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Female bonobos show social swelling by synchronizing their maximum swelling and increasing bonding

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Different Old World primates show conspicuous anogenital swelling, with the Maximum Swelling Phase (MSP) signaling the ovulatory phase. MSP synchronization between females has been linked to social dynamics. In bonobos, characterized by female dominance, MSP is not a fully reliable signal of fertility because it may cover anovulatory periods. We investigated whether bonobo females synchronized their MSP and whether this phenomenon was modulated by social factors. Data were collected at *La Vallée des Singes* (France). In the period 2009–2022, swelling cycles data were collected daily on bonobo females (N = 9). In the period 2018–2022, ethological data (aggression/affiliation/socio-sexual behaviors) were also collected. We found that: (i) females synchronized their MSP and most likely experienced MSP onset following the MSP onset in other females; (ii) synchronization increased as the years spent together by females increased; (iii) synchronization preferentially occurred between females that affiliated less; (iv) synchronization on the MSP was linked to increased female-female socio-sexual contacts, which probably favored MSP synchronization maintenance. Hence, in bonobos MSP can be modulated by social factors and its synchronization, possibly underlying autonomic contagion, might have been positively selected during evolution in relation to the benefits females obtain in terms of intra-group cohesion.

In several Old World monkey species (catarrhines), females show a conspicuous swelling of the anogenital area (and sometimes other correlated areas) occurring during the ovulatory phase^{1,2}. In baboons^{3–5}, geladas (*Theropithecus gelada*), also showing vesicles on neck and chest⁶, different macaque species⁷, sooty mangabeys (*Cercocebus atys*)⁸, and chimpanzees (*Pan troglodytes*)^{9,10} ovulation occurs within few days before the start of swelling deturgescence (deflation) and the Maximum Swelling Phase (MSP) encompasses ovulation. Hence, the MSP is strictly linked to the ovulatory phase¹¹.

Conspicuous sexual swelling has evolved multiple times in the course of primate evolution¹ and the hypotheses on its functional significance have been mainly focused on the context of sexual selection, with the MSP functioning as a signal increasing intra- and inter- sex competition^{1,12}. Within sexual cycles, the MSP may extend the mating period, promote multiple mating and enhance male-male competition when the ovulation probability is at its highest point (*Graded Signal Hypothesis*)². Across sexual cycles, males may distinguish between conceptive and post-conceptive maximum swellings (e.g., size and turgidity) to detect when a female is actually fertile (*Papio anubis*¹³; chimpanzees¹⁰, *Differentiating Between Cycles Hypothesis*). Finally, males might gain information on mate quality by differentiating females based on their maximum swelling features, although this hypothesis remains controversial (*Signaling Differences Between Individuals Hypothesis*^{12,14,15}). Moreover, by either promoting (via signaling ovulation) or reducing (via mating period prolongation) paternity certainty, swelling might enhance paternal care (*Paternity Care Hypothesis*)¹².

An important element to be added to the previous scenario is that females can undergo MSP (informing estrus) simultaneously or not (synchronous vs asynchronous). Females can increase their mate choice when they undergo synchronous MSP because the monopolization potential of males is reduced¹⁶. Although not common, when present synchrony has been linked with the social dynamics between females. In hamadryads

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(*Papio hamadryas*)—in which a single alpha male exerts a strict control over females within a One Male Units (OMU)—synchronization of MSP might be linked to female-female competition over the limited male sperm¹⁵. In other species, synchronization appears to be related to increased female-female affiliation. In gelada females (*Theropithecus gelada*)—living in OMUs characterized by a high level of tolerance—close reproductive synchrony is associated with female-female highly affiliative relationships, also enhanced by infant handling^{17,18}. Chimpanzee females have been observed to occasionally synchronize their MSP especially in association with social contact¹⁶. In women, menstrual cycle synchronization has been described in certain cohorts but not in others¹⁹. When described, synchronization has been mostly reported between socially bonded females (e.g., room-mates, friends) but not for random female dyads, thus suggesting the social factors may contribute to modulate the ovulatory cycle in *Homo sapiens*²⁰.

The above framework suggests that while MSP is a biological signal mainly directed to males, its synchronization may be influenced by social factors concerning females' relationships. So far, the role that MSP may have in relation to other females has been neglected. The bonobo is an excellent species to investigate this understudied aspect because the MSP shows peculiar features in this species. As it occurs in other primate species, the size and turgidity of female bonobos' anogenital region vary in the course of the ovulatory cycle²¹. Contrary to other species, MSP is not a fully reliable signal of fertility mainly because it can last for a very long period of time (up to 30 days) covering anovulatory periods, such as early adolescence, pregnancy and lactation ("pseudo-estrus"^{22,23}). Moreover, the inter-swelling interval (interval between the last days of successive MSP) does not always reflect the inter-menstrual interval as ovulation occurs during MSP (most frequently;²⁴) but also outside the MSP²⁵.

To our knowledge, no studies have ever been conducted on MSP synchronization in bonobos, although this species shows several features that might favor its presence. Bonobos share with chimpanzees and humans (both possibly showing occasional cycle synchronization,^{16,19,20} the last common ancestor living around 5–8 million years ago²⁶. Chimpanzees and bonobos share a similar social structure (fission–fusion, multi-male/multi-female groups and male philopatry) but bonobos show female dominance (and not male dominance as chimpanzees)²⁷. Bonobo females are highly cohesive and form alliances to support each other not based on kinship (owing to female dispersal from the natal group) (28–30). In bonobo females, the swelling phase can modulate the affiliation preferences of females³¹ and there may be a neurobiological basis for the link between bonobo female sexuality and sociality³². In particular, in bonobos MSP is attractive not only for males, but also for females³³. When in MSP, females receive more affiliation³¹ and engage more in socio-sexual contacts via Genito-Genital Rubbing (GGR;²¹ GGR is a socio-sexual contact during which two females embrace each-other, frequently face to face, and rub their genitals by moving their hips side to side³⁴. With other behaviors (e.g., grooming, sit-in-contact), GGR concurs to establish and maintain social relationships between females^{31,35}.

This long-term study aims at examining for the first time whether bonobo females show MSP synchronization and, if so, whether such synchronization is influenced by social factors (including rank and affiliation). To this purpose we formulated the following prediction and sub-predictions.

As the MSP seems to be used by females as a social passport to establish or reinforce social relationships with other females, we expected that: (i) females would show synchronized MSP (*prediction 1a*) especially in case of long-term permanence in the same group (*prediction 1b*); (ii) a female could most likely show MSP onset after that another female had undergone MSP onset (*prediction 1c*); in the short-term socially distant females needing to strengthen their relationship (low vs high ranking or weakly bonded females) may most likely show MSP synchronization (*prediction 1d*); females synchronized on the MSP may most likely engage in socio-sexual contacts than unsynchronized females (*prediction 1e*).

Methods

Data collection and operational definitions. Data on sexual swelling were gathered in the morning on a daily basis from July 2009 to April 2022 and involved 9 mature bonobo females (Table 1) that were living in a stable social group ranging from 5 to 18 individuals depending on the period (Table 1) housed at *La Vallée des Singes* (Romagne, France).

Trained keepers collected data on sexual swelling, reproductive status of females and possible pharmacological treatments. For each adult female keepers noted sexual swelling changes in size, firmness and coloration following Furuichi's method³⁶. Sexual swelling was coded according to three phases: minimum (1), maximum (3), and intermediate when it could not be categorized as either maximum or minimum (2) (Fig. 1). Hence, intermediate swelling was a non-homogeneous category that encompassed the turgidity and size stages during both increasing and decreasing swelling periods (i.e., from minimum to maximum and vice-versa; stages 2–3 as *per*²³).

A urine-based rapid pregnancy test for women (Clearblue) was carried out once a month on each adult female. Phase 0 indicated the absence of changes in the sexual swelling due to late pregnancy, first part of the lactation period or temporary administration of contraceptive. In total, 28,033 records were collected (mean \pm SE = 3,114.78 \pm 439.43).

For five years, in 2018 (April–May), 2019 (July–August), 2020 (August–September), 2021 (April–June), and 2022 (March–April), we collected behavioral observational data on the group including seven females (all the females from Table 1 except Nakala and Lisala). Because grooming and sit-in-contact between females (affiliation patterns) are particularly frequent behaviors, data on these patterns were collected via 10-min scan sampling³⁷. Affiliation frequencies were calculated as the number of scans in which grooming and sit-in-contact were observed in a given dyad normalized over the number of scans in which both individuals of the dyad were present.

Via all occurrences sampling³⁷ we collected data on genito-genital socio-sexual contacts (GGR; Table S1) and agonistic encounters between females, spanning overt aggression and less intense competitive interactions (e.g., displacements, avoidance, food priority; Table S1). The conflicts were classified as "decided" if a winner

Subject, sex	Observation period ^a	Year of birth	Year of arrival at VDS
Daniela, F	2009/2022	1968	2009
Nakala, F	2014/2017	2008	2014
Lisala, F	2012/2016	1980	2012
Ukela, F	2011/2022	1985	2011
Lucy, F	2012/2022	2003	2012
Ulindi, F	2013/2022	1993	2013
Yahimba, F	2017/2022	2009	2017
Khaya, F	2009/2022	2001	2009
Lingala, F	2011/2022	2003	2011
Kirembo, M	–	1992	2009
David, M	–	2001	2009
Diwani, M	–	1996	2009
Kelele, M	–	2004	2011
Loto, M	–	2009	2013
Luebo, M	–	2006	2012
Bondo, M	–	1991	2012
Moko, M	–	2012	2012
Lokoro, M	–	2015	2015
Khalessi, F	–	2012	2012
Yuli, F	–	2014	2014
Swahili, F	–	2014	2014
Kymia, F	–	2017	2017
Kyara, F	–	2020	2020
Yago, M	–	2021	2021

Table 1. Bonobo females involved in the study and individuals belonging to the *La Vallée des Singes* group.
^aOnly for the females involved in the analyses.

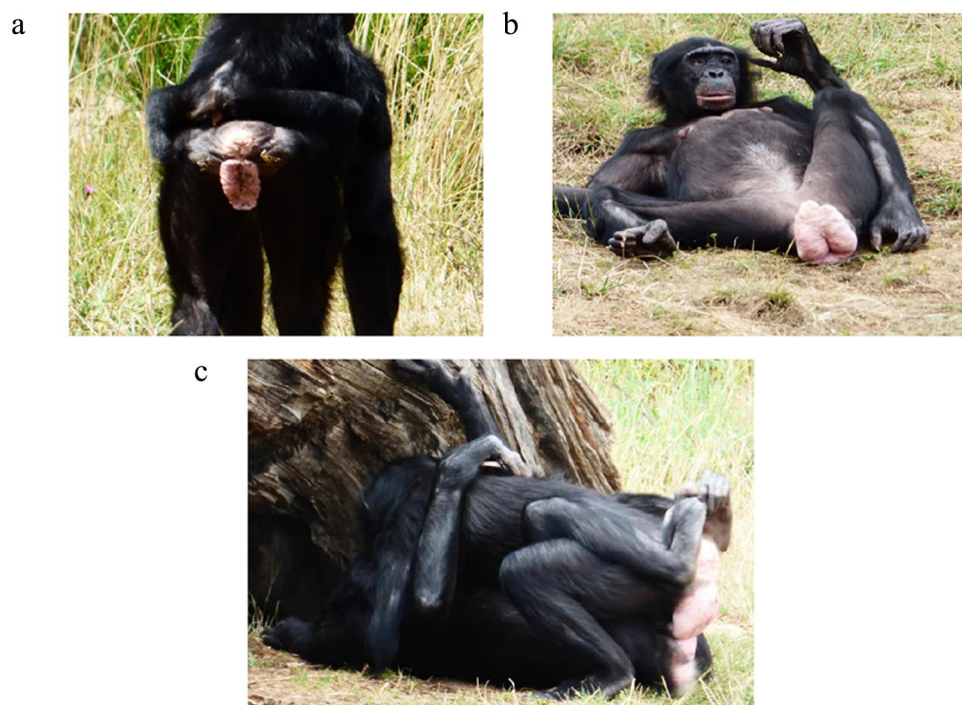


Figure 1. Figure showing: (a) minimum swelling phase; (b) maximum swelling phase; (c) genito-genital rubbing (GGR) between two females in maximum swelling.

and a loser were undoubtedly recognizable and as “undecided” otherwise. Specifically, a subject was labeled as the loser of the aggressive interaction when they fled, screamed, left the food or the place to the other subject, or emitted submissive vocalizations and/or showed submissive facial expressions (Table S1). The frequency of dyadic agonistic interactions was determined as the number of interactions of a given dyads over the observation time of such dyad. Affiliation and agonistic interaction levels were calculated for each data collection period.

Data sort-out and statistical elaboration. We determined the individual ranking position based on decided agonistic interactions (ethogram: Table S1) via Normalized David's Scores (NDS³⁸). NDS were individually determined via an aggression sociomatrix including the frequency of decided agonistic encounters/dyad (R ‘steepness’ package; CRAN.R-project.org/package = steepness). Further details are provided in Appendix S1.

In the subsequent analyses, for each female we excluded the periods when they were in phase 0, under pharmacological treatment, or when their swelling cycle did not show a complete fluctuation (from phase 1 to 3 and vice-versa). Moreover, for the purpose of this study (showing synchronization in the maximum swelling phase), we considered maximum swelling (3) and the minimum (1) as a control condition to make sure that synchronization applied to the maximum swelling phase. Intermediate swelling did not represent a homogenous category, as explained above, so it could not be included in the analysis.

Owing to the small sample size ($N < 10$) not testable for normality ($N_{\text{females}} = 9$), we applied the non-parametric, the Wilcoxon signed-rank test to compare the number of days each female spent in maximum and minimum swelling phase. This analysis was necessary to check whether the possible synchronization on maximum swelling could be byproduct of the fact that females spent more time in maximum than minimum swelling. We used the same test to verify whether the MSP onset in a female could contribute to inducing the MSP onset in another female. In this respect, we compared the frequency of MSP onset of each female between two conditions: (i) when at least another female had previously experienced MSP onset within three days and (ii) in absence of previous MSP onset by other females in the same time window. In both conditions, data were normalized over the total number of opportunities (cases of MSP onset + cases of no MSP onset in the target female). In both conditions, unclear cases (i.e. cases in which other females already showed MSP—but not its onset—or cases in which the MSP of a given female ended right before the three day time window) were excluded from the analysis owing to the impossibility to single out MSP onset (as possible MSP inducer in other females) or (for a female) to undergo MSP onset. Exact probability values were selected following Mundry and Fischer³⁹.

The first Generalized Linear Mixed Model (GLMM₁; $N_{\text{max_min_swelling_days}} = 5256$) was focused on checking whether females showed MSP synchronization. Specifically, via GLMM₁ we verified whether two females would show same swelling phase on the same day (synchronized swelling) and, if so, on what factors could influence swelling synchronization. The daily presence/absence of synchronization between females was selected as binomial, target variable (different/same swelling phase = 0/1). The following fixed factors were included: (i) the age of the two females in every year of data collection (numeric); (ii) daily swelling phase (binomial; 1 = min/3 = max); (iii) years spent by the two females in the study group (numeric). For this analysis we considered the days when females were in minimum or maximum swelling phase and showed a regular swelling cycle (as explained above).

GLMM₂ ($N_{\text{MSP_onset_days}} = 52$) was focused on the social factors possibly leading to MSP synchronization between females in a three-day time window. Specifically, GLMM₂ was run to check whether dominance relationship and affiliation levels between females would elicit swelling synchronization on the MSP. We set the binomial, target variable based on whether the onset of the MSP in one female (hereafter the ‘trigger’) on a given day was followed within three days (or not) by the onset of the MSP in another female (hereafter the ‘follower’). Three days is the periovulatory period and within the range to detect progesterone changes²³.

We included as binomial, fixed factors the dyadic affiliation levels (high: affiliation frequency > median value; low: affiliation frequency ≤ median value) and dominance relationships (trigger rank > follower rank or vice-versa) between female dyads. The reduced dataset available for GLMM₂ is justified by the fact that this analysis (carried out on behavioral data collected over five years) only included the days of the onsets of MSPs and the trigger-follower dyads characterized by females showing regular swelling cycles (as explained above).

GLMM₃ ($N_{\text{dyad_observation_days}} = 153$) was run to check for a possible social function of MSP synchronization. To this purpose via GLMM₃ we verified whether socio-sexual contacts between females were influenced by synchronization on MSP and/or by affiliation levels. The daily presence/absence of socio-sexual contacts was introduced as binomial, target variable. We included as binomial, fixed factors: (i) the dyadic affiliation levels (high: affiliation frequency > median value; low: affiliation frequency ≤ median value) and (ii) whether females were synchronized on the MSP on a given day or not. This analysis was restricted to the days of behavioral observations (indicated above), when females showed minimum or maximum swelling and a regular swelling cycle. In all GLMM_s dyad identity (including both females) and day (Julian date) were included as random factors.

The models were fitted in R (R Core Team, 2018; version 3.5.3⁴⁰) by using the function *glmer* of the R-package *lme4*⁴¹. We first verified if full (all factors) and null model (random factors only) were significantly different⁴² via the likelihood ratio test (ANOVA with argument ‘Chisq’⁴³). Subsequently, by using the R-function “*drop1*”, the p-values for the individual predictors based on likelihood ratio tests between the full and the null model were calculated⁴⁴. As the dependent, response variable was binary, a binomial error distribution was used (link function: logit).

Via the freeware Behatrix 0.9.11⁴⁵ we carried out a sequential analysis to assess the probability of temporal association between the presence of female-female genito-genital socio-sexual contacts on a given day, female-female synchronization or no-synchronization on the MSP on the same day, and female-female synchronization or no-synchronization three days after the socio-sexual contact. We ran a permutation test on behavioral transition counts (‘Run random permutation test’ Behatrix function, 10,000 permutation test). Based on this, we

Predictors	Estimates	SEM	CI ₉₅	Effect size	χ^2	p
GLMM₁	Full vs. null model: $\chi^2 = 202.894$; $df = 4$; $p < 0.001$					
(Intercept) ^a	0.164	0.410	-0.640, 0.969	a	a	a
Females age 1	-0.002	0.010	-0.022, 0.018	0.641	-0.176	0.861
Female age 2	-0.019	0.018	-0.055, 0.016	0.681	-1.068	0.285
Swelling (max) ^b	1.006	0.076	0.858, 1.155	0.734	13.249	<0.001
Years together	0.072	0.026	0.021, 0.124	0.733	2.767	0.006
GLMM₂	Full vs. null model: $\chi^2 = 7.683$; $df = 2$; $p = 0.021$					
(Intercept) ^a	0.476	0.914	-1.315, 2.268	a	a	a
Dominance relationship (trigger rank > follower rank) ^b	0.147	0.870	-1.558, 1.852	0.371	0.169	0.866
Affiliation level (high) ^b	-2.496	1.088	-4.627, -0.364	0.635	-2.295	0.022
GLMM₃	Full vs. null model: $\chi^2 = 8.944$; $df = 2$; $p = 0.011$					
(Intercept) ^a	-6.122	2.493	-11.009, -1.235	a	a	a
Swelling phase (sync on MSP) ^b	2.598	1.318	0.015, 5.181	0.102	1.972	0.049
Affiliation level (strong) ^b	3.077	2.559	-1.938, 0.093	0.127	1.203	0.229

Table 2. Full results of GLMM₁ on factors that could influence swelling synchronization ($N_{\text{cases}} = 5256$); GLMM₂ on factors that could elicit swelling synchronization on MSP ($N_{\text{cases}} = 52$); and GLMM₃ to check if females socio-sexual contacts were influenced by synchronization on MSP and/or by affiliation levels ($N = 153$). For all models dyad identity and Julian date were included as random factors. Significant values are in bold.

^aNot shown as not having a meaningful interpretation. ^bThese predictors were dummy-coded, with the reference category as follow: swelling: “min”; dominance relationship: “trigger rank < follower rank”; affiliation level: “low”; swelling phase: “no sync on MSP”.

generated a flow diagram of behavior-to-behavior significant and non-significant transitions. For all the analyses the threshold of probability significance was set at $\alpha = 0.05$.

Results

As a preliminary analysis, we verified that there was no significant difference in number of days that females spent in minimum or maximum swelling phase (Exact Wilcoxon's sign-rank test: $N_{\text{female}} = 9$, $T = 16.00$, $z = -0.770$, $p = 0.496$).

GLMM₁ (target variable: daily presence/absence of swelling synchronization) including all fixed factors (female age, swelling phase, and years spent together) significantly differed from the null model (likelihood ratio test: $\chi^2 = 202.894$, $df = 4$, $p < 0.001$). Hence, the variance explained by the test predictors as a collective was significantly different from the variance explained by the variables in the null model. To be able to interpret the effect of individual predictors rather than their combined effect on the response we moved on with the ‘drop1’ procedure. We found that the swelling phase had a significant effect on swelling synchronization ($p < 0.001$), with females being most frequently synchronized when in the Maximum Swelling Phase (MSP; Table 2; Fig. 2a). Moreover, the years spent together in the same group influenced synchronization ($p = 0.006$), which increased as the number of years increased (Table 2; Fig. 2b). Age had no significant effect (Table 2). Hence, swelling synchronization between bonobo females was enhanced by MSP and long-term permanence in the same group.

We found that it was more likely that a female experienced the onset of MSP within three days after the MSP onset in at least another female than when no MSP onset in other females occurred (Exact Wilcoxon's sign-rank test: $N_{\text{female}} = 9$, $T = 5.00$, $z = -2.073$, $p = 0.039$; Fig. 3). Hence, the onset of MSP in a female probably concurred in eliciting MSP onset in other females.

GLMM₂ (target variable: the onset of a female's MSP followed within three days or not the onset of another female's MSP) including all fixed factors (dominance relationship and affiliation level) significantly differed from the null model (likelihood ratio test: $\chi^2 = 7.683$, $df = 2$, $p = 0.021$). Thus, we moved on with a drop1 procedure. We found that only the affiliation level had a significant effect on the probability that the onset of a female's MSP followed within three the onset of another female's MSP ($p = 0.022$), with weakly bonded females following each other more frequently than strongly bonded females (Table 2; Figs. 4a, 5). The dominance relationship had no significant effect. Hence, social proximity enhanced MSP synchronization.

GLMM₃ (target variable: daily presence/absence of genito-genital socio-sexual contacts) including all fixed factors (synchronization or not on the MSP and affiliation level) significantly differed from the null model (likelihood ratio test: $\chi^2 = 8.944$, $df = 2$, $p = 0.011$). We found that MSP synchronization, but not affiliation levels, had a positive, significant effect on the presence of genito-genital socio-sexual contacts between females ($p = 0.049$) (Table 2; Fig. 4b). Thus, MSP synchronization (rather than affiliation per se) appears to function as an enhancer of geno-genital contacts.

The behavioral sequence analysis showed significant temporal transitions from the presence of socio-sexual contacts to MSP synchronization ($p < 0.001$) and vice-versa ($p < 0.001$). A significant transition was also found from synchronization to no-synchronization on MSP in absence of genito-genital socio-sexual contacts ($p = 0.002$). The transitions from no-synchronization to synchronization on MSP in absence of socio-sexual contacts was not significant ($p = 0.998$), as it was not significant the transition from the presence of socio-sexual contacts to no-synchronization on MSP ($p = 0.492$) and vice-versa ($p = 0.487$) (Fig. 6).

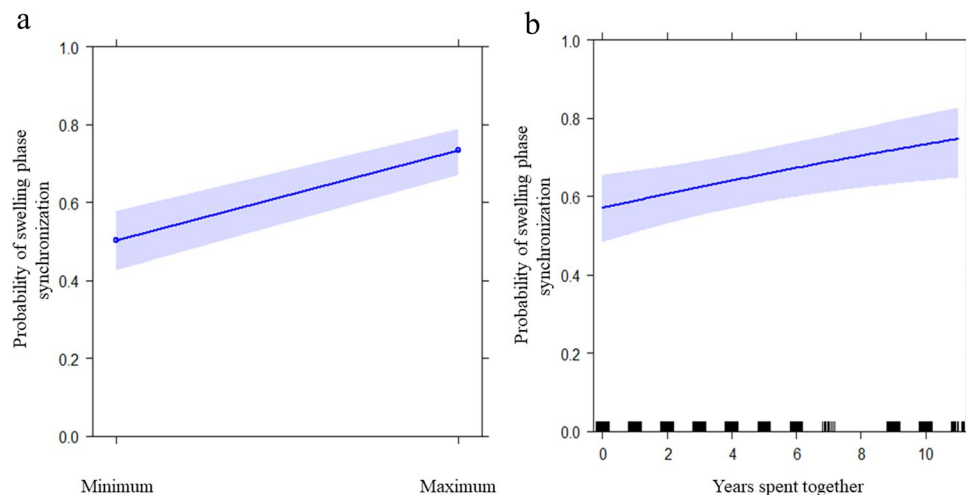


Figure 2. Effect plot of the variables having a significant influence on the swelling synchronization in GLMM₁ (a,b; Table 2). (a) The probability of swelling phase synchronization (Y axis) was higher in maximum swelling phase (MSP) than in the minimum swelling phase (X axis); (b) the probability of swelling phase synchronization (Y axis) increased as the number of years spent together increased (X axis).

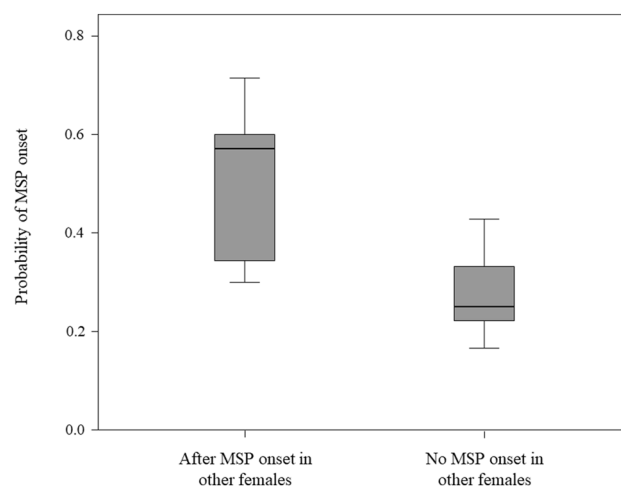


Figure 3. Box plot shows that females were most likely to experience MSP onset after that another female had experienced MSP onset in a three-day time window. Solid horizontal lines: medians; box length: interquartile range; thin horizontal lines: value range.

Ethics approval. This study was purely observational and did not require any animal manipulation or disturbance. Thus, no ethical approval was necessary according to the current regulation.

Discussion

Our results show that in our study group: (i) bonobo females synchronized on their Maximum Swelling Phase (MSP; prediction 1a supported; Table 2; Fig. 2a), especially if they stayed long-term in the same group (prediction 1b supported; Table 2; Fig. 2b); (ii) females were more likely to experience MSP onset after that at least another female had undergone MSP onset in the three previous days than when no other female had experienced MSP onset (Fig. 3; prediction 1c supported); (iii) in the short term, synchronization preferentially occurred between females that affiliated less, with no significant effect of rank (prediction 1d partially supported; Table 2; Fig. 4a); (iv) MSP synchronization was linked to increased frequency of genito-genital socio-sexual contacts between females (prediction 1e supported; Table 2; Fig. 4b), with socio-sexual interactions probably exercising a positive feedback in the maintenance of MSP synchronization (Fig. 5).

The bonobo females of our study group synchronized on their MSP (Table 2; Fig. 2a), which suggests that swelling may be at least in part under the influence of social factors, and not just under the hormonal control related to ovulation. The fact that bonobo females synchronized significantly on the maximum rather than on the minimum swelling phase, despite these two phases showing similar duration, suggests that synchronization

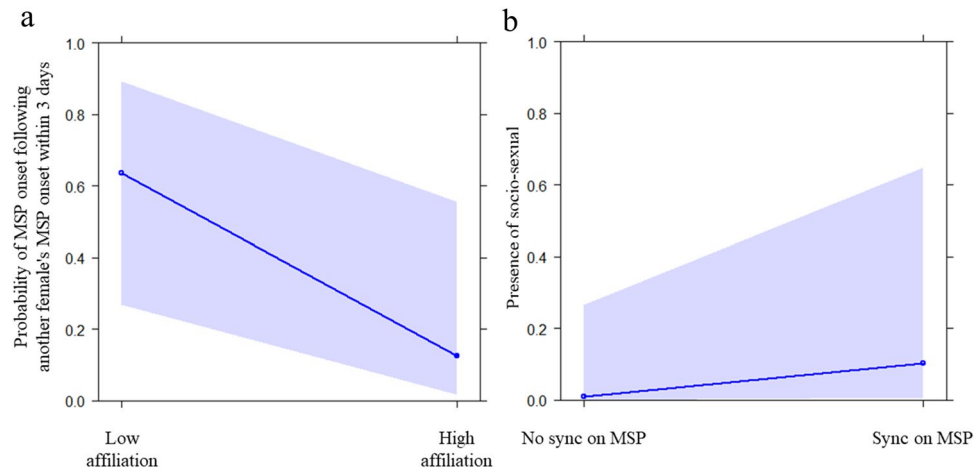


Figure 4. Effect plot of the variables having a significant influence on the occurrence of socio-sexual contacts in GLMM₂ and GLMM₃ (a,b; Table 2). (a) The probability of the MSP onset following another female's MPS onset within three days (Y axis) was highest between females with low affiliation levels (X axis); (b) the occurrence of socio-sexual contacts between females (Y axis) increased when females were synchronized on MSP (Y axis).

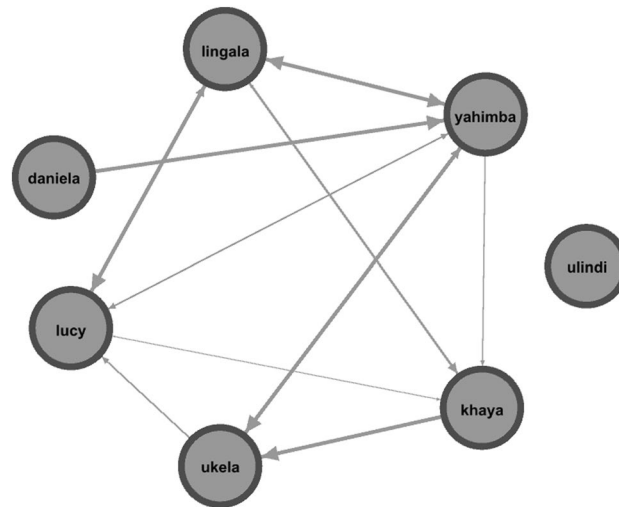


Figure 5. Swelling synchronisation network based on 5 years of data (2018–2022) obtained via freeware Gephi 0.9.7. The nodes are females (grey round circles), and edges show synchronization between females on the maximum swelling phase. In particular, directional edges go from the synchronizing female (follower) to the female eliciting synchronization (trigger). Synchronization occurred within 3 days.

may not simply be an artifact of prolonged MSP in bonobos. During evolution, MSP in primates with conspicuous swelling may have emerged as a signal to males¹² but might have been then co-opted as a signal to females inducing synchronization. Synchronization can be advantageous and therefore adaptive to females under different circumstances, such as when it is beneficial to reduce male monopolization potential, gain access to limited male sperm, or increase female-female affiliation^{15,16,18}. Indeed, reproductive synchronization may not be less important as a female mating strategy in bonobos as in chimpanzees or hamadryas baboons, due to the lack of infanticide risk. MSP synchronization may have been co-opted as a social strategy in bonobos (possibly in both intra-sexual and inter-sexual contexts), for example to gain dominance over males⁴⁶.

Our results show that females are most likely to experience MSP onset after that another female had experienced MSP onset (Fig. 3), thus suggesting that the MSP onset in one female may contribute to inducing MSP onset in others. Although cycle synchronization may be mediated by chemical signals, social contacts or environmental factors^{23,28,47}, our result suggests that synchronization might fall within the domain of autonomic contagion. Automatic synchronization (motor or autonomic) via contagion may occur when a subject perceives a change in the internal state in another subject (e.g., informed by visual and olfactory cues) and—by activating shared neural representations and related endocrinological processes—replicates a similar state (extended *Perception–Action Mechanism*^{48,49}). This phenomenon can occur over different time scales, depending on what

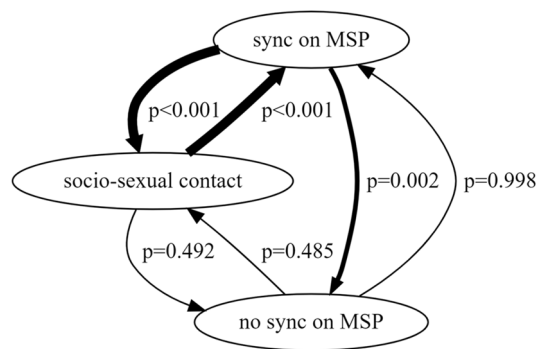


Figure 6. The flow diagram—generated by Behatrix 0.9.11—representing the transitions and their probability between synchronization and no-synchronization on MSP and socio-sexual contacts. Thick arrows indicate significant transitions (socio-sexual contacts → synchronization on MSP: $p < 0.001$; synchronization on MSP → socio-sexual contacts: $p < 0.001$; synchronization on MSP → no-synchronization on MSP: $p = 0.002$).

is replicated (e.g., pupil size mimicry occurs within 1 s and yawn contagion can occur within minutes^{48,50}). Interestingly, it has been observed in the same bonobo group that the swelling cycle in females can promote yawn contagion, associated with inter-individual coordination⁵¹. In humans, apes and other mammalian species synchronization phenomena such as automatic mimicry or yawn contagion may be socially modulated (e.g., increasing in strongly bonded individuals or in-group members), although modulation may not occur in all cohorts and may not always follow the same trend^{48,50–58}.

In primates, sexual cycle synchronization has been related to either female-female competition¹⁵ or affiliative social contacts^{16,18}. Because in bonobos the MSP is prolonged, females are dominant and males cannot monopolize females for mating²³, it is very unlikely that MSP synchronization is associated with female-female competition over resources (limited sperm availability). Our results suggest that long-term bonding more than short-term affiliation exchange may be effective in favoring synchronization, possibly because MSP synchronization represents a social passport that increases the opportunity to positively interact with other females. In the long-term, the females that had spent more years in the same group synchronized most frequently on their MSP (Table 2, Fig. 2b) whereas in the short term bonobo females that affiliated less were most likely to synchronize with each other on the MSP (Table 2; Fig. 4a) possibly because they needed to establish and reinforce relationship within their social group. These females can also have more conflicts and—therefore—an increased necessity of regulating social tension and reconcile conflicts, e.g., via socio-sexual contacts.

Indeed, MSP synchronization was associated with highest rate of genito-genital socio-sexual contacts (Table 2; Fig. 4b) which is in line with previous studies showing that females engage more in socio-sexual contacts via GGR when in the MSP^{21,59} and may receive more affiliation in general^{31,33}. Moreover, it has been recently shown that GGR plays a fundamental role in promoting the high levels of female cooperation among female bonobos as this behavior stimulates the release of oxytocin³². Although not frequently observed, GGR between females can also occur in chimpanzees where it has been associated with increased affiliation^{60,61}. In our case, socio-sexual contacts seem to promote MSP synchronization more than the other way around. The temporal analysis (Fig. 5) showed that MSP synchronization was preceded and followed by socio-sexual contacts in a significant amount of transitions (positive feedback allowing the maintenance of synchronization) but synchronization is not observed in absence of socio-sexual contacts (with MSP synchronization being temporally followed by a lack of synchronization). Indeed, autonomic synchronization can enhance inter-individual cohesion^{48,49} and in bonobos, MSP synchronization may be another way to reinforce social connections and alliances between females.

In conclusion, our study shows for the first time that bonobo females can synchronize their MSP, and that synchronization can be affected by social factors and might promote cohesion. Within extant Hominini, sexual cycle synchronization has been occasionally observed in chimpanzee females¹⁶ and—with respect to the ovulatory cycle (without swelling)—may be possibly present at least in certain cohorts of women (e.g.,²⁰). Hence, a parsimonious scenario is that the potential for synchronization was present in the last common ancestor between bipedal hominins and the *Pan* genus (and even before, if we consider African monkeys showing synchronization)^{15,18}. However, synchronization may have been especially enhanced in bonobo where female social relationships are a prominent feature in the society. A broader implication of this study is that MSP synchronization might to a certain extent underlie autonomic contagion and might have been positively selected over the course of evolution in relation to the benefits that females obtain in term of cohesion, alliances and intra-group dynamics.

Data availability

The raw data supporting results and conclusion of this article are provided as supporting material to the article.

Received: 25 May 2022; Accepted: 12 October 2022

Published online: 21 October 2022

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Acknowledgements

The authors wish to thank Lolita Bertrand, Marielle Brun, Jeremy Mergault for taking care of bonobos and assisting during data collection. Clara Mazzanti, Laura Vannini, Vittorio Sordella for helping with data entering. Anita Genovese, Emilio Russo, Gabriele De Meo, Alessandro Gallo, Giada Sangiovanni for field assistance in the different years of data collection.

Author contributions

E.D. and I.N.: conceived the manuscript. I.N., M.C., E.D.: wrote the manuscript. C.M., F.A., M.C., E.D.: collected data. I.N., M.C. and E.D.: entered and sorted out data. I.N. and M.C.: analysed data. E.D.: field's assistance training for data collection. J.-P.G.: provided access to resources and facilities. All authors: revised the manuscript.

Funding

This study was funded to Ivan Norscia by Università degli Studi di Torino (Grant No. NORI_RILO_21_01). Elisa Demuru has received financial support from the LabEX ASLAN – Advanced Studies on LAnguage complexity (ANR-10-LABX-0081) and from the IDEXLYON (ANR-16-IDEX-005 and ANR-11-IDEX-0007) of the University of Lyon.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-022-22325-7>.

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