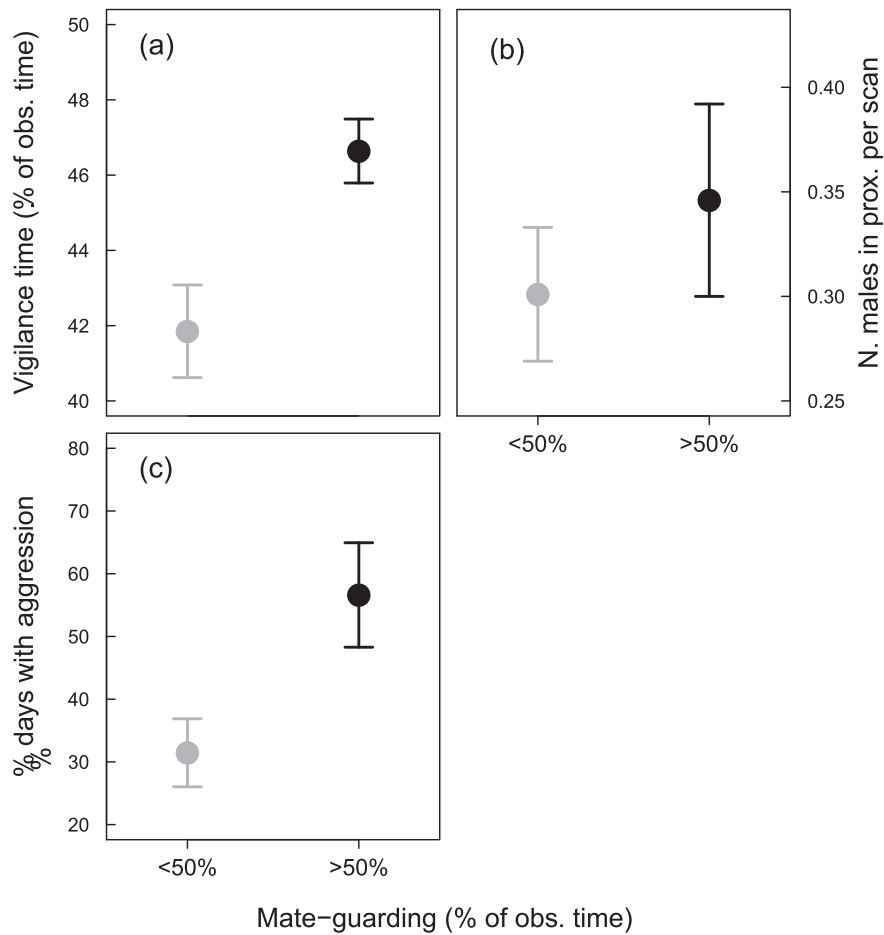
Fig. 3. Influence of mate-guarding intensity on a) males' vigilance time, b) number of males in proximity, and c) percentage of day with male-male aggression. Grey dots depict results from days in which males spent <50% of observation time mate-guarding and black dots those in which they did this >50% of observation time. The mean ± SE over all males is depicted for each of the parameters. Please note that these graphs are no substitute for the statistical models presented in Table 3.

et al., 2014) in a context in which they trade-off feeding time (Girard-Buttoz et al., 2014) against vigilance time (this study). Glucocorticoids may provide the male with more readily available energy (Sapolsky, 2002) used to compensate for the reduced food intake (Girard-Buttoz et al., 2014) and that may also be allocated towards vigilance, which is by nature energetically demanding and stressful (Warm et al., 2008).

Similar to long-tailed macaques during mate-guarding, other mammals commonly trade-off feeding time/efficiency against vigilance (Fortin et al., 2004; Illius and Fitzgibbon, 1994) and males of diverse taxa are, generally, more vigilant during the reproductive season (birds, Reboreda and Fernandez, 1997; mammals, Li et al., 2012) and particularly when paired to females (Guillemain et al., 2003). Overall, increased
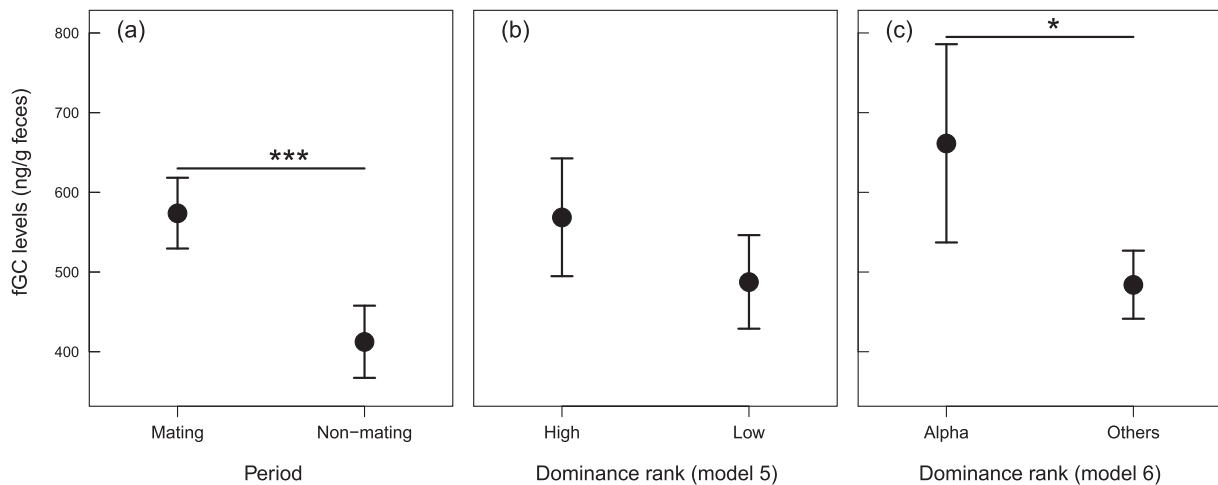
Fig. 4. Influence of period (a) and rank (b and c) on fGC levels. The mean ± SE fGC levels over all males in each of the periods (mating and non-mating) (a) and the mean ± SE fGC levels over males in each rank category as defined in model 5 (b) and in model 6 (c) are also depicted. In model 5 dominance rank is categorized as high (alpha + beta males) or low (other males) and in model 6 as alpha or other males. * P = 0.029, *** P < 0.001.

vigilance derives from the need to monitor conspecifics in a highly competitive context. In long-tailed macaques, however, increased vigilance time during mate-guarding might not be directly linked to male-male competition since males were less vigilant when more males where in proximity (discussed below). In many taxa, increased vigilance is associated with increased predation risk (Quenette, 1990). Yet, in our study, males had more males in proximity while mate-guarding females and hence most likely faced a lower predation risk. We therefore argue that increased vigilance during mate-guarding might serve the male to better prepare for females attempt to escape, particularly since females are promiscuous and often seek to copulate with multiple males (de Ruiter et al., 1994).

Interestingly, from a certain degree of investment into mate-guarding, our study males had higher fGC levels when they were less vigilant. The lack of vigilance while mate-guarding females intensively may generate psychological stress in male long-tailed macaques steaming from the fear of failing to monopolize the female efficiently. It is known for humans and non-human primates that the stress response might be strongly influenced by the perceived degree of control individuals have over their environment (Levine and Ursin, 1991; Marmot, 2004; Ray, 2004; Crockford et al., 2008). In long-tailed macaques, being more vigilant during mate-guarding may enhance a male's perception of the control he has over the females which may in turn lead to the observed decrease in stress hormone levels under condition of high levels of vigilance. In addition, the fact that this effect is most pronounced when males mate-guard the female most intensively might be related to the reproductive value of the guarded female. Male long-tailed macaques mate-guard more intensively high-ranking than low-ranking females (i.e. female producing higher quality offspring more likely to survive until adulthood and to achieve high-rank in the future, Engelhardt et al., 2006; van Noordwijk and van Schaik, 1999). Furthermore, high-ranking males can reliably assess the female fertile phase and increase their mate-guarding effort around this period (Engelhardt et al., 2006). The importance/quality of the female may thus be a source of additional psychological stress.

In addition to its effect on the male physiological stress response, similar to other vertebrates (e.g. mammals, Mass et al., 2009; reptiles, Ancona et al., 2010; and birds Steele et al., 2007), mate-guarding also had a positive effect on male-male aggressions. We did not measure injuries systematically in our study animals, but aggression is known to inherently increase the risk of injury in vertebrates (Blanchard et al., 1988; Clutton-Brock et al., 1979; Drews, 1996). In line with our prediction, we show that in long-tailed macaques, a capital breeder species with a low degree of female cycle synchrony (Engelhardt et al., 2006), males are more likely to engage in male-male aggressions during mate-guarding. In capital breeders, the guarded female is often the only fertile female in the group (e.g. Engelhardt et al., 2006), thus further concentrating male-male competition. In income breeders, in contrast, several females can be sexually receptive at the same time so that several high-ranking males may concurrently access different females, which may lead to a reduction in intensity of male-male competition. Surprisingly, in our study, male-male aggression rate did not significantly influence male fGC levels, although increased aggression rate during male-male competition for access to mates often leads to a concurrent increase in fGC levels in primates (e.g. Arlet et al., 2009; Ostner et al., 2008a; Surbeck et al., 2012). This might be explained by the overall low rate of aggression observed in our study males ($0.2\ h^{-1}$). Increased aggression rate during mate-guarding may thus not in itself dramatically impact male stress physiology. It may constitute, however, a physical cost since, in long-tailed macaques, male-male aggressions sometimes result in severe injuries directly impairing male ability to mate-guard females. For example, during our study period, two high ranking males (one alpha and one beta) from two different groups got severely injured and had to isolate themselves socially from the group for over a week to recover. During this period, they did not access/mate-guard females despite the presence of sexually active females in the group.

In our study, males had more males in proximity on mate-guarding days than on other days most likely resulting from males' interest in the guarded female. Interestingly, although mate-guarding increased aggression between males, having more males around during mate-guarding reduced male stress hormone levels. This result might partly derive from our definition of vigilance which were "monitoring the surrounding environment by looking in different directions, being either still or moving, and while not involved in feeding or social activity". This definition aimed at creating mutually exclusive activity categories and hence at avoiding recording under "vigilance" the monitoring of surrounding directly associated with foraging or grooming itself. Yet our definition is relatively broad and we could not assess whether males where monitoring other conspecifics or being vigilant against predators. Therefore, it may be that the presence of other males in proximity provides a mate-guarding male with the benefit of collective vigilance against predators (reviewed in Elgar, 1989 and Quenette, 1990) and/or extra-group males attempting to enter the group and access females (e.g. Engelhardt et al., 2006). Our finding that our study males were less vigilant when they had more males in proximity supports this idea. The presence of other male group members may thus alleviate the need to monitor the surrounding and better focus on monitoring the guarded female hence reducing his physiological stress levels since guarded females may more effectively be controlled. This might be particularly the case in a species like long-tailed macaques where alpha male tenure and male residence duration are relatively long (on average 25 and 45 months respectively, van Noordwijk and van Schaik, 2001), which provides the opportunity for stable long-term alliances and coalitionary support against extra-group males. Under such conditions and in periods of hierarchy stability (as in our study), group males can thus be allies rather than challengers so that their presence will be beneficial to high-ranking males. The presence of other males may function as kind of "social buffering" (i.e. the presence of known social partners moderates the rise in GC levels in response to a stressor, reviewed in Hennessy et al., 2009) by modulating high-ranking perception of the degree of control they have over their environment (see above).

Beyond the direct effect of mate-guarding on male fGC levels, in our study, all males (i.e. mate-guarding and non-mate-guarding males) were in general more physiologically stressed during the mating periods than during the non-mating ones confirming previous finding in the same population (Girard-Buttoz et al., 2009). This pattern is in line with many studies in vertebrates that found a clear rise in glucocorticoid levels during the reproductive period (Barrett et al., 2002; Fichtel et al., 2007; Moore and Jessop, 2003; Mooring et al., 2006, for a review see Romero, 2002). Interestingly, being at the top of the dominance hierarchy appears to be physiologically stressful for male long-tailed macaques independently of competition for access to females. In our study, alpha males had significantly higher fGC levels than other males in the group during but also outside of the mating season. A similar finding has been recently shown for savannah baboons (Gesquiere et al., 2011). Alpha male long-tailed macaques maintain their rank through contest competition (van Noordwijk and van Schaik, 1985) and face the risk of rank challenges year-round. In contrast, in species in which males attain high dominance status through succession, such as rhesus macaques (Berard, 1999), dominance rank influences fGC levels only during a period of the reproductive season with an unstable dominance hierarchy (Higham, et al., 2012). These differences illustrate how the process of rank achievement may modulate the relationship between dominance rank and stress hormone levels in primates and potentially in other group living mammals as well.

The potential physiological and physical costs of mate-guarding and the cost of being alpha-male per se may altogether explain, at least partially, the deviation from the PoA model observed in long-tailed macaques (Engelhardt et al., 2006). Whereas short term increases in glucocorticoid levels during mate-guarding is most likely a proximate adaptive mechanism favoring the maintenance of a balanced energetic

status (Girard-Buttoz et al., 2014, see also discussion above), long-term exposure to high cortisol levels can be highly deleterious for the males. Chronic stress may suppress the immune system (Grossman, 1985; Setchell et al., 2010) and testicular function (Hardy et al., 2005; Sapolsky, 1985) and hence affect males' health and ability to reproduce. In long-tailed macaques, the need for the males to prevent the detrimental effects of aggression and exposure to chronic stress may prevent them from mate-guarding all the females in a group even when their fertile phases do not overlap (Engelhardt et al., 2006).

The possibility for the alpha male to monopolize as many females as expected by the PoA model and/or the need to limit his monopolization potential to certain females may depend on the degree of reproductive seasonality in primates. In long-tailed macaques the timing of female fertility is unpredictable and females can potentially cycle year round (van Schaik and van Noordwijk, 1985). Males thus face a high risk of exposure to chronic stress since, in order to monopolize access to all females, they would have to mate-guard females over extended periods of time. Mountain chacma baboons, in contrast, live in a seasonal and predictable environment. Conceptions are clustered during the first half of the year and males mate-guard females to the extent predicted by the PoA model (Weingrill et al., 2000). In this species, males do not seem to be limited in their monopolization potential even though they bear the cost of elevated fGC levels during mate-guarding (Bergman et al., 2005).

Given the strong effect of fruit availability on fGC levels in our study males, ecological factors may in addition play an important role in male mate-guarding decisions and may further explain the deviation from the PoA model. In order to prevent the exposure to chronic stress, males may need to stop mate-guarding females in periods of food shortage (i.e. when their fGC levels are naturally high). Such a phenomenon has been described in other taxa: food availability influenced the decision to engage or not in costly courtship and/or mate-guarding for example in crabs (Kim et al., 2008) and fish (Kolluru et al., 2009). The influence of food availability on mate-guarding decisions in male long-tailed macaques remains to be investigated but may be challenging to assess under natural conditions.

Our study shows that male long-tailed macaques may endure physiological (in the form of exposure to chronic stress) and potentially also physical (in the form of increased aggression and associated injuries) costs of mate-guarding. Even though the rise in glucocorticoids most likely serves an adaptive proximate function – i.e. reallocating resources during mate-guarding - it may, ultimately limit male mate-guarding abilities. We suggest that the degree to which these costs of mate-guarding act to limit male monopolization potential in different species depends on the species' reproductive seasonality. Males of seasonally reproducing species can most likely afford to engage fully in stressful, aggressive male-male competition and female guarding over a short period of time without facing the high risk of exposure to chronic stress. In contrast, males of species with highly unpredictable timing of reproduction are more likely to face long-term exposure to physiological stress and may thus have evolved an "incomplete female monopolization strategy" in order to avoid this cost. We therefore encourage future model developers to incorporate physiological costs of mate-guarding into reproductive skew models and to take into account the extent to which reproductive seasonality and rank achievement modes influence the interplay between costs of mate-guarding, dominance and male monopolization potential.

Acknowledgments

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