

**Title**

Sexual adaptation: Is female-male mounting a supernormal courtship display in Japanese macaques?

**Short title**

Functionality of female-male mounting

**Authors**

Noëlle Gunst<sup>1</sup>, Jean-Baptiste Leca<sup>1,2</sup> & Paul L. Vasey<sup>1</sup>

**Affiliations**

<sup>1</sup> Department of Psychology, University of Lethbridge, AB, Canada

<sup>2</sup> School of Natural and Engineering Sciences National Institute of Advanced Studies, Bangalore, India

**Corresponding author**

Noëlle Gunst

Department of Psychology, University of Lethbridge, 4401 University Drive West, Lethbridge, AB, T1K3M4, Canada

Email: [noelle.gunstleca@uleth.ca](mailto:noelle.gunstleca@uleth.ca)

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### **Summary**

We analysed heterosexual consortships in a free-ranging group of Japanese macaques in which adult females routinely perform female-to-male mounting (FMM). We tested whether FMM is more efficient (i.e., a “supernormal courtship” behavioral pattern) than species-typical female-to-male sexual solicitations (FMSS) at prompting subsequent male-to-female mounts (MFM). In a context of high female-female competition for male mates, we found that (1) FMM functioned to focus the male consort partner’s attention as efficiently as FMSS and prevented him from moving away, and (2) FMM was *more* efficient than species-typical FMSS at expediting MFM (i.e., the most fitness-enhancing sexual behavior of a mating sequence). We concluded that FMM could be considered a supernormal courtship behavioral pattern in adult female Japanese macaques. This population-specific sexual adaptation may result from a combination of favorable socio-demographic conditions. This study has implications for the evolutionary history of non-conceptive mounting patterns in Japanese macaques and non-conceptive sexuality in humans.

### **Keywords**

female-to-male mount, supernormal courtship, sexual solicitation, non-conceptive sex, sexual adaptation, Japanese macaques, non-human primates.

## Introduction

In adult mammals, mounting is overwhelmingly considered a male-typical behavior that females perform infrequently, or sometimes never (Baum, 1979). In certain species (e.g., moose, elephant seals, howler monkeys), it appears that only males engage in mounting behavior (i.e., male-to-female mounts, hereafter MFM; Dagg, 1984; Bagemihl, 1999). In other taxa (e.g., dogs, goats, bisons), mounts are occasionally performed by females, although always at lower frequency than males (Dagg, 1984; Bagemihl, 1999). There are two types of non-conceptive mounts performed by females: those directed to same-sex sexual partners (i.e., female-to-female mounts, hereafter FFM, for example in Australian sea lions and Canada geese; Bagemihl, 1999) and those directed to opposite-sex sexual partners (i.e., female-to-male mounts, hereafter FMM, for example in grey seals and mute swans; Bagemihl, 1999).

Previous descriptive studies in various mammal taxa suggest that FMM can be considered a proceptive sexual behavior, that is, a form of female-to-male sexual solicitation, that may serve to stimulate males with low levels of sexual motivation and performance and prompt subsequent male-female copulations (Beach, 1976; Dagg, 1984). Thorough literature reviews showed that adult FMM was phylogenetically widespread among mammals, with reports of this behavior in 43 mammalian species. In 36 of these species, FMM were performed in a context of sexual excitement, that is when females were sexually attractive, proceptive, and receptive to male mates, or during the breeding season (e.g., rats, mice, Guinea pigs, lemmings, marmots, squirrels, mongoose, shrews, cats, dogs, pigs, sheep, camels, monkeys, great apes; Beach, 1968, 1976; Dagg, 1984). However, none of the studies cited in these reviews are based on a quantitative and empirical investigation of the mechanisms and function of FMM (but see Afonso & Pfaus, 2006 for an experimental study on captive rats).

To date, the hypothesis that FMM is a form of courtship that may function to trigger MFM has not been formally tested (e.g., via a sequential analysis of sexual behaviors) and systematically examined in an observational research setting. Until now, there is no empirical evidence that FMM is as efficient as, or even more efficient (i.e., a female-to-male “supernormal courtship” behavioral pattern) than species-typical female-to-male sexual solicitations (hereafter FMSS, such as pushing, ground-smacking, body spasm, and shrieking vocalizations; Vasey et al., 2008a; Wolfe, 1979) in non-experimentally manipulated animals. A phenotypic stimulus (e.g., behavioral trait) is defined as “supernormal” if it triggers the expression of the normal pattern of behavior even more strongly than the normal stimulus (Tinbergen, 1951). The term “super-solicitational” behavior applied to FMM was coined by Afonso & Pfaus (2006, p. 30) in an experimental study conducted in captive rats. In this study, the performance of FMM by females facilitated the expression of MFM by castrated non-copulating males when typical female-to-male solicitations, such as hops-and-darts and anogenital touching, failed to prompt MFM (Pfaus et al., 1999; Afonso & Pfaus, 2006).

In certain populations of Japanese macaques (*Macaca fuscata*), adult females are bisexual, routinely engaging in both sexual interactions with adult opposite-sex and same-sex mates within the context of temporary, but exclusive, sexual associations during the mating season, known as consortships (Gouzoules & Goy, 1983; Huffman, 1991, 1992; Vasey, 2006; Leca et al., 2014a; Wolfe, 1979). Sexual behaviors expressed during such consortships include vocal, facial, and gestural sexual solicitations, and mounting behaviors, including FFM, FMM, and MFM (Vasey et al., 2008a; Leca et al., 2015; Gunst et al., 2020; Wolfe, 1979). In addition to sexual solicitations and mounting behaviors, 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 (Vasey et al., 2008b).

In the present study, we focused on a free-ranging group of Japanese macaques living at Arashiyama-Kyoto, Japan, in which adult females mount both adult males and adult females (Vasey et al., 2006; Vasey & Duckworth, 2008). This research fits into the scheme of a broader investigation of the

functionality of non-conceptive mounting patterns observed in Japanese macaques and a reconstruction of their evolutionary history. Vasey and VanderLaan (2012) proposed a four-stage model invoking step-by-step changes in mounting behavior over evolutionary time, which relies on developmental and socio-cultural explanations, as well as proximate and ultimate mechanisms. This model holds that: (Stage 1) play mounting among immature males evolved as a mechanism to solicit the mountee's attention and prolong play bouts; (Stage 2) adult females exploited this evolutionary "loophole" for their own adaptive ends by using FMM to focus their male consort partners' attention and expedite MFM in a context of high female competition for male mates (Figure 1); (Stage 3) subsequently females evolved the capacity to derive immediate sexual reward from female-male mounting via vulvar stimulation; and (Stage 4) female homosexual behavior (i.e., FFM) then evolved as a neutral by-product of selection for FMM and, as a result of the proximate ability of females to derive sexual reward from mounting. Stage 1 of this model has been partly verified: juvenile males employ double foot-clasp mounts as sociosexual signals for acquiring the mountee's attention, thereby facilitating, but not significantly prolonging subsequent social play (VanderLaan et al., 2012; Gunst et al., 2013). Stage 3 has been verified: when mounting males, females acquire sexual gratification by stimulating their anogenital area (Vasey & Duckworth, 2008). The evolutionary component of Stage 4 has been verified: cross-population comparisons and movement analyses showed that female-male mounting is the ancestral homologue of female-female mounting (Leca et al., 2014b; Ottenheimer Carrier et al., 2015). Finally, the sexual reward component of Stage 4 has also been verified: during homosexual mounts, female mounters rub their anogenital regions against their female partners' backs via pelvic thrusting or, they stimulate their anogenital region with their tails, thereby gaining pleasurable feedback (Vasey & Duckworth, 2006; Vasey et al., 2006).

As for Stage 2 (i.e., testing the functionality of FMM), a previous study employed the "design-feature argument" by drawing on the temporal structure of FMM in Japanese macaques to infer possible functional components of this behavior (Gunst et al., 2020). The T-pattern detection and analysis (TPA) – a methodological tool that explores the temporal organization of behavior by identifying recurring series of behavioral events (i.e., T-patterns) within a behavioral sequence – showed that the occurrence of FMM conferred further functional constraints to mating sequences with more hierarchically organized courtship behavioral patterns than in mating sequences without FMM (Gunst et al., 2020). Specifically, we found that (1) FMM was an integral part of mating sequences, like other sexual solicitations, (2) when FMM was expressed in a mating sequence, the level of functionality of this courtship behavior may be sufficient to reduce the need for the female partner to repeat potentially less effective sexual solicitations, (3) when examining the order of first expression of the different female-male sexual solicitations, FMM was performed after species-typical FMSS (e.g., sexual vocalizations, ground-smacking, hindquarter presentation, grasping), and (4) heterosexual mating behavioral sequences that included FMM ended more often with male ejaculation than those sequences without FMM (Gunst et al., 2020). This result partly supported the view that FMM is an efficient courtship behavioral pattern in some populations of Japanese macaques that females may employ to prompt sexually disinterested or sluggish senescent males to engage in sexual interactions with them (Gunst et al., 2020; see also Vasey, 2002; Leca et al., 2014b).

To date, no study has been designed to test the "FMM as a (supernormal) courtship behavior" hypothesis in an unequivocal manner. First, none of the aforementioned studies addressed the multivariate question of whether FMM serves the function of expediting MFM, *as efficiently as*, or *more efficiently than*, species-typical FMSS in the context of high female competition for male mates in Japanese macaques. Second, the reliability and validity of the results obtained by Gunst et al. (2020) were limited by the conservative methodological procedure we employed. Indeed, the TPA required us to control for a number of potentially confounding variables, which significantly reduced our sample size (i.e., the number of mating sequences analyzed). Third, despite a clear tendency for FMM to be performed after the most frequent FMSS, these differences did not reach statistical significance (Gunst et al., 2020).

Therefore, our results were only in partial agreement with the expectation that FMM was performed by the female after most (other) courtship behaviors have failed to prompt MFM. Only a systematic analysis of the sequential organization of heterosexual consortships (including the most relevant sexual and social variables in an environment of sexual competition) could provide a robust test of whether, and to what extent, FMM is a (supernormal) courtship behavioral pattern in adult Japanese macaques.

There are two central questions in this study. First, in a context of high female competition for male mates in Japanese macaques, can a non-conceptive sexual mount, and more specifically FMM, serve the function of (1) focusing the male consort partner's attention *as efficiently as* FMSS, and (2) preventing him from moving away? Second, when it comes to expediting MFM – which is the only conceptive, hence the most fitness-enhancing sexual behavior of a consortship – is FMM *more efficient than* species-typical FMSS? One of the reasons for FMM being hypothetically more efficient at prompting MFM than FMSS is that mounting behavior involves contact between multiple body parts. Thus, FMM may provide a more intense signal than FMSS, including those involving physical contact. This is because any FMSS involving physical contact would be limited to a single area of the body (e.g., grabbing some part of the consort partner's body with one's hands; cf. VanderLaan et al., 2012). To answer these two questions, we generated and tested the following five original hypotheses, focusing on the effects of FMM on the male consort partner's behaviors, and whenever relevant comparing them with the effects of FMSS (Table 1).

First, the “Preventing Male Distraction” hypothesis holds that FMM and FMSS function to focus the male consort partner either when his attention is drawn away from the consortship by a sexually relevant external disturbance (e.g., the male sexually solicited or was sexually solicited by third party females), or when he attempts to move away from the female consort partner (Hypothesis #1). Second, the “Deadweight” hypothesis holds that, due to the physical constraints it imposes (Vasey, 2006; Gunst et al., 2020), FMM contributes to keeping the male consort partner immobile or limiting his movement while being mounted (Hypothesis #2). Third, the “Post-FMM Female Repositioning” hypothesis holds that FMM increases the probability that the female consort partner will reposition herself in front of the male immediately after dismounting him, thus facilitating subsequent MFM (Hypothesis #3). Fourth, the “Expediting Male Mount” hypothesis holds that FMM is a more intense, thus more efficient, signal than FMSS at expediting MFM by shortening the time window of its occurrence after FMM (Hypothesis #4). Fifth, the “Post-Insemination Decreased Courtship” hypothesis holds that, once FMM has achieved its putative function and led to male ejaculation during the final MFM, the female consort partner's motivation to perform FMM (just like FMSS) decreases (Hypothesis #5).

Based on each of these hypotheses, we generated specific and directional predictions that we statistically tested by using behavioral data mostly pertaining to the sequential organization of heterosexual consortships (Table 1). If the outcome of these tests indicates that FMM is *as efficient as* species-typical FMSS, then FMM could accurately be described as a regular courtship behavioral pattern in adult female Japanese macaques. If our results show that FMM is *more efficient than* species-typical FMSS, then FMM could be considered a “supernormal courtship” behavioral pattern in adult female Japanese macaques.

## Materials and methods

### *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; Nigi, 1975). 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 and behavioral records on individually identified monkeys are available from years of collaborative research between observers working at this site (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 for 101 adult females). 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 ( $40.8 \pm 28.9$  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 behavioral sampling technique was a modified version of continuous video-recorded focal-animal sampling (Altmann, 1974). Focal data were collected for both the female and her male consort partner simultaneously because the two individuals were typically no more than 1 m apart and interacting with one another within a heterosexual consortship. When two consortships occurred simultaneously, the one for which fewer data had been collected was selected.

A heterosexual *consortship* was defined as a temporary, but exclusive, sexual association between two adult opposite-sex mates (Huffman, 1991, 1992). It took the form of a mating behavioral sequence with series-mounting (i.e., three or more mounts within a 10-min period) separated by inter-mount intervals, that included vocal, facial, and gestural sexual solicitations exchanged between partners. In addition, sexual solicitations could be performed by third-party competitors seeking to disrupt consortships (Enomoto, 1974; Huffman, 1987). Consortships were deemed to have terminated if the main two sexual partners were not in proximity (separated by a distance of more than 1 m) 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 ( $\geq 5$  years) were sampled as focal subjects, along with a total of 19 adult male consort partners ( $\geq 7$  years). 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*

In Japanese macaques, MFM is typically performed in a double foot-clasp dorso-ventral posture, whereas different FMM postures are performed at Arashiyama, including single or no foot-clasp dorso-ventral mounts, double foot-clasp dorso-ventral mounts, reclining mounts, and sitting mounts (Leca et al., 2014b, 2015). However, in these analyses, we did not distinguish between different mounting postures. Sexual solicitations (or courtship behaviors) occurred during inter-mount intervals and functioned to

prompt mounting behavior (Vasey et al., 2008a). Inter-mount intervals were defined as the period between two consecutive mounts. Sexual solicitations included proceptive behavioral patterns without physical contact between the consort partners (i.e., *bird-dogging*, *body spasm*, *crouching-while-shrieking*, *glancing*, *ground-smacking*, *hindquarter presentation*, *hindquarter-sniffing*, *inclined-back presentation*, *lip-quivering*, and *sexual vocalizations*) and with physical contact between the consort partners (i.e., *grasping*, *hands-on-hindquarters*, and *pushing*; Table 2).

Non-sexual behaviors also occurred during inter-mount intervals, including agonistic interactions and displays (Table 2), affiliative interactions (i.e., allo-grooming), and other behavioral categories (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 behavioral patterns) for each of the 49 sampled adult female subjects. The first author also scored the direction of expression of the mounts, sexual solicitations, and non-sexual behaviors listed above. If the female focal subject was the performer, then the recipient (i.e., male mate or third-party individual) was noted. If the female focal subject was the recipient, then the performer (i.e., male mate or third-party individual) was noted.

To further characterize the spatio-temporal dynamic of heterosexual consortships, the first author scored two behavioral variables, namely (1) the distance between the two consort partners throughout the duration of the consortship (i.e., body contact, not in body contact but within arm reach, beyond arm reach but within 3 m, beyond 3 m but in view, and out of view); and (2) the positioning (i.e., body orientation) of the female relative to the male during intermount intervals (i.e., ventro-ventral, ventro-dorsal, ventro-side, dorso-ventral, dorso-dorsal, dorso-side, side-ventral, side-dorsal, and side-by-side). Finally, to test whether FMM contributes to keeping the male consort partner immobile or limiting his movement, the first author scored whether and how far the male moved while being mounted by a female consort partner (i.e., immobile, moved less than 2 meters, and moved more than 2 meters). We decided on this distance threshold because we aimed to distinguish between moving only a few steps (possibly due to the physical constraint associated with carrying a monkey on one's back) and being able to move around as during typical locomotion. Since the average head-and-body length of an adult male Japanese macaque is 0.6 meter (Fooden & Aimi, 2005), we chose 2 meters to differentiate a few steps versus further away.

To measure inter-scorer reliability, the second author transcribed a total of 11 hr of video-records (i.e., 10% of the data set). The comparison of the transcriptions obtained from the first and second authors for frequency of the behavioral patterns analyzed in this study yielded a strong inter-scorer consistency ( $k = 0.80$ ).

For most analyses, we selected 22 adult females with a minimum of 90 min of focal time, and whose age range was 5 – 26 years (mean  $\pm$  SD = 12.8  $\pm$  4.9 years). Selected subjects were representative of adult female Japanese macaques at Arashiyama with regards to the degree of heterosexual activity exhibited and the range of sexual behaviors performed (Vasey et al., 2006, 2008a, b; Leca et al., 2015; Gunst et al., 2020). Among these 22 adult females, we selected 10 subjects for Prediction 4a because they were the only subjects with the required temporal sequence of mounts (i.e., a MFM before and after a FMM). We selected 21 subjects for Predictions 5a and 5b because one of the original 22 adult females was never the recipient of MFM leading to ejaculation.

For all analyses (except those pertaining to Prediction 4a), 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” (Faraone & Dorfman, 1987). Depending on what direction in time we decided to choose (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 two types of lag sequential analysis, depending on the type of transitions between a Criterion and a Target. First, a “time lag” sequential analysis that requires the comparison of the same time window before and after the Criterion, and considers transitions between a Criterion and a Target within these specific time windows, independent of how many other events are 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. Second, we used a “state lag” sequential analysis considering the transitions between a Target that directly followed or directly preceded a Criterion (i.e., lag +1 or lag -1, respectively).

For Prediction 1a, we used a time lag sequential analysis to compare the frequency of FMM (i.e., Target) within two 60-sec windows. The first 60-sec window was centered around the male consort partner's attention being drawn away from the consortship, and/or when he attempted to move away from the female consort partner (i.e., Criterion). The 30 seconds before the Criterion were meant to measure the female consort partner's response in anticipation of the male moving away (e.g., when he was sexually solicited by third party females), whereas the 30 seconds after the Criterion were meant to measure the female consort partner's response as a direct consequence of the male moving away. The second 60-sec window immediately preceded the first 60-sec window (Figure 2a). For Predictions 1b and 1c, we used the same analysis, except that the Target was “FMSS without physical contact between the consort partners” and “FMSS with physical contact between the consort partners”, respectively. For Prediction 2a, we used a 30-sec time lag sequential analysis to compare how often the male was immobile versus moving less than 2 meters (i.e., Target) while being mounted by the female consort partner (i.e., Criterion). For Prediction 2b, we used a 30-sec time lag sequential analysis to compare how often the male moved within 2 meters versus beyond 2 meters (i.e., Target) while being mounted by the female consort partner (i.e., Criterion). We chose a 30-sec window because some FMM do not last more than 30 sec; therefore, any time windows beyond 30 seconds after the start of FMM would be too long to measure any male movement (or lack thereof) during FMM. For Prediction 3, we used a state lag sequential analysis to compare how often the female consort partner adopted a dorso-ventral position (i.e., Target) immediately before (i.e., lag -1) versus immediately after (i.e., lag +1) the FMM (i.e., Criterion; Figure 2b). For Prediction 4b, we used a 2-min time lag sequential analysis to compare the frequency of MFM (i.e., Target) before versus after a FMM (i.e., Criterion). For Prediction 4c, we used the same analysis, except that the Criterion was FMSS. For Prediction 4d, we compared the respective effect of FMM and 10 of the 13 FMSS listed in Table 2 on the subsequent occurrence of MFM. These 10 FMSS were *body spasm*, *crouching-while-shrieking*, *glancing*, *grasping*, *ground-smacking*, *hands-on-hindquarters*, *hindquarter presentation*, *inclined-back presentation*, *pushing*, and *sexual vocalizations*. The three remaining FMSS (i.e., *bird-dogging*, *hindquarter-sniffing*, and *lip-quivering*) were excluded from this analysis because they were only male-to-female sexual solicitations (Table 2) and only relevant to test Hypothesis 1. We used a 2-min time lag sequential analysis to directly compare the proportion of FMM and each of these 10 FMSS (i.e., Criterion) that were followed within 2 minutes by MFM (i.e., Target). For Prediction 5a, we compared the baseline rate of FMM (i.e., the mean number of FMM per min of observation before a MFM leading to male ejaculation) and the frequency of FMM within 2 min after a MFM leading to male ejaculation (obtained from a 2-min time lag sequential analysis). We chose a 2-min time window because some FMM, particularly sitting mounts and reclining mounts, can last more than one minute, and there should be



enough time for the female to dismount and any subsequent MFM. Unlike Prediction 4b, Prediction 4a was not tested via a Lag Sequential Analysis that compares the *frequency* of the Target behavior (i.e., MFM) before and after the Criterion behavior (i.e., FMM). Instead, Prediction 4a was based on the comparison of *time intervals* between (1) a given FMM and the subsequent MFM and (2) the previous MFM and this same FMM.

### *Statistics*

For Hypothesis 2, testing within-individual differences in male's movement, or lack thereof, when mounted by the female consort partner, we used a Friedman test followed, if significant, by post-hoc pairwise comparisons using Wilcoxon signed-rank tests (i.e., Predictions 2a and 2b). For Prediction 4d, we used a Pearson's chi-squared test with a 2 x 11 contingency table containing the number of MFM within two minutes following (versus not following) FMM and each of the 10 aforementioned FMSS. Post hoc analysis involved the examination of adjusted standardized residuals with a Bonferroni correction to control for false positives. For all the other predictions, 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 our predictions were directional, we conducted one-tailed tests. Statistical analyses were performed using the IBM-SPSS Statistics-26 analytical program. For all predictions, significance levels were set at  $\alpha = 0.05$ , except Prediction 4d, for which the statistical significance was set at  $0.05/11 = 0.004$ .

### *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. It was also approved by the authors' institutional Animal Welfare Committee.

## **Results**

### *"Preventing Male Distraction" hypothesis*

FMM occurred significantly more when the male consort partner's attention was drawn away from the consortship, and/or when he attempted to move away from the female consort partner than before the male was distracted or moved away (mean frequency of FMM per min  $\pm$  SD:  $0.10 \pm 0.06$  and  $0.04 \pm 0.04$ , respectively; Wilcoxon signed-rank test,  $N = 22$  females,  $z = -3.629$ ,  $p < 0.001$ ,  $r = 0.77$ ). Therefore, Prediction 1a was supported.

FMSS without physical contact occurred significantly more when the male consort partner's attention was drawn away from the consortship, and/or when he attempted to move away from the female consort partner than before the male was distracted or moved away (mean frequency of FMSS without physical contact per min  $\pm$  SD:  $1.07 \pm 2.26$  and  $0.33 \pm 0.39$ , respectively; Wilcoxon signed-rank test,  $N = 22$ ,  $z = -3.911$ ,  $p < 0.001$ ,  $r = 0.83$ ). Therefore, Prediction 1b was supported.

FMSS with physical contact occurred more significantly more when the male consort partner's attention was drawn away from the consortship, and/or when he attempted to move away from the female consort partner than before the male was distracted or moved away (mean frequency of FMSS with physical contact per min  $\pm$  SD:  $0.09 \pm 0.09$  and  $0.04 \pm 0.04$ , respectively; Wilcoxon signed-rank test,  $N = 22$ ,  $z = -3.510$ ,  $p = 0.012$ ,  $r = 0.53$ ). Therefore, Prediction 1c was supported. Overall, the "Preventing Male Distraction" hypothesis was supported.

### *"Deadweight" hypothesis*

When mounted by the female consort partner, there was a statistically significant difference in the frequency of male's movement, or lack thereof (Friedman test,  $N = 22$ ,  $\chi^2 = 35.179$ ,  $df = 2$ ,  $p < 0.001$ ). Posthoc pairwise comparisons indicated that the male consort partner was immobile significantly more often than mobile (i.e., moving less than 2 meters [Wilcoxon test,  $z = -4.109$ ,  $p < 0.001$ ], or moving more than 2 meters [ $z = -4.032$ ,  $p < 0.001$ ]). Therefore, Prediction 2a was supported.

However, there was no statistically significant difference between how often the male consort partner moved less or more than 2 meters when being mounted by the female ( $z = -1.302$ ,  $p = 0.193$ ). Therefore, Prediction 2b was not supported. Overall, the "Deadweight" hypothesis was partly supported.

#### *"Post-FMM Female Repositioning" hypothesis*

The female consort partner adopted a dorso-ventral position significantly more often immediately after dismounting the male than immediately before mounting the male (mean frequency of dorso-ventral repositioning  $\pm$  SD:  $9.6 \pm 14.7$  and  $3.1 \pm 8.4$ , respectively; Wilcoxon signed-rank test,  $N = 22$  females,  $z = -3.732$ ,  $p < 0.001$ ,  $r = 0.80$ ). Therefore, Prediction 3 and the "Post-FMM Female Repositioning" hypothesis were supported.

#### *"Expediting Male Mount" hypothesis*

We found that the time interval between a given FMM and the subsequent MFM was significantly shorter than that between the previous MFM and this same FMM (mean time interval  $\pm$  SD:  $2.9 \pm 1.8$  min and  $4.7 \pm 2.6$  min, respectively; Wilcoxon signed-rank test,  $N = 10$  females,  $z = -2.701$ ,  $p = 0.007$ ,  $r = 0.85$ ). Therefore, Prediction 4a was supported.

The male consort partner mounted the female more often within 2 min after the performance of a FMM than within 2 min before the performance of a FMM (mean number of MFM per min  $\pm$  SD:  $0.19 \pm 0.13$  and  $0.15 \pm 0.12$ , respectively; Wilcoxon signed-rank test,  $N = 22$ ,  $z = -2.632$ ,  $p = 0.008$ ,  $r = 0.56$ ). Therefore, Prediction 4b was supported.

There was no statistically significant difference in the frequency of MFM within 2 min after the performance of a FMSS (either without physical contact, or with physical contact, but excluding FMM) and within 2 min before the performance of FMSS (mean number of MFM per min  $\pm$  SD:  $0.14 \pm 0.05$  and  $0.14 \pm 0.06$ , respectively; Wilcoxon signed-rank test,  $N = 22$ ,  $z = -0.506$ ,  $p = 0.613$ ,  $r = 0.11$ ). Therefore, Prediction 4c was not supported.

Finally, there was an omnibus statistically significant effect of the different types of FMSS and FMM on the subsequent (i.e., within 2 min) occurrence of MFM (Pearson chi-squared test:  $\chi^2 = 125.74$ ,  $df = 10$ ,  $p < 0.001$ ). Post-hoc analysis of residuals showed that, after the Bonferroni correction, only FMM reached statistical significance ( $p < 0.001$ ). This means MFM was significantly more likely to occur shortly after FMM than shortly after any FMSS. Comparatively, none of the 10 FMSS (namely, *body spasm*, *crouching-while-shrieking*, *glancing*, *grasping*, *ground-smacking*, *hands-on-hindquarters*, *hindquarter presentation*, *inclined-back presentation*, *pushing*, and *sexual vocalizations*) reached statistical significance ( $p > 0.05$ ) in their effect on the subsequent occurrence of MFM. Therefore, Prediction 4d was supported.

Taken together, these results showed that FMM was more efficient than FMSS at expediting MFM. Therefore, the "Expediting Male Mount" hypothesis was supported.

#### *"Post-Insemination Decreased Courtship" hypothesis*

The baseline rate of FMM was significantly higher before a MFM leading to male ejaculation than the rate of FMM after a MFM leading to male ejaculation (mean frequency of FMM per min  $\pm$  SD:  $0.27 \pm$

0.24 and  $0.01 \pm 0.02$ , respectively; Wilcoxon signed-rank test,  $N = 21$  females,  $z = -4.016$ ,  $p < 0.001$ ,  $r = 0.88$ ). Therefore, Prediction 5a was supported.

The baseline rate of FMSS was significantly higher before a MFM leading to male ejaculation than the rate of FMSS after a MFM leading to male ejaculation (mean frequency of FMSS per min  $\pm$  SD:  $1.46 \pm 0.72$  and  $0.36 \pm 0.39$ , respectively; Wilcoxon signed-rank test,  $N = 21$ ,  $z = -3.841$ ,  $p < 0.001$ ,  $r = 0.84$ ). Therefore, Prediction 5b was supported. Overall, the “Post-Insemination Decreased Courtship” hypothesis was supported.

## Discussion

In this study, we used sexual and social variables pertaining to the sequential organization of heterosexual consortships to address the following two multivariate questions. First, in a context of high female competition for male mates in Japanese macaques, can a non-conceptive sexual mount, and more specifically FMM, serve the function of (1) focusing the male consort partner’s attention *as efficiently as* FMSS, and (2) preventing him from moving away? Second, when it comes to expediting MFM – which is the only conceptive and hence, the most fitness-enhancing sexual behavior of a consortship – is FMM *more efficient than* species-typical FMSS? To answer these questions, we tested five hypotheses, focusing on the effects of FMM on the male consort partner’s behaviors, and whenever relevant comparing them with the effects of species-typical FMSS. Overall, our results supported the view that FMM was a courtship behavior because FMM was *as efficient as* FMSS in soliciting a male consort partner for sex (Hypothesis 1, Table 1). Additionally, we showed that FMM could be considered a *supernormal* courtship behavior in adult female Japanese macaques because it was more efficient at prompting MFM, compared to FMSS (Hypothesis 4, Table 1).

First, we found that FMM and FMSS were more often performed either when the male consort partner’s attention was drawn away from the consortship or when he attempted to move away from the female consort partner. Therefore, FMM and FMSS may function to focus the male consort partner in an environment of sexual competition. In other words, the “Preventing Male Distraction” hypothesis was supported (Hypothesis 1; Table 1). The significant increase in the frequency of FFM and FMSS following the male mate’s distraction may be interpreted in terms of strong reactivity of female consort partners in the context of disruption to their temporary, but exclusive, sexual associations (i.e., the consortships). In Japanese macaques, this disruption can take two main forms: either a spatial distancing between consort partners (i.e., the male mate moves away from the female consort partner), or the male mate’s attention is drawn away from the consortship by a sexually relevant external disturbance (e.g., the male sexually solicited, or was sexually solicited by, third party female competitors/intruders).

Regarding the larger effect size obtained for FMSS without physical contact (Prediction 1b), compared to FMSS with physical contact (Prediction 1c), we propose two explanations. First, FMSS without physical contact were, on average eight to 11 times more frequent, and almost four times more diverse than FMSS with physical contact; female consort partners may have to perform a larger number of more diverse FMSS without physical contact to compensate for their relatively low intensity and efficiency. This interpretation is supported by the outcome of Prediction 4d showing that *glancing* and *sexual vocalizations* (i.e., two examples of FMSS without physical contact) were significantly less efficient than FMM in prompting MFM, even though they were expressed very often by the female consort partner. Second, female consort partners may be parsimonious in their performance of FMSS with physical contact because the intensity of the behavioral patterns (i.e., pushing or grabbing their male mate) could make them easy targets of severe aggression by the male (Enomoto, 1981; Leca et al., 2014a). Previous research on the development of female sexual behavior in the Arashiyama population of Japanese macaques indicated that sexual solicitations with body contact might be slow-developing behavioral patterns because they involve attracting attention to oneself and, even more importantly, close interactions with

potential male mates who may not only be disinterested, but also be overtly aggressive (cf. Leca et al., 2014a). *A fortiori*, mounting interactions (and, in the case of this study, FMM) involve coordinating with established mates who may have demonstrated a degree of trustworthiness.

Second, we found that FMM contributed to keeping the male consort partner immobile while being mounted. However, when the male did move while being mounted, FMM did not significantly limit the distance he walked. Therefore, the “Deadweight” hypothesis was *partly* supported. While performing a FMM, a female may act as a “dead weight” on her male partner's back and constrain the male's movement, thus preventing or restraining him from leaving the consortship (Vasey, 2006). Indeed, a FMM is an interaction that necessitates contact between multiple body parts, including the male's hind limbs, rump, and back, that are involved in locomotion.

It is noteworthy that although males occasionally moved around (even beyond 2 meters) while being mounted by their female consort partners (this study), they tolerated FMM and seldom tried to push or shake off the female mounter (Gunst et al., under revision). 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 may be the result of a voluntary decision on the male's part. Interestingly, some males actively solicited FMM and even engaged in masturbation during FMM, further underscoring males' voluntary participation in FMM (Gunst et al., under revision). The lack of agonistic response from male mountees is consistent with a previous inter-population comparative study showing that FFM 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., 2014b). 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., 2014b).

Why would female Japanese macaques occasionally employ a male-typical behavior (i.e., mounting) to retain their male consort partners? In an environment of sexual competition, this demonstrative courtship behavior could signal possession of the male to potential female and male competitors in a more conspicuous manner than species-typical FMSS. Because the ratio of sexually mature males to sexually mature females present in the Arashiyama population is skewed towards females, there is increased intra-sexual female competition for male mates compared to other populations, which is associated with more frequent FMM at Arashiyama (Leca et al., 2014b). As a showy signal of sexual interest, FMM could be viewed as a form of mate-guarding. 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 competitors to disrupt consortships (i.e., intrusion, sexual coercion, and sexual harassment; Gunst et al., 2015; Vasey, 2004).

Third, our results showed that FMM increased the probability that the female consort partner would reposition herself in front of the male immediately after dismounting him, thus facilitating subsequent MFM. In other words, the “Post-FMM Female Repositioning” hypothesis was supported. Wolfe (1978) noted that during heterosexual consortships, male Japanese macaques routinely sit with their ventral surfaces against their female partners' backs. Vasey et al. (2008b) provided quantitative confirmation of this observation: Heterosexually consorting males sat with their ventral surfaces against their partners' backs significantly more often than the reverse. Consorting males may prefer this ventral-to-dorsal sitting posture because their female partners are in front of them and, as such, this is a better position from which to execute a mount. In addition, it may be easier for males to mate guard while adopting this orientation, as they can (and often do) wrap both hands around their partners' bodies and clasp onto them during inter-mount intervals (Vasey et al., 2008b). Our results showed that the performance of FMM does not disrupt this male preference since the female consort partner actively

repositions herself by sitting in front of the male with her back turned to his chest immediately after dismounting him.

Fourth, we found a much closer temporal relationship (i.e., a shorter time interval) between a given FMM and the subsequent MFM than between the previous MFM and this FMM. This result is consistent with previous findings obtained in the same group of Japanese macaques using a different methodology (Gunst et al., 2020) and supports the view that FMM is a sexual adaptation that functions to expedite a successful series of MFM (Figure 1). From a fitness-enhancing perspective, the first key result from the present study is that males mounted females significantly more often shortly after the performance of a FMM rather than shortly before the performance of a FMM. Importantly, a similar effect was not found with the performance of FMSS. The second key result, directly comparing the effects of FMM and FMSS, is that MFM was significantly more likely to occur shortly after FMM than shortly after any FMSS. Therefore, the “Expediting Male Mount” hypothesis was supported: FMM was *more* efficient than FMSS at expediting MFM. This result on the functionality of FMM is more robust than that reported by Gunst et al. (2020) because, first, it was obtained from a larger sample (i.e., a total of 1892 min of heterosexual mating sequences sampled from 22 female subjects versus a total of 300 min of heterosexual mating sequences sampled from 10 female subjects, respectively). Second, unlike Gunst et al. (2020), we compared the effect of FMM and FMSS, which allowed us to demonstrate that FMM is a “supernormal courtship” behavioral pattern.

Fifth, we found that the rate of FMM after a MFM leading to male ejaculation was significantly lower than the baseline rate of FMM before a MFM leading to male ejaculation. A similar difference was obtained with the rate of FMSS. Therefore, the “Post-Insemination Decreased Courtship” hypothesis was supported. This result is consistent with the view that, once FMM has achieved its fitness-enhancing function and led to male ejaculation during the final MFM, the female consort partner’s motivation to perform FMM (just like FMSS) decreases.

Behaviorally, the Arashiyama group of Japanese macaques does not seem to be species-typical in that females have expanded their repertoire of sexual solicitations by adopting a non-conceptive, but intense, showy, and powerful mating tactic (i.e., FMM) that may have positive reproductive consequences by impacting intra-sexual competition for male mates and ultimately increasing chances of conception. A combination of favorable socio-demographic conditions—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., 2014b)—likely favors the expression of this population-specific sexual adaptation. Although the Arashiyama macaques are *behaviorally* unique in this regard, all female Japanese macaques may have the *psychological* capacity to engage in these behaviors given the appropriate socio-demographic conditions.

FMM has been anecdotally reported in other primate species with social structures and mating systems similar to that of Japanese macaques, including rhesus macaques, pigtailed macaques, and bonnet macaques (Bagemihl, 1999). In most cases, FMM has been described and interpreted as a proceptive behavior, based on the hormonal status of the females exhibiting this behavior (Beach, 1968, 1976). As such, the underlying motivation of FMM is more sexual than sociosexual (Beach, 1976; Dagg, 1984). However, because quantitative behavioral data on the mechanisms of expression of FMM are not available in these non-human animal taxa, any empirically-grounded discussion about the causation and adaptive value of FMM beyond Japanese macaques remains limited. While the present study represents an improvement on the existing literature, we urge researchers to replicate this type of analysis in other species.

By providing empirical evidence for the functionality of FMM, this study lends further support to Vasey and VanderLaan’s (2012) model on the evolutionary history of non-conceptive mounting patterns in Japanese macaques. Our research may also have implications for the evolution of sexuality in humans. To the best of our knowledge, no study on human courtship shows that a *particular* female-to-male

courtship behavior is more *effective* than others at attracting males. However, when women direct a *high number* of different courtship behaviors in combination towards men, then they are *more likely* to be approached by these men, compared to women who court men, but employ a smaller number and less diverse combination of courtship behaviors (Moore, 1985; Moore & Butler, 1989). Consequently, there appears to be an additive effect of courtship behaviors (e.g., hair flipping, averting the gaze downward, head tossing, etc.) that signals high female interest (Grammer, 1990) and enhances the functionality of female courtship in humans (Moore, 1985; Moore & Butler, 1989).

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Figure 1a.

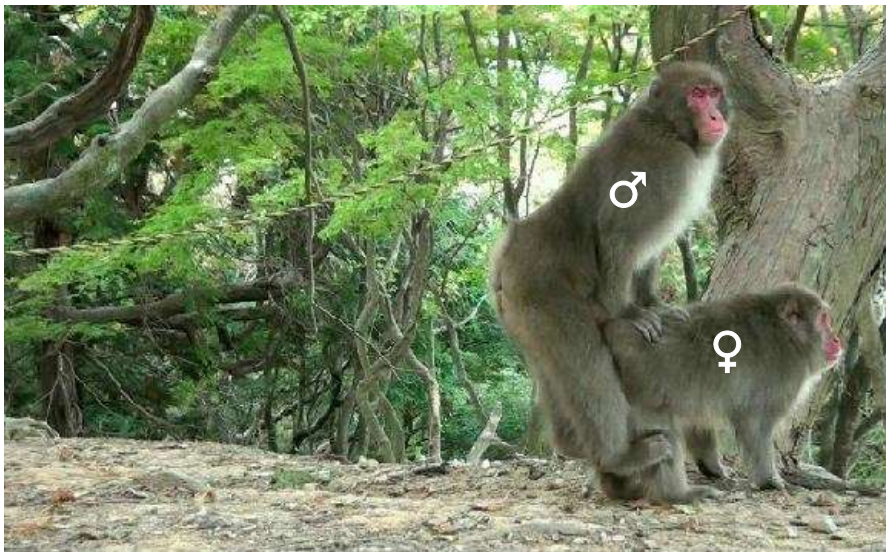


Figure 1b.

**Figure legend**

Figure 1. Female-to-male mount (a) followed by male-to-female mount in a heterosexual consortship in Japanese macaques at Arashiyama, Kyoto.

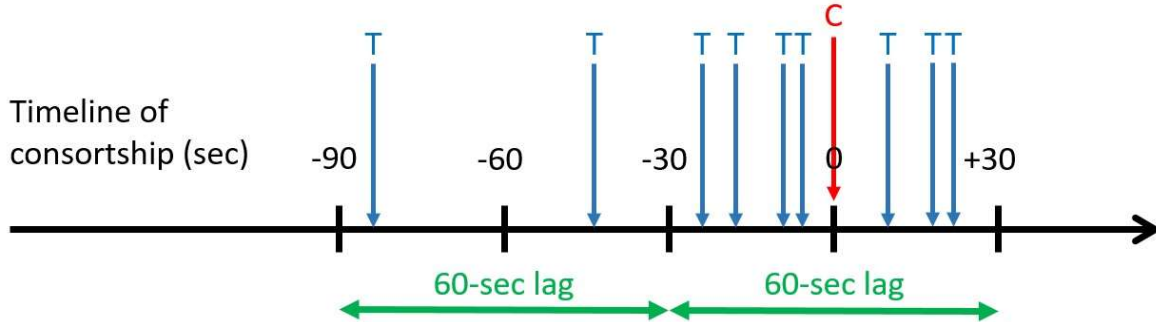


Figure 2a. Example of a 60-sec time lag sequential analysis used in Hypothesis #1 to compare the frequency of a Target behavior (T) within a 60-sec window before and within a 60-sec window around (i.e., 30 sec before and 30 sec after) the male consort partner's attention was drawn away from the consortship, and/or when he attempted to move away from the female consort partner (i.e., Criterion: C). In Predictions 1a, 1b, and 1c, T was FMM, FMSS without physical contact, and FMSS with physical contact, respectively.

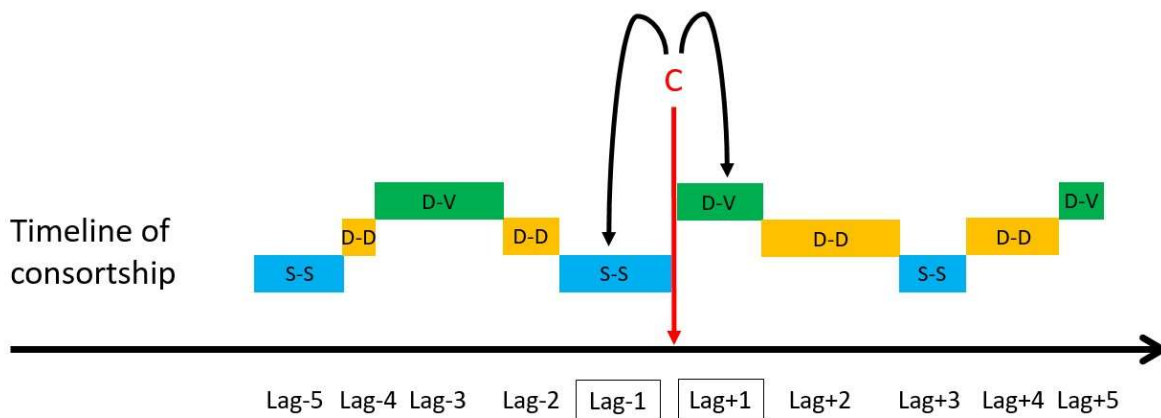


Figure 2b. Example of a state lag sequential analysis used in Hypothesis #3 to compare the frequency of a dorso-ventral (D-V) position (i.e., Target) adopted by the female consort partner immediately before (i.e., lag -1) versus immediately after (i.e., lag +1) the FMM (i.e., Criterion: C). Other positions relative to the male consort partner during intermount intervals include dorso-dorsal (D-D) and side-by-side (S-S).

Hypothesis	Prediction # and focus	Prediction	Outcome of prediction	Effect size result	Effect size outcome
1. <b>"Preventing Male Distraction"</b> : FMM (and FMSS) functions to focus the male consort partner either when his attention is drawn away from the consortship by a sexually relevant external disturbance (e.g., the male sexually solicited or was sexually solicited by third party females), or when he moves away from the female consort partner.	1a. Focus: FMM	FMM should be more frequent either when the male consort partner's attention is drawn away from the consortship, and/or when he moves away from the female consort partner than before the male distraction/moving away.	Supported	0.77	Large
	1b. Focus: FMSS without physical contact	FMSS without physical contact should be more frequent either when the male consort partner's attention is drawn away from the consortship, and/or when he moves away from the female consort partner than before the male distraction/moving away.	Supported	0.83	Large
	1c. Focus: FMSS with physical contact	FMSS with physical contact should be more frequent either when the male consort partner's attention is drawn away from the consortship, and/or when he moves away from the female consort partner than before the male distraction/moving away.	Supported	0.53	Medium
2. <b>"Deadweight"</b> : Due to its constraining form, FMM contributes to keeping the male consort partner immobile or limiting his movement while being mounted.	2a. Focus: FMM	When mounted by the female consort partner, the male should be more often immobile than on the move (less or more than 2 meters).	Supported	n.a.	n.a.
	2b. Focus: FMM	When moving while being mounted by the female consort partner, the male should move less often beyond 2 meters than within 2 meters.	Not supported	n.a.	n.a.
3. <b>"Post-FMM Female Repositioning"</b> : FMM increases the probability that the female consort partner will reposition herself in front of the male immediately after dismounting him, thus facilitating subsequent MFM.	3. Focus: FMM	To facilitate subsequent MFM, the female consort partner should adopt a dorsoventral position (i.e., sitting in front of the male with her back turned to his chest) more often immediately after dismounting the male than immediately before mounting the male.	Supported	0.80	Large
4. <b>"Prompting Male Mount"</b> : FMM (and FMSS) serves the function of expediting MFM by shortening the time window of its occurrence after a FMM.	4a. Focus: FMM	If the performance of a FMM is motivated by a long time interval without MFM, and if the FMM serves the function of prompting MFM, there should a closer temporal relationship (i.e., a shorter time interval) between a given FMM and the subsequent MFM than between the previous MFM and this FMM.	Supported	0.85	Large
	4b. Focus: FMM	If FMM is a sexual solicitation that serves the function of prompting MFM, the male should mount the female more often shortly after the performance of a FMM than shortly before the performance of a FMM.	Supported	0.56	Medium
	4c. Focus: FMSS	If FMSS (either without physical contact, or with physical contact, but excluding FMM) serve the function of prompting MFM, the male should mount the female more often shortly after the performance of FMSS than shortly before the performance of FMSS.	Not supported	0.11	Small
	4d. Focus: FMSS and FMM	If FMM is a supernormal sexual solicitation, it should be more efficient than FMSS at prompting subsequent MFM. Specifically, MFM should more likely occur shortly after FMM than shortly after FMSS.	Supported	n.a.	n.a.
5. <b>"Post-Insemination Decreased Courtship"</b> : Once FMM has achieved its putative function and led to male ejaculation during the final	5a. Focus: FMM	If FMM serves the function of prompting the male to ejaculate, the baseline rate of FMM should be higher before a MFM leading to male ejaculation than the rate of FMM after a MFM leading to male ejaculation.	Supported	0.88	Large

<p>MFM, the female consort partner's motivation to perform FMM decreases.</p>	<p>5c. Focus: FMSS</p>	<p>If FMSS (either without physical contact, or with physical contact, but excluding FMM) serve the function of prompting the male to ejaculate, the baseline rate of FMSS should be higher before a MFM leading to male ejaculation than the rate of FMSS after a MFM leading to male ejaculation.</p>	<p>Supported</p>	<p>0.84</p>	<p>Large</p>
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Table 1. Hypotheses, corresponding predictions, outcomes, and effect sizes. When appropriate, Bonferroni corrections were applied to the level of statistical significance (<sup>a</sup>:  $\alpha = 0.017$ ; <sup>b</sup>:  $\alpha = 0.025$ ). Categories and ranges for effect sizes: Small (0.00-0.30), Moderate (0.31-0.60), and Large (> 0.60).

<b>Behavioral patterns</b>	<b>Definitions</b>
<i>Agonistic interactions and displays</i>	Threat-staring, submissive bared teeth, lunging, chasing, fleeing, hitting, biting, and tree-shaking
<i>Sexual solicitations</i>	
Bird-dogging	Male gazes at female in frozen stance and exaggerated strut with the tail up
Body spasm	Sudden burst of trembling throughout one's body
Crouching-while-shrieking	Female consort partner either hunched on the ground or lowered her body stance by bending her limbs while emitting a loud and high-pitch vocalization
Glancing	Swift movement of the eyes towards consort partner
Grasping	Grabbing the consort partner with one's hands and pulls it towards oneself
Ground-smacking	Hitting the ground with one or both of his hands
Hands-on-hindquarters	Placing both hands on the hindquarters of potential mountee
Hindquarter presentation	Standing quadrupedally with one's arms and legs flexed and perineum oriented toward potential mounter
Hindquarter-sniffing	Male brings its nose very close to female partner's hindquarters and sniffs it
Inclined-back presentation	Sitting with one's forearms slightly bent, and back inclined and oriented towards potential mounter
Lip-quivering	Male purses his lips and moves them in a trembling motion towards female
Pushing	Shoving the consort partner with one's hands
Sexual vocalizations	Screaming and chuckling calls

Table 2. Behavioral patterns and definitions (after Enomoto, 1974; Enomoto et al., 1979; Fedigan, 1982; Huffman, 1991, 1992; Vasey et al., 2006, 2008a,b; Gunst et al., 2015, 2020; Leca et al., 2015)