Title

- Do males know? Evidence-driven rainmaking mating strategy by male bonobos to meet the fertile window of females

Short Title

- Male mating efforts allocation based on female fertility

Authors

Heungjin Ryu,[1,2]* Chie Hashimoto,[2] David A. Hill,[3] Keiko Mouri,[2] Keiko Shimizu,[4] Takeshi Furuichi[2]

Affiliations

[1]School of Life Sciences, Ulsan National Institute of Science and Technology, Ulsan, South Korea.

[2]Primate Research Institute, Kyoto University, Aichi, Japan.

[3]Wildlife Research Center, Kyoto University, Kyoto, Japan

[4]Faculty of Science, Okayama University of Science, Okayama, Japan

*Corresponding author. Email: heungjin.ryu.26v@kyoto-u.jp

Abstract

Female bonobos exhibit prolonged receptivity, one suggested function of which is to lower male mating competition. However, it is questionable whether easier access to receptive females can reduce male-male competition, given the exclusive nature of male reproductive success. We tested whether males could determine the fertile phase of females. We found that ovulation probability predicted male mating effort. High-ranking males copulated with females with higher fertility, and male-male agonistic interactions increased when there were fertile females in the party. When there were multiple females with maximal swelling, males concentrated their mating effort on females with an older infant whose maximal swelling started earlier, and they continued mating efforts until detumescence (rainmaking). These findings suggest that male bonobos distinguish between fertile and non-fertile phases of females and that having more receptive females in the party does not reduce male-male competition for fertile females.

Teaser

Males use the rainmaker's rule to meet the periovulatory phase of the female bonobo for better reproductive success.

Introduction

Male-male competition over mates and female choice shapes the behavior, physiology, and social systems of the species (*1*, *2*). Bonobos (*Pan paniscus*) are known for their peaceful and mild social characteristics (*3–5*) compared with those of chimpanzees (*Pan troglodytes*). One proposed mechanism for their peaceful nature is their high operational sex ratio that influences male competition over mates. This is the estrus sex ratio hypothesis (*6*). Based on findings that female bonobos are receptive for a longer period than female chimpanzees, this hypothesis proposes that the prolonged receptivity of female bonobos – achieved by prolonged and frequent maximal swelling phases – results in milder mating competition between male bonobos compared to chimpanzees. According to this hypothesis the main role of prolonged receptivity is, therefore, to confuse certainty of paternity as well as reducing the tension surrounding male reproductive success by allowing males to increase their chance of mating. Prolonged receptivity in bonobos is signaled by prolonged maximal swelling periods, as female bonobos achieve maximal swelling during the early lactation periods when the infant is younger than 2 years (*7*), and even during pregnancy (*8*, *9*), whereas female chimpanzees do not (*10*).

Some researchers suggested that prolonged periods of maximal swelling in bonobos might help females conceal ovulation (*8*, *11*). In line with this suggestion, female bonobos are known to have the longest period of maximal sexual swelling among species that exhibit it (*6*, *8*, *11*). Moreover, the probability of ovulation during the maximal swelling phase in bonobos is the least predictable among those species with exaggerated sexual swelling (*11–13*). The lower predictability of ovulation in bonobos might support the idea that the prolonged periods of maximal swelling function to conceal ovulation. However, it is uncertain to what extent mating competition is reduced by easier access to mating due to the greater number of receptive females within a group and low predictability of ovulation. In addition, the estrous sex ratio hypothesis implies that males may not pay much attention to producing offspring if they are able to mate with a female with maximal swelling. Otherwise male bonobos should be deceived by the signal of ovulation from the sexual swelling, so they do not get much reproductive benefit from male-male competition. However, it seems unlikely that male mating competition is unimportant in determining male reproductive success as there is a very high reproductive skew to high-ranking males (*14*, *15*), and male bonobos do compete over access to mates, sometimes with the support of their mothers (*16*).

In previous studies on bonobos (*11*, *12*, *17*, *18*), female reproductive events including lactation and pregnancy were not considered thoroughly as important factors in determining the resumption and continuation of the menstrual and swelling cycle. For example, the maximal swelling phase may less reliably indicate ovulation for females with younger infants, particularly when the infant is younger than 2-years-old (*19*). The maximal swelling phase of such females may also vary in length more than it does for females with older infants (*20*). Male bonobos may also respond differently to the sexual swelling of females with young infants, as those females might have a lower probability of getting pregnant, given that the mean inter-birth interval is 4.8 years (*19*). In such cases, the sexual swelling of females with young infants can be considered less meaningful for male mating decision-making.

Despite the lower predictability of ovulation from the onset of maximal swelling in bonobos among primates, over half of the ovulation occurs in the second half of maximal swelling periods (*11*, *17–19*); but see also (*12*). In addition, we do not have any hormonal evidence that explains how ovulation can deviate from sexual swelling, given the antagonistic effect of estrogen and progesterone on both. Therefore, if sexual swelling somewhat reliably signals ovulation, male mating activity should have been selected to occur more frequently in the second half of maximal swelling periods in which the fertile phase, also referred to as a fertile window (*21*), or peri-ovulatory periods – POP; (*22*, *23*), is likely to be. In chimpanzees, male mating efforts, in particular, those of the alpha male who can exert the most influence on male mating competition, more concentrate their mating efforts on the fertile phase of females (*24*, *25*). These findings are in line with predictions from the graded signal hypothesis, which implies that sexual swelling provides a graded signal of the probability of ovulation, so that it distributes males' mating attempts with their social dominance (*26*, *27*). Considering the similarity in genetics and mating systems between bonobos and chimpanzees, it is unlikely that bonobo males cannot determine the fertile phase of females unless ovulation is independent of maximal sexual swelling. However, given the genetic similarity with chimpanzees and exaggerated color and size of sexual swelling in bonobos, the basic hormonal mechanism that regulates sexual swelling in bonobos may not be very different from other Old World primates (*19*).

In chimpanzees, males adopt a coercive mating strategy or mate-guarding to restrict promiscuous mating of females during maximal swelling periods (*28*, *29*). The efficiency of male mate-guarding probably depends on the number of males in the group (*30*) and the

degree of synchrony of ovulation (*31*, *32*). Nevertheless, it is highly beneficial for male chimpanzees if they can determine the fertile phase (peri-ovulatory phase; POP) of females within the maximal swelling periods, for better reproductive outcomes. In contrast to chimpanzees, male coercive mating does not occur in bonobos (*33*). Alongside which, the high social status of females (*4*, *34*) might facilitate female choice and prevent males from using a coercive mating strategy in bonobos as well. Therefore, male bonobos might deploy different strategies to increase their reproductive success compared with male chimpanzees. However even if males' behavioral responses to fertile females are different in bonobos, it would be adaptive for male bonobos if they could judge the probability of ovulation and adjust their behavior in relation to the ovulation probability. Following previous studies and the above assumptions, we hypothesize that male bonobos can determine the fertile phase of females with some precision – the "males know" hypothesis. The fertile phase of this study is defined as a 4-day fertile window, which includes 3 days preceding ovulation and the day of ovulation (*23*). This hypothesis predicts that

P1: Males' mating efforts, as indicated by intensive following (defined in the methods section), will coincide with higher "reproductive quality" of females. Here reproductive quality is determined based on the swelling status that may indicate the probability of ovulation, and the age of the female's infant, if she has one. More specifically, when there are several females with maximal swelling, males will focus their mating efforts on a more fertile female whose infant's age is older, and whose onset of maximal swelling was earlier.

P2: The number of copulations, interventions, and solicitations of copulation will increase with the probability of ovulation and infant age.

P3: Male-male agonistic interactions will increase when there is a female who gets close to ovulation in the party, particularly when the female has an old infant. This might also result in a higher copulation rate between high-ranking males and females with higher reproductive quality than for low-ranking males.

Our hypothesis will be supported if male bonobos can determine/detect the fertile phase of female bonobos based on sexual swelling and one's infant age somehow. Therefore, our study will provide an opportunity to examine whether sexual swelling is a reliable signal indicating ovulation and male mating efforts will be predicted from the changes in sexual swelling in bonobos. To test this hypothesis and predictions, we will investigate the male

mating efforts including following over females, copulations, and aggressions in relation to the probability of ovulation (or sexual swelling) and infant age. After we evaluate the relevance of the hypothesis, we will suggest a male decision-making rule for mating effort allocation and a possible mechanism that can cause a loose relationship between ovulation and maximal swelling. We then propose that detumescence of the maximal swelling is a key phenomenon to understanding male decision-making as we assume that the mechanism of detumescence sexual swelling in Old World Monkeys – an increase of serum progesterone concentration after ovulation results in detumescence (*35*, *36*) – is probably the same for bonobos (*11*). To test the effect of detumescence on male mating effort, we will modify the previously proposed calculation of ovulation probability and fertility from the onset of maximal swelling (*23*). Finally, based on our findings and the new calculation of ovulation probability, we will propose and discuss a decision-making model, called a lottery model (evidence-driven rainmaking), that explains how males allocate their mating efforts toward females with different reproductive qualities for the best reproductive outcomes.

Results

We determined 14 ovulatory cycles and 5 anovulatory cycles in 19 maximal swelling phases from 7 females (table S1A) with the daily sexual swelling record and using 660 urine samples collected from September 2013 to April 2015. The 14 ovulatory maximal swelling phases were only found in 5 females whose infants were more than 2.0 years old (fig. S1). The earliest ovulation of females was for a female (Jk) whose infant was 24 months old. There was one possible case of ovulation from a female (Nv) whose infant was 20 months old. However, the exact date of ovulation could not be determined because of a 5-day sampling gap, so this case was not included in data analysis.

Male dominance hierarchy

The male subjects of this study were 3 adolescent and 7 adult males (table S1B). The male dominance hierarchy was not stable during the 2 years of study. During Study Period 1, one male named JR temporally occupied the highest rank of the group (table S2A). In this period, however, the h□ index was 0.84 which indicates unclear linearity of the male dominance hierarchy (*16*, *37*). During Study Periods 2 and 3, JR was frequently the recipient of aggressive behaviour from the top 3 ranking males and his rank dropped to 5th (table S2B). To take into account this dominance fluctuation, we separated the male dominance hierarchy in Study Period 1 from Study Period 2 and 3.

Male intensive following behavior toward females

In total, male intensive following behavior after females – following the target female over 5 minutes within 10m distance while keeping eyes on the target – was observed on 95 days among 250 observation days. The number of males who intensively followed females at some point on the same day ranged from 0 to 8 (1.4 ± 2.1 males per day). Of these 95 days, there were only 6 days when two females were the targets of the male intensive following at the same time. To investigate the effect of infant's age, sexual swelling status, and ovulation on male behavior, we used hurdle modeling that divided the data set into two parts to deal with many zeros values – there were many days when no males intensively followed females (*38*). Further details are provided in materials and methods.

For the first part of the hurdle model, we ran a generalized linear mixed model (GLMM) with the data that contained all 250 observation days that included days of no male's intensive following was observed (GLMM-1A in Table 1). We confirmed that the number of males who intensively followed a female increased when the target female had an older infant and maximal swelling (Fig. 2A and 2B). Female age, which probably reflects the parity of females, did not explain the number of males who intensively followed females which suggests no preference for older females in bonobos. This result is in contrast to what was found in chimpanzees (*39*). The number of males and the number of females with maximal swelling (FMS) in the daily ranging party were not responsible for the increased number of males in the intensive following. Interaction between infant age and the swelling score was not included in the GLMM-1A given the large proportion of data from females without maximal swelling, but with an infant.

For the second part of the hurdle model, we ran a GLMM with a reduced data set, which only consisted of the days when females exhibited maximal swelling (205 days). With this data set, we investigated the effect of the days from the detumescence of the maximal swelling and one's infant age on male's intensive following behavior (GLMM-1B in Table 1). We found that the number of males who intensively followed females increased when maximal swelling was nearing detumescence. Infant age was also positively related to the number of males engaged in the intensive following. More males followed females with maximal swelling for which ovulation was detected during or right after the maximal swelling phase (14 ovulations) compared to females with maximal swelling for which no ovulation was detected within or after the maximal swelling phase (fig. S2). Such an anovulatory maximal

swelling phase maybe because it was post-conception or anovulatory swelling or we might miss ovulation due to insufficient data. The other predictor variables were not responsible for the number of males engaged in the intensive following. Importantly, however, there was a significant interaction between the days from detumescence and infant age on males' intensive following over females. This suggests that the increase in the number of males involved in intensive following close to the day of detumescence was more rapid (or the slope of increase was steeper) with an increase in the age of the infant – females with older infants attracted more males when they exhibited maximal swelling (Fig. 3A).

We also investigated how males chose a female with maximal swelling for the intensive following when there were two or more two females with maximal swelling in the same party using a binomial GLMM (GLMM-1C in Table 1). The days when there was only one female with maximal swelling were excluded for this analysis. In total, we found 77 days when there were more than two females with maximal swelling. Using this data, we tested the effect of infant age, the day from the onset of maximal swelling, female age, and the number of males in a day on male's choice among females with maximal swelling. Similar to previous results, male bonobos chose females with older infants, and whose maximal swelling started earlier – significant interaction term (Fig 3B). However, the number of males did not influence male choice, which indicates that males do not alternate their choice even when there were same-sex competitors in a party. Although female age was significant in this model, it could be caused by small female age variations in the reduced data set as seen in fig. S3 – compared with infant age and the onset of maximal swelling (fig. S3A and S3B), female age data was distributed widely and the two medians in between were almost identical (fig. S3C).

We finally tested the effect of days from ovulation (not detumescence) on male behavior (GLMM-1D) using a data set that only included 14 ovulatory-detected maximal swelling phases from 5 females (138 days in total). By doing so, we also tested the reproducibility of the results from GLMM-1B. There were some sampling gaps within a maximal swelling phase in the data and the largest gap was 6 consecutive days from Sl (fig. S1). We assumed the female continued to exhibit maximal swelling throughout this gap, so this female was considered to have started maximal swelling 18 days before ovulation. As detumescence of maximal swelling preceded the ovulation day in this cycle, we included the day without maximal swelling until the day of ovulation in the data set. Similarly, when the maximal swelling phase was continued after ovulation, these days were also included in the data (*24*).

There were also no sampling gaps over 1 day during POP (4 days of fertile phase) in the data set. GLMM-1D showed similar results to GLMM-1B except for a non-significant interaction term between the days from ovulation and infant age (Table 1). The number of males who intensively followed a given female increased when females were near to ovulation (Fig. 4), as well as with increase in age of female's infant. The other predictor variables did not predict the number of males intensively following the given female. The lack of a significant interaction between the probability of ovulation and infant age may be related to the small size of the data set, or less likely, that males can indeed detect ovulation precisely, so males follow a female regardless of her infant's age when ovulation coincides with maximal swelling phase.

Day-specific ovulation probability and fertility

To evaluate the effect of detumescence on male behavior, we first calculated ovulation probability and fertility from the day of onset of maximal swelling. The day-specific probability of ovulation and fertility were calculated using the 14 ovulatory cycles from 5 females that were used for GLMM-1D. The equation for the calculation of day-specific ovulation probability has been used in previous studies of chimpanzees and bonobos (*12*, *23*) and also described in Materials and Methods in detail. The day-specific ovulation probability from the onset was widely distributed from the 8th to 27th days from the onset of maximal swelling (closed circle with black lines in Fig. 5A). The peak probability of ovulation was on the 19th day from the onset of maximal swelling. This pattern is similar to that of a previous report on wild bonobos from Luikotale (*12*), except that no ovulation was found before the onset of maximal swelling. The day-specific probability of fertility – the probability that the egg coincides with sperm – did not exceed 0.3 (open circle with red lines in Fig. 5A), which also resembles the previous finding (*12*).

To better understand whether ovulation results in detumescent and why males stopped following females after detumescence, we calculated the day-specific probability of ovulation and the fertility from the detumescent day using the same equation used for Fig. 5A (see Materials and Methods). Fig. 5B only differs from Fig. 5A in that day 0 was rearranged to the onset of detumescence. Compared with Fig. 5A, the day-specific probability of ovulation was concentrated to the detumescence day of maximal swelling and showed a clear peak 4 days before detumescence. This result also suggests that progesterone that is released from the corpus luteum after ovulation probably results in detumescence of maximal swelling. Due to the high probability of ovulation before detumescence in our current study, the day-specific

fertility exceeded 0.8 from 5 to 4 days before detumescence then decreased rapidly and became zero one day before detumescence. This result indicates that copulation around detumescence would more likely result in pregnancy than copulation on other days.

The distribution of the probability of ovulation and fertility regardless of calculation methods resembles the distribution of the number of males that intensively followed females. The number of males that exhibited intensive following was widely distributed when plotted with the days from the onset of maximal swelling (Fig. 5C). In contrast, the number of males exhibiting intensive following was more concentrated to the day to detumescence (Fig. 5D). Particularly, the median number of males in intensive following increased 5 to 1 day before detumescence and no males followed females when detumescence just started. This result suggests a possibility that males might predict ovulation before detumescence which indicates females are signaling and males take advantage of it.

Male's copulation, intervention, and solicitation of copulation

Ten males copulated with the 9 female subjects 570 times in 250 days (table S1B). The frequency of copulation was 0.066 times/hour/male for males (570/8609 of total presence counted by one-hour party attendance; party presence counts) and 0.070 times/hour/female (570/8137) for females. Of 570 observed copulations, 492 (86.3%) involved females with maximal swelling. We observed 440 solicitations of copulation from a male to a female, regardless of success or failure in 250 days (0.051 times/hour/male; 440 in 8609 party presence counts). Intervention of copulation was observed 80 times in 250 days (0.009 times/hour/male; 80 in 8609 party presence counts). Male-male aggression, including dyadic and more than 2 individuals, were observed 873 times in 250 days (0.101 times/hour/male; 873 in 8609 party presence counts).

To test the effect of ovulation on male copulation-related behaviors, we also used data from 14 ovulation-detected maximal swelling phases from 5 females as in GLMM-1D. We then limited the data to only contain -14 to 0 days from ovulation to remove the effect of extreme values. Minus 14 to 0 days from the ovulation were selected given the average length of the maximal swelling phase of bonobos is around 14.0 days – based on mean maximal swelling phase length from published studies (Table S3) – and one day after ovulation is still fertile given the lifespan of an egg. The final data set contained 104 days among 250 total observation days. In total, 209 copulations involving 22 dyads (of a possible 48 dyads; except

2 mother-son dyads) were included in the data set and the frequency of copulation was 0.041 times/hour/dyad (in 5040 dyad-party hours; total presence count of a dyad found in the same party). We observed 201 instances of solicitation in 5040 dyad-party hours (0.040 times/hour/dyad). The intervention of copulation between males was observed 42 times in 5040 dyad-party hours (0.008 times/hour/dyad). The number of male-male aggressive interactions in the 104 days was divided by the party presences counts of all males. In total, 472 male-male agonistic interactions were observed in 104 days (4203 party presence counts in total; male-hours) and the frequency was 0.112 times/hour/male (472/4203).

To investigate further the effect of ovulation, infant age, female age, male age, and rank (highest: 1, lowest: 10) on the number of copulations, interventions, and solicitations of copulation, we ran three GLMMs (Table 2). We confirmed in the GLMM-2A that the number of copulations increased when the ovulation day of a given female was getting close (Fig. 6A). Infant age was negatively related to the number of copulations – males copulated more with the females with younger infants (Fig. 6B). Male rank was positively related to the number of copulations – high-ranking males did more (Fig. 6C), and male age was negatively related to the number of copulations (Fig. 6D). Female age did not predict the number of copulations (Fig. 6E). The interaction between infant age and days from ovulation was not significant.

As males did more copulation with females with younger infants whose reproductive quality is assumed to be lower, we further investigated whether this result came from a greater number of copulations from low-ranking males with such females. To test this possibility, we ran a GLMM with the same data set used for GLMM-2A. In this model, we converted male rank to a categorical variable (1-3: high-ranking, 4-10: low-ranking), and a three-way interaction between male rank (category), infant age, and the days from ovulation was also included. Female age was removed as the model failed in converging. The top 3 ranking males (JR, NB, KT in periods 3 and KT, NB, GC in period 3) were selected as the three males and their mother Jk (JR's mother) and Ki (NB and KT's mother) competed for alpha position during the study period. The top 3 ranking males accounted for 78.9% of all copulations (165 in 209 copulations). GLMM-2B showed a similar tendency of GLMM-2A in that significance and the effect of variables were identical in between (Table 2). Importantly, the 3-way interaction term was significant for high-ranking males. This significant interaction indicates important contrasts of males' copulation depending on their rank. The ovulation probability was responsible for the increased number of copulations for the high-ranking males, but not

for low-ranking males. Such skewed copulation tendency was mostly because even high-ranking males could copulate more with a female with younger infants (fig. S4). This result suggests that females with low reproductive quality also copulate more frequently with high-ranking males, not with low-ranking males. Low-ranking males, therefore, have less chance to copulate even with females with low reproductive quality which is different from the prediction of the estrus sex ratio hypothesis. This result also demonstrated that females are choosier when their reproductive quality gets high and reduce the copulation rate even with high-ranking males.

The number of interventions of copulation between males (GLMM-2C in Table 2) increased when the ovulation day was getting close (Fig. 6F) and increased for females with older infants (Fig. 6G). High-ranking males intervened more frequently in other males' copulation attempts (Fig. 6H). It is probably easier for high-ranking males to intervene than it is for other males. Male age and female age were not related to the number of interventions of copulation (Fig. 6I, 6J). This result indicates that even though older females have a higher rank than younger females, the intervention of copulation between males may not be influenced by the rank of females in copulation attempts.

Males solicited copulation more often when the day of ovulation of a given female was about to occur (Fig. 6K, GLMM-2D in Table 2). Infant age did not predict the number of solicitations of copulation by males (Fig. 6L). This finding suggests that the increased number of copulations in females with younger infants in GLMM-2A was not due to increased solicitation of copulation by males. Both high-ranking and younger males solicited copulation more frequently (Fig. 6M, 6N). Female age was not related to the number of solicitations, which suggests that older females are not more attractive for male bonobos.

Finally, we tested whether the number of females with maximal swelling on a given day was related to the number of male-male aggressions using all 250 observation days in a generalized linear model (GLM-2D in Table 2). We included the number of females with maximal swelling and the existence of the male intensive following as explanatory variables. To control the number of males of the day and observation hours, we include the two variables in the offset term of the model. We found that the number of male-male aggressions on a given day increased on days when the male intensive following was observed (Fig. 7A). The number of male aggressions was also increased with the number of females with maximal

swelling of the day (Fig. 7B). These results suggest that the availability of receptive/attractive females with maximal swelling in a party does not influence male-male aggression, which contrasts with the prediction of the estrus-sex ratio hypothesis.

Discussion

In the current study, we showed that male mating efforts were skewed toward females with older infants and whose maximal swelling was close to detumescence, which describe as the female having higher reproductive quality. Males, regardless of rank, intensively followed females with higher reproductive quality. More specifically, the number of males in intensive following increased for females whose maximal swelling was close to detumescence and whose infants were older. When there were more than two females with maximal swelling, males followed females with older infants whose maximal swelling started earlier. The significant interaction between infant age and sexual swelling makes sense since males did not follow females, even with maximal swelling, when their infants were younger than 2 years old. It is worth noting, however, that when the data set was reduced to 14 ovulation cycles from 5 females, the significance of the interaction term disappeared. This non-significant interaction suggests that male bonobos, regardless of infant age of females, may be able to determine an ovulatory maximal swelling phase more precisely, though this result could also be due to sampling bias in the reduced data set.

Despite increasing the number of copulations close to ovulation day, high-ranking males copulated more frequently with females with younger infants, contrary to the results of males' intensive following. High-ranking males also intervened in the copulation attempts of other males when the other males tried to copulate with females with older infants whose ovulation day was approaching (higher reproductive quality). These results suggest that male-male competition for access to females with older infants is more intense so the copulation frequency might be lower between them, or females are more selective for mating when they have higher reproductive quality. Males solicited copulation more often from females whose ovulation was approaching. However, solicitation frequency did not change with infant age. Male-male aggression also increased when there were more females with maximal swelling. There were more aggressive interactions between males after controlling the number of males in the party, especially on days when males' intensive following was observed. Contrarily to a prediction from the estrus sex ratio hypothesis, this result suggests that the availability of

receptive/attractive females is not an important influencing factor determining male-male agonistic interaction in bonobos.

Overall, our results support the predictions from the males know hypothesis but did not support the estrus sex ratio hypothesis. The three predictions of the males know hypothesis regarding male mating were well related to the reproductive quality of females except for the effect of infant age on females in the ovulatory maximal swelling phase. This exception, however, makes the hypothesis even stronger as this result implies that males can recognize an ovulatory swelling cycle. Therefore, our study supports the notion that male bonobos can determine the fertile phase of females with some precision and they allocate mating efforts to the females with higher reproductive quality. These results are also in line with previous findings in other primate species where females have exaggerated sexual swelling, including chimpanzees and Old World monkeys (*24*, *40*, *41*). We suggest, therefore, that male bonobos use information from sexual swelling and age of the female's infant for decision-making on mating effort allocation, and that the sexual swelling of females is a reliable indicator of ovulation in bonobos.

Male intensive following and fertility of females

Males intensively followed females with maximal swelling more than females at other sexual swelling stages. When the female had an older infant and the sexual swelling was near to the detumescence, a higher number of males intensively followed the female (GLMM-1A and 1B). Therefore, males appear to be able to distinguish females with higher reproductive quality even when several females exhibit maximal swelling which suggests a possibility that males use not only sexual swelling but also other factors from females such as lactation status, olfactory and behavioral cues.

Although males may be able to make a better choice by combining the information from sexual swelling and reproductive history, there can be two females with similar reproductive quality at the same time by menstrual synchrony. If there is some degree of the synchronized menstrual cycle (maximal swelling as well), it would be difficult for high-ranking males to monopolize copulation. Here, some degree of synchrony represents loose synchrony in which the ovulation date of each female coincides within a or two weeks so thus their maximal swelling also overlaps. As seen in the table S1A, in E1 group, two females often gave birth in the same month (within 2 weeks) which suggests a possibility of loose synchrony of the

menstrual cycle. If there is such loose synchrony, it can also allow females to test the physical durability of males, as higher-ranking males need to maintain mating efforts for longer periods. It may also reduce female-female competition over mates by differentiating the short fertile phase (within 4 days from ovulation). This loose synchrony in menstrual cycles, therefore, can play as a counterstrategy to the male's monopolizing mating strategy and allow females to exert control on males. In such a case, we could recall the estrus hypothesis that the high availability of receptive/attractive females in the bonobo group has some regulative roles in male-male competition. However, a narrow synchrony window may result in a competitive situation between females and so is unlikely to be beneficial for them.

We confirmed that more males intensively followed a female whose ovulation was about to occur (Fig. 4). Our way of determining ovulation may be strict; ovulation was not determined unless the average of PdG was above the threshold (mean ± 2SD) for 10 days after the ovulation day. This might be why we could not detect ovulation from females with young infants whose age was less than 2, contrary to the previous finding (*12*). However, ovulation in those females might not have much influence on male behavior since males were not interested in females with such young infants, even when the females had maximal swelling (Fig. 3).

As seen in Fig. 5D, the number of males in intensive following seems to decrease one or two days before detumescence. This suggests that male bonobos are better than human observers at evaluating subtle changes in sexual swelling. Or males may have some ability to detect ovulation based on olfactory and other visual cues (*42*). However, such discussion goes beyond the scope of this study. Given that detumescence of maximal swelling is a good predictor of male responses, it is likely that male bonobos also rely on the sexual swelling as an important indicator of ovulation just like males of other primate species with exaggerated sexual swelling, such as yellow baboons (*41*), Barbary macaques (*43*), and chimpanzees (*24*). A more important question might then be whether the seemingly unpredictable ovulation of female bonobos, possibly concealed by the maximal swelling phase (*12*, *13*), would be manipulative enough to confuse male mating decision making and to regulate male-male mating competition.

Male intensive following behavior was not directed toward females whose infants were less than 2 years old, except for 2 days during Nv's maximal swelling phase, and that was only

by 2 males when her infant was 21 months old. Male intensive following sometimes continued all day, from the bed site in the morning to dusk when group members started making their beds for the night. In this case, males would even make beds around the target female. This might be because high-ranking males do not want males other than themselves sneaking copulations during the night or early next morning. Such all-day-long male intensive following was most noticeable when the sexual swelling of females with old infants (over 4) reached its maximal swelling phase. This might be related to the inter-birth interval, which was 4.8 ± 0.8 years in this study group (*19*). In the future, it will be interesting to see if the duration of intensive following of a given male varies depending on the reproductive quality of the female. Females may be also able to test the durability of males that participate in all-day-long intensive following to make a better mate choice. Together with the possibility of the loose synchrony of ovulation, such a female mating strategy might be challenging, particularly for the highest-ranking male, who would have to invest more energy for longer periods than lower-ranking males (*44*).

In all models (GLMM-1A to 1D), the number of males and females with maximal swelling in a party did not predict the number of males who intensively followed females. This indicates that the spatio-temporal distribution of males each day was not responsible for the increase in the number of males in the intensive following. This strengthens the finding that male bonobos selectively choose the target of intensive following, rather than just following any female with maximal swelling.

Male mating efforts and competition for access to fertile females

As predicted from the "males know" hypothesis, the number of copulations within a dyad increased when ovulation was about to occur. However, infant age had a negative influence on the number of copulations, which is contrary to the prediction of the hypothesis. It may be that females with older infants are be more selective in their choice of copulation partners, or that mate guarding by high-ranking males more is intense for females with older infants, so they cannot copulate so easily. Male rank was also positively correlated with the number of copulations. High-ranking males may be chosen more often by females for copulation, or high-ranking males may increase their chance of copulation by staying closer to the female with high reproductive quality (*4*, *45*). Maintaining proximity to a female with high reproductive quality can also be an effective strategy of male bonobos, given the prominence of female choice in bonobos, because of the high social status of females (*4*, *46*, *47*). A

negative binomial GLMM using the proximity data from individual focal sampling confirmed that the number of females with maximal swelling within 1 meter was negatively related to male age (Z = -3.46, SE = 0.21, P < 0.001) and positively related to male rank – higher-ranking males had more females around (Z = -2.01, SE = 0.18, P = 0.044). This result indicates that it is not always the high-ranking males who are closer to more females with maximal swelling and their access to copulation was not simply explained by the availability of females with maximal swelling in proximity. This result is also consistent with GLMM-2A and 2B that younger males copulated more frequently (Table 2). The high frequency of copulations in younger males, therefore, might be due to their close spatio-temporal relationship with females. Young males might get extra benefit from having their mother in the group, since the mother can influence the availability of females around their son directly and indirectly (*4*, *16*, *48*, *49*).

Although copulation in bonobos is assumed to be open for low-ranking individuals (*4*), our results suggest that male-male competition over mates results in high-ranking males having a higher number of copulations with with highly fertile females. Such skewed mating causes the exclusion of low-ranking males from mating with fertile females. The estrous sex ratio hypothesis (*4*) predicts that low-ranking males may seek access to females even with lower reproductive quality to maximize chances of copulation and reproductive success. If this is the case, low-ranking males may copulate more with females of lower reproductive quality, such as those with younger infants, but with maximal swelling. However, our results do not support this prediction. Instead our results demonstrated that high-ranking males occupy most of the copulations during the fertile window and they also copulate more with females with younger infants (GLMM-2B, and fig. S4). This was not because males solicited copulation more frequently with females with younger infants (GLMM-2D). It is possible that females with a younger infant are more responsive, or females with an older infant are more selective about responding to a copulatory invitation. Females may also prefer high-ranking males to low-ranking males for mating. Investigating female choice will therefore clarify how female mate choice shapes male-male competition and its outcome that results in variations in male reproductive success depending on male rank.

It was suggested that paternity in bonobos seems to be skewed towards high-ranking males (*50*), as found in chimpanzees (*51*). Recent studies demonstrated that the paternity of bonobos is indeed skewed towards high-ranking males, and even more so than in chimpanzees.

Our current study suggests that male bonobos can discriminate a narrow fertile window using female sexual swelling and infant age and that this ability could explain this skew in paternity. Together with the previous finding that male rank is important in bonobos for mating success (*16*), we suggest that male-male competition is also an important characteristic of bonobo society, and male-male competition may cause reproductive skew toward high-ranking males who are more durable and can monopolize mating opportunities with females with higher reproductive quality. Such monopolization is probably not solely down to the competitive ability of the male, but also to the female preference for the male with high durability in pursuing mating efforts as well.

The number of interventions by high-ranking males increased for females with older infants when their ovulation was about to occur. Males may also intervene in the copulation of young females more, though this was not statistically significant ($P = 0.053$, GLMM-2c in Table 2). If this was the case, it might be because old females are usually high ranking (*46*, *47*) and their high social status might restrain males from intervening in their copulations. High-ranking and young males solicited copulation from females. Male's solicitation of copulation also increased with ovulation probability. Unlike the results of the result of copulation, solicitation of copulation did not increase with the infant age which denies one of our second predictions (P2). This finding also suggests that males do not discriminate between females for copulation if females exhibit maximal swelling. However, females' willingness to copulate may vary depending on their reproductive quality or probability of conception.

The number of male aggressive interactions increased on days when male intensive following behavior was observed (Fig. 7A). More importantly, the number of females with maximal swelling resulted in a greater frequency of male-male aggression. The increase in male aggressions might be simply due to the increase in the number of males in the daily ranging party, as the number of males increased when there were more females with maximal swelling (Poisson GLM; $\chi^2(1) = 43.18$, $P < 0.001$). However, since the number of males was included as an offset term to control the effect of the number of males in GLM-5E and the number of males did not vary depending on the occurrence of male's intensive following (Poisson GLM; $\chi^2(1) = 1.25$, $P = 0.26$), male mating competition over access to ovulating females probably caused more male-male aggression in the current study.

Male mating strategies to cope with the low predictability of ovulation

We found that the onset and detumescence of maximal swelling were significant predictors of male mating efforts. Therefore, males seem to rely on the sexual swelling of female bonobos as a signal to make decisions for mating. However, as shown in Fig. 5A, the day-specific probability of ovulation was distributed widely from the onset of maximal swelling. The predictability of ovulation from the onset of the maximal swelling phase is therefore also low in the Wamba population, as found in the Luikotale population (*12*). Although sexual swelling of bonobos was suggested to deviate from that of other primates in that ovulation does not match well with maximal swelling (*12*), the physiological and hormonal mechanisms that result in such deviation in bonobos have yet to be proposed. However, the role of estrogen and progesterone that regulates sexual swelling in bonobos may have not changed much from that of chimpanzees (*19*). Moreover, although maximal swelling could play an important role in female-female interactions (*49*), what is the benefit in keeping this costly signal if it does not indicate ovulation? Therefore, we may have missed some important keys, or we are stuck with noise or artifacts from the previous model to calculate daily ovulation probability in evaluating sexual swelling of bonobos.

Bonobo females resume swelling cycles in early lactation periods: 225.4 days on average after giving birth even when their estrogen level is still low (*19*). In addition, as seen in fig. S5, some females have very long maximal swelling around 30 days, particularly in those with younger infants. Such variation may not be due to the small sample size in the current study as other studies also reported such variations in the length of maximal swelling (*11*, *12*). We propose, therefore, that the inter-and intra-individual variations in the length of the maximal swelling phase are the reason (or the source of noise) why the probability of ovulation calculated from the onset of the maximal swelling is low in bonobos. In other words, as the equation calculate the daily probability by summing up all probabilities of a given day from all defined ovulatory cycles, a great individual variation in the length of the maximal swelling phase results in poor predictability of ovulation. In such a case, poor predictability of ovulation is not because ovulation deviates from the maximal swelling phase. Instead, it is the inter-and intra-individual variations in the length of the maximal swelling phase that cause such low predictability of ovulation. So even if ovulation usually occurs in last half of the maximal swelling phase, as reported in the previous study (*11*, *17*) and this one, the day-specific probability of ovulation and fertility is low in bonobos.

The equation to calculate day-specific ovulation probability and fertility in the current study (see method section) was proposed in a study on chimpanzees (*23*). Although this equation has provided a solid framework with which to understand and investigate the relationship between sexual swelling and ovulation, it does not take into account the greater variation in the length of the follicular phase compared to the luteal phase between and within individuals across menstrual cycles (*52*). Such variation in the length of the follicular phase would inevitably cause low predictability of ovulation when using the equation as seen in the current study. This in turn may mislead researchers to conclude that ovulation is unpredictable based on the change in sexual swelling, particularly for species such as bonobos in which the length of the maximal swelling phase varies greatly. Nevertheless, our current study does not deny the notion that the predictability of ovulation from sexual swelling is low in bonobos. The predictability of ovulation from the onset of maximal swelling is low in the current study (Fig. 5A). As demonstrated in the current study and paternity data from the wild bonobo population (*14*, *15*, *53*), males may be just able to cope with well such low predictability of ovulation for better reproductive outcomes. How would males be able to match their mating efforts near to ovulation and detumescence of maximal swelling if ovulation is barely predictable in bonobos? In addition, if ovulation is so difficult to predict, how can paternity be skewed to high-ranking males in bonobos? Our result implies that female choice alone cannot explain such a skew.

Although sexual swelling is, in general, a reliable signal indicating ovulation probability of females, the reliability may be lowest in bonobos (*12*, *13*, *19*). Despite such low reliability, detumescence is a reliable indicator that predicts male behavior in bonobos, as seen in Fig. 5B thus suggesting that detumescence can be a reliable indicator of ovulation. However, even if ovulation causes detumescence of maximal swelling in bonobos, male bonobos may not be able to predict ovulation (or detumescence) of females due to the greater inter-and intra-individual variation in the length of the maximal swelling phase. We propose a decision-making model of males to cope with such difficulties in predicting ovulation. This model does not need to assume that males can pinpoint the detumescence day, although such a possibility exists in bonobos. Instead, males can simply follow the females with older infants and maximal swelling over days if the detumescence does not happen on that day (today) as the day-specific probability of ovulation will get higher and higher over days until detumescence. Our model would be also applicable to understanding male mating effort allocation, not only in species where sexual swelling is found but also in species that have any graded signals

indicating ovulation (e.g., changes in face colors, odors, behaviors with ovulation probability). The model assumes that male bonobos, as well as males in the species proposed above, use simple rules to allocate their mating efforts for the best reproductive outcome – here we propose three-layered rules.

The first rule in the basement layer is called the 'just-do-it' rule. This layer assumes that males are highly motivated for copulation, which is plausible considering that more mating, in general, gives males better reproductive outcomes (*54*). Therefore, male bonobos seek any copulation opportunities and whenever an opportunity is available, males are willing to engage in copulation. This rule could be predominant particularly for young males throughout their puberty as more copulations might allow them to become better at copulation as well.

The second rule in the second layer is that males allocate more mating effort to access to females with older infants (called 'check-infant'). This rule requires an assumption that the attractiveness of females with maximal swelling to male bonobos changes depending on the infant's age. This rule does not necessarily assume that males should recognize infant age as humans do. It can work if the male can somehow discriminate among females with different reproductive histories based on some signal or cue related to infant growth. Holding this rule by males does not necessarily result in skewed copulations toward the females with older infants, since male-male competition and female choice might influence the outcomes of copulation.

The final rule in the third layer is more complicated and arguable. This rule is called 'rain-making' as males are following females until the detumescence of maximal swelling. If maximal swelling (or any indicative signal of ovulation) continued from yesterday, then males simply increase mating efforts or keep a similar degree of mating efforts toward the female on that day compared to yesterday. Males, in particular high-ranking males, might skew their mating efforts more toward females with older infants and whose maximal swelling started earlier or is close to detumescence. This does not mean that they can predict detumescence or ovulation. They can make wrong decisions, particularly when the ovulations of several females are closely synchronized. It is also plausible that males are interested in a female from the onset of her maximal swelling phase, particularly for a female accompanied by an old and weaned infant. For such a female with higher reproductive qualities, males maintain their mating interests and efforts until the day of detumescence. After detumescence, they will not

pay attention, since the probability that the sexual swelling becomes detumescent before ovulation is low (though not zero). Since social-ecological factors, such as the presence of the mother, party composition that influences male relative rank, vary over time for males, these social dynamics can cause individual specificity of the rainmaking rule. Therefore, the strategy of each male for the 3rd layer might vary between individuals as well as within an individual over his lifetime.

Overall, this male mate decision-making model explains the results of this study that male mating efforts get more intense around the time of ovulation without an assumption of male's ability to pinpoint ovulation day. We call this hypothetical model a "lottery" model since it is somewhat similar to the way lotteries work. In lotteries, as the prize money increases when there are no winners for several weeks, more people buy lottery tickets. The increased number of lottery buyers will increase the chance of a winner coming out. Although the probability of ovulation does not change due to an increase in male interest and mating efforts, such an increase in male followers will help females exert more influence over sperm competition or female choice. It is also possible that males can predict the fertile phase more precisely using multiple signals (or cues), including female behavior and olfaction. This might also explain the subtle decrease in the number of males engaged in intensive following even before detumescence (Fig. 3A, 5D). However, our data is not enough to test this possibility.

It has been reported that the size of sexual swelling gradually increased until the fertile phase (POP) in chimpanzees (*24*, *55*) and olive baboons (*56*). Males might, therefore, be able to discriminate the subtle change in the size of sexual swelling (*24*). However, an increase in the size of sexual swelling may simply reflect the gradual increase of serum estrogen level until ovulation, and males do not need to discriminate precisely the subtle size variation within a maximal swelling phase (*43*). In such a case, the gradual increase of size within the maximal swelling phase can only have significance when it is presented to the males with a continuous time scale. This possibility will be examined in future studies. With a more precise measurement of female signals, the future study will clarify whether males can discriminate subtle increases of size and color (or even olfactory cues) and adjust their mating efforts precisely to the narrow fertile window. This will provide us with a valuable opportunity to understand how males have evolved to recognize and respond to females' signaling on ovulation probability, not only in bonobos, but in all primate species with such graded signals.

An increase of serum progesterone concentration caused by ovulation results in detumescence in primates with sexual swelling (*35*, *57–59*). If there is a mechanism that can explain how an increase in progesterone would not result in detumescence, it would be important to look deeper into the reason why. However, it is unlikely that the physiology of sexual hormones has changed much only in bonobos. Instead, reproductive events, such as lactation, pregnancy and early miscarriage of pregnancy (*60*), might be related to the great variation in the length of maximal swelling phase, as these events add more instability to the follicular phase in primates including bonobos. For example, as seen in fig. S6A, there could be a short post-conception swelling (around 1 week) right after implantation within 3 weeks from fertilization (ovulation). Such post-conception swelling is probably due to a surge of estrogen being earlier than a surge of progesterone after implantation and such relative concentration difference between estrogen and progesterone will be one (or the only) plausible mechanism of post-conception swelling in bonobos and other primate species with sexual swelling. In addition, if an early loss occurs after the emergence of post-conception maximal swelling as in fig. S6B, this post-conception maximal swelling can be defined as anovulatory by the researcher. Male bonobos may also be confused by such post-conception swelling as losing mating opportunity is more costly than allocating mating efforts, even for the post-conception swelling. If such early miscarriage frequency in bonobos is similar to that of humans, over 20% (*60*), this will be an important reason that causes sexual swelling to deviate from ovulation as well. Together with the proposed possibility of high sensitivity to estrogen of cells in bonobo sex skin (*19*), the physiological variations from reproductive history might, therefore, be important sources of the noise which causes inter-and intra-individual variation in the length of maximal swelling. Although this variation in the length of maximal swelling causes the loose relationship between the probability of ovulation and sexual swelling in bonobos, males do not have much difficulty meeting their mating efforts to ovulation, as suggested in the current study. Further studies on molecular level hormonal sensitivity of sex skin and hormone–swelling dynamics induced by fertilization events will elucidate the source of noise and will help us to understand better the mechanism and evolution of such presumably noisy ovulatory signals in bonobos.

In this study, we confirmed that male-male competition does occur in bonobos, as found previously (*16*), and male mating competition is important for males to access females with high reproductive quality. This result suggests that male mating efforts and interests are not manipulated by the poor predictability of ovulation from the onset of the maximal swelling.

Instead, as we suggested in the three-layered model, males might be able to cope with the low predictability of ovulation and their mating efforts using simple rules based on female sexual swelling and infant growth. Although the high availability of receptive/attractive females achieved by the more frequent and prolonged maximal swelling in bonobos may have some regulative role in male mating competition as suggested in the estrus-sex ratio hypothesis, we could not find evidence to support it. Together with the possibility that females are getting more selective when their infant gets older, future studies should examine and clarify the regulative role of sexual interactions between males and females with low reproductive quality.

Chimpanzee society is characterized as male-centered and aggressive, while bonobo society is recognized as female-centered and peaceful (*3–5*, *47*, *61*). The prolonged receptivity/attractiveness from the early resumption of maximal swelling and long-lasting maximal swelling phase of bonobos have been suggested as the key to understanding the difference in social characteristics between chimpanzees and bonobos (*4*, *9*, *12*, *49*). Although more open chances of mating even for low-ranking males due to higher availability of receptive/attractive females in bonobos may lower male-mating competitions in bonobos (*4*, *6*), it has not yet been tested thoroughly whether more opportunities for copulation for low-ranking males lower mating competition among male bonobos. As suggested in the current study, it becomes questionable whether the prolonged period of maximal swelling phase does indeed conceal ovulation in bonobos. In addition, we do not know whether concealed ovulation lowers mating competition in bonobos as when ovulation is concealed, males may need to allocate more efforts toward mate guarding and sexual activity of females for a longer time (*52*, *62*). The main perspective and insight from this study are therefore that the extended periods of maximal swelling through frequent and prolonged maximal swelling phases are not sufficient to explain the social differences between chimpanzees and bonobos.

In contrast to female chimpanzees, female bonobos make coalitions against male aggression (*47*, *63*). The female-female cooperation may contribute to the high social status of female bonobos, and the high social status of females may in turn may allow more room for female choice that eases male-male competition over mates. We suggest therefore that the high operational sex ratio and lower predictability of ovulation may not be the only causation of less aggressive and more tolerant (namely peaceful) bonobo society compared with that of chimpanzees. Instead, milder and more tolerant characteristics of bonobo society and less

restricted sexual interactions in bonobos can be rather the outcome from the social status of females, which is as high, or equivalent to, that of males (matriarch hypothesis). Nevertheless, a high operational sex ratio in bonobos caused by prolonged sexual swelling may play some regulative roles in male competition. As a result, we propose that to comprehend the characteristics of bonobo society, we must investigate the socio-ecological factors underlying how females achieved high social status in their society, as well as the mating competition and strategies of females and males.

Materials and Methods

Study site and subjects

We conducted the study on a fully habituated free-ranging wild bonobo group, called E1, at the long-term bonobo field site at Wamba (00˚ 11□ 07.6□ N, 022˚ 37□ 57.5□ E; WGS84) in the northern sector of the Luo Scientific Reserve, D. R. Congo (*7*, *64*). The group's home range consists of primary, secondary, and swamp forests. Although there is no clear division of dry and wet seasons, the amount of rainfall and fruits availability are lower in January and February than in the other months (*65*). E1 group was comprised of 32 to 38 individuals, including 9 adult and 3 adolescent immigrant females and 7 adult and 4 adolescent males during the study periods from 2013 to 2015. The age classes of females and males were defined following a previous study (*66*). Focal data were collected on 9 adult females and 7 adult and 3 adolescent males. Further information on the study subjects is given in tables S1A and S1B. Three adolescent females who had no previous birth records were not subjects of the current study. Although one adolescent male became 8 years old in October 2014, he was not a subject animal, since he had not shown any sign of dominance challenges, which can be a good indicator of adolescence (*16*). All adult females had immigrated into E1 group and had at least one successful birth after their immigration (*67*).

Behavioral observation

The first author RH collected behavioral data on adult males and females during three study periods (Period 1; September 2013 to February 2014, Period 2; July 2014 to September 2014, Period 3; November 2014 to April 2015). Bonobos were followed from their bed site, located at around 6 AM, until they made a new night bed, usually after 5 PM. When they split into several parties, the largest party was followed as far as possible. To control for the effect of the number of available group members, party composition was recorded every single hour

following the one-hour party method (*68*). Daily ranging party size and membership were defined as the number and identities of all individuals who were found during a given day when the total observation time of the day was longer than 2 hours.

For continuous focal sampling, one of the bonobos in the party was randomly selected based on a random order which was previously generated before field work began. RH and one research assistant searched for the first target focal animal in the random order for at least 30 minutes, after bonobos were located in the morning. If we could not find the first one, we chose the second one in the order, and if we could not find the second one either, we moved to the next one and so on. To compensate for the lack of focal sampling data due to the fission-fusion social system of the species (*69*), we also gave priority to some individuals with fewer data for focal animal selection. One focal session continued for 20 minutes and was terminated when a focal animal was out of sight for more than 5 minutes within a focal session. Only focal sessions that were conducted for longer than 15 minutes were included in data analysis. After an individual was followed once, it was not followed for another focal sampling before at least 100 minutes. All activities involving the focal animal, including feeding, moving, resting, and social interactions were recorded during a focal session. To estimate neighboring individual patterns, the names, and behaviors of neighboring individuals within 5m of the focal animal were recorded at 5-minute intervals, including a scan at the beginning of the focal session (5 scan points within a focal session). All rare events, such as sexual and agonistic interactions, were also recorded as far as possible during the party following. We recorded the individual ID of the participants of the interactions as well as time and duration. All copulations, genito-genital rubbings, and agonistic interactions (e.g., bite, hit, displacing, and chase), were recorded whenever observed by RH and at least one research assistant – ad libitum sampling.

Ejaculation during copulation was not always possible to confirm. Therefore, complete heterosexual intercourse without any interruption by others was counted as copulation. The intervention in copulation included direct aggression towards a male who solicited copulation from a female, and direct intervention which targeted the male during copulation. Intervention directed towards females nunmbered only 22 attempts and most of them led to counter-aggression from females, or were otherwise ineffective. Only 5 cases of intervention directed towards females were successful in stopping copulation. Solicitation of copulation was counted only when a clear target was identified. Male bonobos often have an erect penis

during feeding while watching females, and so only the presence of erection was not counted as a solicitation. For solicitation, an erection should coincide with other behaviors such as directed hand or body gestures (*70*) or shaking, bending, or dropping branches or twigs to get attention from the target female.

We also recorded agonistic interactions whenever there was a clear target, regardless of physical contact. Therefore, undirected display behaviors, such as charging and branch dragging, were not considered agonistic interactions (*71*). When a counterattack was performed by the target within 5 seconds of the directed aggression to the target, we considered it as a tied interaction. To evaluate males' interests towards females in the party, we defined **male intensive following** behavior as when a male maintains proximity (within 10m maximum), to the target female for more than 5 minutes while moving, without losing the target female from his sight. If a male's following behavior fulfilled these criteria, we considered this male to be intensively following the target female.

In total, we followed bonobos for 1462.3 hours on 255 days (5.73 ± 1.25 hours per day). The total focal following time for all individuals was 280.22 hours (858 focal sessions: 14.75 ± 2.01 hours per individual). The average length of a focal session was 19.6 ±1.0 minutes and each focal session consisted of 4.88 ± 0.34 scans (4189 scans in 858 focal sessions). Of the 255 days we excluded two days on which we were able to follow bonobos for less than 1 hour. There was one day with very heavy rain so that no males were confirmed, and two days on which we could not see any females. These 5 days were removed from all data analyses, apart from calculation of the male dominance relationships.

Assessment of sexual swelling

Daily variation in sexual swelling of female bonobos was scored in relation to the firmness and size of each individual's swelling (*8*, *49*). The sexual swelling status was assigned to one of three categories. Fig. 1 shows an example of changes in sexual swelling of one individual, named Fk. Swelling 1 (Fig. 1A) is for non-swelling status; swelling 2 (Fig. 1B) is for intermediate swelling status; swelling 3 (Fig. 1C) represents maximal swelling status. Unlike female chimpanzees, the sexual swelling of female bonobos is always visible, even in the non-swelling status. Therefore, the practical definition of non-swelling status (swelling 1) is that the swelling is within range of its minimum size. The swelling size variation of an individual between swelling 2 and 3 was sometimes not definitive. Therefore, firmness and

shininess of the surface and movement of the sexual swelling during locomotion were the key features for distinguishing swelling 2 and 3. The detumescence day was set to the first day when the maximal swelling started shrinking so lost its firmness and shininess and the swelling score moved from 3 to 2. The maximal swelling phase was defined from the onset of the maximal swelling to the end of maximal swelling. If sexual swelling recovers from 2 to 3 within 3 days, it was considered that the maximal swelling phase was continuous. Since this study followed a conventional method (*8*) for scoring sexual swelling stages, there could be subjective bias in scoring between observers. To reduce observation errors and bias on sexual swelling scoring, at least one researcher and two research assistants discussed and decided on the sexual swelling status of each female during field observations at a daily meeting every evening.

Urine sample collection and hormonal measurement

Urine was collected using filter paper (Whatman #1 Ø 5.5cm) during a day. After a female finished urination, RH or a research assistant collected urine from the leaves of terrestrial plants or small trees. We put the edge of the filter paper (around 1/4 of the whole) into the urine drops and waited until it absorbed to around 2/3 of the paper. By putting only the edge of the paper into the urine, we avoided contamination of dirt from leaves. To avoid disturbing the bonobos, we collected urine after they had left the place, so that we could keep at least 5m distance between the collector and the bonobos. When the urine was mixed with their feces or others' urine or feces, we did not collect the urine. Further information on our sampling collection and handling is found in a published work (*19*) and the supplementary material (Urine sample handling after collection). We used enzyme immunoassay (EIA) to measure urinary metabolites of estrogen (E_1C) and progesterone (PdG). In total 660 urine samples from 9 females were successfully recovered urinary E_1C and PdG and used to determine ovulatory cycles. The number of urine samples and examined swelling cycles are available in table S1A. Further details about the EIA analysis and validation are available in the supplementary material (Enzyme immunoassay and its validation) and a published paper (*19*).

Defining the fertile phase (POP) and probability of ovulation and conception on a given day within a swelling cycle

The date of ovulation was estimated based on sustained urinary PdG rise above the baseline (*19*). In brief, the baseline was defined as the mean of urinary PdG concentration of

the 10 days preceding a given day. When the PdG concentration on the given day was more than two standard deviations above the baseline for 3 successive days within a week, one day before the first day of the sustained PdG rise (over 2 standard deviations) was considered ovulation date. We used the 4-day fertile window, which starts from 3 days prior to ovulation, based on findings that sperm are fertile within three days in the reproductive tracts and eggs are fertile within 24 hours after ovulation (*72*, *73*). This criterion has already been used in several studies in several primate species including wild chimpanzees in Taï (*23*) and wild bonobos in Luikotale (*12*).

To calculate the probability of ovulation on a specific day within a cycle, we used the following equation proposed previously (*23*). When the onset of maximal swelling phase was not observed (6 cases) or the detumescence day was not observed (4 cases), the start day and/or the end day was determined as to when a female was first observed with maximal swelling and/or the last day when she was observed with maximal swelling.

$$P(T = t) = \frac{n_t}{n}, t = 1,2,3\ldots$$

In this equation, $P(T = t)$ refers the probability of ovulation on a given day; *t* refers to a specific day within the maximal swelling phase which starts from the onset of maximal swelling; n_t is the total number of cycles in which ovulation occurred on day *t*; *n* is the total number of ovulatory cycles (14 in the current study).

We also calculated the daily probability of fertility (the probability that the sperm can meet the egg; fertilization) using the equation in the same study (*23*).

$$P(X(f) = 1) = \sum_{t=f}^{f+3} P(T = t)$$

$P(X(f) = 1)$ refers to a probability of fertility (conception) on a given day within the maximal swelling phase. More simply the probability of fertilization on a day is the sum of the probability of ovulation on the given day f and the following 3 days of from the given day f that are calculated in the previous equation. By following the same equation used previously, we can directly compare our results between species, as well as between populations of the same species.

Estimating male dyadic dominance hierarchy

Male dominance relationships were assessed on the basis of dyadic agonistic interactions. Agonistic interactions with physical contact included biting, hitting, and trampling. Agonistic interactions without physical contact included chasing, charging, and directed display (sometimes with branch dragging). We only used dyadic agonistic interactions which had a clear outcome of loser and winner. A loser was defined when the recipient of the aggression showed submissive behaviors such as grimace, screaming, running away, or retreating. We did not include tied agnostic interactions for calculation of relative dominance. In total, we observed 844 dyadic agonistic interactions. Only 16 dyadic interactions were followed by counter-aggressions. Therefore, in total 828 dyadic interactions (p1: 314, p2: 162, p3: 352) were selected to calculate male dominance hierarchy (table s2A and s2B). We used the 'steepness' package (*74*) to build a dominance hierarchy and David's score. We also checked h□ index (*75*) – a modified version of Landau's linearity index (*76*) – using the 'igraph' package (*77*) to decide whether the male dominance hierarchy was linear or not.

Statistical analysis

We used R 4.0.2 (*78*) with R studio 1.3.1056 (*79*) for all analyses. We used generalized linear mixed models (GLMM) or generalized linear models (GLM) with negative binomial, binomial error distributions along with several packages including 'lme4', and 'lmertest' to fit our models to the data. Mixed models that included random effects were done to control the repeated measure of the behavior from the same individual. More details of each model will be described later in this section. We also checked multicollinearity between independent variables in the model based on variance inflation factors (VIFs) after we ran all mixed models. In all models, the maximum VIF was less than 3 (only over 2 in GLMM-1C), therefore the multi-collinearity among the predictor variables is of serious concern (*80*). All models were also significantly better in explaining the data compared with null models.

In bonobos it has been reported that a male's copulation rate is related to other social factors, such as the mother's support and relative dominance rank caused by changes in party composition in a group (*16*). Therefore, we may need to consider those factors as predictor variables in the models. However, the 4 subject males whose mothers were in the group, were almost always with their mother in the party. There were only 23 out of 744 days (sum of days when the 4 males were observed) that any of the 4 males were found without their mother

(only 3.1%). Therefore, we did not include this factor in the models. Fluctuation of the relative rank between days because of change in party composition was not the main predictor, since our question is more generally whether the male rank within the community is an important factor for understanding male mating efforts. In addition, the alpha male was the highest-ranking male on 188 days of the 253 observation days on which we observed males (74.3%). The beta male occupied the highest position on 33 days (13.0%), the 3rd ranking male for 9 days (3.6%) and the 4th for 17 days (6.7%).

We also considered that the reproductive quality of female bonobos has two main components. One is the increased chance of getting pregnant with the growth of infants over time, regardless of the menstrual cycle on a wide time scale. The other is changes in the probability of fertility (the chance of fertilization – a sperm meets an egg) within a menstrual cycle depending on changes in the probability of ovulation over time. In chimpanzees, these two components are closely related to each other probably because energetic constraint from lactation has a regulative role in the menstrual cycle (*10*). This is probably similar to female bonobos, although bonobo females resume their swelling cycle much earlier (*6*, *19*). To integrate the effect of a dependent infant on the female reproductive quality, we integrated infant age, as a proxy for female body condition. To examine the effect of ovulation, we also included the number of days from ovulation, or detumescence, or the onset of maximal swelling as a predictor variable in each model depending on our question because the chance of fertilization increases until the day of ovulation. The day of ovulation (or detumescence) was coded 0 and one day before the ovulation was -1, two days before was -2, and so on. The days after the ovulation were 1, 2, and so on. The onset of maximal swelling was coded 1, the next day was 2, and so on. In some analyses, we confined the data from -14 days before ovulation to the ovulation day (15 days, -14 to 0) to control large inter-and intra-individual variations in the length of the maximal swelling phase.

Infant age was coded on an ordinal scale by putting together 6 months as 0.5 years. It ranges from -1 to 5.5. From the day of birth to 6 months, the infant age was coded 0.5. From six months before parturition to the day of parturition were therefore coded -0.5. We also coded -1 from the detumescent day of maximal swelling which coincided with ovulation which resulted in successful deliveries of an infant. Finally, to avoid the high VIF and convergence errors of the model, we standardized all predictor variables (male rank, days from ovulation/detumescence/onset, infant age, the number of males and females) to make all

variables have a mean of 0 and standard deviation of 1. To make figures more intuitive and easier to interpret, they were made with the original scale.

- **Male intensive following after a female with different reproductive quality**

To investigate factors that influence male intensive following of a certain female, we ran two GLMMs with negative binomial distribution following the hurdle model approaches (*38*). In the first model (GLMM-1A), we tested whether maximal swelling and increase in infant age (explanatory variables) predict the number of males (response variable) who intensively followed a certain female using all data (250 days). Female age was also included as a fixed effect to examine whether female age influences male intensive following. The number of males and females with maximal swelling were also included as fixed effects to examine whether the spatio-temporal distribution of males and females with maximal swelling on the day influences the number of males who intensively follow the female. Female ID was the random factor in the model. One row of the data set comprised swelling status on a given day (ordinal 1 to 3), and infant age of a certain female as well as her age. In the same row, the number of males and females with maximal swelling of the given day was also placed. There were on average 6.4 ± 2.4 females in a day in the data set.

In the second part of the hurdle model, we took a subset of the data, which consisted only of those females with maximal swelling (205 days), to examine the effect of detumescence of maximal swelling and infant age (GLMM-1B). The average number of females with maximal swelling per day was 2.7 ± 1.3 (range: 1 to 8 per day). In this model, the days from detumescence of maximal swelling was included as an explanatory variable instead of swelling scores. The other variables were the same with GLMM-1A, except the inclusion of the interaction term between detumescent day and infant age, and a categorical variable that divides maximal swelling phase into ovulation detected or not – 209 ovulation-detected female-days and 336 ovulation-undetected female-days. Here a female-day represents a row in the data set that includes other explanatory and response variables of a given female on the given day. The inclusion of the interaction term was to test whether there would be a dependency between the two terms on male's intensive following. The categorical variable for the maximal swelling phase (ovulatory vs anovulatory) was included to test whether males can discriminate ovulatory cycles between maximal swelling phases. Our division of maximal swelling into ovulatory or anovulatory is a rough estimation as we could categorize an

ovulatory cycle into anovulatory, but not likely vice versa. However, it would provide therefore a conservative estimation of the effect of ovulation on male behavior.

We also investigated how males chose the target of the intensive following using a binomial mixed model (GLMM-1C) with the data when there were more than 2 females with maximal swelling in a daily ranging party (77 observation days). In this model, the number of days from the onset of maximal swelling and infant age as well as their interaction were included as explanatory variables. Female age and the number of males of the day were also included as in the two previous models. There were on average 3.2 ± 1.3 females with maximal swelling in the data set. Using ovulation-detected menstrual cycle from 14 females which cover 138 observation days, we finally tested the effect of ovulation on the intensive following behavior (GLMM-1D). In this model, other explanatory variables were identical with GLMM-1B except that we changed days from detumescence to days from ovulation (ovulation day is coded 0). As in other models, it was fitted to a negative binomial distribution.

- **Copulation, intervention, solicitation of copulation, and male-male aggression**

Male behaviors including copulation and intervention in copulation, and solicitation of copulation are probably directly related to male mating efforts. To examine the number of these three events between male-female dyads on a given day, three separated GLMMs with negative binomial distribution were conducted. For these three analyses, we used the 14 ovulation-detected maximal swelling phases from 5 females and limited the data from -14 to 0 days from ovulation (104 days in total). Within this ovulatory maximal swelling phase, there were temporary drops from maximal swelling to intermediate swelling (swelling score 2). The maximal swelling temporarily dropped to the intermediate swelling on 11 days from 5 females (fig. S1). These 11 days were excluded from data analysis. However, within the menstrual cycle of a female called Sl, 3 days of the fertile phase were outside of the maximal swelling phase. These 3 days of the intermediate swelling phase remained in the data set as a fertile window is situated in the days (*24*).

Each model (copulation: GLMM-2A and 2B, intervention: GLMM-2C, solicitation: GLMM-2D) has the number of copulations, interventions, and solicitations of copulation observed within a male-female dyad on a given day as a response variable. The number of events was controlled by the hours that the male and female of the given dyad were observed together (total counts of a one-hour party on a given day) using the offset function. The

explanatory variables were the number of days from ovulation, infant age, male rank, male age, and female age. Males with their mothers have better copulation opportunities and advantages during male-male competition (*4*, *16*). To include these social dynamics to some extent male age was included in all three models as the probability of having mothers in the group will be higher for younger males. In the GLMM-2B, male rank was converted into two categories, high (1st to 3rd ranking) and low (4th to 10th ranking) to further investigate the effect of 3-way interaction between days from ovulation, infant age, and the male rank on the number of copulations. The female-male dyad that was nested within a certain menstrual cycle was integrated into all models as a random variable (coded as dyad ID: cycle name). We did not use the 'dyad ID*cycle name' term because of a convergent error.

To test whether the number of females with maximal swelling influences the number of male-male aggression, we ran a GLM with a negative binomial distribution (GLM-2E). As male-male aggression might be also related both directly and indirectly with the male mating competition, we included the existence of male intensive following (O or X) as a fixed effect along with the number of females with maximal swelling on a given day. Both following hours of the day and the number of males of the given day were included as an offset term to control the effect of observation hours and the number of males in a daily ranging party. The random effect could not be defined as the number of male-male aggression was pooled within a day. One row of the data included the total number of aggressions of the day, the existence of intensive following and the number of females with maximal swelling, and so on.

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Acknowledgments

We thank our research assistants at Wamba for their great help and members of the Department of Ecology and Social Behavior and CICASP of the Primate Research Institute of Kyoto University for their support for fieldwork and valuable comments. We thank in particular K. Hosaka, T. Miyabe-Nishiwaki, F. Bercovitch, M. Nishikawa, A. MacIntosh, K. Graham, Y. Kawaguchi for valuable comments and reviews on the manuscript. We finally thank the Ministry of Scientific and Technological Research of the D.R. Congo for research permissions (MIN.ESURS/SG-RST/13/2013, MIN.ESURS/SG-RST/007/2014, MIN.ESURS/SG-RST/026/2014 to HR) and the Research Center of Ecology and Forestry for helping us and maintaining Luo Scientific Reserve.

Funding:
Environment Research and Technology Development Fund D-1007 (TF)
Japan Society for the Promotion of Science (JSPS) Grants-in-aid for Scientific Research 22255007 (TF)
JSPS Grants-in-aid for Scientific Research 25304019 (CH)
JSPS Grants-in-aid for Scientific Research 25257409 (HI),
JSPS Asia-Africa Science Platform Program 2012-2014 (TF)

Author contributions:
Conceptualization: HR
Methodology: HR, CH, KM, KS
Investigation: HR
Visualization: HR
Supervision: TF, DAH, CH
Project Administration: TF
Writing—original draft: HR
Writing—review & editing: HR, CH, DAH, KM, KS, TF

Competing interests: Authors declare that they have no competing interests.

Data and materials availability: All data are available in the main text and supplementary materials. Raw and other related data may be requested from the authors.

Supplementary Materials

Supplementary materials for this article are available in a separate file.

Figures and Tables

Fig. 1. Morphological changes in sexual swelling of a female named Fk. (A) non swelling; swelling score 1, (B) intermediate swelling; swelling score 2, (C) maximal swelling; swelling score 3.

Fig. 2. The number of males in intensive following across all 250 observation days. (A) the number of males in intensive following after females increased with the size of sexual swelling. (B) the number of males in intensive following after females increased with infant age of females. Sexual swelling 1 is non-swelling, 2 is intermediate swelling, 3 is the maximal swelling. Infant age ranges -1 to 5 and the minus value represents pregnant periods which included post conception swelling which resulted in a successful delivery. Infant age 0 is from birth to within 1year, and infant age 1 is from 1 to <2 years and so on. Due to many zero, medians are 0, and only a small box that shows 75th percentile and an upper whisker is seen in figure 2B. The points are the number of males in the intensive following of the day divided by daily observation hours.

Fig. 3. Male intensive following after females with maximal swelling. (A) More males intensively followed a female with an older infant and detumescence of the maximal swelling of the female was close. The fitted line (red) was generated by the 'lowess' function with default value in r which is based on locally weighted least squares regression. (B) The probability of males' intensive following increased when a female with an older infant and the onset of maximal swelling of the female started earlier. The fitted line (red) was generated by logistic regression and each. Each dot is a single data point for each day. Day 0 is the day that the maximal swelling of a given female became detumescent (A) or one day before the onset of maximal swelling (B).

Fig. 4. Male intensive following concerning the day of ovulation (14 cycles in 5 females). The number of males each day who intensively followed females in relation to the days from ovulation increased when ovulation was approaching. Detumescence of maximal swelling started after 1.9 ± 2.4 days from ovulation day on average. The median number of males in the intensive following after a given female was highest on the day of ovulation. Due to many zero numbers of males, the median is mostly zero except the periovulatory phase and one day after ovulation. Day 0 is the day that ovulation occurred. The upper and lower edges of the box represent 75th and 25th percentile respectively. A line within a box is median and whiskers are 1.5 times of interquartile range, and the dots are all data points.

Fig. 5. Probability of ovulation and male behaviors. (A) The probability of ovulation and fertility days from the onset of maximal swelling phase, and (B) from the detumescence of the maximal swelling phase. Black closed circles and lines are the day-specific ovulation probability, and red open circles and lines are the day-specific probability of fertility. (C) The number of males who intensively followed females with the onset of maximal swelling is widely distributed as found in the probability of ovulation in A. (D) The number of males who intensively followed females concerning days from the detumescence of maximal swelling shows a similar distribution as found in the probability of ovulation in B. Day 1 is the day of onset of maximal swelling phase (A, C). Day 0 is the day of detumescence (B, D). The upper and lower edges of the box represent 75th and 25th percentile respectively. A line within a box is median and whiskers are 1.5 times of interquartile range, and the dots are all data points.

Fig. 6. Prediction plots of males' copulation, intervention, solicitation of copulation. (A to E) The predicted copulation rate within a dyad (GLMM-2A) in relation to the ovulation day, infant age, male rank, male age, and female age. (F to J) The predicted rate of intervention of copulation by the male within a female-male dyad in relation to the ovulation day, infant age, male rank, male age, and female age. (K to O) The predicted rate of solicitation of copulation by a dyadic male in relation to ovulation day, infant age, male rank, male age, and female age. Asterisks (*) on each plot indicate *P*-value (ns: not significant, *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$).

Fig. 7. The number of male-male aggression concerning females with maximal swelling. (A) When males' intensive following behavior was observed, there were more aggressions per hour between males. (B) The number of male-male aggression also increased when there were more females with maximal swelling in a daily ranging party. Each dot represents each data point (total 250). The upper and lower edges of the box represent 75th and 25th percentile respectively. A line within a box is median and whiskers are 1.5 times of interquartile range.

Table 1. Summary statistics of GLMM-1A to 1D.

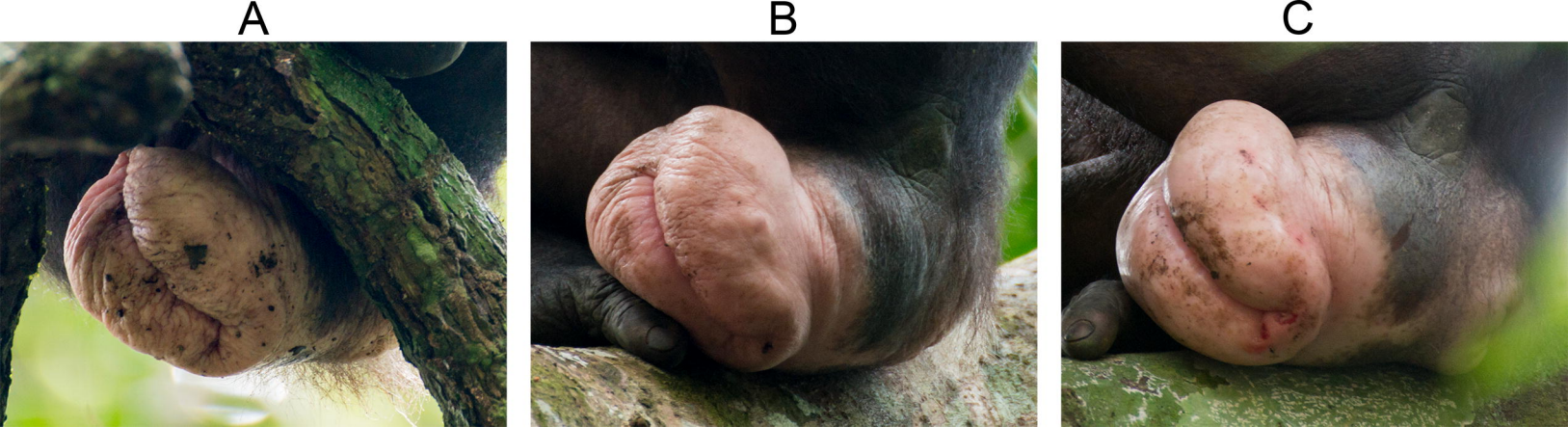
GLMM results of the number of males who intensively followed a given female in relation to infant age, sexual swelling, days from detumescence/onset of maximal swelling, ovulation, female age, and the number of males and females with maximal swelling. All predictor variables were standardized (mean of 0 and a standard deviation of 1) and the maximal variance influence factor, VIF was 2.95 for days from onset of MS in GLMM-1C. Asterisks indicates significance, *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$. FMS: female with maximal swelling, MS: maximal swelling.

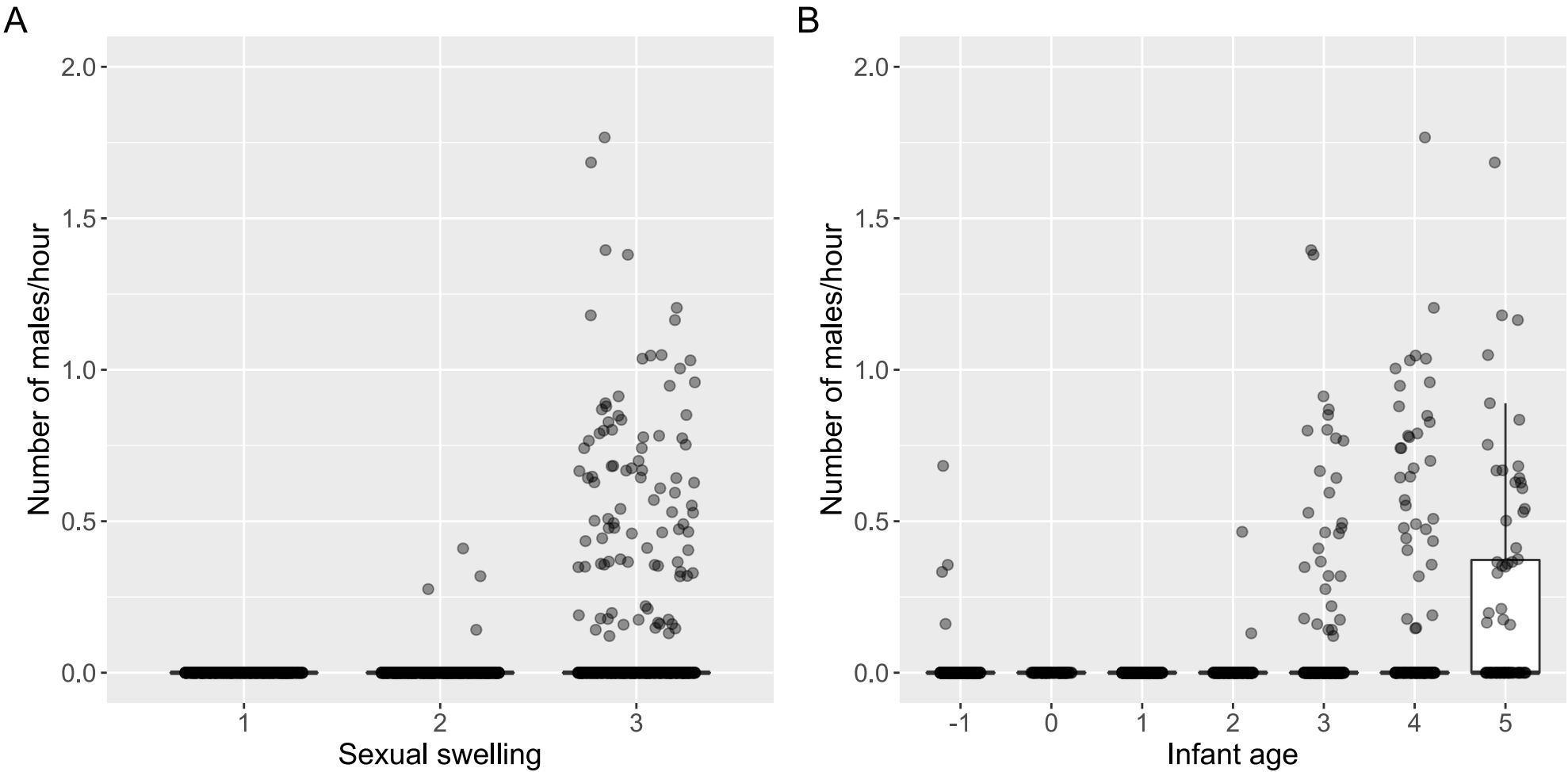
Models	Predictors	Estimates	SE	*Z*	*P*
GLMM-1A (Figure 2)	Intercept	-7.98	0.85	-9.43	<0.001***
	Infant age	2.76	0.52	5.33	<0.001***
	Swelling score	2.48	0.33	7.44	<0.001***
	Female age	-0.02	0.59	-0.04	0.971
	Number of males	-0.17	0.17	-1.01	0.312
	Number of FMS	-0.03	0.15	-0.18	0.854
GLMM-1B (Figure 3A)	Intercept	-3.00	0.21	-14.42	<0.001***
	Infant age[1]	0.39	0.18	2.22	0.026*
	Days from detumescence[2]	1.25	0.21	6.06	<0.001***
	Female age	0.10	0.12	0.85	0.393
	Number of males	-0.10	0.12	-0.81	0.419
	Number of FMS	-0.07	0.12	-0.55	0.582
	Ovulation undetected vs detected	-1.13	0.28	-4.03	<0.001***
	Interaction between 1 & 2	1.36	0.25	5.44	<0.001***
GLMM-1C (Figure 3B)	Intercept	-3.00	0.38	-7.89	<0.001***
	Infant age[3]	3.44	0.55	6.21	<0.001***
	Days from onset of MS[4]	2.24	0.39	5.82	<0.001***
	Female age	0.84	0.38	2.20	0.028*
	Number of males	-0.02	0.22	-0.08	0.939
	Interaction between 3 & 4	1.92	0.47	4.12	<0.001***
GLMM-1D (Figure 4)	Intercept	-2.97	0.38	-7.87	<0.001***
	Infant age[5]	1.59	0.42	3.83	<0.001***
	Days from ovulation[6]	1.74	0.23	7.58	<0.001***
	Female age	-0.26	0.31	-0.82	0.413
	Number of males	0.17	0.14	1.23	0.217
	Number of FMS	0.10	0.13	0.78	0.434
	Interaction between 5 & 6	-0.04	0.27	-0.14	0.887

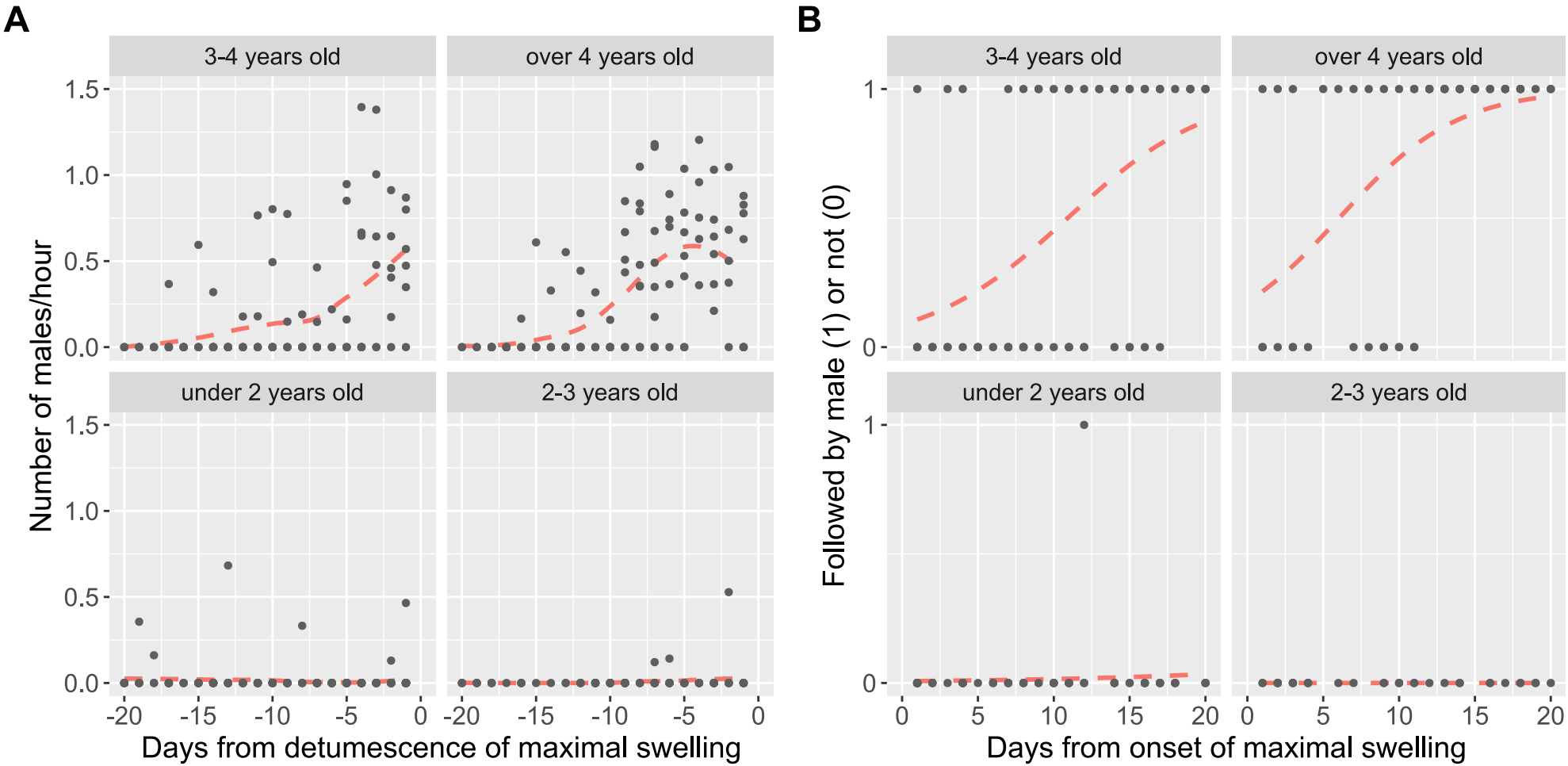
Table 2. Summary statistics of GLMM-2A to GLM-2E

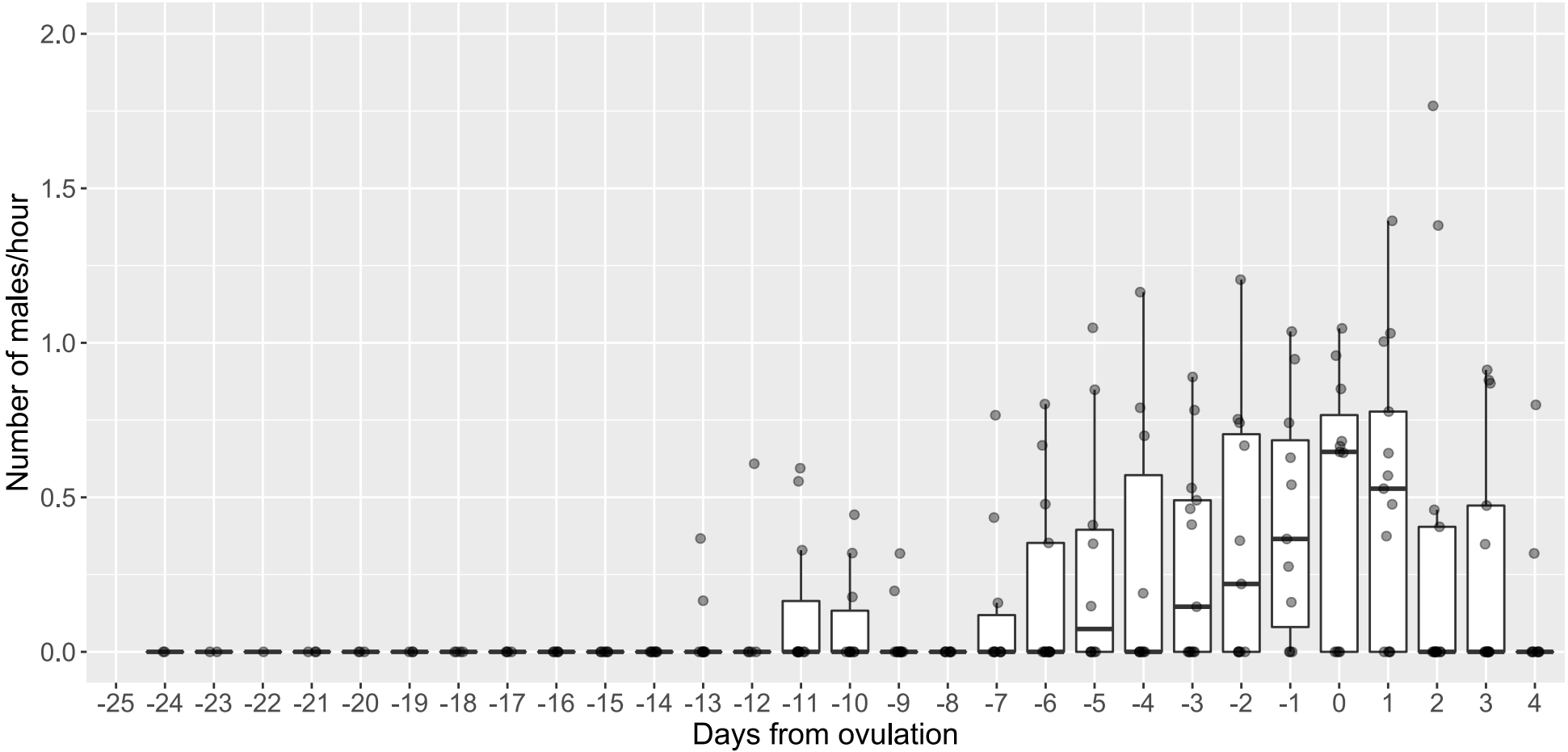
GLMM (2A to 2D) results of the number of copulations, interventions, and solicitations of copulation between male-female dyads in relation to days from ovulation (-14 to 0), infant age, female age, male rank (1: highest to 10: lowest in GLMM-2A, 1 to 3: high and 4 to 10: low in GLMM-2B), and male age in 104 days. GLM-2E shows results of the number of male-male aggression in relation to the existence of male intensive following and the number of females with maximal swelling. All predictor variables were standardized and the maximal VIF was 1.26 for female age in GLMM-2C. Asterisks indicates significance, *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$. FMS: female with maximal swelling.

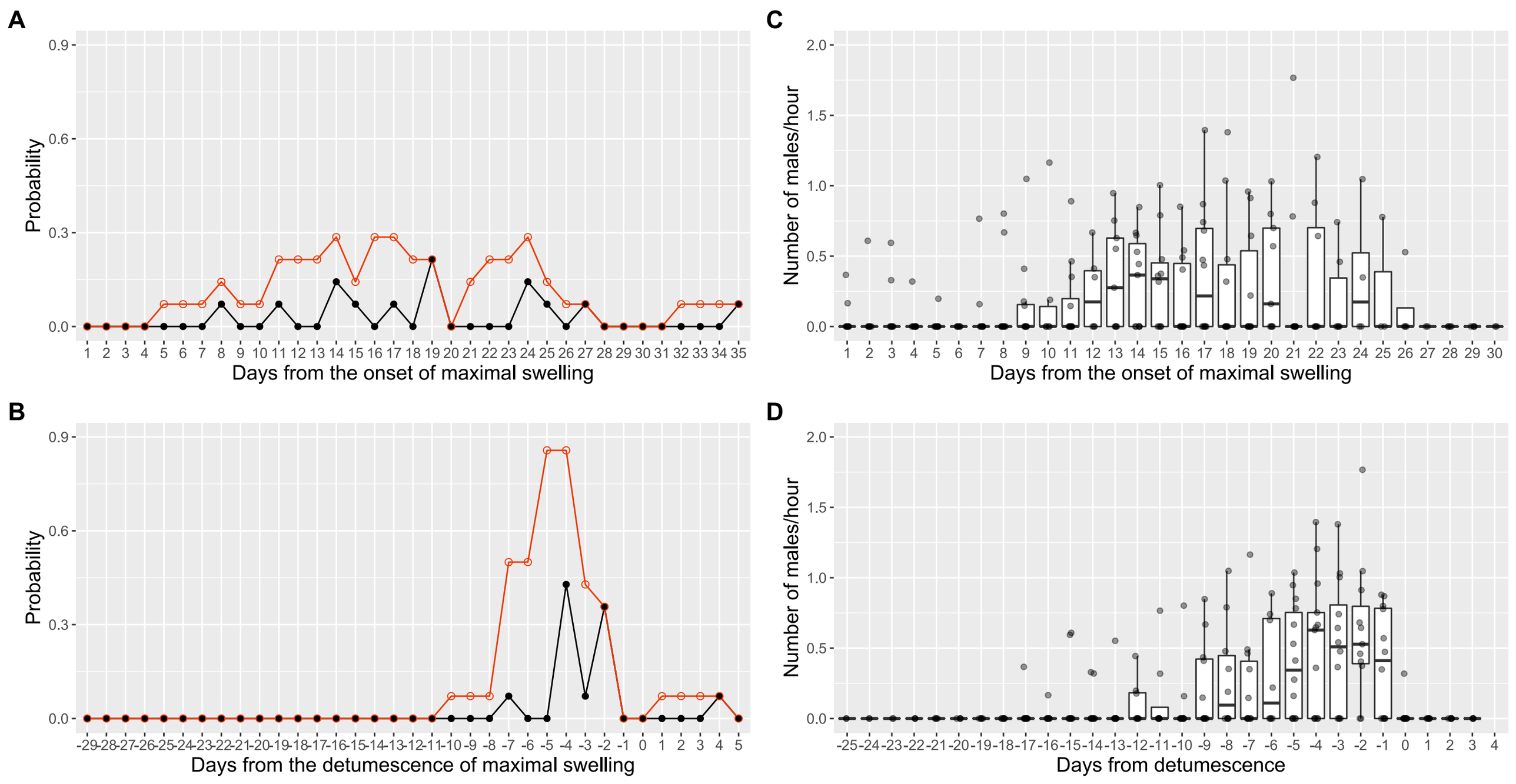
Models	Predictors	Estimates	SE	*Z*	*P*
GLMM-2A Copulation	Intercept	-4.89	0.27	-18.19	<0.001***
	Days from ovulation	0.24	0.10	2.49	0.013*
	Infant age	-0.48	0.18	-2.65	0.008**
	Male rank (ordinal 1 to 10)	-0.44	0.17	-2.65	0.008**
	Male age	-1.28	0.22	-5.79	<0.001***
	Female age	0.02	0.19	0.11	0.911
GLMM-2B Copulation	Intercept	-4.07	0.30	-13.61	<0.001***
	Days from ovulation[1]	0.30	0.10	3.01	0.003**
	Infant age[2]	-0.50	0.17	-2.86	0.004**
	Male rank low (base) vs high	-1.35	0.34	-3.99	<0.001***
	Male age	-1.23	0.22	-5.62	<0.001***
	Interaction 1, 2 & male rank (high)	-0.42	0.14	-3.01	0.003**
	Interaction 1, 2 & male rank (low)	0.24	0.14	1.70	0.090
GLMM-2C. Intervention	Intercept	-7.94	0.82	-9.70	<0.001***
	Days from ovulation	0.85	0.25	3.43	<0.001***
	Infant age	0.81	0.36	2.26	0.024*
	Male rank	-2.14	0.57	-3.77	<0.001***
	Male age	-0.58	0.41	-1.42	0.157
	Female age	-0.47	0.25	-1.93	0.053
GLMM-2D. Solicitation	Intercept	-4.53	0.23	-19.59	<0.001***
	Days from ovulation	0.29	0.10	2.84	0.005**
	Infant age	-0.10	0.15	-0.68	0.499
	Male rank	-0.34	0.14	-2.45	0.014*
	Male age	-1.25	0.19	-6.43	<0.001***
	Female age	0.15	0.15	1.00	0.318
GLM-2E. Male-male aggression	Intercept	-2.32	0.08	-27.41	<0.001***
	Intensive following (x: o)	-0.58	0.11	-5.07	<0.001***
	Number of FMS	0.20	0.06	3.42	<0.001***

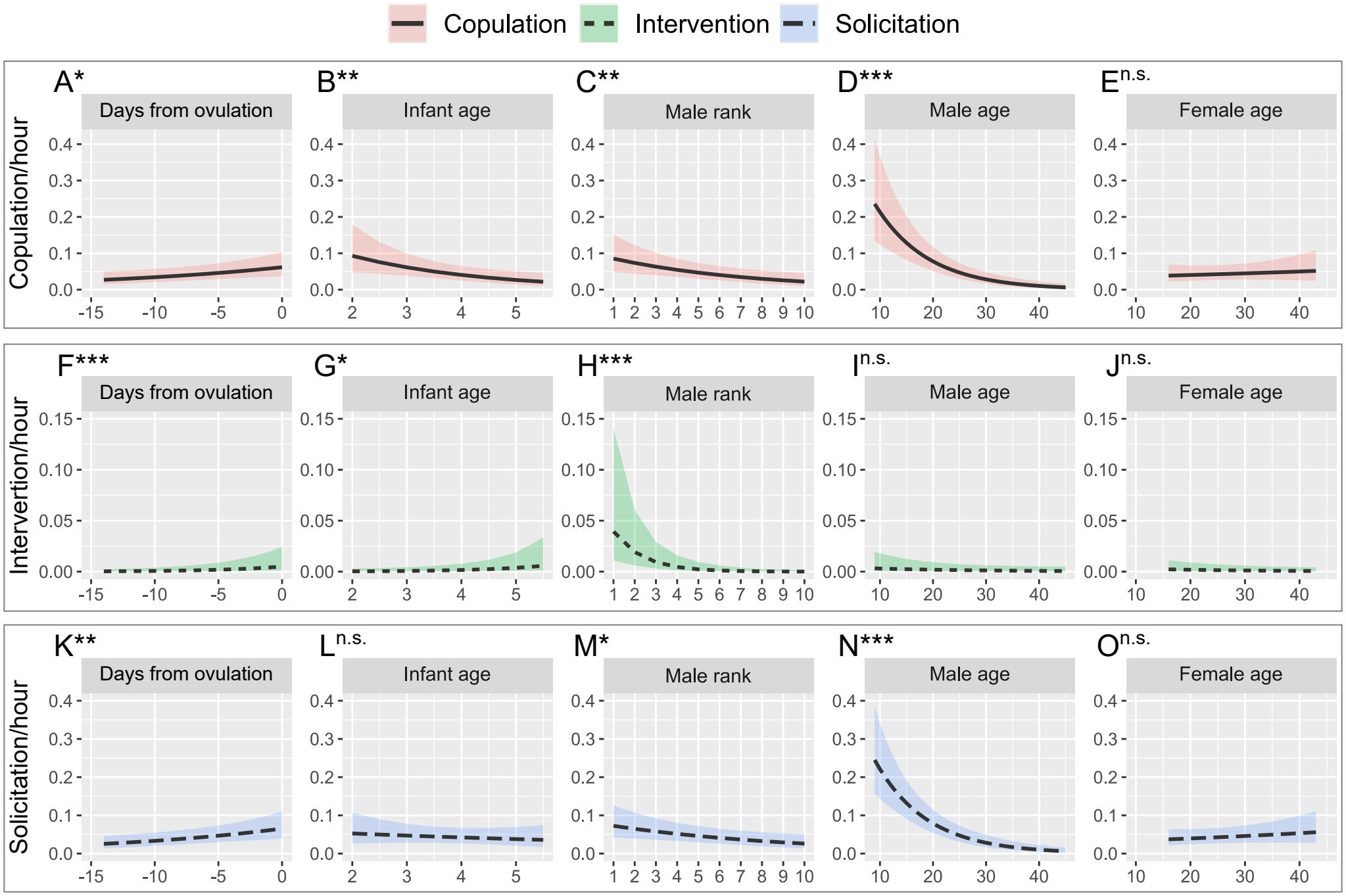

A
B
C

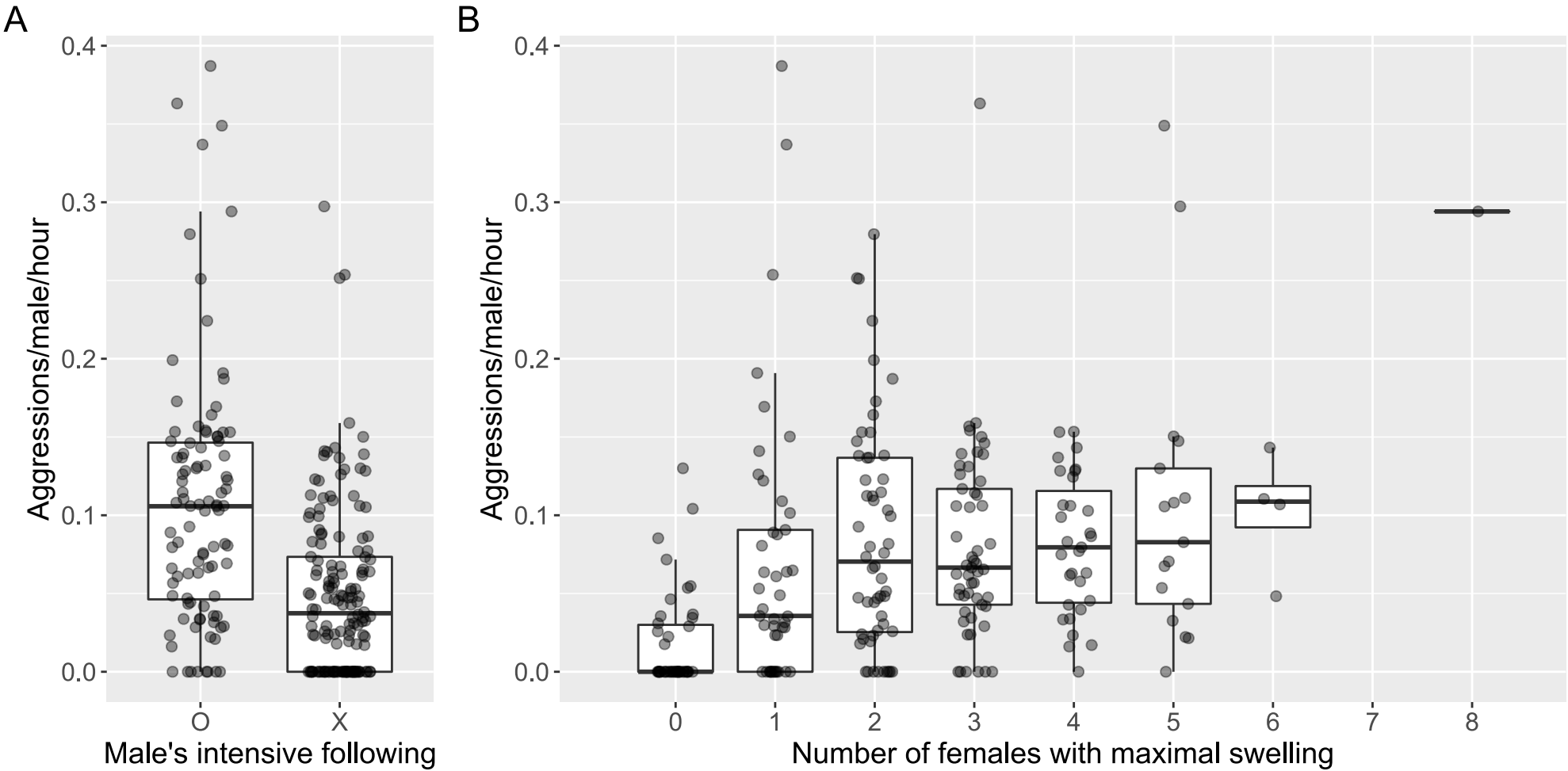

A
B
Number of males/hour
2.0
1.5
1.0
0.5
0.0
1
2
3
Sexual swelling
-1
0
1
2
3
4
5
Infant age


A
3-4 years old
over 4 years old
under 2 years old
2-3 years old
Number of males/hour
1.5
1.0
0.5
0.0
-20
-15
-10
-5
0
Days from detumescence of maximal swelling
B
3-4 years old
over 4 years old
under 2 years old
2-3 years old
Followed by male (1) or not (0)
1
0
0
5
10
15
20
Days from onset of maximal swelling


Number of males/hour
2.0
1.5
1.0
0.5
0.0
-25 -24 -23 -22 -21 -20 -19 -18 -17 -16 -15 -14 -13 -12 -11 -10 -9 -8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4
Days from ovulation


A
Probability
0.9
0.6
0.3
0.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35
Days from the onset of maximal swelling
B
Probability
0.9
0.6
0.3
0.0
-29 -28 -27 -26 -25 -24 -23 -22 -21 -20 -19 -18 -17 -16 -15 -14 -13 -12 -11 -10 -9 -8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5
Days from the detumescence of maximal swelling
C
Number of males/hour
2.0
1.5
1.0
0.5
0.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
Days from the onset of maximal swelling
D
Number of males/hour
2.0
1.5
1.0
0.5
0.0
-25 -24 -23 -22 -21 -20 -19 -18 -17 -16 -15 -14 -13 -12 -11 -10 -9 -8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4
Days from detumescence


Copulation
Intervention
Solicitation
A*
Days from ovulation
B**
Infant age
C**
Male rank
D***
Male age
E n.s.
Female age
Copulation/hour
F***
Days from ovulation
G*
Infant age
H***
Male rank
I n.s.
Male age
J n.s.
Female age
Intervertion/hour
K**
Days from ovulation
L n.s.
Infant age
M*
Male rank
N***
Male age
O n.s.
Female age
Solicitation/hour


A
B
Aggressions/male/hour
0.0
0.1
0.2
0.3
0.4
O
X
Male's intensive following
0
1
2
3
4
5
6
7
8
Number of females with maximal swelling