

Post-copulatory grooming: a conditional mating strategy?

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Abstract Animals of diverse taxa show different conditional mating strategies: they adjust their behaviour according to social and environmental situations, which may bring diverse (fitness) advantages for an individual. Especially in primates, mating is often associated with other social behaviours, such as grooming. Here, we study Barbary macaque post-copulatory grooming: we investigate for the first time whether males and females modify their grooming initiations after mating depending to the type of copulation (i.e. with or without ejaculation) and female lactation state. Our results show that males and females adjust grooming initiations conditional on copulation type, with males initiating grooming after copulations with ejaculation and females after non-ejaculatory mating. Moreover, lactating females tend to start grooming the males they just mated with more than vice versa, whereas there is no such a difference for grooming initiations after copulations with non-lactating females. These data indicate that Barbary macaques show post-mating grooming strategies that vary depending on the type of copulation that occurred and in dependence of female reproductive state. These grooming initiation patterns may reflect sex-specific mating interests and potentially serve to increase fitness: females, in particular lactating females, may benefit from initiating grooming to secure protection for themselves and their

offspring and reduce harassment. Males may profit from grooming females after ejaculatory copulation by keeping them from mating with another male and thus potentially decreasing sperm competition.

Keywords Barbary macaques · Mating · Ejaculatory copulations · Non-ejaculatory copulations · Single mount ejaculations

Introduction

Individuals of a species often have different sets of behaviours and a number of decision rules they use to determine under which conditions to express each behaviour (Dominey 1984). These decisions may be based on social and environmental factors. For instance, males of many jumping spider species display different courtship behaviours depending on where they encounter a female (visual displays in the daylight or tactile displays inside the nest) and in accordance to female maturity (Jackson 1992). Similarly, males of the bug species *Jadera haematoloma* adjust their mate guarding rates to the operational male-to-female sex ratios within a population (with more mate guarding occurring in male-biased environments, Carroll 1988), which suggests plasticity in these insects' behavioural responses to social conditions (Bretman et al. 2011) and an adaptive function of these conditional behaviours (Jackson 1992). Furthermore, the decision on which behaviours to express under specific circumstances is usually influenced by the status of an individual (Gross 1996): whether a chimpanzee female who mates with a male emits a copulation call or not depends on the presence of higher-ranking females in the audience as well as on the social rank of her mating partner (Townsend et al. 2008; Townsend and Zuberbuhler 2009). Thus, these conditional responses allow

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individuals of genetically monomorphic species to fine-tune behaviour to minor, short-term, momentary conditions and changes in their environment (Gabriel et al. 2005; Bretman et al. 2011).

Especially in primates, mating is often associated with other social behaviours, such as grooming, both before and after copulation. Generally, grooming is an interesting candidate to evaluate conditional behavioural responses to different mating contexts (e.g. in herb-field mouse: Stopka and Graciová 2001). Diverse studies investigating grooming outside mating situations in primate species show that this behaviour, which acts as a form of social ‘glue’ in many primates (Dunbar 1991), is employed differently depending on environmental and social conditions (e.g. Crockford et al. 2008; Wittig et al. 2008; Cheney and Seyfarth 2009; Sonnweber et al. 2015), which ultimately may result in fitness advantages (Silk et al. 2003; Silk 2007a, b, 2014). But does this hold for grooming in mating contexts too?

Theoretical and empirical research suggests that the value of mating may differ between the sexes and that males and females may often have different sexual interests (Trivers 1972; Johnstone et al. 1996; Baldwin and Baldwin 1997). Therefore, it seems likely that males and females express different behavioural responses to mating. For instance, a survey on university and college students found clear differences in male and female post-coital behaviour (Hughes and Kruger 2011). Whilst females initiated and engaged in bonding behaviour after copulation, males preferentially showed behaviours that were extrinsically rewarding (e.g. smoking) or increased the likelihood of repeated copulation (e.g. continued sexual activity). Similarly, male and female snub-nosed monkey mating partners huddle together or allogroom after copulations, and females initiate more of such post-mating grooming than males (Li and Zhao 2007). Amongst chimpanzees, in contrast, males groom females after inspecting their hindquarters and often initiate post-copulatory grooming (Nishida 1997). These studies suggest that socio-positive behaviours immediately after copulation might follow species-specific, sex-specific patterns that may follow from differences in social structure and/or ecology (e.g. dispersal patterns).

Whether or not grooming is initiated after copulation can depend on various factors, such as audience effects (Overduin-de Vries et al. 2012), mating partners’ age (Kuester and Paul 1992), the social bond between mating partners (Smuts 1985) or the cycle stage of the female (Wallis 1992; Nishida 1997; Van Belle et al. 2009). Likewise, the motivation to initiate grooming may vary. Previous studies indicate that mating frequencies can be managed by post-copulatory grooming. By grooming the male copulation partner, a female may keep the male in an aroused state and obtain additional matings (Slob et al. 1986; Rao 1995; Bancroft 2005; Lee et al. 2009) or avoid further mating with the same partner (Gumert

2007). Furthermore, the female potentially gains social support and reduces the risk of harassment from the male by initiating grooming (Smuts 1985). Male-initiated grooming on the other hand may keep the female from mating with other males, reducing sperm competition (Berenstain and Wade 1983; Berard et al. 1994), and/or lead to additional mating (Kuester and Paul 1992). Thus, males and females may use post-copulatory grooming strategically to follow sex-specific reproductive interests.

Within a sex, differences in post-copulatory grooming behaviour can also be expected depending on the type of mating and the physiological state. In mammals, several studies indicate that females nursing offspring may show lactation-associated reduced fertility (Wilson et al. 1983; Maeda et al. 1991; Mitsunaga et al. 1994; Kondo et al. 2003; Wallner et al. 2011), which may lead to differential grooming responses. Whilst non-lactating females show typical changes in oestrogen and progesterone throughout the ovarian cycle, females nursing offspring often lack pronounced changes in progesterone and oestrogen concentrations, which leads to irregular menstrual cycles (Maeda et al. 1991; Mitsunaga et al. 1994). This may be due to the increased energetic costs of lactation (Prentice and Prentice 1988). Thus, decreased female fertility associated with lactation may be relevant to differences in post-copulatory social behaviour expressed by and directed towards lactating versus non-lactating females. Other motivational factors may also influence lactating females’ post-copulatory social behaviour: Previous research suggests that females with infants may be inclined to bond with male (mating) partners as they can offer protection and social support for the females and their infants (Palombit et al. 1997, 2001; Lemasson et al. 2008) and thus potentially increase offspring survival.

Similarly, the type of copulation may have consequences for post-copulatory behaviours. Interestingly, amongst multiple mammalian species, copulations do not always lead to ejaculation (e.g. voles: (Dewsbury 1973); opossums: (McManus 1967); mice: (McGill 1962); and amongst primates muriquis: (Possamaia et al. 2005); golden monkeys: (Ren et al. 1995); and chimpanzees: (Goodall 1986); for a review, see (Dewsbury 1972)). Although non-ejaculatory mating can still lead to fertilization through pre-ejaculatory fluid (Lampiao 2014), when ejaculation occurs, the likelihood of egg fertilization increases dramatically. Consequently, non-ejaculatory copulations have been largely neglected in the literature and have often been excluded from analyses in studies on reproduction and mating strategies (Furtbauer et al. 2011; Dixson 2012; Young et al. 2013) or evaluated solely outside reproductive periods in seasonally breeding species (Li et al. 2007). But given the number of species, in which non-ejaculatory mating is seen, this behaviour deserves closer scrutiny. In particular, the implications of ejaculatory and non-ejaculatory copulations may differ between the sexes and

possibly impact their motivation to initiate post-copulatory grooming.

In the current study, we investigated for the first time whether individuals showed different post-copulatory grooming strategies conditional on the type of mating that had just occurred. Grooming behaviour can be described and quantified through different measures (e.g. grooming duration, grooming frequency or grooming reciprocity), which may provide information about different qualities of a social interaction. Individuals who initiate grooming show motivation for social interaction (Tsukahara 1990). Thus, differential patterns of grooming initiation may reflect differences in current motivational states. When one individual of a mating pair initiates grooming right after copulation, this indicates a relatively high motivation to engage in social interactions after mating.

We were particularly interested in differences in post-mating grooming initiations between and within the sexes: Do males and females initiate grooming differently conditional on the type of mating? Do lactating and non-lactating females express different patterns of grooming initiations? To address these questions, we studied free-ranging Barbary macaques over two consecutive mating seasons. These macaques are promiscuous with high mating partner turnover rates (Taub 1980; Small 1990b; Kuester and Paul 1992), and the majority of females tend to mate no more than twice in succession with a male before copulating with another partner, but repeated copulations in succession have also been observed (Kuester and Paul 1992). Moreover, their mating system seems to be primarily shaped by female choice (Taub 1980; Small 1990b; Brauch et al. 2008), although data restricted to fertile periods challenge this claim (Kuester and Paul 1992). Barbary macaques breed seasonally and have single-mount-to-ejaculation patterns (Taub 1982), thus ejaculation often occurs at the first instance of a male mounting a female. Whilst frequencies of ejaculatory copulations increase around female fertile periods, non-ejaculatory mating occurs throughout the mating period (Heistermann et al. 2008; Pfefferle et al. 2008). Finally, about two thirds of all matings are associated with post-mating close body contact or grooming, with males being the more active groomers (Kuester and Paul 1992). Hence, Barbary macaques (like various other primate species) constitute a promising model species to examine conditional post-mating grooming strategies.

Material and methods

Subjects and study site

Free-ranging, adult male and female Barbary macaques (*Macaca sylvanus*) inhabiting the Rock of Gibraltar, Gibraltar, UK were observed over two consecutive mating seasons

(October 2004–February 2005 and October 2005–March 2006). All females were cycling and some were nursing offspring from the previous season (three in the first, nine in the second season). In the first season, we collected data on the ‘Apes Den’ group (AD), which encompassed 13 adult females and nine adult males (six of whom immigrated from neighbouring groups). In addition, AD had six subadult individuals, eight juveniles and five infants (age was classified following Burton 1972). In the second season, AD consisted of 14 adult females and nine adult males (two of which emigrated at the beginning of the season), as well as nine subadults, five juveniles and seven infants. Additionally, in the second season, we observed the ‘Prince Phillip’s Arch’ group (PPA), consisting of 12 adult females and six adult males (and 12 subadult individuals, eight juveniles and seven infants). Two females in the PPA group had contraceptive implants. Contraceptive implants can affect social and sexual behaviour in macaques (Pazol et al. 2004), and therefore the two females on hormonal contraceptives were excluded from data analysis. Thus, in total, we observed 31 adult individuals (18 females and 13 males) of which 17 (11 females and 6 males) were observed in two consecutive seasons. The home ranges of the two study groups had good accessibility and allowed for a good view over the territory. The Gibraltar Ornithological and Natural History Society (GONHS) provisioned the animals with fruits and vegetables on a daily basis. Due to the provisioning, all individuals gathered around the feeding sites in the course of the day. Nevertheless, data were also collected in the periphery of the groups’ home ranges to avoid a bias towards more central individuals in the data.

Behavioural data collection and sampling

Behavioural data collection spanned 109 days in the first and 115 days in the second season. Observations started at 08:00 and ended at 17:00. In the first season, AD was observed daily. In the second season, data collection alternated between groups: after a day of observations at AD, data were collected at PPA the following day. We collected behavioural data ad libitum (Altmann 1974). To establish rank hierarchies, we collected data on intra-sex agonistic interactions. Furthermore, we recorded copulations and consecutive grooming between adult male and female individuals. When copulation occurred, we noted identities of the copulation partners and the type of copulation (ejaculatory or non-ejaculatory). Ejaculatory copulations were clearly identifiable by an ejaculatory pause in pelvic thrusting and visible sperm threads either on the male or female genitalia after copulation (as described earlier in Kuester and Paul 1984; Brauch et al. 2007). Non-ejaculatory mating was recorded when a male had mounted a female, performed pelvic thrusts after intromission and subsequently un-mounted the female. The sex that initiated grooming and grooming direction (female initiates grooming of the male or

vice versa) that occurred within 30 s after the male dismounted the female was recorded.

Data analysis

We used intra-sexual dyadic agonistic interactions (Deag 1974) between adult individuals to establish male and female rank hierarchies (per group and season). Wins and losses were entered into dominance matrices. Mat Man 1.0 (de Vries et al. 1993) was used to calculate linear dominance ranks (Landau's indices for females: AD, season 1 = 0.49; AD, season 2 = 0.52; PPA, season 2 = 0.86; Landau's indices for males: AD, season 1 = 1; AD, season 2 = 0.57; PPA, season 2 = 1). As the number of males and females differed across seasons and groups, we calculated relative rank positions by dividing the absolute rank by the number of rank places in the groups. Due to insufficient data, three young males in the PPA group (second season) and males immigrating into the AD group during the first season were not assigned a dominance rank.

We entered all observed copulations twice in our data set, once for the male and once for the female mating partner and added information on whether the individual initiated grooming after the mating (binary data: either the individual initiated grooming or the individual did not initiate grooming). These data were entered into binomial generalized linear mixed models with a logit link function (GLMM, using the lme4 package in R, Bates et al. 2014) to assess the relationship between male and female post-copulatory grooming after ejaculatory and non-ejaculatory copulations and in relation to female lactation state. Since individuals were sampled repeatedly and over consecutive seasons, we used a repeated measures design. Our response variable was the binary grooming initiation variable. Intercepts for male and female identity nested in group and season were entered as random factors into our models. As all copulations were entered twice in the data set, a unique copulation identification number was also included as a random effect. We fitted a full model, containing the following predictor variables: (i) type of copulation (ejaculatory or non-ejaculatory), (ii) the sex of the individual (male or female), (iii) female lactation state (lactating or not lactating), (iv) female and male relative rank, (v) the interaction between the copulation type and individual's sex, (vi) the interaction between lactation state and sex, (vii) the interaction between the ranks of the mating partners, (viii) the interaction between copulation type and lactation state, (ix) the three-way interaction between copulation type, sex and lactation state, (x) the three-way interaction between the copulation type, female rank and sex as well as (xi) the three-way interaction between the copulation type, male rank and sex. By reducing the set of predictor variables (stepwise reduction procedure: we eliminated the parameter that explained the least variance in the data and build a new model), we evaluated the model that fits the data best. We calculated Akaike information

criterion (AIC) scores controlled for small sample sizes (AICc) and Akaike weights (wAICc) to compare competing models and to select the model most efficiently predicting the probability of grooming to occur (Burnham and Anderson 2002; Aho et al. 2014). The variable elimination procedure was repeated until variable reduction no longer decreased AICc scores and thus did not increase the explanatory power of the model. The final model contained fewest predictor variables amongst the candidate models, which differed less than two AICcs from each other.

With regard to our repeated measures design, for post hoc testing of interaction effects, we split the data frames (according to significant predictors in the final model) and re-ran models. All statistics were computed with R (version 3.1.1 (July 10, 2014), Core Team 2014), all tests were two-tailed and alpha was set to 0.05.

Results

A total of 490 copulations between 18 adult females and 13 males were observed throughout the observation period. In the first season, one female who was old and sick and two young males who immigrated from neighbouring groups were never observed mating. In the second season, six young females (three from AD and three from PPA) and two young males, who immigrated into PPA, were never seen copulating. The number of copulations varied across individuals: between three and 58 copulations per female (mean±standard deviation (SD)=9.5±8.87) and between two and 83 copulations per male (mean±SD=14.25±14.1) were recorded in the first season. In the second season, between two and 41 copulations per female (6.89±6.77) and between two and 40 copulations per male (10.08±6.92) were observed. Two hundred twenty-four (45.71 %) of the 490 copulations were ejaculatory, and 266 (54.29 %) occurred without ejaculation. Two hundred thirty-five (47.96 %) copulations with lactating females and 255 (52.04 %) matings with non-lactating females were observed (for a detailed overview, see Table 1). When grooming occurred after ejaculatory mating, females were responsible for 38.17 % and males for 61.83 % of grooming initiations. Grooming after non-ejaculatory mating was initiated by females in 82.05 % and by males in 17.95 %.

To analyse the factors influencing grooming initiations after copulation, we ran a GLMM including many predictor variables (as described in the methods above). The best fitting model (Table 2; the full model is provided in the Online Resources 1) included the type of copulation, the sex of the individual, female lactation state, the two-way interaction terms of copulation type and sex, copulation type and lactation state, sex and lactation state, male and female relative rank as well as the three-way interaction of copulation type, sex and lactation state. However, the only significant predictors of

Table 1 Overview of distribution of grooming initiations

	General 490 observations (%)	Ejaculatory 224 observations (%)	Non-ejaculatory 266 observations (%)	Copulations with lactating females 235 observations (%)	Copulations with non-lactating females 255 observations (%)
No grooming initiated	49.39	41.52	56.02	48.94	49.80
Male-initiated grooming	20.82	36.16	7.89	16.60	24.71
Female-initiated grooming	29.79	22.32	36.09	34.47	25.49

The numbers indicate percentages of (i) no grooming initiated, (ii) grooming initiated by the male and (iii) grooming initiated by the female

grooming initiations in this model were the type of copulation, the sex of the individual and the interaction of copulation type and sex. Additionally, the interaction of sex and lactation state was close to significant ($P=0.056$).

Copulation type and sex of the individual significantly predicted post-copulatory grooming initiations. In general female-initiated grooming rates after mating were higher than males', irrespective of the type of copulation that occurred (Table 2). Overall grooming initiation rates were significantly higher after mating with ejaculation than after non-ejaculatory copulations (Table 2).

Because the interaction of copulation type and sex of the individual had a significant effect on grooming initiations, the dataset was split into subsets (by copulation type and sex; Fig. 1 shows individuals' average grooming initiation ratios by copulation type and sex). Post hoc models revealed several differences in post-copulatory grooming behaviour. Analysis of grooming initiations within sex showed that females initiated more grooming after copulations with ejaculation than after non-ejaculatory matings ($z=-3.716$, standard error

(SE)=0.236, $P<0.001$; Fig. 1). Males initiated more grooming after ejaculatory mating than after copulations without ejaculation ($z=6.654$, SE=0.303, $P<0.001$; Fig. 1).

Comparing the two sexes revealed that males initiated less grooming after copulations without ejaculation than females ($z=7.268$, SE=0.268, $P<0.001$; Fig. 1) but more after mating with ejaculation ($z=-2.961$, SE=0.217, $P=0.003$; Fig. 1). Because the interaction between lactation state and individual sex was very close to being significant ($P=0.056$), we also performed post hoc tests on these data (for visualization, see Fig. 2), again by running simple models on split datasets. This revealed that lactating females initiated more grooming than the males they had mated with ($z=4.350$, SE=0.223, $P<0.001$), whereas non-lactating females and their mating partners started grooming after mating at similar rates ($z=0.528$, SE=0.211, $P=0.598$). A detailed examination of nursing and non-lactating female grooming initiations after ejaculatory and non-ejaculatory copulations showed that non-lactating females initiated grooming less after copulations with ejaculation than after non-ejaculatory ones ($z=-2.792$,

Table 2 The final model on the probability of an individual to groom its mating partner after copulation

Linear mixed-effects model fit by maximum likelihood					
	AIC	BIC	logLik	Deviance	df residuals
	852	926.9	-410	820	782
Scaled residuals					
	Min	1Q	Median	3Q	Max
	-0.915	-0.649	-0.369	-0.237	3.949
Fixed effects					
	Estimate	Standard error	z value	P value	
Intercept	-3.316	0.651	-5.090	<0.001	
Copulation type	4.800	0.847	5.667	<0.001	
Sex	1.250	0.370	3.384	0.001	
Lactation state	-1.774	1.080	-1.642	0.101	
Copulation type × sex	-2.904	0.538	-5.398	<0.001	
Copulation type × lactation state	-0.790	1.307	-0.604	0.546	
Sex × lactation state	1.138	0.596	1.910	0.056	
Female relative rank × male relative rank	-0.025	0.049	-0.509	0.611	
Copulation type × sex × lactation state	0.658	0.776	0.848	0.396	

Female and male identity nested in group and season as well as the copulation identification number were included as random factors. P values of significant predictors are displayed in bold typeface

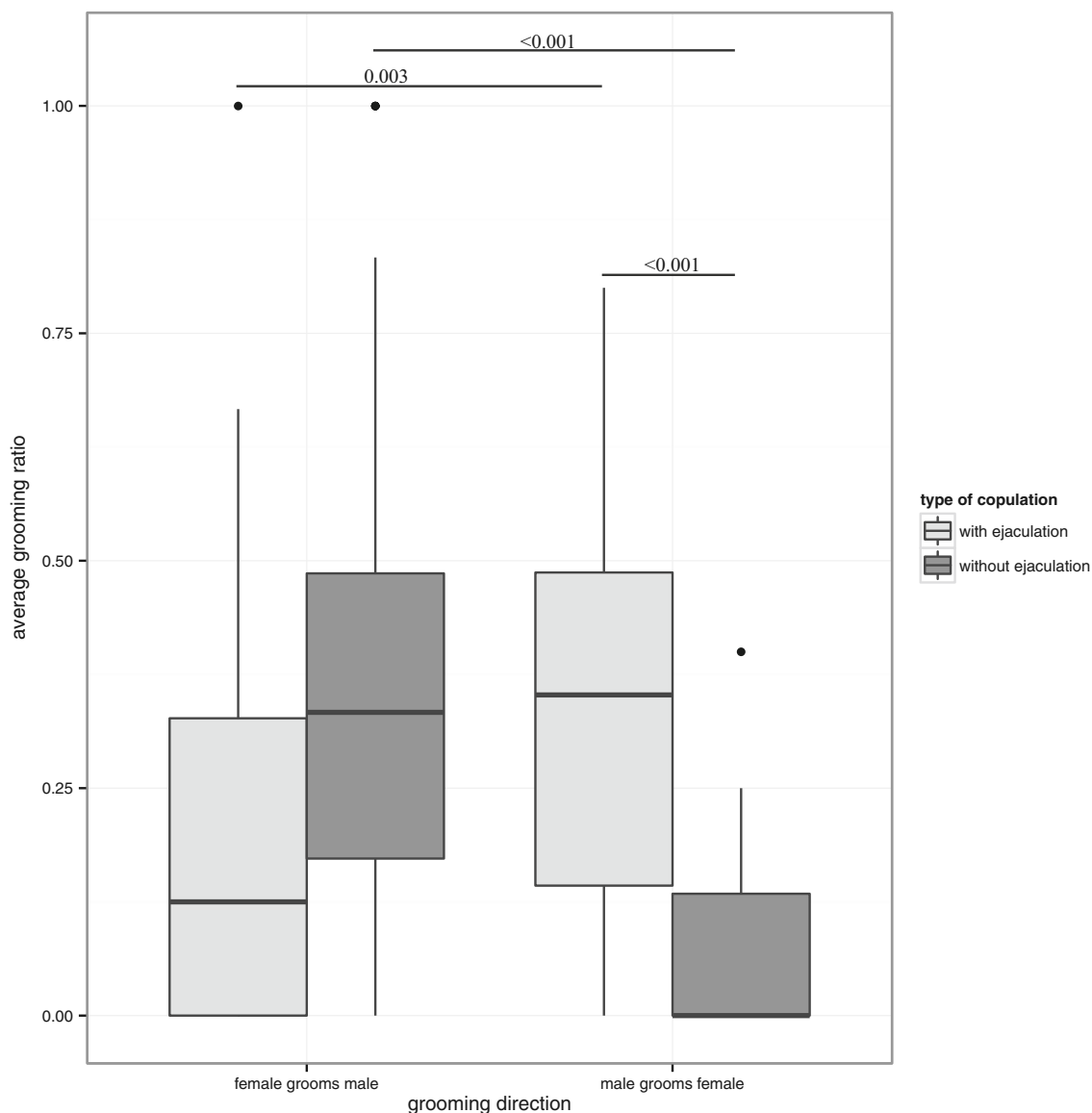


Fig. 1 Average grooming ratios (i.e. the number of instances when grooming occurred divided by the total number of copulations) for females and males after copulations with ejaculation (*light grey boxes*)

and after copulations without ejaculation (*dark grey boxes*). Median, quartiles and range are plotted. Only P values for significant differences are indicated

$SE=0.598$, $P=0.005$). In contrast, females nursing offspring from the previous season initiated as much grooming after copulations with ejaculation as after non-ejaculatory ones ($z=-0.364$, $SE=1.301$, $P=0.716$). Males did not differentiate between lactating and non-lactating females when initiating grooming ($z=-1.456$, $SE=0.3117$, $P=0.145$).

Discussion

Overall, our results show that male and female Barbary macaques express post-copulatory grooming patterns that depend on the type of mating that occurred. The proportion of male-initiated grooming is higher after ejaculatory copulations than

after matings without ejaculation. This increased frequency of grooming initiations after ejaculatory copulations may be driven by males' increased social activity (e.g. Soltis 1999; Koyama et al. 2012) associated with heightened ejaculation rates (Heistermann et al. 2008) around the time of female ovulation. Potentially, grooming the female after ejaculatory mating may keep her from copulating with other males, ultimately reducing sperm competition. Thus, males may employ grooming after ejaculatory copulations as a conditional mating strategy to increase their own fitness.

Whilst males initiate grooming more after ejaculatory mating than females, females initiate grooming more than their male partners after non-ejaculatory copulations. This relative increase in female grooming after non-ejaculatory mating

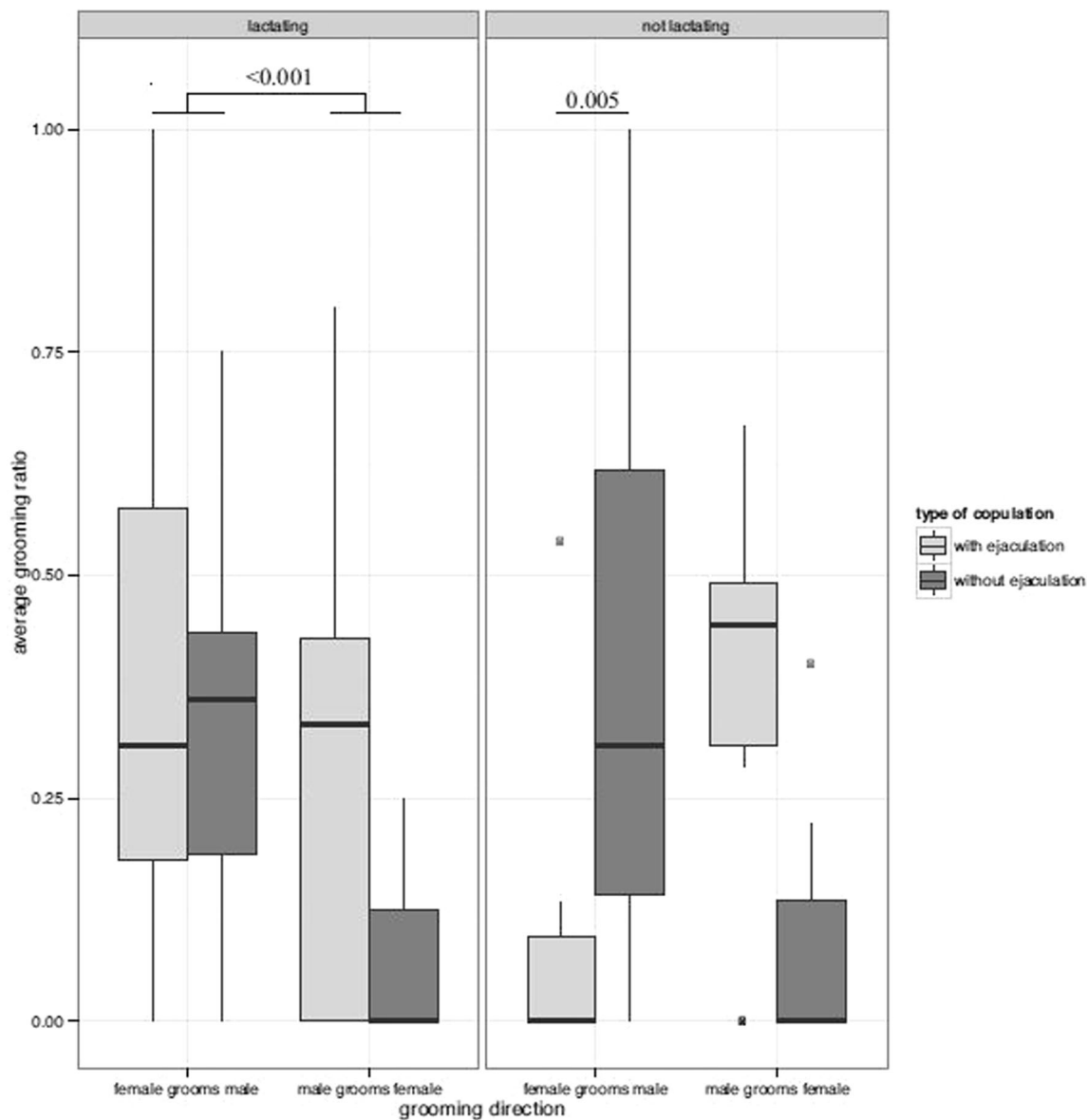


Fig. 2 Average grooming ratios for males and lactating (*left side*) and non-lactating (*right side*) females after copulations with ejaculation (*light grey boxes*) and after copulations without ejaculation (*dark grey boxes*).

Median, quartiles and range are plotted. Only *P* values for significant differences are indicated

could simply be a response to a decrease in male grooming: if the male fails to start grooming after a mating, the likelihood of the female initiating grooming should increase. The female may simply react to the absence of male social activity (in the future data on when grooming was initiated within the 30 s after mating may help answer this question). Alternatively, females may be more inclined to initiate grooming in response to the type of copulation that occurred, implying that females respond differently to whether an ejaculation occurred or not. Females may use post-copulatory grooming to avoid further matings with the male: Gumert (2007) showed that female grooming of males reduces subsequent copulation frequency. Alternatively, females may profit from direct potential gains, such as male support and reduction of harassment, particularly

relevant to females nursing offspring from a previous mating season (Palombit et al. 1997, 2001; Lemasson et al. 2008). Comparing nursing and non-lactating females showed that lactating females initiated grooming at similar rates after either copulation type, whilst non-lactating females initiated grooming more after non-ejaculatory copulations than after ejaculatory matings. Males however did not initiate grooming differentially between lactating and non-lactating females, suggesting that the female differential grooming initiations after ejaculatory and non-ejaculatory copulations are not a simple response to male behaviour. This pattern supports the notion that females themselves respond to the type of mating they receive, showing conditional behavioural responses to copulation type.

Comparing the two sexes, female-initiated grooming after copulation (across copulation types) occurs more often than male-initiated grooming. Taking female lactation state into account reveals that this holds for nursing females only: Our data show that males and non-lactating females initiate grooming at similar rates after copulations. Nursing females however express higher grooming initiation rates than their male partners. This finding suggests that this post-copulatory grooming pattern between males and lactating females is female-driven. Nursing females increase post-copulatory grooming initiations after copulations, whilst males initiate grooming with lactating and non-lactating equally often. Furthermore, we found that copulations with ejaculation were more frequently followed by grooming than non-ejaculatory matings—an effect probably driven by lactating females' increased grooming. But why do lactating females in particular show these increased grooming initiation rates? On the one hand, increasing grooming may increase the likelihood of repeated copulation (e.g. Matsumoto-Oda 1999). Male lemurs have been shown to keep female mating partners interested (and thus gain additional copulations) by post-copulatory mountings, a behaviour solicited by females (Parga 2010). A similar mechanism might underlie lactating female post-copulatory grooming in Barbary macaques: increasing grooming rates might increase repeated copulation likelihood (further studies collecting data on copulation rates following groomed and non-groomed mating would help to answer this question) (but see Gumert 2007). This may be particularly relevant to lactating females, as lactation can reduce female fecundity (Maeda et al. 1991; Mitsunaga et al. 1994; Kondo et al. 2003; Wallner et al. 2011). Through repeated copulations, lactating females might still be successful in conceiving new offspring. On the other hand, females nursing offspring from the previous season may gain protection and social support (Palombit et al. 1997; Palombit et al. 2001; Lemasson et al. 2008) from their male copulation partners and thus benefit from establishing stable, long-term social relations (usually established, maintained and repaired by social grooming) or 'friendships' with them (Massen et al. 2010; Massen and Sterck 2013). Barbary macaque males show some care for infants, both to later gain mating access to the mother and to use infants as social tools for 'agonistic buffering' in conflicts with other males (Deag and Crook 1971; Small 1990a; Paul et al. 1996; Ménard et al. 2001). Thus, good social relations with their previous mate may be important to a female trying to establish good social bonds.

Overall, grooming followed about half of all observed copulations, whilst after the other half of observed matings no grooming was initiated, which is consistent with earlier findings in Barbary macaques (Taub 1980; Small 1990b; Kuester and Paul 1992). This itself suggests that post-copulatory grooming is employed conditionally in response to external, environmental and/or internal, motivational states.

Macaques may refrain from grooming for multiple reasons. Chimpanzee females often do not call whilst mating when higher-ranking females are in vicinity (Townsend et al. 2008; Townsend and Zuberbuhler 2009), and Barbary macaques similarly may not initiate grooming after copulation when dominant competitors are nearby. For macaques, audience effects on grooming have been shown previously (Overduin-de Vries et al. 2012). Furthermore, previous data on Barbary macaques suggest that refraining from social interactions potentially reduces the risk of interference or attacks by higher-ranking females (Kuester and Paul 1996) or males, although high-ranking male Barbary macaques are relatively tolerant towards subordinate males (Kuester and Paul 1992). Additionally, the age of the male mating partner may impact the likelihood of grooming being initiated after copulation. Kuester and Paul (1992) showed that contacts between females and young subadult males often stopped right after mating or were terminated by other males. Also, female cycle stage may influence whether grooming is initiated or not, as general social activity between males and females has been shown to increase around the time of female ovulation (Wallis 1992; Nishida 1997; Van Belle et al. 2009) and at peak of female fertility indicator conspicuousness (Rowell 1963; Higham et al. 2009). A final factor that may influence the occurrence of post-copulatory grooming is the quality of the social bond between the mating partners (Smuts 1985). Massen et al. (2012) did not find a direct exchange of grooming for mating in rhesus macaques, but 'friendship' between male and female rhesus macaques predicted male mating success. Male and female Barbary macaques may potentially have already established social bonds with their mating partners before the mating season, and non-ejaculatory copulations may function as social copulations. Analyses of social network data between males and females, using longer-term data than available here, as well as hormonal samples to monitor female ovarian cycles may help to shed light on these issues in future studies.

Generally, multiple factors may affect post-copulatory grooming strategies, influencing whether grooming is initiated after copulation or not and by whom. Our current data do not allow us to disentangle all of these factors, and further studies are required to answer these questions. However, our data clearly indicate that grooming right after copulations is expressed conditionally in response to the type of mating that occurred and depending on female lactation state. We hope that this study will spur further investigations to increase our understanding of the underlying mechanisms and the ultimate functions of post-copulatory grooming.

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Ethical standards All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The nature of the study was purely observational: No invasive methodologies were applied at any point of the study. The Gibraltar Ornithological and Natural History Society (GONHS) approved data collection for the study. All procedures were in accordance with British, Austrian and European Union law.

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