Title

When males have females on their backs: Male's tolerance, solicitation, and use of female-male mounting in Japanese macaques

Short running title

Male's response to female-male mounting

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Accepted in *American Journal of Primatology* (May 11, 2022)

Abstract

Previous research on Japanese macaques has shown that female-to-male mounting (FMM) is performed by some females as an exaggerated form of sexual solicitation that may occur in the context of high female competition for male mates. This supernormal courtship behavior functions to prompt subsequent male-to-female mounting. In this report, we focused on the male consort partners' responses to FMM. We studied a free-ranging population of Japanese macaques at Arashiyama, Japan, in which FMM is frequent and prevalent. We analyzed 240 consortships involving 31 females and 19 males. We tested three hypotheses regarding male's tolerance, solicitation, and use of FMM. First, we found that FMM was tolerated by male mountees who were no more likely to aggress their female partners during a short time window around a FMM, than they were during the rest of the consortship period. Second, we showed that FMM could be triggered by male recipients, via explicit male-to-female sexual solicitations. Third, we found that some males may utilize FMM in a quest for their own sexual stimulation, which sometimes culminated in masturbation by the male during FMM. Our findings indicate that male partners facilitate the expression of FMM both passively (via their tolerance) and actively (via their solicitation). In addition, FMM appears to enhance the sexual arousal of male partners during consortships. We argued that, for females to have expanded their repertoire of sexual solicitations by adopting FMM, male mates must have played a role in the evolutionary origins and maintenance of this non-conceptive, but intense and powerful female mating tactic.

Keywords

Female-male mounting, sexual adaptation, male arousal, masturbation, *Macaca fuscata*

Research Highlights

- Previous research in Japanese macaques has shown that female-to-male mounting (FMM) is a supernormal courtship behavior that functions to prompt subsequent male-to-female mounting.
- Because mounting is a male-typical behavior, we studied male consort partners' responses towards FMM in a free-ranging population of Japanese macaques in which this behavior is particularly frequent and prevalent.
- By tolerating and triggering the performance of FMM in their female mates, males may have passively and actively contributed to the evolution and maintenance of this sexual adaptation, while deriving sexual gratification from this behavior.

Introduction

In mammals, mounting behavior is usually considered a male-typical behavior. Male-to-female mounting (hereafter MFM) is generally characterized as primarily sexual and reproductive, with possible secondary sociosexual functions, including adaptive social goals (e.g., dominance expression; Dixson, 2012; Wickler, 1967). In contrast, female mammals display mounting behavior infrequently, if at all (Baum, 1979). In some species (e.g., dogs, goats, bisons), mounts are occasionally performed by females, even though these always occur at lower frequency than mounts performed by males (Bagemihl, 1999; Dagg, 1984). Female mounting is obviously a non-conceptive behavior that has typically been explained in terms of sociosexual benefits (e.g., affiliation, tension-reduction, reconciliation), with sexual motivation playing little or no role (Bagemihl, 1999; Dixson, 2012; but see Vasey, 2006; Vasey & Duckworth, 2008).

There are two types of mounts performed by females: those directed to same-sex sexual partners (i.e., female-to-female mounting, hereafter FFM) and those directed to opposite-sex sexual partners (i.e., female-to-male mounting, hereafter FMM). Previous studies in diverse mammal taxa propose that FMM is a proceptive sexual behavior. As a female-to-male sexual solicitation, FMM may serve to stimulate males with low levels of sexual motivation and performance, and prompt subsequent male-to-female copulations (Beach, 1968; Dagg, 1984). Adult FMM is phylogenetically widespread among mammals, with reports of this behavior in 43 mammalian species. In 36 of these species, FMM was performed during the breeding season or in a context of sexual excitement, such as when females were in heat and ready to mate (e.g., Guinea pigs, marmots, squirrels, cats, dogs, pigs, sheep, camels, monkeys, great apes; Dagg, 1984).

In certain populations of Japanese macaques (*Macaca fuscata*), some adult females are bisexual. During the mating season, these females routinely engage in sexual interactions with adult opposite-sex and same-sex mates. They do so within the context of temporary, but exclusive, sexual associations involving mount series between partners, and that are known as consortships (Dixson, 2012; Leca et al., 2015a; Vasey, 2006). Sexual behaviors expressed during consortships include vocal, facial, and gestural sexual solicitations. During heterosexual consortships, MFM and FMM are also expressed, and FFM is a defining feature of female homosexual consortships (Gunst et al., 2020; Leca et al., 2015b; Vasey et al., 2008a). In addition to mounting behaviors and sexual solicitations, consortships are characterized by a close spatial proximity between the two sexual partners. During heterosexual consortships, for example, the female often sits in front of the male with her back turned to his chest; this dorso-ventral positioning may facilitate subsequent MFM (Dixson, 2012; Vasey et al., 2008b).

Previous research in a free-ranging group of Japanese macaques living at Arashiyama-Kyoto, Japan, showed that adult females mount both adult males and adult females (Vasey et al., 2006; Vasey & Duckworth, 2008). In a recent study focusing on this population, we investigated whether mounting is employed by some female Japanese macaques as an exaggerated form of sexual solicitation that may occur in the context of high female intra-sexual competition for male mates (Gunst et al., in press). We demonstrated that FMM is more efficient (i.e., a "supernormal courtship" behavior pattern) than species-typical female-to-male sexual solicitations at prompting subsequent MFM (Gunst et al., in press). As per Tinbergen (1951), we defined "supernormal" as a behavioral stimulus that triggers the expression of the normal pattern of behavior even more strongly than a normal stimulus. The same study also revealed that FMM is an intense and conspicuous proceptive sexual behavior that is triggered when a male consort partner's attention is drawn away from his female mate. Our data showed that FMM contributed to limiting the male consort partner's movement while being mounted. Indeed, FMM necessitates contact between multiple body parts, including the male's hind limbs, rump, and back, that are involved in locomotion. While performing a FMM, a female may act as a "dead weight" on her male partner's back, thereby constraining the male's movement and preventing or restraining him from leaving the immediate area in which the consortship is taking place (Vasey, 2006).

Although FMM has been reported in several groups of Japanese macaques (e.g., Minoo, Takasakiyama), this behavior is particularly frequent and prevalent at Arashiyama (Figure 1 in Leca et al., 2014a). Females at Arashiyama have expanded their repertoire of sexual solicitations by adopting a non-conceptive, but showy and powerful mating tactic (i.e., FMM). FMM may have positive reproductive consequences by impacting intra-sexual competition for male mates, via male retention, and ultimately increasing the chances of conception by expediting MFM (Gunst et al., in press). This population-specific sexual adaptation may be the result of favorable socio-demographic conditions, namely few resident males, most of them being old, sexually under-motivated, and less aggressive and controlling than the average male Japanese macaques (Leca et al., 2014a).

If demonstrated, a lack of agonistic response from male mountees in the Arashiyama population could be interpreted as male-to-female sexual tolerance within the context of established consortships. This would be consistent with a previous inter-population comparative study showing that FMM was more tolerated in groups of Japanese macaques (like Arashiyama) with lower levels of male-to-female sex-related aggressiveness, as measured by fewer cases of intense male sexual harassment (Leca et al., 2014a). Male mates at Arashiyama were described as more "mellow" (i.e., less coercive, less controlling, and more affiliative) than those from other populations, a social style that is likely conducive to the expression and maintenance of FMM as a population-specific and cultural non-conceptive sexual behavior (Leca et al., 2014a). In this context, tolerance of unsolicited FMM (i.e., an atypical behavioral pattern in mammals: Baum, 1979) could be interpreted as acceptance on the part of the male mountee. Previous research on the development of female sexual behavior in the Arashiyama population of Japanese macaques suggested that sexual solicitations with body contact are slow-developing behavior patterns because they involve attracting attention to oneself and, even more importantly, close interactions with potential male mates who may be overtly aggressive (cf. Enomoto, 1981; Leca et al., 2014b). *A fortiori*, mounting interactions (and, in the case of this study, FMM) involve coordinating with established male consort partners who may have demonstrated a "degree of trustworthiness" (Leca et al., 2014b, p. 1209).

In the present study, we broadly aimed to further our understanding of the favorable socio-cultural conditions that could explain why FMM is more frequent and widespread among adult female Japanese macaques in Arashiyama, than in other troops of this primate species where FMM, if present, is rare (Leca et al., 2014a). We specifically focused on the male consort partners' responses towards FMM. We examined the degree of tolerance males exhibited in response to being the recipients of this proceptive behavior. We then assessed whether male consort partners were proactive towards FMM by soliciting this behavior from their female mates. In addition to a possible reproductive advantage (as FMM functions to prompt MFM: Gunst et al., 2020), we investigated whether males could derive proximate benefits from being mounted by females, via mechanistic processes (e.g., sexual gratification by means of masturbation).

First, we tested the hypothesis that male partners passively participated in the expression of FMM at Arashiyama. Because FMM is an unusual behavior at the species level (Leca et al., 2014a), and a physically constraining sexual solicitation, we assumed that most male Japanese macaques were not evolutionarily prepared to be mounted by females. Still, FMM is frequent and prevalent at Arashiyama. Therefore the "male partner's tolerance towards FMM" hypothesis holds that FMM is tolerated by Arashiyama male recipients (Hypothesis 1). Based on this hypothesis, we predicted that males would not aggress their female consort partners more often immediately (i.e., 30 sec; see Methods for explanation) after being the recipients of a FMM, than immediately before a FMM (Prediction 1a). We also predicted that males would be no more likely to aggress their female consort partners during a short time window around a FMM, than they would during any other time window of the same duration in the rest of the consortship period (as a baseline), but in which FMM did not occur (Prediction 1b).

Second, we tested the hypothesis that male partners actively participated in the occurrence of FMM at Arashiyama. The "male partner's solicitation of FMM" hypothesis holds that FMM is solicited by

Arashiyama male recipients (Hypothesis 2). Based on this hypothesis, we predicted that males would perform all types of sexual solicitations towards their female consort partners more often shortly (i.e., 1 min; see Methods for explanation) before a FMM, than shortly after (Prediction 2a). We then tested two male-to-female solicitations (i.e., *hindquarter presentations* and *inclined-back presentations*) for similar sequential effects because their behavioral structure is *specifically* oriented towards the expression of FMM by female partners. These two male-to-female solicitations expose the male's rear end to the female partner, and thus are likely to facilitate subsequent FMM; we expected males to perform these two solicitations more often shortly (i.e., 1 min) before a FMM than shortly after (Prediction 2b). Then, we considered a third male-to-female solicitation allowing the male to grab and pull his female partner towards him to either trigger a FMM or physically maintain the female on his back during the FMM: *grasping*; we expected a higher rate of *grasping* during a 1-minute time window around the occurrence of a FMM than during the rest of the consortship period (Prediction 2c).

We did not expect more structurally and functionally *generic* male-to-female solicitations to facilitate subsequent FMM. Male-to-female solicitations that do not involve exposure of the male's rear end to the female partner and do not allow the male to grab and pull his female partner towards him should not be performed more often shortly (i.e., 1 min) before a FMM than shortly after. This expectation applied to male-to-female solicitations without physical contact between the consort partners (i.e., *bird-dogging*, *glancing*, *hindquarter-sniffing*, *lip-quivering*, and *sexual vocalizations*; Prediction 2d), and those with physical contact between the consort partners (i.e., *body spasms, ground-smacking*, *hands-on-hindquarters*, and *pushing*; Prediction 2e).

Third, in a previous study, we found that (1) FMM functioned to prompt MFM (Gunst et al., in press), and (2) a few males were anecdotally reported to engage in masturbation without ejaculation while being mounted by their female partners (unpublished data in Gunst et al., in press). In this study, we tested the "male partner's sexual arousal during FMM" hypothesis, which holds that FMM functions to enhance the male partner's sexual arousal during the consortship (Hypothesis 3). Based on this hypothesis, we predicted that males would masturbate significantly more often shortly (i.e., 1 min) after the start of a FMM than shortly before (Prediction 3a). We also predicted that, when the male consort partner engaged in masturbation while being mounted by a female, the most frequent FMM posture (i.e., with the highest percentage of expression among all FMM postures) should be the one involving the largest area of body contact and the maximum number of body parts between the two partners, namely reclining mounts, which necessitate contact between the female's torso and ventral areas, as well as the inside of all four limbs, and the male's back, rump, and hind limbs (Prediction 3b; after VanderLaan et al., 2012). We also predicted that males would perform male-to-female sexual solicitations more often shortly (i.e., 1 min) before engaging in masturbation during FFM, than shortly after (Prediction 3c). If male masturbation is associated with a long interval without MFM during which penile erection is lost, and if male masturbation functions to prompt MFM, then there should be a shorter time interval between a given masturbation bout and the subsequent MFM, than between the previous MFM and the same masturbation bout (Prediction 3d).

Methods

Ethical statement

This research was exclusively observational and non-invasive. Our study was conducted in accordance with the Guide for the Care and Use of Primates prepared by the Primate Research Institute, Kyoto University, and in compliance with the American Society of Primatologists Principles for the ethical treatment of non-human primates. It was also approved by the authors' institutional Animal Welfare Committee.

Study species, group, and site

Japanese macaques are seasonally breeding primates, and females ovulate only during the mating season (i.e., autumn and winter months). Like other macaque species, they are characterized by a multimale-multifemale mating system (Dixson, 2012). Observations were conducted on the free-ranging Arashiyama-E group at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture, Japan. The Arashiyama population of Japanese macaques is one of the longest continuously studied non-human primate populations in the world (Huffman et al., 2012). Long-term genealogical records on individually identified monkeys are available from years of collaborative research between observers working at this site, including longitudinal data sets on hierarchical ranks (Leca et al., 2012). The members of the Arashiyama-E troop belonged to 15 separate matrilineages and their exact ages were known. During the first study period (2001), the group consisted of 171 individuals – 124 females and 47 males of all age classes, with a qualified sex ratio of 0.28, that is 28 adult males (≥ 7 years) for 101 adult females (≥ 5 years; see Leca et al., 2007, 2014c for age classes). During the second study period (2003), the group consisted of 146 individuals (115 females and 31 males of all age classes, with a qualified sex ratio of 0.20, that is 19 adult males for 97 adult females). The Arashiyama E-group was larger than the average group of free-ranging Japanese macaques (40.8 ± 28.9 individuals; Fooden & Aimi, 2005) and its qualified sex ratio was more skewed towards females than that of the average group of free-ranging Japanese macaques (0.65; Fooden & Aimi, 2005), which probably exacerbated female-female competition for male mates in our study group. These monkeys were provisioned at least three times per day with fruits and vegetables by the park staff and were very well habituated to human presence.

Data collection

Behavioral data were collected daily, during the mating season, in October-December 2001 and October-December 2003 by the third author. The observer recorded the identities of all the group members. Observations occurred primarily between 7h00 and 14h00 when the monkeys are most sexually active (Vasey & Duckworth, 2006). The selection of sampled consortships was partly opportunistic (i.e., on a "first encountered, first selected" basis) and partly corrected: when two consortships occurred simultaneously, the one for which fewer data had been collected was selected. Once a consortship was selected, the observer used a modified version of continuous video-recorded focal-animal sampling (Altmann, 1974). Therefore, focal data were collected for both male and female consort partners simultaneously (i.e., as a dyad) because the two individuals were typically in close proximity (i.e., in physical contact or up to about 10 m apart when they occasionally moved together) and interacting with one another, allowing the observer to generally video-record both consort partners within the same video frame.

A heterosexual *consortship* was defined as a temporary, but exclusive, sexual association between two adult opposite-sex mates, also referred to as consort partners (Huffman, 1991, 1992). It took the form of a mating sequence with series-mounting (i.e., three or more MFM or FMM mounts in any combination within a 10-min period; Vasey & Duckworth, 2008; Vasey et al., 2006) separated by inter-mount intervals, that included vocal, facial, and gestural sexual solicitations exchanged between partners, as well as self-directed masturbation. In addition, sexual solicitations could be performed by third-party competitors seeking to disrupt consortships (Enomoto, 1974). Consortships were deemed to have terminated if the main two sexual partners were not in close proximity and exhibited no mounting for 10 min (Vasey, 2004).

Data were recorded until the termination of the consortship unless the observer lost sight of the consort pair. Focal data were video-recorded by using a Sony Video Hi8 Handycam Vision (CCD-TR58 NTSC) video-camera with a colour LCD monitor. A total of 49 adult females and 19 adult male consort partners were sampled as focal subjects. During the two study periods, a total of 110.5 hrs of focal data (i.e., 66.5 hrs in 2001 and 44.0 hrs in 2003) were collected on heterosexual consortships.

Behavioral definitions and categories

In Japanese macaques, MFM is typically performed in a double foot-clasp dorso-ventral posture, whereas FMM postures performed at Arashiyama include this type of mount, but also single or no foot-clasp dorso-ventral mounts, reclining mounts, and sitting mounts (Table 2; Leca et al., 2014a, 2015b). Sexual solicitations (or courtship behaviors) occurred during inter-mount intervals and functioned to prompt mounting behavior (Vasey et al., 2008b). Inter-mount intervals were defined as the period between two consecutive mounts. Aside from three types of male-to-female solicitations (i.e., *hindquarter presentation*, *inclined-back presentation*, and *grasping*) whose behavioral structure was specifically oriented towards the expression of FMM, the other solicitations were grouped into those performed without physical contact between the consort partners (i.e., *bird-dogging*, *glancing*, *hindquarter-sniffing*, *lip-quivering*, and *sexual vocalizations*) and those performed with physical contact between the consort partners (i.e., *body spasm*, *ground-smacking*, *hands-on-hindquarters*, and *pushing*; Table 2; Enomoto, 1974; Enomoto et al., 1979; Fedigan, 1982; Huffman, 1991, 1992; McDonald, 1983; Vasey et al., 2006, 2008a,b; Gunst et al., 2015, 2020; Leca et al., 2015b).

Non-sexual behaviors also occurred during inter-mount intervals, including agonistic interactions and displays (see Table 2), affiliative interactions (i.e., allo-grooming), and other behaviors (i.e., approaching, leaving, resting, self-grooming, stone handling, and foraging). All courtship and non-sexual behaviors could also be directed toward third-party individuals (i.e., non-consort partners).

Data analysis

The first author was the sole video-scorer of all the mating sequences and used the aforementioned composite ethogram for heterosexual consortships in Japanese macaques. The first author used *The Observer XT 12* (i.e., a video scoring/analysis software by Noldus) to score the video-recorded mating sequences and generate event-log files (i.e., series of consecutive behavior patterns) when one of the 49 sampled adult female subjects and one of the 19 sampled adult male subjects were engaged in a heterosexual consortship. The first author also scored the direction of expression of the mounts (i.e., whether the mounts were MFM or FMM), sexual solicitations, and non-sexual behaviors listed above. When the male focal subject performed, or was the recipient of, a mount, then the recipient, or the performer (i.e., female mate or third-party individual) was noted. Mounting or being mounted by a third-party individual did not mean the termination of the ongoing consortship unless the two consort partners were not in close proximity (i.e., more than 10 m apart) and exhibited no mounting for 10 min (Vasey, 2004).

To measure intra-scorer reliability, the first author transcribed twice a total of 1.5 hr of video-records representing five heterosexual consortships, involving 102 sexual solicitations and 84 mounts. The comparison of the two transcriptions for frequency and duration of the behavior patterns yielded a high score of coder consistency (mean $k = 0.91 \pm 0.05$).

For the analyses pertaining to Predictions 1a, 1b, 2a-e, 3a, and 3b, we reduced our sample to 31 adult females with a minimum of 0.5 hour of focal time per female consort partner that performed FMM and whose age range was 5 – 26 years (mean ± SD = 13.0 ± 4.9 years). For Prediction 1b, we compared the frequency of agonistic interactions from male to female consort partners (1) during a 1-minute time window around the occurrence of a FMM (i.e., 30 sec before and 30 sec after FMM) and (2) during the rest of the consortship period (i.e., a baseline number of male-to-female agonistic interactions per minute), but in which FMM did not occur. For Prediction 2c, we compared the frequency of male-to-female grasping, as a sexual solicitation (1) during a 1-minute time window around the occurrence of a FMM (i.e., 30 sec before and 30 sec after FMM) and (2) during the rest of the consortship period (i.e., a baseline number of male-to-female grasping interactions per minute), but in which FMM did not occur. For Prediction 3c, we limited our analyses to the 20 female subjects whose male partners engaged in masturbation while being the recipients of FMM. For Prediction 3d, we limited our analyses to the 32 mating sequences that temporally contained a MFM before and after a masturbation bout.

For the analyses pertaining to Predictions 1a, 2a, 2b, 2d, 2e, and 3a, and 3c, we used *The Observer XT 12* to run a series of lag sequential analyses. Lag Sequential Analysis is a type of temporal analysis applied to behavioral sequences (such as mating sequences or consortships) that calculates the frequency of transitions between pairs of events (i.e., behaviors or positioning in our case) within a certain lag. The first event of the pair is called "Criterion" and the second "Target". Depending on what direction in time we chose (i.e., positive or negative), we calculated how often the Criterion (e.g., Event A) was followed by the Target (e.g., Event B), or how often Target (e.g., Event B) preceded the Criterion (e.g., Event A), respectively. We used a "time lag" sequential analysis, which considers transitions between a Criterion and a Target within a specific time window, independent of how many other events occur between them. We calculated the number of transitions from a Criterion to those Targets occurring within a specific time window following or preceding the Criterion. We used a time lag sequential analysis that requires the comparison of the same time window before and after the Criterion.

For Prediction 1a, we used a 30-sec time lag sequential analysis to compare the frequency of male-to-female agonistic interactions within consortships (i.e., Target) immediately before versus immediately after a FMM (i.e., Criterion). We chose a 30-sec time window because if a male consort partner does not tolerate being mounted by his female mate, one can expect an immediate reaction. For Predictions 2a-d, we used several 1-minute time lag sequential analyses to compare the frequency of various male-to-female sexual solicitations within consortships (i.e., Target) before and after being mounted by the female consort partner (i.e., Criterion). We chose a 1-min time window because (1) some FMM, particularly sitting mounts and reclining mounts, can last more than 30 sec, and there should be time for the expression of post-FMM male-to-female sexual solicitations to compare with pre-FMM male-to-female sexual solicitations, and (2) any time windows longer than one minute pre-/post-FMM may be too long to infer any causal relationships between any male-to-female sexual solicitations and FMM. For Prediction 3a, we used a 1-min time lag sequential analysis to compare the frequency of male masturbation bouts (i.e., Target) before versus after a FMM (i.e., Criterion). We chose a 1-min time window because (1) even if a FMM triggers a male masturbation bout, male sexual arousal should be associated with a physiological response (Roth et al., in press) that may not immediately follow the beginning of the FMM, and (2) FMM did not typically last more than one minute. For Prediction 3c, we used a 1-min time lag sequential analysis to compare the frequency of male-to-female sexual solicitations (i.e., Target) before versus after a male masturbation bout (i.e., Criterion). We chose a 1-min time window because this prediction combined aforementioned justifications about the time needed for the expression of male-to-female sexual solicitations and male masturbation after the beginning of the FMM.

Statistics

For most of our predictions (i.e., 1a,b, 2a-e, and 3a), we used Wilcoxon signed-rank tests to test within-individual differences in behavioral frequencies (i.e., Target) before versus after a particular behavior (i.e., Criterion). Because all these predictions were directional, we conducted one-tailed tests. Statistics of effect size for Wilcoxon signed-rank tests used Pearson's r correlation coefficient and reported the degree to which one group had data with higher ranks than the other group, with $r = Z/(\sqrt{(2 \times N_{pairs})}$. Categories and ranges for effect sizes were as follows: Small: ≤ 0.25, Medium: 0.26-0.34, and Large: > 0.35 (Gignac & Szodorai, 2016). To test the association between the occurrence of FMM and the occurrence of masturbation bouts across consortships, we used a Pearson chi-square test with continuity correction, and examined adjusted residuals for post hoc tests. To test the association between the number of male masturbation bouts and the number of FMM across consortships involving male masturbation, we used a Spearman's rho correlation coefficient. The measure of dispersion around the mean was the standard deviation. Statistical analyses were performed using the IBM-SPSS Statistics-26 analytical program. Significance levels were set at $\alpha = 0.05$.

Results

We analyzed a total of 240 consortships involving 31 females and 19 males, and during which FMM was expressed. This data set amounted to an average (± SD) of 2.1 ± 1.3 hours of consortship/female focal subject, range: 1.0-4.8 hours.

"Male partner's tolerance towards FMM" (Hypothesis 1)

Even though male-to-female agonistic interactions within consortships were, on average, about 4 times more frequent 30 seconds after a FMM (0.42 ± 0.48 aggressions/min) than 30 seconds before a FMM (0.12 ± 0.24 aggressions/min), this difference was not statistically significant (Wilcoxon signed-rank test, N = 31 females, z = -1.890, p = 0.059). Therefore, Prediction 1a was supported.

We found that male-to-female agonistic interactions within consortships were significantly less frequent during a 1-minute time window around the occurrence of a FMM (mean frequency per min ± SD: 0.01 ± 0.01) than during the rest of the consortship period (0.05 ± 0.04), which was taken as a baseline of heterosexual interactions (Wilcoxon signed-rank test, N = 31, z = -3.782, p < 0.001). Because males did not initiate agonistic interactions towards their female partners more often around the occurrence of a FMM than during the consortship baseline, Prediction 1b was supported.

"Male partner's solicitation of FMM" (Hypothesis 2)

The average frequency of all types of male-to-female sexual solicitations within consortships was 0.15 ± 0.13 solicitations/min. We found that males performed sexual solicitations towards their female partners significantly more often one minute before (mean frequency per min: 0.24 ± 0.26) than one minute after being the recipients of a FMM (0.11 ± 0.16; Wilcoxon signed-rank test, N = 31 females performing FMM, z = -2.983, p = 0.003). Therefore, Prediction 2a was supported.

We found a similarly significant effect with two types of male-to-female solicitations that explicitly expose the male's rear end to the female partner, namely *hindquarter presentations* and *inclined-back presentations* (N = 31 females, z = -2.547, p = 0.011). Therefore, Prediction 2b was supported.

We also found a similarly significant effect with grasping, a type of male-to-female solicitation allowing the male to grab and pull his female partner towards him to either trigger a FMM or physically maintain the female on his back during the FMM. This behavioral pattern was significantly more frequent during a 1-minute time window around the occurrence of a FMM than during the rest of the consortship period (mean frequency of male-to-female *grasping* per min ± SD: 1.45 ± 3.64 and 0.06 ± 0.08, respectively; Wilcoxon signed-rank test, N = 31 females, z = -2.253, p = 0.024). Therefore, Prediction 2c was supported.

As expected, we found no statistically significant effect for other types of male-to-female solicitations that are more structurally and functionally generic in the sense that they do not involve exposure of the male's rear end to the female partner and do not allow the male to grab and pull his female partner towards him. This was true regardless of whether these generic solicitations were performed without physical contact between the consort partners (e.g., *bird-dogging*, *glancing*, *hindquarter-sniffing*, *lip-quivering*, and *sexual vocalizations*; N = 31 females, z = -1.859, p = 0.063), or with physical contact between the consort partners (e.g., *body spasms, ground-smacking*, *hands-on-hindquarters*, and *pushing*; N = 31 females, z = -0.378, p = 0.705). Thus, Predictions 2d and 2e were supported, respectively.

"Male partner's sexual arousal during FMM" (Hypothesis 3)

Out of a total of 19 male consort partners, three individuals engaged in a total of 169 masturbation bouts during 50 heterosexual consortships involving 20 different females. The first male, named Mi-63-69-74-94, aged seven years during the first part of the study period (i.e., 2001), engaged in 85 masturbation bouts during 34 consortships out of 79 consortships sampled for this individual. Only one of these 85 masturbation bouts occurred during a consortship that did not involve FMM. The remaining 84

masturbation bouts were distributed over 33 consortships that involved FMM, with an average of 2.5 ± 2.3 masturbation bouts per consortship (range: 1 – 13). The second male, named Mi-63-69-74-83-90, aged 11 years during the first part of the study period (i.e., 2001), engaged in 83 masturbation bouts during 15 consortships out of 35 consortships sampled for this individual. All of these masturbation bouts were distributed over 15 consortships that involved FMM, with an average of 5.5 ± 4.9 masturbation bouts per consortship (range: 1 – 20). The third male, named Bl-59-64-75-84, aged 17 years during the first part of the study period (i.e., 2001), engaged in one masturbation bout during one consortship (out of nine consortships sampled for this individual), that did not involve FMM.

Interestingly, the two males performing 168 of these 169 masturbation bouts (i.e., Mi-63-69-74-94 and Mi-63-69-74-83-90) were, respectively, the alpha (i.e., highest-ranking) and beta (i.e., second highest-ranking) males in the Arashiyama population during the study period. They were also the two males with the two highest percentages of consortships recorded across all male group members during the study period (i.e., 18.0% and 14.2%, respectively; Leca et al., 2018).

Among the two aforementioned males, we found a statistically significant association between the occurrence of FMM and the occurrence of masturbation bouts across all their consortships (Pearson chi-square with continuity correction, $\chi^2 = 39.850$, df = 1, $p < 0.001$). Adjusted residuals showed a significant co-occurrence of FMM and masturbation (i.e., 67.1% of consortships with FMM included masturbation) and a significant co-absence of FMM and masturbation (i.e., 95.3% of consortships without FMM did not include masturbation). We also found a positive and statistically significant correlation between the number of masturbation bouts and the number of FMM across consortships involving male masturbation (Spearman's rho correlation coefficient: Rs = 0.839, N = 50 consortships, $p < 0.001$). These male masturbation bouts were relatively short (mean duration: 3.5 ± 2.6 sec, range: 1.0 – 28.7 sec) and none led to ejaculation.

We found that males engaged in masturbation significantly more often one minute after the start of a FMM than one minute before a FMM (Wilcoxon signed-rank test, N = 31 females performing FMM, $z = -3.474$, $p < 0.001$). Therefore, Prediction 3a was supported.

When the male consort partner engaged in masturbation while being mounted by a female, the most frequent FMM postures performed were reclining mounts (62.4%). Other FMM postures were double foot-clasp dorso-ventral mounts (25.4%), and the remainder (12.2%) included sitting mounts and single or no foot-clasp dorso-ventral mounts. Therefore, Prediction 3b was supported.

We found that males performed all types of male-to-female sexual solicitations significantly more often one minute before than one minute after engaging in masturbation while being mounted by their female partners (mean frequency of male-to-female sexual solicitations per min ± SD: 0.03 ± 0.04 and 0.01 ± 0.02, respectively; Wilcoxon signed-rank test, N = 20 females whose male partners engaged in masturbation while being the recipients of FMM, $z = -2.599$, $p = 0.009$). Therefore, Prediction 3c was supported.

We found that the time interval between a given male masturbation bout and the subsequent MFM was significantly shorter than that between the previous MFM and this masturbation bout (mean time interval ± SD: 1.3 ± 1.0 min and 4.4 ± 3.1 min, respectively; Wilcoxon signed-rank test, N = 32 relevant mating sequences, $z = -4.432$, $p < 0.001$). Therefore, Prediction 3d was supported.

Discussion

In this study, we examined FMM—a population-specific, cultural, and non-conceptive sexual adaptation—from the perspective of male consort partners. To do so, we used social and sexual variables pertaining to the sequential organization of heterosexual consortships in the free-ranging population of Japanese macaques living at Arashiyama, a suburb of Kyoto, Japan. At the outset, we hypothesized that for females to have expanded their repertoire of sexual solicitations by adopting FMM, male mates must have played a role in the origin and maintenance of this non-conceptive, but powerful female mating

tactic (Gunst et al., 2020). Our findings indicate that male partners both passively and actively participate in the expression of FMM at Arashiyama, and suggest that FMM functions to enhance the sexual arousal of some male partners during heterosexual consortships.

Our results supported the "male partner's tolerance towards FMM" hypothesis, which holds that FMM is tolerated by Arashiyama male recipients, even though this sexual solicitation is physically intense and constrains male partners. As expected, we found that, statistically speaking, males did not initiate aggressive interactions toward their female consort partners more often immediately after, than immediately before, being the recipients of FMM. Similarly, males did not initiate aggressive interactions toward their female consort partners more often during a short time window around the occurrence of FMM, than during the rest of the consortship period.

When a female Japanese macaque mounts her male consort partner, the weight she imposes on the male's back contributes to constraining the male's movement, making it more difficult for the male to leave the area of the ongoing consortship (Vasey, 2006). In agreement with this proposition, Gunst et al. (in press) found that during FMM, male mountees were immobile significantly more often than mobile. However, these male mountees did occasionally move around (even beyond 2 meters) while being mounted by their female consort partners (Gunst et al., in press). The fact that male mountees *can* move, regardless of the distance walked, is evidence that FMM is not physically constraining to the point of eliminating any male motion. Therefore, staying immobile while being the recipient of a FMM appears to be the result of a voluntary decision on the male's part.

Moreover, the infrequency of male-to-female agonistic responses during FMM is suggestive of male-to-female sexual tolerance within the context of established heterosexual consortships. This result is in line with a previous study showing that, in the E-group of the Arashiyama population of Japanese macaques characterized by relatively low levels of male-to-female sex-related harassment and aggressiveness, FMM was tolerated by males (Leca et al., 2014a). In that study, male mates at Arashiyama were described as more "mellow" and affiliative than those from other populations, which could have facilitated the expression and maintenance of FMM (Leca et al., 2014a; see also Amici et al., 2020; Kaigaishi et al., 2019 for other studies in Japanese macaques showing inter-group variation in food-related tolerance). In a sexual context, tolerance of FMM could be interpreted as acceptance of this mount type on the part of the male mountee. Taken together, these findings are consistent with the view that male partners *passively* contributed to the expression of FMM at Arashiyama via their tolerance of FFM.

We also tested the hypothesis that male consort partners *actively* participate in the expression of FMM in this population of Japanese macaques. Our results supported the "male partner's solicitation of FMM" hypothesis, which holds that FMM are solicited by male recipients. As expected, we found that males performed sexual solicitations towards their female consort partners more often shortly before, than shortly after, being the recipients of FMM. More specifically, we found a similarly significant effect with two specific types of male-to-female solicitations that explicitly expose the male's rear end to the female partner, namely *hindquarter presentations* and *inclined-back presentations*, and function as requests to be mounted. We also found that *grasping*, a type of male-to-female solicitations that allows the male mountee to prompt the FMM and physically maintain his female consort partner on his back during the FMM, was more frequent around the occurrence of a FMM than during the rest of the consortship period. These effects were not found for other types of male-to-female solicitations that were less intense or involved less explicit exposure of the male's perineum. Overall, these findings indicate male consort partners solicit FMM by performing conspicuous proceptive behavior patterns directed toward their female mates. It is noteworthy that some these male-to-female sexual solicitations (e.g., *hindquarter presentations* and *inclined-back presentations*) are structurally similar to some female-to-male sexual solicitations in Japanese macaques (cf. Vasey et al., 2008a).

Why would male Japanese macaques at Arashiyama actively participate in the maintenance of FMM in this population by prompting their female consort partners to mount them? Here we suggest two

adaptive explanations and a third more mechanistic one. The first explanation is that FMM is a population-specific (i.e., cultural; Leca et al., 2014a) sexual adaptation that functions to expedite subsequent male-female mounting, which may lead to impregnation (Gunst et al., 2020, in press). Therefore, by tolerating and soliciting FMM, a female sexual strategy to promote male mating behavior, these males actually facilitate a behavior that has positive reproductive consequences by ultimately increasing the chances of conception and thereby enhancing their own fitness (Gunst et al., in press).

Second, male-to-female sexual solicitations that tend to trigger FMM (i.e., a female-to-male sexual solicitation; Gunst et al., in press) are demonstrative courtship behaviors. As such, they could be viewed as a combination of signals produced to advertize consort partners' strong and exclusive sexual bonds to third-party individuals (i.e., potential intruders) in an environment of intense intra-sexual competition for mates (i.e., male-male and female-female competition; Gunst et al., 2015). In the former type of intra-sexual competition, the male mountee tolerates the presence of a female mounter on his back and occasionally moves around while carrying his female partner on his back (Gunst et al., in press), which could further communicate bond strength to potential male bystanders. Additional data may allow us to test this hypothesis by quantifying the potential effect of FMM on the frequency of sexually motivated behavioral tactics by third-party male competitors aimed at disrupting the heterosexual consortships in question (i.e., intrusion, sexual coercion, and sexual harassment; Gunst et al., 2015; Vasey, 2004).

Third, male Japanese macaques at Arashiyama may use FMM to enhance their own sexual reward, which may prompt them to masturbate while being mounted by their female partners. Indeed, our results supported the "male partner's sexual arousal during FMM" hypothesis, which holds that FMM functions to enhance the male mate's sexual arousal during consortships. The present study allowed us to quantify masturbatory behavior mainly performed by two young adult males in the context of heterosexual consortships. We found that almost all (i.e., 167 out of 169) male masturbation bouts were displayed during consortships that involved FMM. We also found that the number of male masturbation bouts was positively correlated with the number of FMM across consortships involving male masturbation. Our findings indicate that, in the context of the consortships involving these two males, male masturbation tends to occur in association with FMM, some of which was solicited by the male mountee. It is noteworthy that previous research conducted on the same population, during the same period, and including the same male subjects showed that male masturbation bouts also occurred outside the context of consortships (Inoue, 2012). Because our data on masturbation were collected in males already involved in consortships, they were not representative of sexually deprived individuals who would use masturbation as an outlet for sexual frustration (but see Inoue, 2012).

As predicted, the most frequent FMM posture associated with male mountee's masturbation was the reclining mount, which involves the largest area of body contact and the maximum number of body parts between the two partners. We argue that such structural features enhance the male mountee's sexual arousal, leading some of them to engage in masturbation while being mounted by their female partners (cf. VanderLaan et al., 2012).

In addition to being driven by proximate sexual reward (i.e., pleasure), male masturbation in our data set could also have a functional explanation. Indeed, we found a significantly closer temporal relationship (i.e., a shorter time interval) between a given masturbation bout and the subsequent MFM than between the previous MFM and this masturbation bout. Therefore, we argue that, in the context of our observations, male masturbation may function to stimulate or maintain penile erection that could be lost during a long time interval without MFM. Because these masturbation bouts were short and not followed by ejaculation, males may masturbate to increase the strength of their erections throughout long consortships that often require multiple mounts with only the last one leading to ejaculation. We found that the two males performing 168 of the 169 masturbation bouts analyzed in this study were the ones with the two highest percentages of consortships within the population. These data are consistent with

the view that more sexually active males may benefit from engaging in masturbation without ejaculation during serial mounting as a way to stimulate or maintain penile erection.

Specifically, unlike older and sexually under-motivated resident males, the two males for whom we have the most data on masturbation (i.e., Mi-63-69-74-94 and Mi-63-69-74-83-90) were frequently involved in over half a dozen consortships every day (Vasey, unpublished data), which maybe have led to sexual fatigue. In other populations and subspecies of Japanese macaques (*Macaca fuscata yakui*), mate guarding by high-ranking males and daily ejaculate production were found to be energetically costly (Matsubara, 2003; Thomsen et al., 2006). Because male Japanese macaques are highly promiscuous serial mounters that are routinely engaged in multiple consortships involving several copulations and ejaculations with different female partners on a given day during the mating season, the demands on their sexual performance are particularly high (Dixson, 2012). In other species of non-human primates, male mating effort is costly as well (Emery Thompson & Georgiev, 2014). For example, in wild tufted capuchin monkeys, males are more physiologically constrained in their daily frequency of ejaculations and as a result, they are also more selective in terms of reproductive timing and mating partners (Lynch Alfaro, 2005).

Overall, our research indicates that, in the Arashiyama population of Japanese macaques, FMM—a supernormal courtship behavior that functions to expedite male-female mounting (Gunst et al., in press)—is not only tolerated but also solicited by males. We argue that male partners' tolerance towards, and solicitation of, FMM may contribute to explaining how this non-conceptive sexual behavior is significantly more frequent and prevalent at Arashiyama than in nine other free-ranging populations of this primate species (i.e., Yakushima, Koshima, Takasakiyama, Miyajima, Awajishima, Shodoshima, Minoo, Jigokudani, and Kinkazan; cf. Leca et al., 2014a). Our study also suggests that, while being mounted by their female mates, some male Japanese macaques at Arashiyama may be sexually aroused to the point of engaging in masturbation. It is noteworthy that our results on male masturbation during FMM may not be generalized to all male Japanese macaques because they were derived from a small sample, and as such, idiosyncratic effects could not be ruled out. Still, this auto-sexual behavior may have both a proximate cause (i.e., sexual gratification) and a functional outcome (i.e., enhanced sexual performance in the competitive context of the mating season) that appeared tied to high mating effort (i.e., a large number of sexual partners during the study period; Leca et al., 2018).

Even though recent research indicates that FMM is a sexual adaptation that functions to prompt MFM in the Arashiyama macaques (Gunst et al., 2020, in press), we cannot entirely rule out the neutral hypothesis. The neutral hypothesis holds that FMM initially emerged in this population for proximate reasons because this behavior was sexually pleasurable (both for the female mounter: Vasey & Duckworth, 2008, and for the male mountee: this study), and then it came under secondary selection due to its adaptive benefits. Future studies should compare (e.g., via paternity tests) the fitness of males that tolerate, solicit, and thus elicit FMM, and those that do not. If the former is higher than the latter, then stronger evidence for the role of males in the evolution of this sexual adaptation will be provided.

Acknowledgements

This study was funded by the following agencies: Natural Sciences and Engineering Research Council of Canada (NSERC-Discovery Grant numbers: 2020-04244 for PLV and 2015-06034 for JBL), Alberta Innovates Health Solutions (AIHS), as well as the Office of the Dean of Arts and Science and the Office of Research Services at the University of Lethbridge, Alberta, Canada. Additional support was provided by National Geographic's *Ultimate Explorer* and Polartec®. We thank Nadine Duckworth and Stefani D. Kovacovsky for their help with field data collection. We thank Nobuo Asaba, Shinsuke Asaba, Jun Hashiguchi, Takeya Kawashima, and Shuhei Kobatake for research permission and fruitful discussion in

the field. We thank the Enomoto family in Arashiyama for logistical support. We thank Karen Bales and Michael Huffman, as well as two anonymous reviewers for helpful comments on previous versions of the manuscript. The authors state no conflict of interest.

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Data Availability Statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Hypotheses	Predictions and behavioral variables tested	Comparisons tested	P	Effect size	Outcome
1. Male Partner's Tolerance Towards FMM	1a. Male-to-female agonistic interactions[1]	Before[a] FMM ≈ After[a] FMM	0.059	0.24	Supported
	1b. Male-to-female agonistic interactions[1]	Around[b] FMM ≈ Rest of consortship	< 0.001	0.68	Supported
2. Male Partner's Solicitation of FMM	2a. Male-to-female sexual solicitations[1] (**all** types)	Before[b] FMM > After[b] FMM	0.003	0.38	Supported
	2b. Male-to-female sexual solicitations[1] **exposing** male's rear end to female partner, without physical contact between partners (i.e., hindquarter presentations and inclined-back presentations)	Before[b] FMM > After[b] FMM	0.011	0.32	Supported
	2c. Male-to-female sexual solicitations[1] with physical contact, not exposing male's rear end to female partner, but **physically maintaining** female partner on male's back during the FMM (i.e., grasping)	Around[b] FMM > Rest of consortship	0.024	0.29	Supported
	2d. Male-to-female sexual solicitations[1] **not exposing** male's rear end to female partner and **not physically maintaining** female partner on male's back during the FMM, **without physical contact** between partners (i.e., bird-dogging, glancing, hindquarter-sniffing, lip-quivering, and sexual vocalizations)	Before[b] FMM ≈ After[b] FMM	0.063	0.24	Supported
	2e. Male-to-female sexual solicitations[1] **not exposing** male's rear end to female partner and **not physically maintaining** female partner on male's back during the FMM, **with physical contact** between partners (i.e., body spasms, ground-smacking, hands-on-hindquarters, and pushing)	Before[b] FMM ≈ After[b] FMM	0.705	0.05	Supported
3. Male Partner's Sexual Arousal During FMM	3a. Male masturbation[1]	Before[b] FMM > After[b] FMM	< 0.001	0.62	Supported
	3b. Male masturbation[1] during different FMM postures	Reclining mount > other FMM postures	n.a.	n.a.	Supported
	3c. Male-to-female sexual solicitations[1] (**all** types)	Before[b] masturbation-during-FMM > After[b] masturbation-during-FMM	0.009	0.33	Supported
	3d. Male masturbation and[2] previous/subsequent MFM	Previous MFM/Male masturbation > Male masturbation/Subsequent MFM	< 0.001	0.56	Supported

Table 1. Hypotheses, predictions, behavioral variables and comparisons tested, p values, effect sizes, and outcomes; [1]: Behavioral frequency and [2]: Time interval; [a]: 30 sec and [b]: 1 min.

Behavioral variables tested	**Definitions**	**Predictions**
Agonistic interactions and displays	Threat-staring, submissive bared teeth, lunging, chasing, fleeing, hitting, biting, and tree-shaking	1a and 1b
Male-to-female sexual solicitations		2a
Hindquarter presentation	Male stands quadrupedally with arms and legs flexed and perineum oriented towards female partner	2b
Inclined-back presentation	Male sits with forearms slightly bent, and back inclined and oriented towards female partner	2b
Grasping	Male grabs the female consort partner with his hands and pulls her towards him	2c
Bird-dogging	Male gazes at female partner in frozen stance and exaggerated strut with the tail up	2d
Glancing	Male makes a swift movement of the eyes towards female partner	2d
Hindquarter-sniffing	Male brings its nose very close to female partner's hindquarters and sniffs it	2d
Lip-quivering	Male purses his lips and moves them in a trembling motion towards female partner	2d
Sexual vocalizations	Male performs chuckling calls	2d
Body spasm	Male exhibits a sudden burst of trembling throughout his body	2e
Ground-smacking	Male hits the ground with one or both of his hands	2e
Hands-on-hindquarters	Male places both hands on the hindquarters of female partner	2e
Pushing	Male shoves the female partner with his hands	2e
Masturbation (male)	Repeated manual rubbing of, or pulling on, the erect penis, which was at least partially erect	3a
Female-to-male mounting postures		
Double foot-clasp dorso-ventral mount	Female grasps with her feet between male's ankles and hips, and with her hands on male's back	3b
Single or no foot-clasp dorso-ventral mount	Female grasps male's back with her hands, while either standing bipedally with her feet on the ground and her knees slightly bent, or standing with one foot on the ground and the other grasping male's hind limb	3b
Reclining mount	Female lays ventrally on male's back, using her feet to grasp male's legs above the ankles and her hands to grasp fur on male's upper back	3b
Sitting mount	Female sits on male's back in a jockey-like position, while grasping male's upper back with her hands and male's lower back with her feet	3b

Table 2. Behavioral variables tested, definitions, and corresponding predictions.