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Effect of Mating Activity and Dominance Rank on Male Masturbation Among Free-Ranging Male Rhesus Macaques

Constance Dubuc*†, Sean P. Coyne†‡ & Dario Maestripieri†‡

* Center for the Study of Human Origins, Department of Anthropology, New York University, New York, NY, USA
† Institute for Mind and Biology, The University of Chicago, Chicago, IL, USA
‡ Department of Comparative Human Development, University of Chicago, Chicago, IL, USA

Correspondence
Constance Dubuc, Center for the Study of Human Origins, Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003, USA.
E-mail: constance.dubuc@nyu.edu

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Abstract

The adaptive function of male masturbation is still poorly understood, despite its high prevalence in humans and other animals. In non-human primates, male masturbation is most frequent among anthropoid monkeys and apes living in multimale–multifemale groups with a promiscuous mating system. In these species, male masturbation may be a non-functional by-product of high sexual arousal or be adaptive by providing advantages in terms of sperm competition or by decreasing the risk of sexually transmitted infections. We investigated the possible functional significance of male masturbation using behavioral data collected on 21 free-ranging male rhesus macaques (*Macaca mulatta*) at the peak of the mating season. We found some evidence that masturbation is linked to low mating opportunities: regardless of rank, males were most likely to be observed masturbating on days in which they were not observed mating, and lower-ranking males mated less and tended to masturbate more frequently than higher-ranking males. These results echo the findings obtained for two other species of macaques, but contrast those obtained in red colobus monkeys (*Procolobus badius*) and Cape ground squirrels (*Xerus inauris*). Interestingly, however, male masturbation events ended with ejaculation in only 15% of the observed masturbation time, suggesting that new hypotheses are needed to explain masturbation in this species. More studies are needed to establish whether male masturbation is adaptive and whether it serves similar or different functions in different sexually promiscuous species.

Introduction

Masturbation, or self-manipulation of the genitalia, is part of the natural behavioral repertoire of many animal species (reviewed in Bagemihl 1999; Thomsen et al. 2003; Dixson 2012), including humans (Laqueur 2003; Dixson 2012), but whether this behavior has an adaptive function is still poorly understood. Although comparative behavioral data on masturbation could help us understand the adaptive function and evolution of this behavior, very few data are available to date.

Different hypotheses have been proposed to explain the function of male masturbation (reviewed by Waterman 2010; see also Dixson 2012). The '*sexual-outlet*' hypothesis proposes that masturbation is a non-adaptive by-product of sexual arousal and serves as an alternative outlet to copulation (Kinsey et al. 1948; Dixson & Anderson 2004; Dixson 2012). This by-product hypothesis implies that males do not gain any fitness benefits, in terms of their health or survival, or increased mating or reproductive success, from masturbation. Second, the '*ejaculate-quality-improvement*' hypothesis posits that masturbation is an adaptive behavior that serves to eliminate degraded gametes or avoid polyzoospermy in order to increase the overall ejaculate quality, thus increasing the probability of impregnation when males copulate with a fertile female (Zimmerman et al. 1965; Baker & Bellis 1993, 1995; Thomsen et al. 2003; Thomsen

& Soltis 2004). While suggesting very different functions of masturbation, these two hypotheses both predict that masturbation should be more frequent among males that have little or no opportunity to mate, and/or occur in periods of infrequent mating (Thomsen et al. 2003; Dixson & Anderson 2004; Thomsen & Soltis 2004; Waterman 2010; Dixson 2012). In addition, the ejaculate-quality-improvement hypothesis predicts that males who have infrequent access to females but masturbate frequently should have higher sperm quality and higher probability of impregnation when compared to males who masturbate less frequently, other things being equal. Finally, according to the '*STI-reduction*' hypothesis, masturbation serves to cleanse the male reproductive tract to decrease the risk of contracting sexually transmitted infections (STIs; Waterman 2010). This hypothesis has been developed more recently to explain the behavioral pattern observed in the highly promiscuous Cape ground squirrels (*Xerus inauris*; Waterman 2010). Contrary to the two other hypotheses, the STI-reduction hypothesis predicts that male masturbation should be more prevalent in periods of high sexual activity, performed by males who mate successfully, and occur shortly after copulation (Waterman 2010). Moreover, it predicts that males who masturbate frequently in these circumstances should be less likely to contract sexually transmitted diseases than males who do not masturbate or do so less frequently and should thus be in overall better health. It should be noted that all three hypotheses are based on the assumption that male masturbation typically leads to ejaculation.

Among non-human primates, the occurrence of male masturbation has been documented at the qualitative level for 30 species of Old World monkeys and apes, whereas it is rare or even absent in New World monkeys and prosimians (reviewed in Thomsen et al. 2003; Dixson 2012). Male masturbation is most frequent in anthropoid primates that live in multimale–multifemale groups (Thomsen et al. 2003) and have large testis volume relative to their body size (Dixson & Anderson 2004). While this observation has been interpreted as being suggestive that male masturbation is functionally linked to sperm competition (*ejaculate-quality-improvement hypothesis*; Thomsen et al. 2003), this observation is also consistent with the sexual-outlet hypothesis because in sexually promiscuous species, 'males possess neuroendocrine specializations for greater sexual arousal and performance' (Dixson & Anderson 2004, p. 366; see also Dixson 2012, p. 192). Such pattern could also be explained by the STI hypothesis because sexually transmitted infections are more likely to spread in species with promiscuous mating system (Waterman 2010).

While no primate studies to date have directly investigated the potential fitness benefits of male masturbation, a handful of studies have investigated the functional hypotheses indirectly, by testing their predictions concerning the frequency of masturbation and its potential association with rank and mating activity within species. In free-ranging red colobus monkeys (*Procolobus badius*), masturbation was performed very rarely (5 instances in 8950 h of observation collected over 5 yr) mainly by alpha males and specifically during intergroup encounters (i.e., when rivals are present) taking place when some females were sexually active, with no copulations reported for either resident or extra-group males (Starin 2004). Male masturbation was much more frequent in two macaques species, in which hundreds of instances were observed over less than 1000 hours of observation collected over 1–2 yr (Nieuwenhuijsen et al. 1987; Thomsen & Soltis 2004). In free-ranging Japanese macaques (*Macaca fuscata*), masturbation is more frequent in males of lower mating success and those of lower dominance rank (Thomsen & Soltis 2004; see also Inoue 2012). No such relation between dominance rank and masturbation frequency was revealed in captive group-living stump-tail macaques (*M. arctoides*; Nieuwenhuijsen et al. 1987). A closer investigation of the latter study's data, however, revealed an opposite pattern of distribution of mating and masturbation rate between the alpha male (409 copulations vs. 30 masturbation bouts) and the beta male (30 copulations vs. 543 masturbation bouts), which suggests a relation between rank, mating, and masturbation similar to that reported in Japanese macaques (cf. Table 3 in Nieuwenhuijsen et al. 1987). Overall, the results obtained for macaques seem more consistent with the ejaculate-quality-improvement and sexual-outlet hypotheses than with the STI-reduction one.

In this study, we examined whether and how access to fertile females influences masturbation rate in free-ranging male rhesus macaques on Cayo Santiago, Puerto Rico. Rhesus macaques are seasonal breeders and on Cayo Santiago that they live in large troops (50–300 individuals). In this rhesus population, male mating and reproductive success are linked to dominance rank, although not strongly (e.g., Berard et al. 1994; Dubuc et al. 2011). High-ranking males form extended consortships with estrous females characterized by frequent copulations and ejaculations, while lower-ranking males mate less frequently and mainly through sneak copulations and short-term associations (e.g., Carpenter 1942; Altmann 1962; Chapais 1983; Berard et al. 1994; Higham et al. 2011). However, middle- and low-ranking males can still enjoy a relatively high reproductive success (e.g., Berard et al. 1994; Dubuc et al. 2011) because high-ranking males are generally unsuccessful at mate-guarding females over the entire course of their fertile phase (Dubuc et al. 2012), thus making it possible for other males to fertilize females through sneaky copulations and sperm competition (see also Bercovitch 1992). While male masturbation has long been known for this species (e.g., Carpenter 1942; Phoenix & Jensen 1973), little is known about the relationship between masturbation and mating activity. Work on captive rhesus macaques has shown that male masturbation takes place even without any sensory contact with females (e.g., Phoenix & Jensen 1973), is eliminated by castration (Phoenix & Jensen 1973; Slimp et al. 1978; Loy et al. 1984), but not by brain lesions that eliminate sexual interactions with females (Slimp et al. 1978).

Here, we explored the possible functional significance of male masturbation by investigating the correlation between masturbation frequency and male dominance rank, and investigating how mating activity influences masturbation behavior in two different ways, by testing (1) whether there is a correlation between masturbation rate and overall mating frequency and (2) whether or not males were more likely to masturbate on days in which they were seen mating. Based on previous findings obtained in macaques, we predicted that the pattern of male masturbations will be more consistent with the sexual-outlet and ejaculate-quality-improvement hypotheses than with the STI hypothesis. Specifically, we predicted that (1) low-ranking males and/or least successful males of a social group should be more likely to be observed masturbating, and (2) males should be more likely to masturbate on days in which they do not mate. In addition, we expected (3) masturbation to lead to ejaculation.

Method

Study Subject and Population

This study was conducted on Cayo Santiago, a 15.2 ha island located 1 km off the coast of Puerto Rico. The rhesus macaque colony was established on this island in 1938 from free-ranging individuals captured in India (Rawlins & Kessler 1986) and is now managed by the Caribbean Primate Research Center (CPRC) of the University of Puerto Rico. The monkeys are provisioned daily with commercial monkey chow and are habituated to human observers. At the time of the study, the population size was approximately 1000 individuals, separated into 6 distinct social groups. All animals in the population have unique tattoos as well as distinct ear-notches to make individual identification easy for observers. In this rhesus population, there is currently a Mar.–Aug. mating season, followed by a Sep.–Feb. birth season (Hoffman et al. 2008). Data collection took place from Apr. to Jun. 2011 on one social troop (group R). At the time of the study, group R comprised 224 individuals, including 83 adult females (≥3 yr old) and 48 adult males (≥5.5 yr old; Manson 1996). Twenty-two males were selected as subjects, but one was dropped from the study because he dispersed from group R during the project. The 21 subjects varied in age ($\bar{x}$: 10.3 ± 4 yr old, range: 6–21) and dominance rank ($\bar{x}$: 15.1 ± 7.3; $\tilde{x}$: 16, range: 1–26; see below).

Behavioral Data Collection

Behavioral data were collected by SC 5–6 d a week, usually from 0700 to 1630. Male–male agonistic interactions and mating behaviors were recorded *ad libitum* (Altmann 1974) for all the males of the group. The 21 subjects were focally observed using 30-min observation sessions (Altmann 1974) twice a week. Observations were counterbalanced between early (0700–1030 hours) and late sessions (1030–1630 hours) on a weekly basis to control for diurnal effects. We collected 201 h of observation on 21 subjects over 10 wk, with each subject being observed, on average, 9.6 ± 0.7 h (range: 8–10.5). During focal observations, mating and masturbation episodes were recorded. Only mounts with intromission and thrusting were considered as mounts. Masturbation was defined as rapid, manual manipulations of the erect penis; the slower, finer self-grooming of the genital area/unerect penis was not considered as masturbation. The occurrence of ejaculation after mounts or masturbation was also recorded. Ejaculation was considered to take place only if an ejaculatory pause and/or sperm were observed. In addition to sexual activity, all social, agonistic, and individual behaviors, such as activity (feeding, resting, drinking) and self-directed behaviors (scratching, self-grooming, yawning, and shaking; see Maestripieri et al. 1992; Higham et al. 2009) involving the focal subject, were recorded. Data were collected using the Behavior software loaded onto a Psion handheld workabout. Data were parsed into Access (Microsoft Corp., Redmond, WA, USA), and Access queries were used to calculate rates and durations of behavior.

Dominance Hierarchy

Of the 48 adult males who resided in the group during the study, reliable data on agonistic interactions (contact and non-contact aggression and submission) were collected for 32 males, the others being too peripheral or not residing long enough in the group to be observed. A total of 418 agonistic interactions were used to assess the dominance hierarchy. The dominance hierarchy was created using the following 'winner–loser' interactions (see Higham et al. 2011 for a similar method): fear grins (winner is grinned at), avoid/displacement (winner is the individual avoided or that physically displaces another individual), and threat, chase, or lunge (winner is aggressor in all interactions). All interactions were compiled into a winner–loser matrix, and Mat-Man 1.1 (Noldus Information Technology, Wageningen, the Netherlands) was used to assign individual dominance rank ($h' = 0.205$, $p = 0.002$;% of unknown relationships: 60.5; directional consistency index = 0.939). The subjects of the study were assigned rank ranging from 1 to 26. Males from the top third of the dominance hierarchy were considered as high-ranking males (ranks 1–8; N = 5 subjects), those of the intermediate part as middle-ranking (ranks 9–17; N = 7 subjects), and males from the bottom third as low-ranking (ranks 18–26); the remaining 6 males were considered as peripheral. The subjects of this study were distributed in all dominance categories: 5 high-ranking, 7 middle-ranked, and 9 low-ranking males.

Data Analyses

Because rhesus macaques are multiple-mount ejaculators, we considered mounts taking place during a focal to be part of a same mating series; we calculated the mating frequency as the hourly frequency with which a subject was seen involved in a mating bout (i.e., number of focals with mounts/total number of hours of observation). Based on the same rationale, we calculated a similar *masturbation frequency* as the hourly frequency with which a subject was observed involved in a masturbating bout (i.e., number of focals with masturbation/total number of hours of observation). In addition, we calculated a *masturbation rate* as the average hourly rate at which a subject was seen masturbating during focal periods (i.e., number of times subject masturbated/hours). Ejaculation following masturbation was observed too infrequently to be analyzed quantitatively (see below).

We tested for the relationship between (1) dominance rank and mating activity, (2) dominance rank and masturbation activity, and (3) mating activity and masturbation activity with linear regressions. All variables but dominance rank were log-transformed to ensure that models met assumptions on the distribution of residuals. To investigate whether males were more likely to be seen masturbating on days in which they were not observed mating, we calculated the proportion of focal periods in which a subject masturbated for days in which he was observed mating and those in which he was not. Because males have fewer opportunities to masturbate during focal observation sessions in which they are mating—simply because they might be busy doing something else—we use *ad libitum* data to assess mating activity. Although *ad libitum* data represent the risk of underestimate the behavioral rate of males with lower observability (i.e., low-ranking and peripheral males), the use of this approach was validated by a strong correlation ($r_s = 0.851$, $p < 0.001$, N = 21) between the mating frequency calculated based on continuous focal observation (see definition above) and the frequency calculated based on *ad libitum* data (average daily number of mount series recorded). We used Wilcoxon signed-rank test to test the prediction that males are more likely to masturbate on days in which they are not seen mating.

Linear regressions were performed in R 2.15.2, and other statistical analyses were performed in IBM SPSS v20. The alpha level was set at $p < 0.05$ for all statistical tests.

Results

Mating and Masturbation Frequencies

We observed 74 mating bouts during focal periods over the course of the 10-wk study, performed by all but one male subjects (95.2% of all subjects), with an average of 3.52 ± 3.06 (range: 0–13) mating bouts per male, and average hourly frequency of 0.37 ± 0.33 bout/h (range: 0–1.37). Mount series ending with ejaculation were observed in 17 instances (23.0% of all mating bouts) and involved 10 males (47.6% of all male subjects), with an average of 0.81 ± 1.33 (range: 0–5) mounts ending with ejaculation per male and an average hourly frequency of 0.09 ± 0.14 event/h (range: 0–0.56).

As for masturbation, we observed 36 bouts over the course of 10 wk, performed by 16 male subjects (72.7% of all subjects), with an average of 1.68 ± 1.58 (range: 0–6) masturbation bouts per male (2.31 ± 1.40 if only those who were seen masturbating are considered). Average masturbation frequency was 0.18 ± 0.16 bout/h (range: 0–0.58) and masturbation rate, 0.35 ± 0.44 time/h (range: 0–1.73) (if only males who were observed masturbating are considered: 0.23 ± 0.13 bout/h and 0.46 ± 0.46 time/h). Masturbation frequency and rate were correlated ($t = -2.699$, $p = 0.014$, $N = 21$), but not if only males who were seen masturbating are considered ($t = 0.843$, $p = 0.413$, $N = 16$). In the majority of the cases (21 of 36, or 58.3%), males manipulated their penis only once during the focal. The rest of the time, masturbation bouts lasted on average 2.22 ± 2.02 min (range: 0.15–6.23 min) with an intermanipulation interval of 41 ± 35 s (range: 5–125 s). Masturbation ending with ejaculation was observed in five instances (13.9% of all masturbation bouts) and involved 5 different males (23.8% of all males). Note that the focal may have ended before the ejaculation could occur (i.e., based on intermanipulation interval; see above) in only 5.56% of the cases (N = 2 bouts, 2 males).

Effect of Dominance Rank

There was a significant effect of dominance rank on mating frequency ($t = -3.486$, $p = 0.002$, $N = 21$), reflecting the fact that high-ranking males accounted for a higher number of observed copulations (Fig. 1a). High-ranking males copulated on average 0.82 ± 0.36 bout/h, while middle- and low-ranking males mated on average 0.24 ± 0.11 bout/h and 0.23 ± 0.18 bout/h, respectively. There is no significant correlation between dominance rank and ejaculation frequency ($t = -1.712$, $p = 0.103$, $N = 21$), probably due to the fact that no middle-ranking males were seen ejaculating (Fig. 1a). High-ranking males were observed ejaculating in a mating context with an average 0.13 ± 0.11 bout/h, while low-ranking males ejaculated only an average of 0.03 ± 0.03 bout/h.

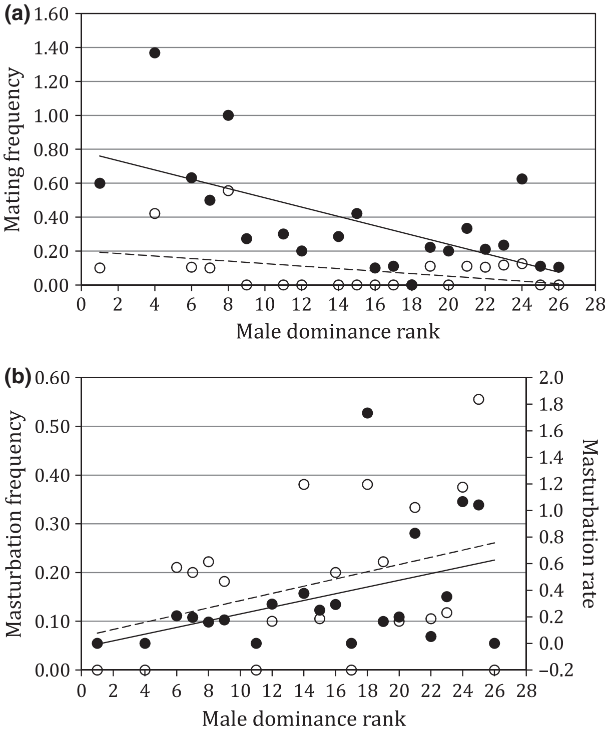

Fig. 1: Relation between male dominance rank and (a) mating activity and (b) masturbation behaviors. (a) Two measures of mating activity are presented: mating frequency (filled circles, full line) and frequency of mating bouts ending in ejaculation (open circle, dashed line). (b) Two measures of masturbation behaviors are presented: masturbation frequency (filled circles, full line) and masturbation rate (open circles, dashed line) (see Method for details).

There was no significant correlation between rank and masturbation frequency ($t = 1.565$, $p = 0.134$, $N = 21$) (Fig. 1b). Yet, low-ranking males still appear to have masturbated twice as frequently as other males: low-ranking males masturbated on average 0.12 ± 0.09 bout/h, while high- and middle-ranking males masturbated on average 0.06 ± 0.06 and 0.07 ± 0.07 bout/h, respectively. However, there was a significant negative correlation between dominance rank and masturbation rate ($t = 2.124$, $p = 0.047$, $N = 21$) (Fig. 1b). Indeed, in all cases of masturbation observed for a high-ranking males, the male manipulated his penis only once (6 bouts of 6), a phenomenon observed in only half of the instances for the other males (middle-ranking males: 6 bouts of 10; low-ranking: 9 bouts of 20). If those bouts are excluded from the analyses, there is a significant negative association between dominance rank and both masturbation frequency ($t = 3.423$, $p = 0.003$, $N = 21$) and rate ($t = 3.328$, $p = 0.004$, $N = 21$). While masturbation leading to ejaculation was too infrequent to be analyzed quantitatively, it is worth mentioning that the four males who were observed to ejaculate were all at the bottom-half of the dominance hierarchy, one mid-ranking male and four low-ranking males (average rank: 19.2 ± 2.4, range: 16–22).

Effect of Mating Activity

There was no significant correlation between mating frequency and both masturbation frequency ($t = -0.756$, $p = 0.459$, $N = 21$) or rate ($t = -1.321$, $p = 0.202$, $N = 21$), although a trend emerges if only bouts involving more than one manipulation are included (masturbation frequency: $t = -1.622$, p = 0.121; rate: $t = -2.020$, p = 0.058). However, on a daily basis, males were more likely to be seen masturbating on days they were not seen mating ($Z = -3.209$, p = 0.001, N = 21) (Fig. 2).

Discussion

In this study, we examined how males' access to fertile females influenced the occurrence of their masturbation behavior by examining the relationship between dominance rank, mating frequency, and masturbation among 21 free-ranging rhesus macaque males. Despite a small sample size (37 masturbation bouts performed by 16 males, 5 of which included ejaculation), we found some evidence that masturbation is more likely to take place when mating opportunities are low. Although there was no significant negative correlation between mating frequency and masturbation measures, the link between mating opportunities and masturbation was also confirmed by the finding that males, regardless of their rank, were more likely to be observed masturbating on days in which they were not observed mating. Furthermore, mating frequency and rate of masturbation measures were associated with dominance rank in opposite directions: higher-ranking males mated more than lower-ranking males, while lower-ranking males tended to masturbate at higher rate than higher-ranking males. Although ejaculation following masturbation was observed only 5 times, all instances of ejaculation involved males in the bottom-half of the dominance hierarchy, further supporting an association between masturbation and low rank.

The results we obtained here for rhesus macaques are similar to those obtained for the closely related Japanese macaques (Thomsen & Soltis 2004; Inoue 2012) and to a certain extent also those for stump-tail macaques (see Introduction). Our results contrast those obtained for red colobus monkeys, in which some high-ranking males were observed masturbating in very few instances and only in context of inter-group encounters during the mating season (Starin 2004). Our results are also in striking contrast to those obtained for promiscuous Cape ground squirrels (*Xerus inauris*) in which high-ranking males masturbated on days of intense mating activity, after copulation occurred—a behavioral pattern that inspired the STI-reduction hypothesis (Waterman 2010). It is possible that different functional hypotheses for masturbation apply to different sexually promiscuous species. Taken together, the results from the macaque studies are more consistent with the predictions of both the sexual-outlet and the ejaculate-quality-improvement hypotheses, than those of the STI-reduction hypothesis.

Interestingly, however, our results revealed that only a small proportion of masturbation events we observed led to ejaculation in the study group (≈15%; Fig. 3). Given that in only two instances (≈5%), males stopped masturbating before the end of the observation period (Fig. 3), it is safe to say that most masturbation bouts did not end in ejaculation (≈80%), which contradicts the assumptions of all three hypotheses proposed to explain male masturbation reported here. It is also very different of the frequency of masturbatory ejaculation reported for other species: while only 22.7% of the ejaculations observed in our study were attributed to masturbation bouts, 50.7% were for Japanese macaques (Thomsen & Soltis 2004). We cannot rule out the possibility that the discrepancy in these results comes from difference in behavioral observation protocol. Indeed, data reported by Thomsen & Soltis (2004) were based on

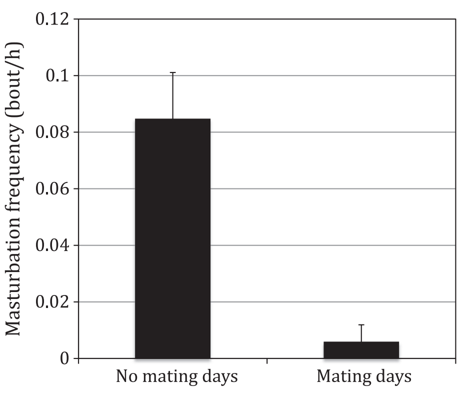

Fig. 2: Comparison of average masturbation frequency between days in which males were seen mating ('Mating days') and those where no mating activity was observed ('No mating days'). Data are presented as average ± SEM.

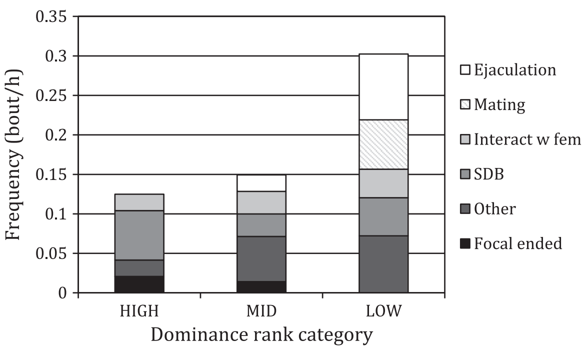

Fig. 3: Frequency of the context in which masturbation took place for each dominance rank category.

all-day continuous observation, while those reported here are based on 30-min focal observations. Supporting this view, ejaculation from mating was also rarely observed in our study (≈25%). Alternatively, it is possible that the hypotheses explaining the function of masturbation currently available do not explain male masturbation in rhesus macaques. Description of the context in which male masturbation takes place can help understand its function.

In our study, masturbation that did not lead to ejaculation took place in two main contexts (25% of all masturbation bouts each): (1) males manipulated their in penis only once in a period of time in which they emitted a large amount of self-directed behaviors; and (2) males stopped masturbating and started interacting with females in a sexual context, a third of which led to mating (Fig. 3). In the remaining cases, the male changed activity or simply stopped with no obvious change of activity. Based on these observations, we propose two hypotheses to explain male masturbation in rhesus macaques. Firstly, we propose that it may be a form of self-directed behavior emitted in context of intense anxiety (Maestripieri et al. 1992), which could or could not be created by a sexual context itself ('masturbation-as-SDB' hypothesis). Masturbation could be more frequent among low-ranked males if their position creates more emotional stress. Alternatively, male masturbation could be aimed at maintaining high level of sexual arousal for males to decrease the length of the next mount series and increase the probability of ejaculating through mating ('sexual-arousal' hypothesis). In rhesus macaques, mount series can last from 1 to 56 min, and long series are more likely to be interrupted by higher-ranking males (Manson 1996). This would be more frequent among non-dominant males that have a lower access to females and mate mainly during short-term associations and sneak copulations.

An unequivocal rejection of the null hypothesis that male masturbation is a non-functional by-product of frustrated sexual arousal would require evidence that interindividual variation in masturbation behavior is associated with variation in male health, emotional stress, ejaculate quality, and/or in fertilization success. While Inoue (2012) showed no correlation between masturbation rate and reproductive success, the fact that mating rate or dominance rank was not taken into account provides little insights about whether males masturbating produced more offspring than predicted based on their mating rate. Some insights into the function of masturbation could also be provided by comparing closely related primate species that live in multimale–multifemale groups that differ in the extent to which the alpha male effectively monopolizes access to fertile females (and in turn, the intensity of sperm competition) or in their mating pattern (i.e., multiple mounters vs. single mounters). Comparing prevalence of male masturbation, the frequency at which it leads to ejaculation, and context in which it takes place within these species could shed some light on whether maintaining a steady supply of high-quality sperm through frequent masturbation is needed to take full advantage of rare opportunities for copulation that become available to individuals who are otherwise consistently prevented from copulating.

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Literature Cited

Altmann, S. A. 1962: A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Ann. N. Y. Acad. Sci. **102**, 338—435.

Altmann, J. 1974: Observational study of behaviour: sampling methods. Behaviour **49**, 227—267.

Bagemihl, B. 1999: Biological Exuberance: Animal Homosexuality and Natural Diversity. St. Martin's Press, New York.

Baker, R. R. & Bellis, M. A. 1993: Human sperm competition: ejaculate adjustment by males and the function of masturbation. Anim. Behav. **46**, 861—885.

Baker, R. R. & Bellis, M. A. 1995: Human Sperm Competition: Copulation, Masturbation and Infidelity. Chapman & Hall, London.

Berard, J. D., Nuernberg, P., Epplen, J. T. & Schmidtke, J. 1994: Alternative reproductive tactics and reproductive success in male rhesus macaques. Behaviour **129**, 177—201.

Bercovitch, F. B. 1992: Sperm competition, reproductive tactics, and paternity in savanna baboons and rhesus macaques. In: Paternity in Primates: Genetic Tests and Theories. (Martin, R. D., Dixson, A. F. & Wickings, E. J., eds). Karger, Basel, pp. 225—237.

Carpenter, C. R. 1942: Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). J. Comp. Psychol. **33**, 143—164.

Chapais, B. 1983: Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. Behav. Ecol. Sociobiol. **12**, 215—228.

Dixson, A. F. 2012: Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human, 2nd edn. Oxford Univ. Press, Oxford.

Dixson, A. F. & Anderson, M. J. 2004: Sexual behavior, reproductive physiology and sperm competition in male mammals. Physiol. Behav. **83**, 361—371.

Dubuc, C., Muniz, L., Heistermann, M., Engelhardt, A. & Widdig, A. 2011: Testing the priority-of-access model in a seasonally breeding primate species. Behav. Ecol. Sociobiol. **65**, 1615—1627.

Dubuc, C., Muniz, L., Heistermann, M., Widdig, A. & Engelhardt, A. 2012: Do males time their mate-guarding effort with the fertile phase in order to secure fertilisation in rhesus macaques? Horm. Behav. **61**, 696—705.

Higham, J. P., MacLarnon, A. M., Heistermann, M., Ross, C. & Semple, S. 2009: Rates of self-directed behavior and faecal glucocorticoid levels are not correlated in female wild olive baboons (*Papio hamadryas anubis*). Stress **12**, 526—532.

Higham, J. P., Heistermann, M. & Maestripieri, D. 2011: The energetics of male-male endurance rivalry in rhesus macaques. Anim. Behav. **81**, 1001—1007.

Hoffman, C. L., Ruiz-Lambides, A. V., Davila, E., Maldonado, E., Gerald, M. S. & Maestripieri, D. 2008: Sex differences in survival costs of reproduction in a promiscuous primate. Behav. Ecol. Sociobiol. **62**, 1711—1718.

Inoue, E. 2012: Male masturbation behavior if Japanese macaques in the Arashiyama E troop. In: The Monkeys of Stormy Mountain: 60 Years of Primatological Research on the Japanese Macaques of Arashiyama. (Leca, J.-C., Huffman, M. A. & Vasey, P., eds). Cambridge Univ. Press, Cambridge, pp. 204—219.

Kinsey, A. C., Pomeroy, W. B. & Martin, C. E. 1948: Sexual Behavior in the Human Male. WB Saunders Co., Phildelphia.

Laqueur, T. W. 2003: Solitary Sex: A Cultural History of Masturbation. Zone Books, New York.

Loy, J. D., Loy, K., Keifer, G. & Conaway, C. 1984: The Behavior of Gonadectomized Rhesus Monkeys. Contributions to Primatology, Vol. 20. Karger, Basel.

Maestripieri, D., Schino, G., Aureli, F. & Troisi, A. 1992: A modest proposal: displacement activities as an indicator of emotions in primates. Anim. Behav. **44**, 967—979.

Manson, J. H. 1996: Male dominance and mount series duration in Cayo Santiago rhesus macaques. Anim. Behav. **51**, 1219—1231.

Nieuwenhuijsen, K., de Neef, K. J., van der Werff, J. J., Bosch, T. & Slob, A. K. 1987: Testosterone, testis size, seasonality and behavior in groupliving stumptailed macaques. Horm. Behav. **21**, 153—169.

Phoenix, C. H. & Jensen, J. N. 1973: Ejaculation by male rhesus in the absence of female partners. Horm. Behav. **4**, 231—238.

Rawlins, R. G. & Kessler, M. J. 1986: The history of the Cayo Santiago colony. In: The Cayo Santiago Macaques: History, Behavior and Biology. (Rawlins, R. G. & Kessler, M. J., eds). State Univ. of New York Press, Albany, pp. 13—45.

Slimp, J. C., Hart, B. L. & Goy, R. W. 1978: Heterosexual, autosexual and social behavior of adult male rhesus monkeys with medial preoptic-anterior hypothalamic lesions. Brain Res. **142**, 105—122.

Starin, E. D. 2004: Masturbation observations in Temminck's red colobus. Folia Primatol. **75**, 114—117.

Thomsen, R. & Soltis, J. 2004: Male masturbation in free-ranging Japanese macaques. Int. J. Primatol. **25**, 1033—1041.

Thomsen, R., Solis, J. & Teltscher, C. 2003: Sperm competition and the function of masturbation in male primates. In: Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions. (Jones, C. B., ed). American Society of Primatologists, Norman, OK, pp. 437—453.

Waterman, J. M. 2010: The adaptive function of masturbation in a promiscuous African ground squirrel. PLoS One **5**, e13060.

Zimmerman, S. J., Maude, M. B. & Moldawer, M. 1965: Frequent ejaculation and total sperm count, motility and form in humans. Fertil. Steril. **16**, 342—345.