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Rank-biased access to females in periovulatory periods but comparable copulation rates across ranks in male bonobos at Wamba

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Rank-biased access to females in periovulatory periods but comparable copulation rates across ranks in male bonobos at Wamba

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Ethical statements

Our field studies of free-ranging bonobos at Wamba in the Luo Scientific Reserve were approved by the Ministry of Scientific Research and the Center for Research on Ecology and Forestry in

the Democratic Republic of Congo. This study adhered to the Animal Research Guidelines of The Graduate University for Advanced Studies (SOKENDAI), Japan, revised on March 23, 2021.

Keywords

Pan paniscus, prolonged sexual receptivity, non-conceptive copulation, intermale mating competition, operational sex ratio

Abstract

Objectives

Bonobos (*Pan paniscus*) are unique among non-human primates in that females exhibit prolonged sexual receptivity to males during the postpartum infertile stage. Although high synchrony in female sexual receptivity has been hypothesized to constrain dominant males' monopolization of reproductive success, recent genetic studies indicate pronounced male reproductive skew in this species. We investigated how prolonged sexual receptivity in female bonobos affects male behavioral patterns.

Materials and Methods

Behavioral observations were conducted on a free-ranging bonobo group at Wamba in the Luo Scientific Reserve, Democratic Republic of the Congo. Periovulatory periods (POPs) were estimated from the timing of detumescence marking the end of the maximal swelling phase, following Ryu et al. (2022). For each male, we calculated the proportion of copulations with POP females. Using all-day focal follows targeting mature males, we tested for rank-related bias in their copulation rates and evaluated the effects of the party-level operational sex ratio (OSR; the ratio of mature males to sexually receptive females) on the focal male's probability of copulation

and intermale aggression.

Results

Higher-ranking males were more likely to copulate with POP females, yet males of all ranks engaged in copulation on most of focal observation days (twice per day, on average). Lower party-level OSR values increased the focal male's probability of copulations while reducing intermale aggression.

Discussion

Prolonged sexual receptivity in female bonobos—yielding a pool of sexually receptive but non-POP females—may broaden male copulation opportunities beyond dominance rank and reduces intermale mating competition, even when POPs are detectable.

1. Introduction

Sexual receptivity refers to the physiological, morphological, and behavioral readiness of a female to accept a male and engage in copulation (Dixson 1998). In most mammals, estrus is the recurring phase of sexual receptivity and typically coincides with the periovulatory period (POP) (Conaway 1971; Weir and Rowlands 1973). Estrous signals—visual, olfactory, or acoustic—advertise fertility, attract males, and facilitate conception (Johns 1980; Semple and McComb 2000; Moreira et al. 2015). However, in some species—particularly among simian primates—female sexual receptivity extends beyond the fertile window (Beach 1976; Small 1988; Rooker and Gavrilets 2020). In species with promiscuous mating systems, copulating with multiple males can obscure paternity and thereby reduce the risk of male-inflicted infanticide (e.g., bottlenose dolphins [*Tursiops* spp.]: Connor et al. 1996; Hanuman langurs [*Semnopithecus entellus*]: Heistermann et

al. 2001; capuchin monkeys [*Cebus capucinus*]: Carnegie et al. 2005). Humans exhibit the most prolongation of female sexual receptivity among mammals (Symons 1979; Hrdy 1981), and ovulatory cues are sufficiently subtle that the POP is difficult for males to detect (Haselton and Gildersleeve 2011). A prominent hypothesis concerning concealed ovulation in humans posits that an obscured fertile window encourages males to maintain pair bonds rather than pursue multiple partners, thereby increasing paternity certainty and eliciting paternal investment in females and their offspring (Alexander and Noonan 1979; Symons 1979; Rodriguez-Girones and Enquist 2001). Thus, the evolution of prolonged female sexual receptivity may have helped shape a social environment advantageous to females.

Female chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are nonseasonal breeders with interbirth intervals of approximately 4–5 years (Thompson and Sabbi 2024). Across ovulatory cycles, females exhibit conspicuous changes in the size, shape, and firmness of the sexual skin around the anogenital region, reflecting fluctuations in estrogen and progesterone levels (Graham et al. 1972; Heistermann et al. 1996; Hashimoto 2023). Sexual skin tumescence ("sexual swelling") functions as an estrous signal indicating sexual receptivity (Furuichi 1987; Nishida et al. 1990). Females of both species continue to show several cycles of sexual swelling after conception and continue to copulate during pregnancy (Tutin and McGinnis 1981; Furuichi 1987; Takahata, Ihobe and Idani 1996; Wallis and Goodall 1993; Douglas et al. 2016). Moreover, in each ovulatory cycle, sexual swellings often persist for more than 10 days (Hasegawa and Hiraiwa-Hasegawa 1983; Wallis 1985; Furuichi 1987; Deschner et al. 2003; Paoli et al. 2009; Douglas et al. 2016), exceeding the fertile window, given that sperm remain viable for up to three days in the female reproductive tract whereas eggs are viable for only ~24 hours postovulation (Wilcox, Weinberg, and Baird 1995; Dunson, Baird, and Wilcox 1999). Prolonged sexual receptivity outside the fertile window in the genus of *Pan* is therefore thought to promote paternity

confusion and reduce the risk of male-inflicted infanticide (Zinner and Deschner 2000; Furuichi and Hashimoto 2002; Wrangham 2002).

The two *Pan* species differ markedly in the timing of postpartum resumption of female sexual receptivity. In bonobos, females resume sexual swellings at a mean of 8.1 months postpartum while still nursing their infants (Hashimoto et al. 2022). By contrast, female eastern chimpanzees typically do not resume sexual swellings until after weaning, at approximately four years of offspring age (Gombe: 46.8 months [Wallis 1997]; Mahale: 55.2 months [Nishida et al. 2003]; Kanyawara: 40.8 months [Thompson and Ellison 2017]), and conception often follows within a year of sexual receptivity resumption (Nishida et al. 1990; Wallis 1997; Furuichi and Hashimoto 2002; Thompson 2013). Female western chimpanzees resume earlier (Tai: 21.6 and 28.8 months postpartum [Deschner and Boesch 2007]), yet female bonobos still resume 13 months earlier on average. In bonobos, the period during which sexual swellings occur prior to conception spans roughly 3.5 years, calculated by subtracting postpartum amenorrhea (8.1 months) and gestation (7.9 months) from the mean interbirth interval of 4.8 years for surviving offspring (Furuichi et al. 1998). The physiological basis of these interspecific differences remains poorly understood; one possibility is that the sexual skin of female bonobos is more sensitive to estrogen than that of female chimpanzees, facilitating earlier resumption of sexual receptivity (Hashimoto et al. 2022).

High synchrony in female bonobos' sexual receptivity has been hypothesized to hinder dominant males' monopolization of reproductive opportunities and thereby reduce intermale mating competition (Furuichi 2006). The operational sex ratio (OSR)—the ratio of mature males to sexually receptive females present at a given time—is widely used as an indicator of the intensity of intermale contest over mates (Kvarnemo and Ahnesjo 1996; Weir, Grant, and Hutchings 2011). In species characterized by multi-male/multi-female groups, long interbirth

intervals, and nonseasonal breeders, such as hominid apes (Thompson and Sabbi 2024), the OSR is typically high. For example, the OSRs in chimpanzee groups are as high as 4.2 at Mahale and 12.3 at Gombe (reviewed by Furuichi and Hashimoto 2002). By contrast, the OSR in a bonobo group at Wamba is 2.8, substantially lower than in chimpanzees, reflecting a relatively higher proportion of sexually receptive females (Furuichi and Hashimoto 2002). Moreover, the mean number of females per party—a flexible subgroup whose membership varies in size and composition over time (Nishida 1968; Kuroda 1979)—is higher in bonobos at Wamba than in eastern chimpanzees at Kalinzu (Mulavwa et al. 2008), whereas it is similar between bonobos at LuiKotale and western chimpanzees at Taï (Surbeck et al. 2021). High rates of interfemale associations in bonobos may therefore further reduce intermale mating competition (Furuichi 2023).

Several studies indicate that intermale mating competition appears both less frequent and less intense in bonobos than in chimpanzees. In eastern chimpanzees, a substantial share of male aggression occurs in mating contexts: 17/100 events (17.0%) at Gombe and 36/100 events (36.0%) at Kanyawara (Goodall 1986; Muller 2002). By contrast, in bonobos at Wamba, the proportion of male aggression during copulations or approaches to sexually receptive females is lower: 2/36 (5.6%), 7/73 (9.6%), and 5/83 events (6.0%) (Furuichi 1989; Shibata and Furuichi 2024; this study). Higher proportions reported for bonobos at Lomako (37/150 events [24.7%], Hohmann and Fruth 2003) and LuiKotale (95 of 431 events [22.0%], Surbeck et al. 2011) likely reflect definitional differences from those studies at Wamba: Hohmann and Fruth (2003) analyzed only contact aggression, which may be disproportionately expressed during intermale mating competition, and Surbeck et al. (2011) broadly classified all antagonistic interactions occurring within 15 minutes before or after copulation as aggression in mating contexts. Additionally, severe intermale aggression—particularly lethal aggression both within and between groups—

characterizes chimpanzees and has not been documented in bonobos (Furuichi 2011; Wilson et al. 2014; Pusey 2022; Shibata and Furuichi 2024). Skeletal evidence from museum specimens likewise indicates higher rates of trauma in chimpanzees than in bonobos (Jurmain 1997).

However, genetic paternity analyses from multiple bonobo groups at LuiKotale, Wamba, and Kokolopori consistently show pronounced male reproductive skew (Surbeck et al. 2017; Ishizuka et al. 2018; Mouginot et al. 2023). Across groups, the most successful males sired a larger share of offspring than in chimpanzees (Mouginot et al. 2023: 69 ± 11% in bonobos; 44 ± 25% in chimpanzees). Male reproductive success also covaries with dominance rank; alpha males in two study groups at Wamba achieved the highest reproductive success (Ishizuka et al. 2018), and alphas in two of three study groups at Kokolopori sired more offspring than expected (Mouginot et al. 2023). These genetic outcomes suggest that male bonobos can discriminate POP from non-POP females with some accuracy, even when both are scored by observers as maximally swollen. Consistent with this possibility, Ryu et al. (2022) have shown that males' intensive following and mate guarding are concentrated on POP females, identified via urinary hormone profiles. Male chimpanzees likewise appear able to detect the POPs (Goodall 1986; Wallis 1992; Deschner et al. 2003; Thompson 2005), although the specific cues used remain untested in either *Pan* species. In addition to the power of dominant males to exclude male competitors (Kano 1996; Hohmann and Fruth 2003; Surbeck et al. 2012; Mouginot et al. 2024), the ability to detect POP females despite high synchrony in female sexual receptivity may help explain the marked male reproductive skew.

Despite pronounced inequality in male reproductive success in bonobos, why is intermale mating competition not expressed in more severe forms of aggression? One possibility is that the presence of multiple sexually receptive females dilutes competition by distributing male copulation attempts. Additionally, if a broad range of males can obtain

copulation opportunities—even though most are nonconceptive—the proximate motivation to compete over POP females may be attenuated. To evaluate the effects of prolonged sexual receptivity in female bonobos on male behaviors, we conducted all-day focal observations of males in a free-ranging bonobo group at Wamba. Specifically, this study addressed the following three questions:

(1) Do dominant males have priority access to POP females? Given the pronounced male reproductive skew, higher-ranking males are expected to copulate more frequently with POP females. To test this prediction, we estimated POPs from daily assessments of each female's sexual swelling status and, for each male, calculated the proportions of his copulations that involved POP females.

(2) Do males of different ranks have comparable opportunities to copulate? If sexually receptive but non-POP females attract males and provide many males with copulation opportunities, copulation rates should differ little across dominance ranks. To test this prediction, we examined a correlation of dominance ranks with copulation rates derived from all-day focal follows, which reduce sampling bias relative to short focal or ad libitum sampling.

(3) Do within-party changes in OSR influence intermale mating competition? If male sexual interest becomes more dispersed at the number of sexually receptive females increases, then lower OSR values should allow males to copulate more easily without contest. To test this prediction, we used continuous records of party composition during all-day focal follows and analyzed how the numbers of mature males and sexually receptive females, and the presence of POP females affected the focal male's probability of copulation and his involvement in intermale aggression.

2. Materials and Methods

2.1 Study site and subjects

Behavioral and ecological studies of free-ranging bonobos at Wamba, in the Luo Scientific Reserve, Democratic Republic of the Congo, began in 1974 (Kano 1992). By 1976, all individuals in the main study group, "E," were identified (Kuroda 1979). Subsequent work showed that the E group actually comprised two independent groups; from 1984 onward tjere were designated "E1" and "E2" (Furuichi 1987; Furuichi and Ihobe 1994). Demographic data—births, deaths, immigration, and emigration—have since been collected primarily for E1. Fieldwork at Wamba was interrupted in 1991–1994 owing to political instability and again in 1996–2002 during the Congo Wars (Furuichi et al. 2012). Artificial provisioning was initially used to facilitate detailed behavioral observations but was discontinued in 1996.

For this study, we collected data on the E1 group from December 1, 2022 to May 2, 2023 (153 days). During this period, E1 ranged from 45 to 48 individuals: 7 adult males (≥15 years), 5 adolescent males (8–14 years old), 16 adult females (≥15 years or older or parous), and 4 adolescent females (8–14 years and nulliparous). Following the resumption of fieldwork in 2004, all E1 individuals were reidentified by 2007; at that time, the group comprised of 24 individuals (10 adult males, 6 adult females, and 2 adolescent females; Hashimoto et al. 2008). E1's size increased gradually after 2009 (Fig. S1), largely due to the immigration of nulliparous females who subsequently reproduced (Toda et al. 2023).

2.2 Behavioral observations

Trained local assistants followed one party of the E1 group continuously from the time the bonobos descended from their night beds (approximately 0600 h) until they constructed new night beds (approximately 1700 h). The first author (KT) and a local assistant, Lokemba Batsindelia

(LB), conducted focal animal sampling (Altmann 1974) throughout the day to collect continuous behavioral data from 6 adult males, 5 adolescent males, 15 adult females, and 4 adolescent females in E1. One adult male (TN; estimated to be 55 years) was excluded from focal sampling because he had been missing from E1 for five months and was absent at the start of this study. Another adult male (TW; estimated to be 51 years) was included in focal follows, but his data were excluded from analyses because he has not been observed copulating or exhibiting erections since at least 2015 (Toda, personal observation).

Each day, we selected a focal subject from party members using a predetermined random order. A focal follow continued until one of the following conditions was met: the focal subject constructed a new night bed; darkness near sunset (approximately 1700 h) precluded identification ; or the subject was out of sight for ≥2 consecutive hours. Focal follows with ≥4 hours of observation were included in our dataset for analyses (i.e., treated as all-day focal data).If a focal subject was lost for ≥2 consecutive hours before reaching 4 hours, a second focal follow was initiated on the same day only if it could start by 1200 h. If the predetermined focal subject could not be located within 30 minutes of the start of the party follow, we selected the next available individual in the predetermined order from among party members present at that time. From the midpoint of the study onward, we prioritized undersampled subjects to balance observation effort. To ensure independence among all-day focal follows, at least 20 days elapsed before resampling the same individual.

During each focal follow, we recorded behaviors, including resting (e.g., sitting, lying, self-grooming), feeding (e.g., taking, chewing, swallowing food), moving (e.g., walking, running, climbing, jumping, brachiating), and social interactions (e.g., playing, social grooming, sexual interactions, agonistic interactions), along with the duration of each activity and the identities of participants. We also noted party composition—defined as the set of adult and adolescent

individuals present during focal follows—at 1-hour intervals from 0600 h to 1700 h using the 1-hour party method (Hashimoto, Furuichi, and Tashiro 2001). In addition, all observed copulatory and antagonistic interactions, including events not involving the focal subject, were recorded ad libitum during focal and party follows.

In total, 349.6 hours of observation were collected from ten males (excluding TN and TW) over 41 days of all-day focal follows conducted by KT (193.2 hours) and LB (156.4 hours). Mean focal time per day was 8.5 hours (SD = 1.8; range = 4.2–11.0 hours), with a median start time of 0630 h (range = 0600–1142 h) and a median end time of 1700 h (range = 1315–1732 h). The median focal time per subject was 35.4 hours (range = 25.1–44.7 hours; Table 1). Party composition was recorded for 422 sessions (not included if the focal male was out of sight for the entire hour. Of these sessions, 413 in which the focal male was visible for more than 15 minutes were retained for analyses.

2.3 Definition of copulation and aggression

Copulation refers to heterosexual interactions in which males mounted females, involving the insertion of the penis into the vagina, accompanied by thrusting movements. Because ejaculation was often not visually discernible, such intercourse was recorded as copulation regardless of whether ejaculation could be confirmed (Hashimoto 1997; Ryu et al. 2022). Aggression refers to directed antagonistic interactions, including physical contacts (e.g., punching, kicking, pushing, tackling, biting) and threat displays (e.g., chasing, charging, charging while branch-dragging, branch-shaking) (Nishida et al. 1999). Undirected displays lacking a clear target were not classified as aggression. We also recorded the target's responses to aggression, including submissive behaviors (e.g., fleeing, grinning, screaming) and retaliations toward the aggressor. To avoid inflating event counts, successive copulations or aggressions involving the same dyad

within 10 minutes were treated as a single event.

2.4 Evaluation of male dominance ranks

To determine the dominance hierarchy of the E1 group, we analyzed 297 aggression events: 124 recorded during all-day focal follows of males, 51 during all-day focal follows of females, and 122 collected ad libitum. In total, 201/297 events (67.7%) elicited submissive responses from the target, allowing us to identify winners and losers. We then computed David's scores (David 1987) for all adults and adolescents from the observed interaction matrix, using dyadic dominance indices that incorporate win-lose proportions and correct for unequal opportunities (de Vries, Stevens, and Vervaecke 2006). Although our primary aim was to evaluate male ranks, both sexes were included because male bonobos are co-dominant with females (Furuichi 1997; Surbeck and Hohmann 2013). Male dominance rank derived from David's score (Table 1) was not significantly associated with age (Spearman's rank correlation test: $\rho = -0.26$, $S = 360$, $p = 0.417$).

2.5 Estimation of female fertile windows

Daily presence of each individual in E1 has been recorded since September 2009 (Sakamaki et al. 2015). In addition, adult and adolescent females' sexual swellings were scored daily on a scale of 1 to 3 based on tumescence (Furuichi 1987; Ryu et al. 2015; Ryu et al. 2022): 1 = no swelling, 2 = intermediate swelling, 3 = maximal swelling.

Douglas et al. (2016) reported that the maximal swelling phase (MSP) in female bonobos at Luikotale is highly variable within and among individuals (mean ± SD = 10.6 ± 6.8 days; range = 1–31 days) and that ovulation timing inferred from urinary hormones varies substantially with respect to both MSP onset and end. By contrast, at Wamba, Ryu et al. (2022) found that ovulation timing peaks four days before MSP end—13 of 14 ovulations occurred toward MSP end (see also

Hashimoto et al. 2022)—although it remains unpredictable from MSP alone. In primates, the fertile window is often defined as the day of ovulation and the three preceding days (Deschner et al. 2003; Douglas et al. 2016), consistent with sperm survival up to ~3 days in the female tract and eggs remaining viable for ~24 hours post-ovulation (Wilcox, Weinberg, and Baird 1995; Dunson, Baird, and Wilcox 1999), Applying this criterion, Ryu et al. (2022) estimated that the probability of sperm coinciding with eggs (i.e. fertility) exceeds 0.3 from 7 to 2 days before detumescence (i.e., MSP end) and falls to ~0 on the day before prior to detumescence.

Although ovulation does not occur during postpartum amenorrhea, female bonobos nevertheless exhibit sexual swellings. To distinguish POP from non-POP females, we operationally defined the POP as the 6-day window from 7 to 2 days before MSP end, following Ryu et al. (2022). Gaps in swelling score records arose when females were absent from party follows or observations were missed. If a female's swelling score was identical immediately before and after a gap of ≤3 days, we interpolated the same score across the gap. When MSP end was obscured by a gap, POP status was treated as indeterminate. If swelling scores dropped from 3 to 2 for a single day and then returned to score 3, the transient score-2 day was included in the MSP. If an MSP lasted <6 days, no POP was assigned for that MSP.

2.6 Data analyses

Statistical analyses were conducted in R version 4.4.2 (R Core Team 2024) using RStudio version 12.0.467 (Posit Team 2024). We fit generalized linear models (GLMs) for non-Gaussian responses with the 'glm' function in the 'stats' package (R Core Team 2024) and generalized linear mixed models (GLMMs) to account for repeated measures within individuals and across observational days (Bolker et al. 2009) with the 'glmer' function in the 'lme4' package (Bates et al. 2015). Because covariate-response relationships can be nonlinear, we included quadratic terms for all

covariates. To reduce collinearity between linear and quadratic terms of the same predictor, all covariates were z-transformed (mean = 0, SD = 1) prior to squaring (Schielzeth 2010). The variables included in each model are described below.

To test the first prediction—that higher-ranking males copulate more frequently with POP females—we evaluated the effect of male dominance rank on the proportion of copulations with POP females versus non-POP females. For each male, we aggregated counts of copulations with POP females and with non-POP females across all events recorded via focal and ad libitum sampling during the study period. These two-column responses (POP, non-POP), constructed with the 'cbind' function, were fit with a binomial GLM using a logit link (Zuur et al. 2009). Male rank (1st–10th) and age (9–48 years) were included as covariates.

To test the second prediction—that male copulation rates differ little across dominance ranks—we examined the rank effect on copulation rates. Because male chimpanzees, in particular dominant males, show greater sexual interest in adult than adolescent females (Muller, Thompson, and Wrangham 2006), we tallied, for each focal day, the focal male's copulations with adult and adolescent females separately. These daily counts were fit with two Poisson GLMMs using a log link, each including an offset for observation time to account for variation among focal follows (Zuur et al. 2009). Male rank and age were included as covariates in both models. In addition, the number of non-mother females with maximal swellings (hereafter termed as MS females) on each focal day (adults: 0–6; adolescents: 0–4) was included as a covariate to capture day-to-day variation in potential copulation opportunities. A random intercept for focal male identity was included in both models to account for multiple observations from the same individual.

To test the third prediction—that lower OSR should allow males to copulate more easily without conflict—we assessed how temporal variation in OSR and the presence of POP females affected the focal male's probability of copulation and intermale aggression. For each 1-hour focal

session from 0600 to 1700 h (11 sessions per day), we coded whether ≥1 copulation and ≥1 intermale aggression involving the focal male occurred (1) or not (0). When an interaction spanned consecutive sessions, it was assigned to the earlier session based on its start time. These binary responses were fit with two binomial GLMMs using a logit link. Fixed effects included the number of mature males except for TW (1–10 individuals), the number of MS females (0–8 individuals), and the presence of non-mother POP females (yes/no) in the party during each session. We also included the duration the focal male spent resting during the session (0–60 minutes) to control for variation in inactivity and the duration he was out of sight (0–45 minutes) to control for variation in effective observational time. Random intercepts for focal male identity, observational date, and hour of day (i.e., session) were included in both models.

We fit GLMs and GLMMs by maximum likelihood (Zuur et al. 2009) and used the Akaike's Information Criterion (AIC) for model selection (Burnham, Anderson, and Huyvaert 2011). The model with the lowest AIC among all subsets of fixed effects was taken as the best model, and we also examined models with $\Delta AIC < 2$ relative to the best model (Burnham and Anderson 2004). For each best model, we evaluated residual normality, dispersion, and outliers using the 'simulateResiduals' function in the 'DHARMa' package (Hartig 2024); none showed violations (Fig. S2–S6). We assessed residual independence with the 'check_autocorrelation' function in the 'performance' package (Lüdecke et al. 2021) and found no significant autocorrelation (minimum *p*-value = 0.176). Multicollinearity was evaluated with the 'check_collinearity' function in the 'performance' package (Lüdecke et al. 2021); variance inflation factors (VIFs) were low in all best models (maximum VIF = 3.07).

3. Results

3.1 Frequency and types of male copulation and intermale aggression

Overall, we observed 67 copulations involving the focal male during 41 all-day focal follows, averaging 0.19 events per observation hour. Individual mean copulation rates ranged from 0.06 to 0.30 events per hour. On 38/41 focal days (92.7%), at least one MS female was in the same party as the focal male; on 33/38 of those days (86.8%), focal males copulated at least once. Including 206 copulations recorded ad libitum, a total of 273 copulations were documented over the study period: 64 (23.4%) with POP females, 186 (68.1%) with non-POP females, and 23 (8.4%) with females of undetermined fertility status. Visible sperm expulsion from the vagina immediately after copulation was confirmed in 17 events (6.2%); eight with POP females, six with non-POP females, and three with females of undetermined status. Ejaculation was more frequently observed in copulations with POP females (8/64 = 12.5%) than overall (17/273 = 6.2%; exact binomial test: $p < 0.001$).

We also recorded 83 intermale aggressions involving the focal male during all-day focal follows, corresponding to a mean of 0.24 events per observation hour. Individual mean aggression rates ranged from 0.08 to 0.42 events per observation hour. The dyad most frequently involved was the maternal brothers, KT and KY (21.7% of all intermale aggressions). Intermale aggression most often occurred when targets were resting on the ground (24.1%), followed by when targets were feeding near aggressors (18.1%). Only five aggressions (6.0%) occurred in mating contexts—when targets approached or solicited MS females, or during/immediately after copulation—and three of these (60.0%) involved contact aggression. Given that the overall proportion of contact aggression in 15/83 (18.1%), contact aggression was more likely to occur in mating contexts than overall (exact binomial test: $p = 0.044$).

383 *3.2 Variation in the frequency of female maximal swellings and the timing of periovulatory periods*
384 *(POPs) after parturition*
385 Based on daily presence records, the mean numbers of MS females per observation day were 2.8
386 adults (range = 0–6, N = 16) and 1.7 adolescents (range = 0–4, N = 4). Across individuals, the
387 percentage of observational days on which each female exhibited maximal swellings ranged from
388 0 to 73.2%. Excluding three pregnant females (Ik, Sc, and Ec) who gave birth during the study
389 period, this percentage was significantly higher in adolescents (56.1 ± 13.5 SD %, N = 4) than in
390 adults (28.7 ± 18.6 SD %, N = 13) (Wilcoxon rank-sum test: W = 46, p = 0.023).
391 We documented 30 MSPs that lasted >6 days. Of these, 21 POPs were identified—based
392 on MPS end—for 10 females (8 adults, 2 adolescents; Table S1). Copulation with mature males
393 occurred at least once in 18/21 POPs (85.7%). Among adults, the 15 POPs accompanied by
394 copulation occurred at 22–91 months postpartum; no female lost her most recent offspring during
395 the study period.
396
397 *3.3 Effect of male dominance rank on access to females in periovulatory periods (POPs)*
398 Figure 1 shows, for each male, the proportion of his copulations that involved POP females. The
399 alpha male, KT, copulated with POP females in 58.1% of his copulations (18/31 events). His
400 mother, Ki, was the alpha female (Table S1). His maternal brothers, KY and NB—ranked second
401 and fourth, respectively—also showed higher proportions (42.9% and 50.0%) than the across-
402 male mean of 23.2% (range = 4.3–58.1%, N = 10). We observed Ki intervene in her sons' agonistic
403 interactions four times; on one occasion, she intercepted another male's copulation attempt.
404 Among males whose mothers were not top-ranking, the third-ranking male, JO, copulated with
405 POP females at a higher proportion (22.2%) than the four lower-ranking males, HC, SE, YD, and
406 NI (range = 4.3–15.8%). Two males without resident mothers, DI and GC, each had only one

copulation with POP females (5.6% and 6.7%, respectively).

The best-fitting binomial GLM for the binary response (POP vs. non-POP) retained male rank (linear term only) as the sole predictor (Table 2A). Male rank had a significant positive effect on the odds that a copulation involved a POP female (estimate = 0.97, SE = 0.19, $z = 5.06$, $p < 0.001$), indicating that higher-ranking males copulated more frequently with POP females than lower-ranking males.

3.4 Relationship of male dominance ranks with copulation opportunities

Figure 2 shows, for each male, the rate of copulations with adult females per observation hour. The best-fitting Poisson GLMM for counts of copulations with adult females included the number of non-mother adult MS females (linear and quadratic terms; Table 2B). The linear term was positive (estimate = 0.94, SE = 0.28, $z = 3.34$, $p < 0.001$), whereas the quadratic term was negative (estimate = –0.47, SE = 0.23, $z = 2.03$, $p = 0.043$), indicating that copulation rates increased with the number of non-mother adult MS females but then peaked out (inverted U-shaped pattern). A competing model that included male rank (linear term only) had a ΔAIC = 2.0, and the rank effect was not significant (estimate = –0.03, SE = 0.16, $z = -0.17$, $p = 0.867$; Table S2A).

Rates of copulations with adolescent females per observation hour are also showed for each male in Figure 2. The best-fitting Poisson GLMM for counts of copulations with adolescent females was the null model with random intercept only (Table 2C), indicating that none of the candidate predictors improved model fit. A model including male rank (linear term only) had ΔAIC = 1.8 and showed a non-significant rank effect (estimate = 0.10, SE = 0.23, Z = 0.45, $p = 0.657$; Table S2B).

3.5 Effects of within-party operational sex ratio dynamics and the presence of females in

periovulatory periods (POPs) on intermale mating competition

Across 1-hour sessions in which the focal male was visible for >15 minutes, the mean (± SD) numbers of party members present were 3.0 ± 1.7 adult males, 2.2 ± 1.3 adolescent females, 6.4 ± 3.6 adult females, and 1.5 ± 1.2 adolescent females. Sessions included, on average, 2.9 non-mother MS females (range = 0–9) and 0.6 non-mother POP females (range = 0–4). At least one non-mother POP female was present in 156/413 sessions (37.8%). Copulations and intermale aggressions were recorded in 60 and 68 sessions, respectively (14.5% and 16.4%). The focal male spent, on average, 23.1 minutes resting and 8/0 minutes out of sight per session.

Figure 3 shows the proportion of sessions in whether the focal male copulated, plotted against (A) the numbers of mature males and (B) the number of MS females. The best-fitting binomial GLMM for copulation occurrence included the following predictors (Table 2D): number of mature males (linear term only), number of non-mother MS females (linear and quadratic terms), presence of non-mother POP females (yes/no), and resting time (linear and quadratic terms). The number of mature males had a negative effect on the focal male's copulation probability (estimate = –0.83, SE = 0.23, z = –3.68, p < 0.001). The number of non-mother MS females had a positive linear effect (estimate = 1.36, SE = 0.30, z = 4.60, p < 0.001) and a negative quadratic effect (estimate = –0.44, SE = 0.15, z = –2.92, p = 0.004), consistent with an inverted-U relationship: copulation probability increased with more non-mother adult MS females, but peaked before the maximum observed counts. The presence of non-mother POP females had no significant effect (estimate = –0.53, SE = 0.35, z = –1.54, p = 0.124).

Figure 3 also shows the proportion of sessions with intermale aggression involving the the focal male, plotted against (C) the numbers of mature males and (D) the number of MS females. The best-fitting binomial GLMM for aggression occurrence included the following predictors (Table 2E): number of mature males (linear term only), number of MS females (linear term only),

and resting time (linear and quadratic terms). The number of mature males had a positive effect on the focal male's aggression probability (estimate = 1.06, SE = 0.22, z = 4.74, p < 0.001), whereas the number of MS females had a negative effect (estimate = –0.56, SE = 0.22, z = –2.58, p = 0.010). A competing model that included presence of POP females (yes/no) had a ΔAIC = 2.0, and the effect was not significant (estimate = 0.04, SE = 0.38, z = 0.10, p = 0.919; Table S2C).

Together, these results indicate that the focal male was more likely to engage in copulation and less likely to be involved in intermale aggression in parties with lower OSRs—i.e., fewer other males relative sexually receptive females—irrespective of the presence of POP females.

4. Discussion

4.1 Validity of the empirical method for inferring female fertility status from the end of the maximal swelling phase (MSP)

Because we conducted all-day focal follows, routine urine collection sufficient to determine ovulation timing was not feasible. As an alternative, we applied an empirical method based on Ryu et al. (2022) to infer periovulatory periods (POPs) of female bonobos from the end of their MSPs. MSPs occurring before 22 months postpartum did not exceed 6 days, and the postpartum POP timing we estimated for adult females (offspring age 22–91 months) largely overlapped the postpartum ovulation timing identified from urinary hormone profiles (24–63 months; Hashimoto et al. 2022). These congruences suggest that clearly non-ovulatory MSPs were unlikely to have been misclassified as POPs. Moreover, the pattern detected with this method—higher-ranking males copulating more often with POP females—accords with genetic evidence of pronounced male reproductive skew in bonobos, supporting its usefulness for rough among-male comparisons of reproductive opportunity. Nonetheless, the method does not pinpoint the exact fertile window and should be interpreted as an approximate proxy.

4.2 Biased reproductive opportunities toward dominant males in bonobos

Consistent with our first prediction, we found that higher-ranking males were more likely to copulate with POP females. This pattern indicates that dominant males enjoy priority access to POP females, aligning with the genetic evidence for pronounced male reproductive skew in bonobos (Surbeck et al. 2017; Ishizuka et al. 2018; Mouginot et al. 2023). It also accords with Ryu et al. (2022), who showed that male bonobos can detect females' POPs to some accuracy and dominants invest greater effort in guarding POP females. In our observations, overt interference with copulations by dominant males was infrequent; nevertheless, dominants may have restricted subordinates' access to POP females, thereby limiting their reproductive opportunities.

For male bonobos, maternal presence is a key determinant of dominance rank and access to sexually receptive females (Kano 1996; Furuichi 1997; Surbeck et al. 2011; Shibata and Furuichi 2023), thereby strongly affecting male reproductive success (Surbeck et al. 2019). In this study, the three sons of the alpha female (Ki)—ranked first (KT), second (KY), and fourth (NB) among E1 males—exhibited higher proportions of copulation with POP females than males whose mothers were ranked lower. In bonobo groups characterized by strong female-female cohesion (Furuichi 1989; Parish 1996; Moscovice et al. 2017), maternal presence likely increases sons' proximity to clusters of females (including their mothers), thereby facilitating access to copulation opportunities (Surbeck et al. 2011; Yokoyama and Furuichi 2022). Moreover, because female bonobos occupy the top position in the dominance hierarchy (Furuichi 1997; Surbeck and Hohmann 2013; Tokuyama et al. 2016), dominant mothers can intervene directly in intermale mating competition on behalf of their sons (Furuichi 1997; Surbeck et al. 2011; Shibata and Furuichi 2023).

Bonobos rarely form intermale coalitions (Furuichi and Ihobe 1994; Shibata and Furuichi

2024; Mouginot et al. 2024), and cooperative relationships between maternal brothers have not been documented. At Wamba, Ihobe (1992) noted frequent spatial proximity among maternal brothers, but this likely reflected simultaneous association with their mothers rather than genuine affiliative bonds between brothers. In this study, we observed a single instance of coalitionary aggression by Ki's sons against a common target; otherwise, they did not form enduring coalitions. Instead, KT persistently directed aggression toward his younger brother, KY, throughout the study period and occasionally toward his older brother, NB. In this case, the maternal brothers appear to have been reproductive competitors, much like other males. By contrast, although documentation on brotherhood in chimpanzees is limited, Bygott (1979) described four cases at Gombe in which males with supportive elder brothers attained alpha status, suggesting that the presence of maternal brothers can confer a reproductive advantage in chimpanzees.

4.3 Relationship between copulation opportunities and dominance ranks in male bonobos

Despite pronounced male reproductive skew, we found that overall copulation rates did not differ appreciably across dominance ranks. This result supports our second prediction that rank-related bias in copulation opportunity is weak in male bonobos and is consistent with the idea that the availability of sexually receptive females during the postpartum amenorrhea provides many males with copulation opportunities. Although dominant males have priority access to females (Kano 1996; Ryu et al. 2022), subordinates may obtain copulation opportunities in contexts where dominants cannot interfere or with females outside of dominants' sexual interest. Assuming that POP detection is not absolute, subordinate males could benefit by maximizing copulation frequency to increase their chances of participating in sperm competition, even if such efforts rarely translate into paternity.

Our finding of comparable copulation rates across dominance ranks in male bonobos

contrasts with prior reports of higher copulation rates for dominant males (Kano 1996; Hohmann and Fruth 2003; Surbeck et al. 2011; Ryu et al. 2022; Yokoyama and Furuichi 2022). A plausible explanation for this discrepancy is methodological differences. Earlier studies were conducted under artificial provisioning (Kano 1996) or relied on short-duration focal sampling (10−60 minutes) (Surbeck et al. 2011; Ryu et al. 2022; Yokoyama and Furuichi 2022). Such approaches can bias observations toward centrally positioned individuals and larger parties, thereby missing copulations at the periphery or in smaller parties (Altmann 1974; Drickamer 1974). Because subordinate males tend to seek copulation opportunities while avoiding dominants (Furuichi and Ihobe 1994; Kano 1996; Shibata and Furuichi 2023), unbiased estimates require sustained focal follows of these males, including periods when they range alone or with only a few companions.

4.4 Impact of prolonged sexual receptivity of female bonobos on intermale mating competition

This study provides, to our knowledge, the first dataset that integrates hourly party compositions with behavioral records from all-day focal follows to test how fluctuations in the operational sex ratio (OSR) predict the occurrence of copulation and intermale aggression involving the focal male. We found that a focal male's probability of copulation increased with more females exhibiting maximal swellings (MS females) and with fewer mature males in the party, whereas his probability of intermale aggression decreased under the same conditions. These results support our third prediction that male bonobos obtain copulation opportunities more readily in parties with lower OSRs—that is, fewer male competitors relative to sexually receptive females. The presence of MS females during postpartum infertility appears to heighten male sexual motivation, suggesting that males may experience proximate physiological and/or neurological rewards from copulation even when conception is unlikely. In humans and rats, the post-ejaculatory state is associated with reduced general arousal, likely mediated by prolactin release (Krüger et al. 2002;

Ågmo and Laan 2022); accordingly, frequent day-to-day access (approximately twice per day, on average) to copulation could lessen males' incentive to engage in costly contests over POP females. Non-invasive monitoring of hormonal activities in male bonobos would help clarify the physiological effects of non-conceptive copulations on behavioral patterns.

Nevertheless, male sexual motivation for non-conceptive copulations may differ from that for conceptive copulations. In several *Macaca* species—Tonkean macaques (*M. tonkeana*: Aujard et al. 1998), Barbary macaques (*M. sylvanus*: Heistermann et al. 2008), and Japanese macaques (*M. fuscata*: Garcia. Shimizu, and Huffman 2009)—the frequency of ejaculatory copulations increases toward ovulation. In Tibetan macaques (*M. thibetana*), copulations observed outside the mating season occur less frequently and feature a shorter mount duration, an absence of vocalization pauses, and less frequent ejaculation (Li, Yin, and Zhou 2007). Similarly, in our dataset—although the number of copulations with confirmed ejaculation was small—ejaculation was observed more often with POP females than non-POP females. Given that ejaculates are costly to produce (Thomsen et al. 2006), male bonobos might have refrained from ejaculating in copulations with non-POP females. Further detailed observations, ideally coupled with hormonal measures, are needed to assess qualitative differences in male sexual motivation between conceptive and non-conceptive copulations.

Genetic evidence of pronounced male reproductive skew in bonobos predicts that males will compete for access to POP females. However, in our dataset, the presence of POP females within parties did not increase the frequency of intermale aggression involving the focal male. This result contrasts with previous findings from LuiKotale (Surbeck et al. 2012) and Wamba (Ryu et al. 2022). At LuiKotale (2007–2009), the presence of "potentially fertile" females—defined as maximal swelling phases occurring within six months prior to conception, inferred by counting back eight months from the subsequent birth—was associated with increased male

aggression (Surbeck et al. 2012). Similarly, at Wamba (2013–2015), male interventions in copulation attempts, including aggression toward male competitors, were more frequent in parties containing POP females identified from urinary hormone profiles (Ryu et al. 2022). Taken together, those studies suggest that subordinate males can engage in direct contests with dominants over POP females, whereas such contests were rare in our dataset.

One factor that could explain the discrepancy between our results and prior works is the stability of within-group dominance hierarchies. Instability may weaken dominants' ability to exclude male competitors, thereby allowing subordinates to increase their reproductive success, as reported in Sanje mangabeys (*Cercocebus sanjei*: Fernandez 2017) and rhesus macaques (*Macaca mulatta*: Milich et al. 2020). During our study period, the mother-son pair of Ki-KT occupied the top ranks in the E1 group; accordingly, there seemed little scope for subordinates to compete successfully with them over POP females. By contrast, during the period studied by Ryu et al. (2022), alpha status in E1 was unstable: the young male JR (son of Jk) began challenging the then-alpha male NB (son of Ki), and antagonistic interactions between them were frequent, sometimes occurring between their mothers (see Shibata and Furuichi 2023). Likewise, during the period studied by Surbeck et al. (2012), the Bompusa group exhibited an unbalanced hierarchy in which mother and son did not jointly hold alpha status (Surbeck et al. 2013). Longitudinal behavioral observations combined with paternity data will help clarify how hierarchy stability shapes alpha male reproductive success.

5. Conclusions

Using behavioral data from free-ranging bonobos in the E1 group at Wamba (December 2022–May 2023), this study presents three key findings: (1) higher-ranking males copulated more frequently with POP females; (2) male copulation rates were broadly similar across dominance

ranks; and (3) lower party-level OSR values increased the focal male's probability of copulation while reducing intermale aggression. Taken together, these results suggest that prolonged female sexual receptivity—which creates frequent copulation opportunities for many males—may attenuate males' proximate motivation to engage in direct contests with dominants over POP females. Nevertheless, because these findings are derived from six months of observations in a single group, additional multi-group, longitudinal datasets are necessary to assess generality. This study emphasizes the importance of all-day focal follows and hormonal measures in elucidating the reproductive strategies of male bonobos and clarifying the adaptive benefits of prolonged female sexual receptivity.

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8. Figure Legends

Fig.1 Proportion of copulations with POP females for each male. Males are ordered from left to right by increasing dominance rank. The curve and shaded band represent the predicted proportion and its 95% confidence interval from the best-fitting binomial generalized linear model (GLM). Point sizes are proportional to the number of copulations for which the female's fertility status (POP vs. non-POP) was determined.

Fig.2 Copulation rates (events per hour of focal follows) for each focal male. Males are ordered from left to right by increasing dominance rank. Gray and white bars denote copulations with adult females and adolescent females, respectively.

Fig.3 Effects of the number of mature males and the number of females with maximal swellings (MS females) present in the party on the probability that the focal male engaged in copulation (A, B) and was involved in intermale aggression (C, D) during 1-hour interval sessions. Point sizes are proportional to the number of sessions observed at each value of (A, C) the number of mature males and (B, D) the number of MS females. Curves and shaded bands represent predicted probabilities with 95% confidence intervals from the best-fitting binomial generalized linear mixed models (GLMMs). Colors indicate predictions evaluated at the 25th (red), 50th (blue), and

75th (yellow) percentiles of the other predictor (i.e., in panel A and C, predictors are computed at these percentiles of the number of MS females; in panel B and D, at these percentiles of the number of mature males).

TABLE 1 Overview of male subjects in the E1 group at Wamba during the study period (December 2022–May 2023).

ID	Age[c] (yrs)	Male rank [David Score]	Observation hours during all-day focal sampling [day]	Number of copulation acts	
				Focal data [number of days copulation occurrence]	Focal + ad-libitum data [POP females, non-POPs]
TN[a]	52*	Not used [-2.9]	Not collected	Not collected	(5 [0, 5])[d]
TW[b]	49*	Not used [-12.9]	(39.2 [4])[d]	(0)[d]	(0)[d]
DI	48*	5th [4.6]	39.7 [4]	7 [3]	19 [1, 17]
NB	35	4th [7.2]	44.7 [5]	9 [5]	31 [14, 14]
GC	33*	8th [-11.2]	37.5 [4]	7 [4]	17 [1, 14]
KT	19	1st [53.4)	36.4 [4]	3 [3]	33 [18, 13]
JO	17	3rd [7.5]	36.7 [4]	11 [4]	38 [8, 28]
KY	14	2nd [10.0]	30.6 [4]	6 [3]	35 [15, 20]
HC	14	6th [-2.7)	32.0 [4]	6 [3]	25 [3, 19]
SE	12	7th [-6.1]	32.6 [4]	9 [3]	20 [3, 16]
NI	10	10th [-28.9]	25.1 [4]	7 [3]	23 [3, 20]
YD	9	9th [-27.0]	34.4 [4]	2 [2]	27 [1, 22]

[a]TN was not included in the focal subject, because he had been lost for a five month in E1 group and was absent at the beginning of this study.

[b]TW had seemed erectile dysfunction before the study period, and thus data on him were not used for the analysis.

[c]Asterisks in the column means estimated ages.

[d]Data in parentheses were not used for the analysis.

[g]Not included when female fertility status could not be determined

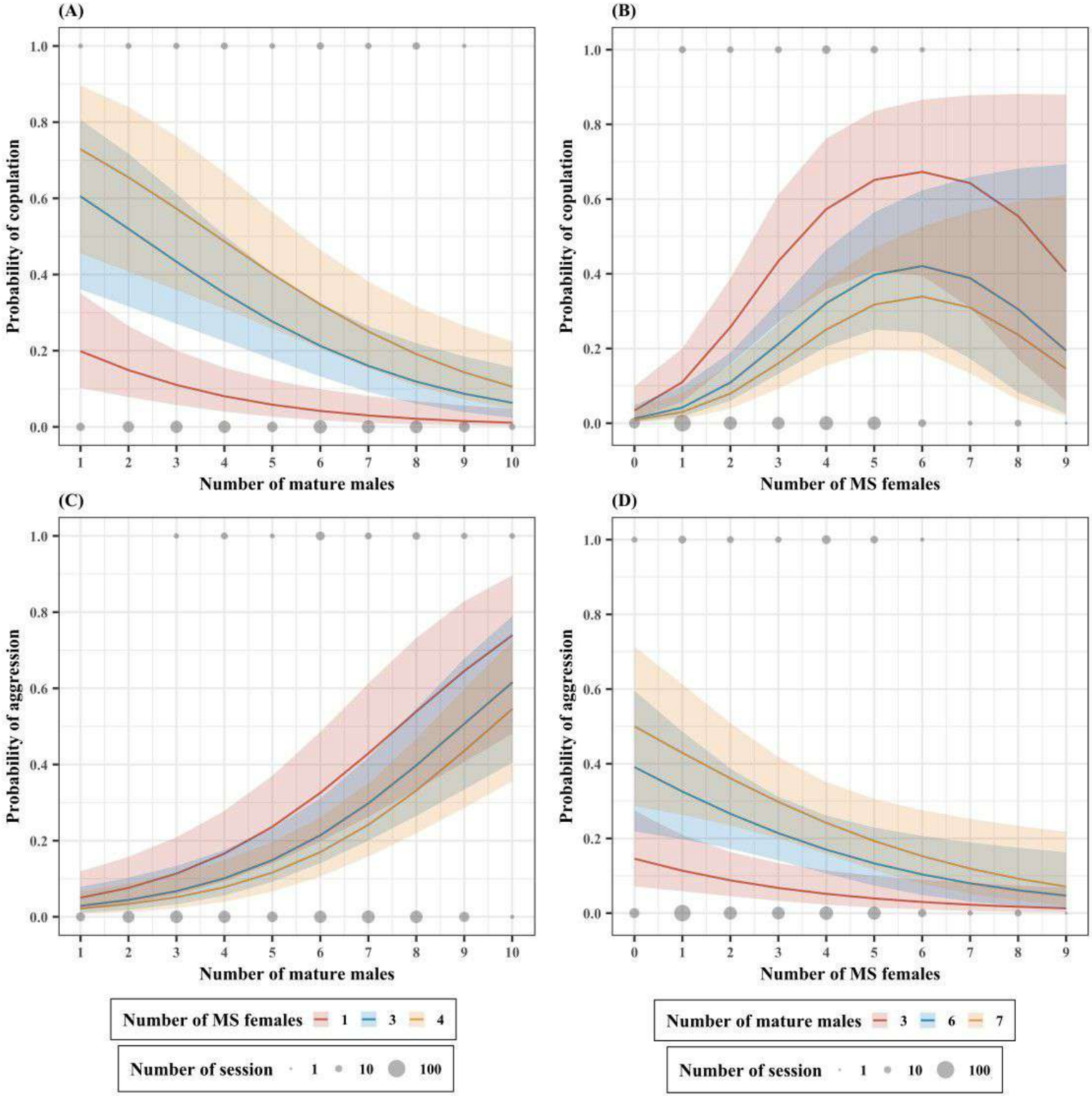
21 **TABLE 2** Parameter estimates from the GLM and GLMMs selected as the best models by AIC

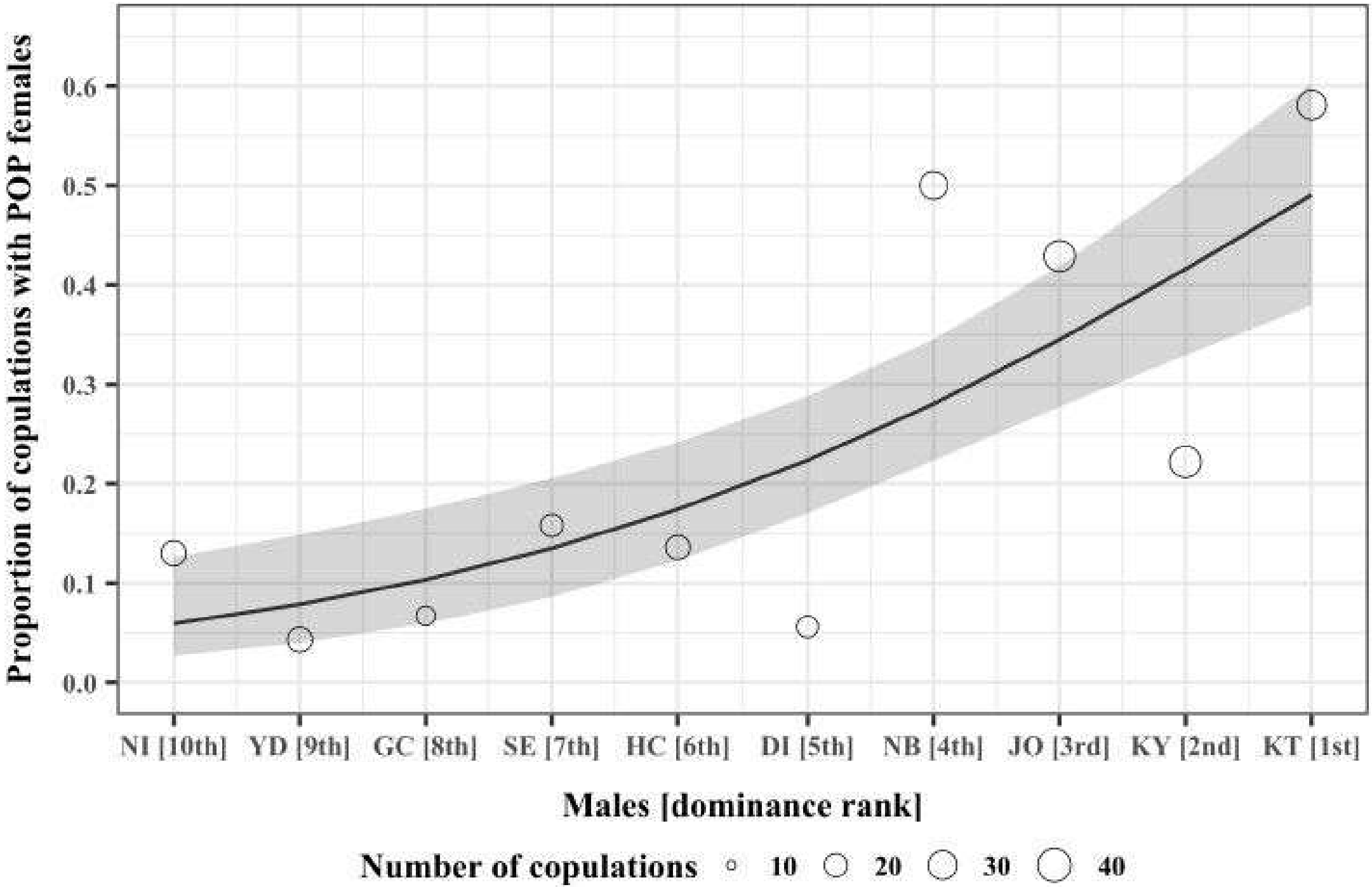
Responses	Predictors	Estimate	SE	Z	*p*-value
(A) Binomial GLM					
Binary data of the proportion whether to copulate with POP or non-POP females	(Intercept)	–1.39	0.19	–7.33	
	Male rank (linear)	0.97	0.19	5.06	< 0.001***
(B) Poisson GLMM 1					
Count data of copulations with adult females for each focal follow	(Intercept)	–2.06	0.23	–8.9	
	Number of MS females (linear)	0.94	0.28	3.34	< 0.001***
	Number of MS females (quadratic)	-0.47	0.23	–2.03	0.043*
(C) Poisson GLMM 2					
Count data of copulations with adolescent females for each focal follow	(Intercept)	–2.06	0.23	–8.9	
(D) Binomial GLMM 1					
Binary data of whether copulation occurred or not per session during focal follow	(Intercept)	–1.16	0.30	–3.87	
	Number of mature males (linear)	–0.83	0.23	–3.68	< 0.001***
	Number of MS females (linear)	1.36	0.30	4.60	< 0.001***
	Number of MS females (quadratic)	–0.44	0.15	–2.92	0.004**
	Presence of POP females (yes/no)	–0.53	0.35	–1.54	0.124
	Resting time (linear)	–0.50	0.21	–2.40	0.017*
	Resting time (quadratic)	–0.45	0.20	–2.28	0.022*
(E) Binomial GLMM 2					
Binary data of whether intermale aggressions occurred or not per session during focal follow	(Intercept)	–1.54	0.29	–5.38	
	Number of mature males (linear)	1.06	0.22	4.74	< 0.001***
	Number of MS females (linear)	–0.56	0.22	–2.58	0.010**
	Resting time (linear)	0.18	0.20	0.90	0.369
	Resing time (quadratic)	–0.61	0.19	–3.24	0.001**

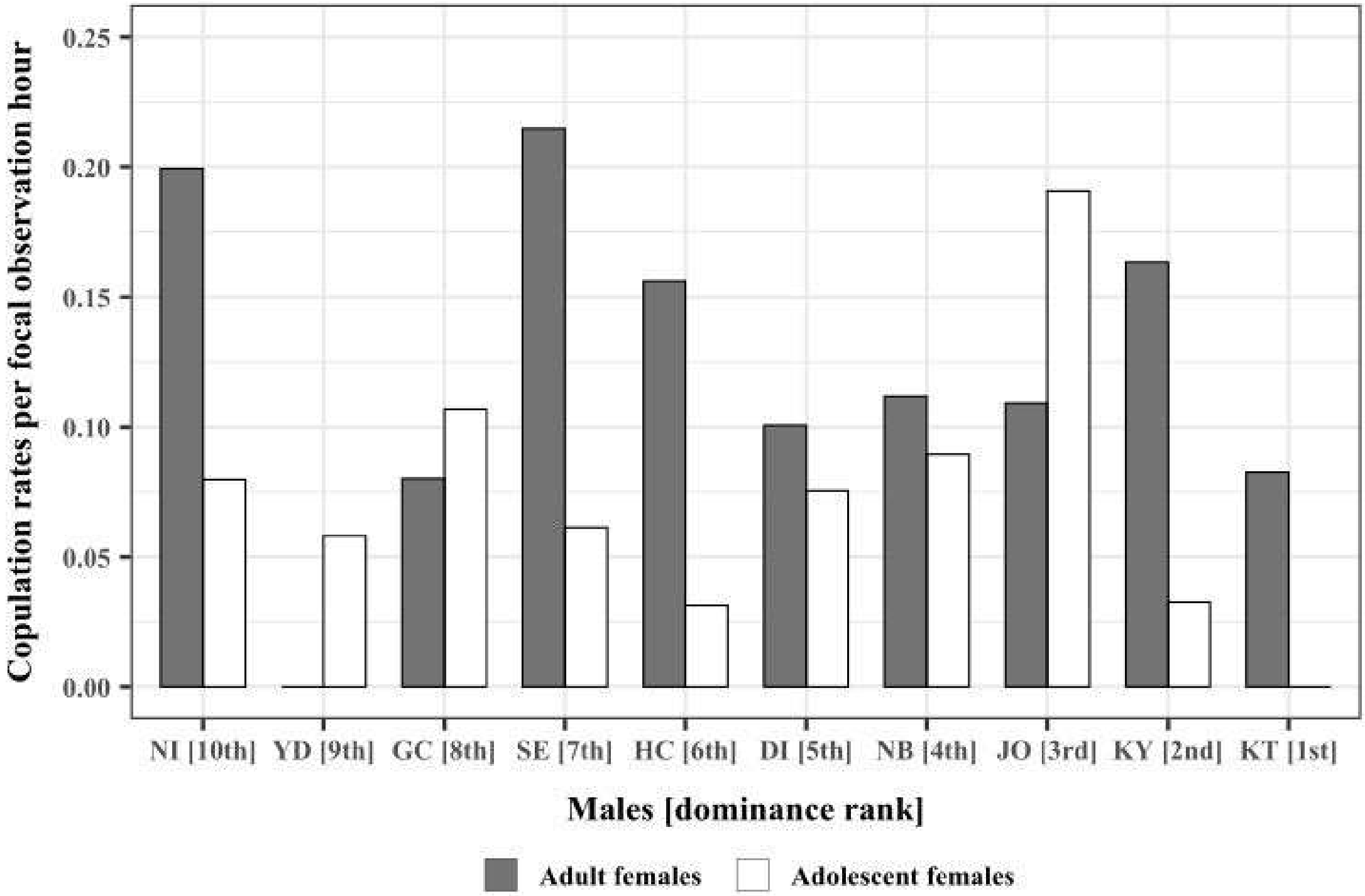
22 Predictors that significantly influence the responses are indicated in bold.

23

24


(A)
(B)
(C)
(D)
Probability of copulation
Probability of aggression
Number of mature males
Number of MS females
Number of MS females 1 3 4
Number of mature males 3 6 7
Number of session 1 10 100


Proportion of copulations with POP females
0.0
0.1
0.2
0.3
0.4
0.5
0.6
NI [10th]
YD [9th]
GC [8th]
SE [7th]
HC [6th]
DI [5th]
NB [4th]
JO [3rd]
KY [2nd]
KT [1st]
Males [dominance rank]
Number of copulations
10
20
30
40


Copulation rates per focal observation hour
0.25
0.20
0.15
0.10
0.05
0.00
NI [10th]
YD [9th]
GC [8th]
SE [7th]
HC [6th]
DI [5th]
NB [4th]
JO [3rd]
KY [2nd]
KT [1st]
Males [dominance rank]
Adult females
Adolescent females