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Communication during sex among female bonobos: effects of dominance, solicitation and audience

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Bonobo females frequently form close bonds, which give them social power over other group members. One potential mechanism to facilitate female bonding is the performance of sexual interactions. Using naturalistic observations and experiments, we found various patterns that determined female-female sexual interactions. First, while low-ranked females interacted with all females, sexual interactions between high-ranked females were rare. Second, during genital contacts, females sometimes produced ‘copulation calls’, which were significantly affected by the rank of the caller and partner, as well as the solicitation direction. Third, there was a significant effect of the alpha female as a bystander, while variables relating to physical experience had no effects. Overall, results highlight the importance of sexual interactions for bonobo female social relations. Copulation calls are an important tool during this process, suggesting that they have become ritualised, beyond their reproductive function, to serve as broader social signals in flexible and potentially strategic ways.

In most Old World primates, females remain in their natal groups whilst the males emigrate in early adulthood¹. As a consequence, females form kin-based matrilineal groups that are often characterised by strong affiliative bonds^{2,3}. Although female migration occurs in some species^{4,5}, this usually leads to weak social bonds between females, presumably because of the lack of kin relations (e.g. *Pan troglodytes*⁶, but see⁷). Female migration has also been linked to despotic social systems and high rates of infanticide. Perhaps as a consequence, females tend to form small family units and generally avoid contact with other group members^{8–10}. Bonobos (*Pan paniscus*) are a noteworthy exception from this general pattern. As in chimpanzees, bonobo females migrate from their natal groups, typically around sexual maturity¹¹, but in contrast to other female-migrating primates, they form enduring affiliations with unrelated females in their new groups^{11–15}. These social bonds provide females with well-documented benefits in terms of resource defence, infanticide avoidance and dominance over males^{15–19}.

A number of behavioural mechanisms have been suggested to underlie the formation and maintenance of female-female bonds in bonobos, such as grooming behaviour, adult play and food sharing^{17,20–22}. In addition, bonobo females engage in habitual genital contacts with each other, a behaviour that appears to facilitate peaceful co-existence and the formation of social bonds^{12,23–25}. Although homosexual genital contacts have been observed in all great apes (*Gorilla gorilla*²⁶; *Pan troglodytes*²⁷; *Pongo pygmaeus*²⁸), female bonobos make particularly strong and habitual use of them, both in the wild and in captivity^{24,25,29,30}. Female genital contacts occur during face-to-face embraces, whilst both participants mutually swing their hips laterally and keep their vulvae in contact²³. Though genital contacts are thought to have numerous social functions^{25,29–30}, they appear to have particular relevance for newly arriving immigrant females, who use sexual interactions to facilitate integration and the formation of bonds with non-related residents^{13,31}.

Although genital contacts clearly have considerable social relevance, assessing the underlying psychological processes has remained a challenge. Here, we examine the communicative signals produced during such interactions, an approach that has proved particularly fruitful in investigating social cognition in other animal species³². During genital contacts, female bonobos sometimes produce individually distinct vocalisations, copulation calls, which have been shown to share the same acoustic structure as those made when copulating with males^{24,33}. Furthermore, although females were more likely to call with male partners, patterns of call usage between homo- and heterosexual contexts were very similar, with females calling more with high-ranked partners, regardless of the partner’s sex³⁴. Moreover, copulation calls were consistently produced only by the lower ranking of the two partners, showing that call production cannot be explained by physical stimulation alone. The



fact that copulation calls given during reproductive and non-reproductive sexual encounters share the same acoustic structure³³ and are used in social interactions indicates that these vocalisations serve a function beyond directly promoting reproductive success.

We reasoned that if sexual interactions were part of a social strategy to affiliate with other females and functioned to develop social bonds then low-ranked females should engage in and solicit more sexual interactions compared to high-ranked females. Moreover, they should seek out and prefer high-ranked and socially established females compared to other females³⁰. If sexual interactions were driven by such social motivations, we expected females to advertise socially important sexual interactions with vocal signals. Particularly relevant are cases where a low-ranked female was invited by a high-ranked female to have sex, especially if this happened in the presence of other socially important group members.

To address these points, we explored the effects of a number of social variables of sexual behaviour and call production, namely the social status of callers and their partners, the identity of the soliciting individuals, the composition of the audience, as well as two potentially relevant physical variables; the spatial position of caller and the overall duration of the interaction. We included the physical variables to address the more general hypothesis that call production during genital contacts is sufficiently explained in terms of the physical stimulation experienced by the caller.

Results

(A) Natural Interactions. Sexual behaviour. Overall, we observed $N = 674$ genital contacts between females, with every female ($N = 14$) engaging in at least one sexual interaction with two or more partners. Controlled for group size and observation time, the highest rates of genital contacts occurred in Group 2 (N genital contacts per female per hour: Group 2 = 0.12; Group 1a = 0.09; Group 1b = 0.06). A relevant point here is that, prior to this study, group 2 experienced a

greater amount of social instability than group 1 (see supplementary information).

The majority of genital contacts occurred between low-ranking females, while interactions between two high-ranked females were rare (low-low: 58%, $N = 390$; low-high: 39%, $N = 264$; high-high: 3%; $N = 20$). Both high- and low-ranking females had more sexual interactions with low- compared to high-ranking partners (mean % interactions: high with low-rank partners = 86% vs. high with other high-ranked partners = 13%; randomization test for two paired samples: $t = 10.11$, $N = 6$, $P < .001$; low with low-ranked partners = 73% vs. low with high-ranked partners = 27%; randomization test for two paired samples: $t = 10.421$, $N = 8$, $P = .0082$). When controlling for the number of possible dyads (low-low: $N = 17$; high-high: $N = 9$; low-high: $N = 32$ dyads), sexual interactions between low-ranked females still occurred significantly more often than expected, while sexual interactions between asymmetric and high-ranked dyads occurred less frequently than expected (goodness of fit test: $G_2 = 283.464$, $df = 2$, $P < .001$; fig. 1).

There was no significant effect of spatial position (top or bottom) of low-ranked females ($N = 8$) compared to high-ranked females ($N = 6$) during sexual interactions (randomization test for two independent samples: $t = -.884$, $N_1 = 8$, $N_2 = 6$, $P > .05$, table S1). However, in asymmetric dyads, high-ranked females showed significant individual positional preferences (i.e. they were consistently either on top or bottom, regardless of partner identity) but there was no overall trend for high-ranking females to occupy the top position ($z = -0.943$, $N = 6$, $p > .05$, fig. S1).

There were significant rank effects relating to direction of solicitation, with low-ranked females significantly more likely to be targeted for sexual contacts by high-ranked females than vice-versa ($X_{\text{high-rank female initiates}} + SD = 6.50 + 2.86$ vs. $X_{\text{low-rank female initiates}} + SD = 1.75 + 2.86$; randomization test for two paired samples: $t = -2.586$, $N = 8$, $P = .044$). No differences were found in dyads composed of either two low-ranked or two high-ranked females. In

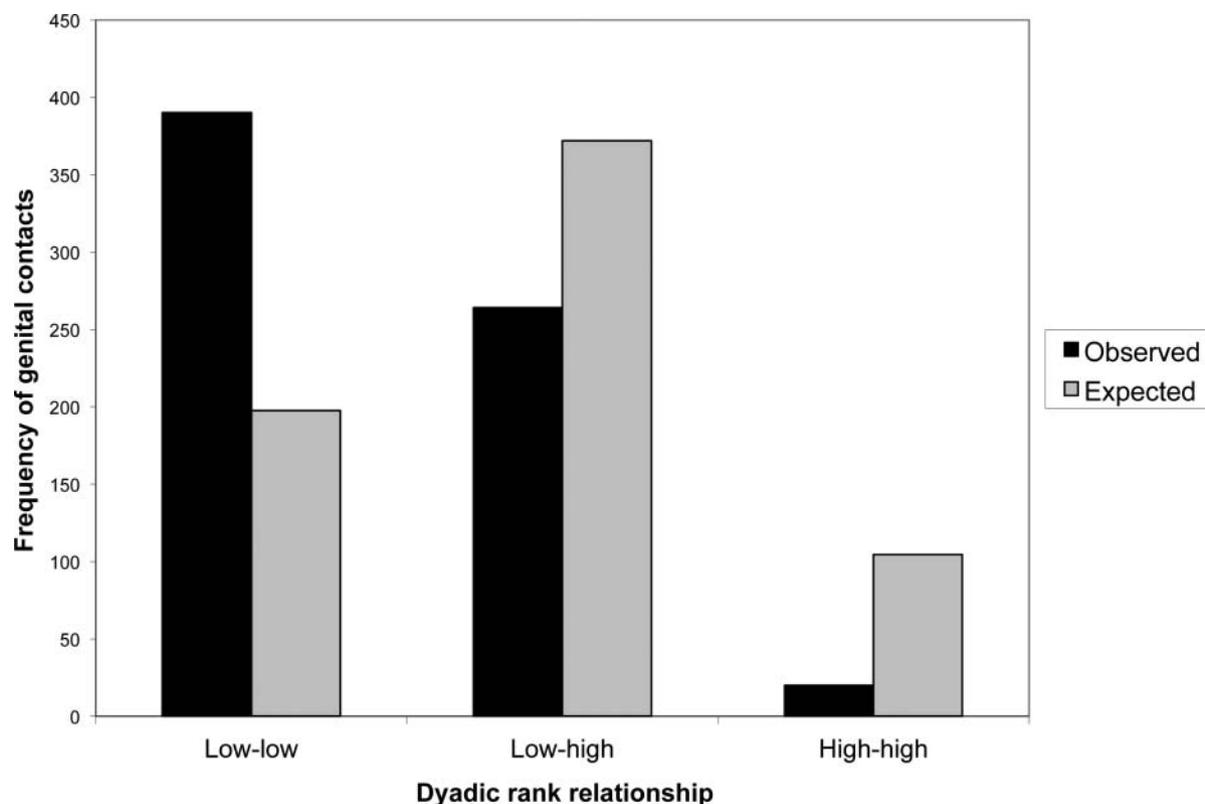


Figure 1 | Frequency of genital contacts between: (1) two low-ranked females ($N = 17$ dyads); (2) asymmetric dyads of a low- with a high-ranked female ($N = 32$ dyads); (3) two-high ranked females ($N = 9$ dyads).



other words, within the low-ranking and high-ranking dyads, the higher ranking partner was not more likely to solicit sex compared to the lower-ranking partner (low-ranked: $X_{\text{higher-rank female initiates}} + \text{SD} = 9.29 + 8.93$ vs. $X_{\text{lower-rank female initiates}} + \text{SD} = 13.65 + 14.64$; randomization test for two paired samples: $t = 1.276$, $N = 6$, $P > .05$; high-ranked: $X_{\text{higher-rank female initiates}} + \text{SD} = 1.44 + 3.97$ vs. $X_{\text{lower-rank female initiates}} + \text{SD} = 0.78 + 1.71$; randomization test for two paired samples: $t = -1.03$, $N = 4$, $P > .05$).

Copulation call production. Copulation calls were only given in a minority of sexual interactions (overall $N = 124/674$ interactions, 18.4%: Group 1a: 12.7%, $N = 424$; Group 1b: 17.9%, $N = 151$; Group 2: 43.4%, $N = 99$).

There was a significant negative correlation between female rank and call production (Spearman's $\rho_s = -0.662$, $N = 14$, $P = .010$; fig. 2), indicating that lower-ranking females were more likely to call than higher-ranked females. In our analyses, all low-ranked females produced copulation calls, suggesting that our results are representative of female copulation calling behaviour more generally. However, we found that spatial position had no effect on call production ($X + \text{SD}$ for N of calls in top position, $N_{\text{females}} = 12$: 5.25 ± 4.43 SD; $X + \text{SD}$ bottom position = 4.41 ± 4.94 ; randomization test for two paired samples: $t = -.637$, $N = 12$, $P > .05$).

Although copulation calling was generally rare, rates were highly dependent on the rank of the female partner with a tenfold increase with high-ranked partners³³. As with genital contacts, the highest calling rates occurred in Group 2 (N genital contacts with calls per

female per hour: Group 2 = 0.05 calls per hour; Groups 1a and 1b = 0.01 calls per hour).

Results from a two-way ANOVA revealed that the direction of initiation (initiate vs. target) and the partner rank (high vs. low) both had significant effects on a female's likelihood to call (Initiation: $F_{1,8} = 6.064$, $P = .039$; partner rank: $F_{1,8} = 27.293$, $P = .001$). Although the interaction of the two terms failed to reach significance ($F_{1,8} = 4.619$, $P = .064$; ANOVA), the effect was strongest for high-ranked partners, with females calling more when were targeted by a high-ranked female compared to when they initiated the interaction (fig. 3).

Audience effects. Group size had no significant effect on call production (overall group size: $t_5 = 2.050$, $P > .05$; N females, $t_5 = 0.819$, $P > .05$; N males, $t_5 = 2.341$, $P > .05$; paired t-tests). However, there was a strong effect of the alpha female with females being significantly more likely to call in her presence than absence ($t_5 = 4.931$, $P = .005$; paired t-test on proportion of events with calls when she was present/absent; fig. 4). The presence of other dominant females, subordinate females or the alpha male had no significant effect (dominant females: $t_5 = -0.46$, $P > .05$; subordinate females: $t_5 = 2.140$, $P > .05$; alpha male: $t_5 = 0.617$, $P > .05$; paired t-tests; table 1). Results from a Generalized Linear Model (binomial-logit) with calling (call versus no call) as the binomial dependent variable revealed that alpha female presence was the only audience-related variable that contributed significantly to the model (alpha female presence: Wald $\chi^2 = 4.579$, $df = 1$, $P = .032$). All other audience related variables were non-significant (all: $P > .05$).

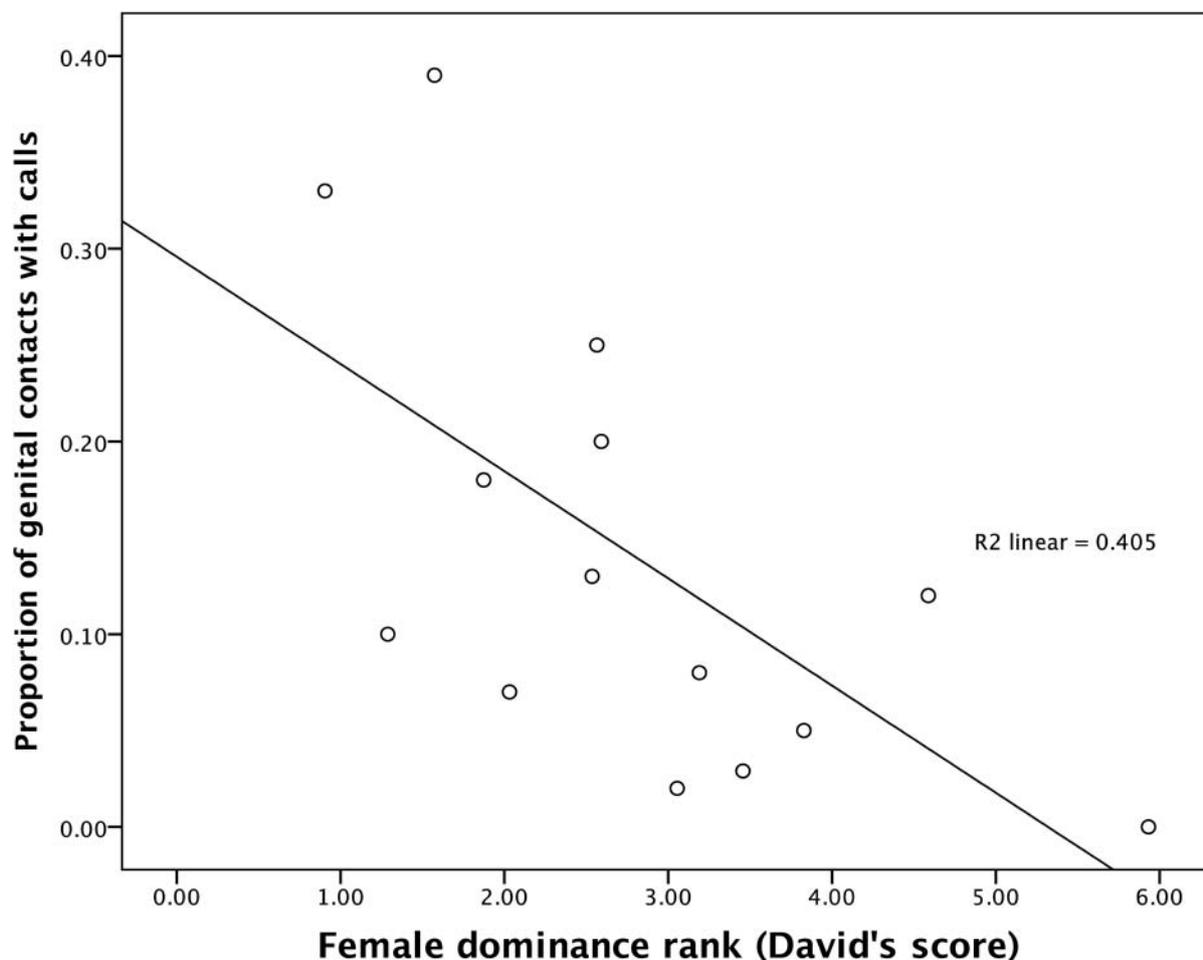


Figure 2 | Scatter-plot showing the relationship between a female's dominance rank and copulation call production during female genital contacts.

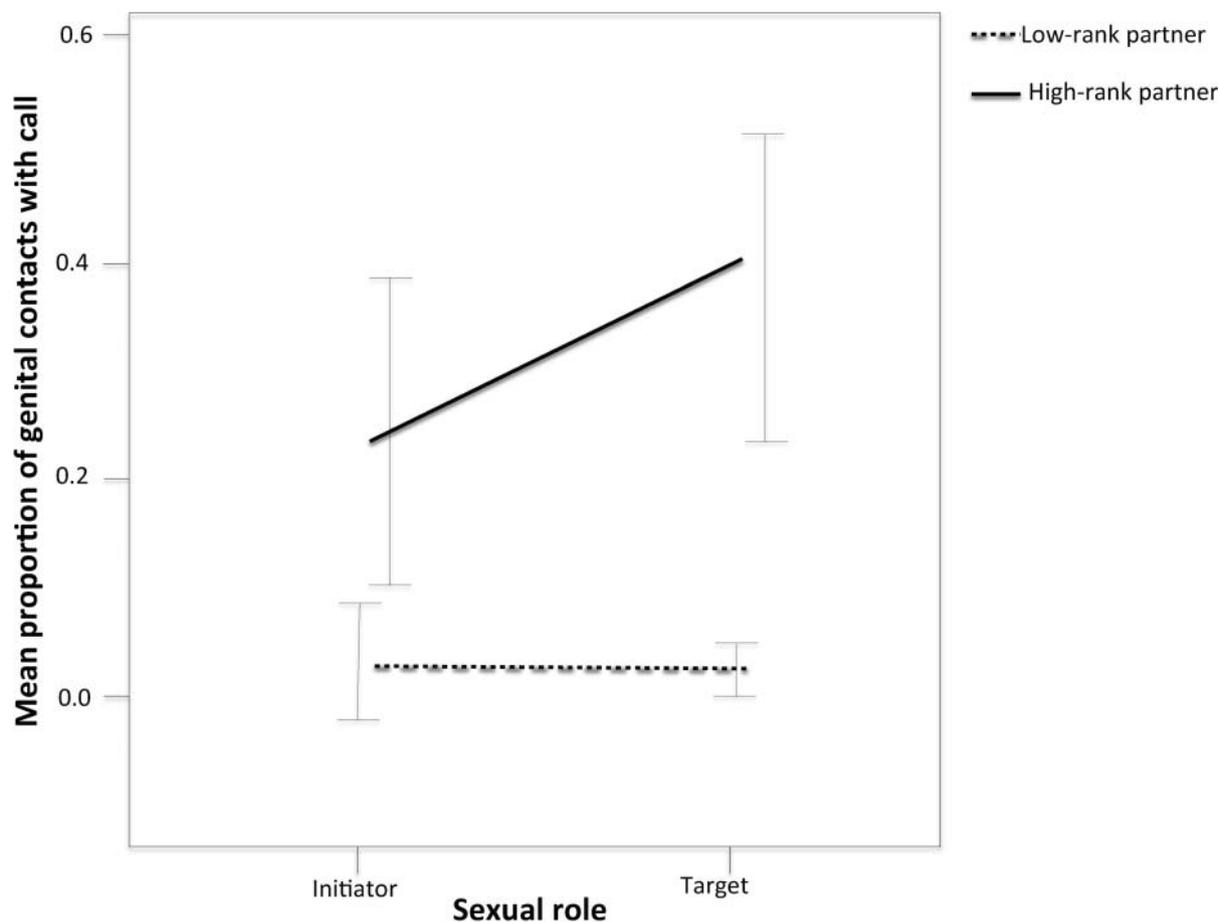


Figure 3 | Line-graph (with SE bars) showing the effect of initiation on call production during female genital contacts ($N = 9$ females) with high-ranked and low-ranked partners.

(B) Interactions in Experimentally Altered Group Compositions.

We conducted 90 experimental trials in which different pairs of females could interact in the presence of different female-only audiences. Overall, behavioural patterns observed in these experimentally induced genital contacts mirrored the natural behaviours observed outdoors, although the effects were generally enhanced.

Sexual behaviour. Rates of sexual interactions were very high (64.4% of trials, 58/90). In 16 of 21 possible dyads, they occurred in at least one trial but differed according to dyad composition (Fisher's exact test; low-low vs. high-high vs. asymmetric dyads: $P = .001$, two-tailed). Low-ranked and asymmetric dyads were significantly more likely to lead to genital contacts than expected (low-low: 67% of trials, binomial test: $(0.5) P = .047$; asymmetric: 74% of trials, binomial test (0.5) , $P = .002$; high-high: 10% of trials, binomial test (0.5) , $P = 0.021$). In contrast, interactions between two high-ranked females were very rare, occurring in just 10% of trials, significantly lower than expected by chance (binomial test (0.5) , $P = 0.021$).

Copulation call production. Of the 58 trials that resulted in a sexual interaction, $N = 29$ (50.0%) were accompanied by copulation calls. In $N = 26$ of these, only one individual produced a call. To reduce ambiguity, we excluded the three other cases of co-calling, resulting in a calling rate of 52.7%. Again, there were strong rank effects for both caller and partner. Call production was restricted to the four low-ranking females. In 20 of 26 cases during which calling occurred the caller interacted with a high-ranked partner (call production with high- vs. low-ranked partners: $\chi^2_1 = 6.48$, $P = .014$).

As with natural observations, spatial position had no influence on call production (N instances when caller on top vs. bottom: $\chi^2_2 = 1.46$, $P > .05$). Equally, the duration of the sexual interaction could not explain the likelihood of calling ($N = 36$ interactions: $N = 6$ silent vs. vocal interactions for LI, KS, NO; Wilcoxon signed-ranks tests: all $P > .05$, table S2).

As with natural observations, there was a significant effect of direction of solicitation on calling behaviour (solicit vs. being targeted: $\chi^2_1 = 3.85$, $P = .050$).

For analyses of audience effects, finally, we combined data of all $N = 55$ events, which replicated the observational data by showing that the presence of subordinate or dominant females had no effect on the likelihood of calling ($\chi^2_1 = 0.53$, $P > .05$; $\chi^2_1 = 0.01$, $P > .05$), while the presence of the alpha female had a significant effect ($\chi^2_1 = 5.106$, $P = .024$; with the $N = 20$ interactions involving alpha female excluded from analysis).

Discussion

In this study, we have focussed on female-female sexual interactions, which have highlighted their social relevance in line with earlier research^{24,25,29–31}. In addition, our data have shown that females use copulation calls, a signal presumably evolved for reproduction, in ways that deviate from its putative reproductive purpose by having taken on more flexible social functions. Low-ranked females engaged most frequently in sexual interactions, both with other low- and high-ranked partners, while genital contacts between high-ranked females were very rare. Genital contacts between high- and low-ranked females were more likely to be initiated by high-ranked partners. These findings are in line with

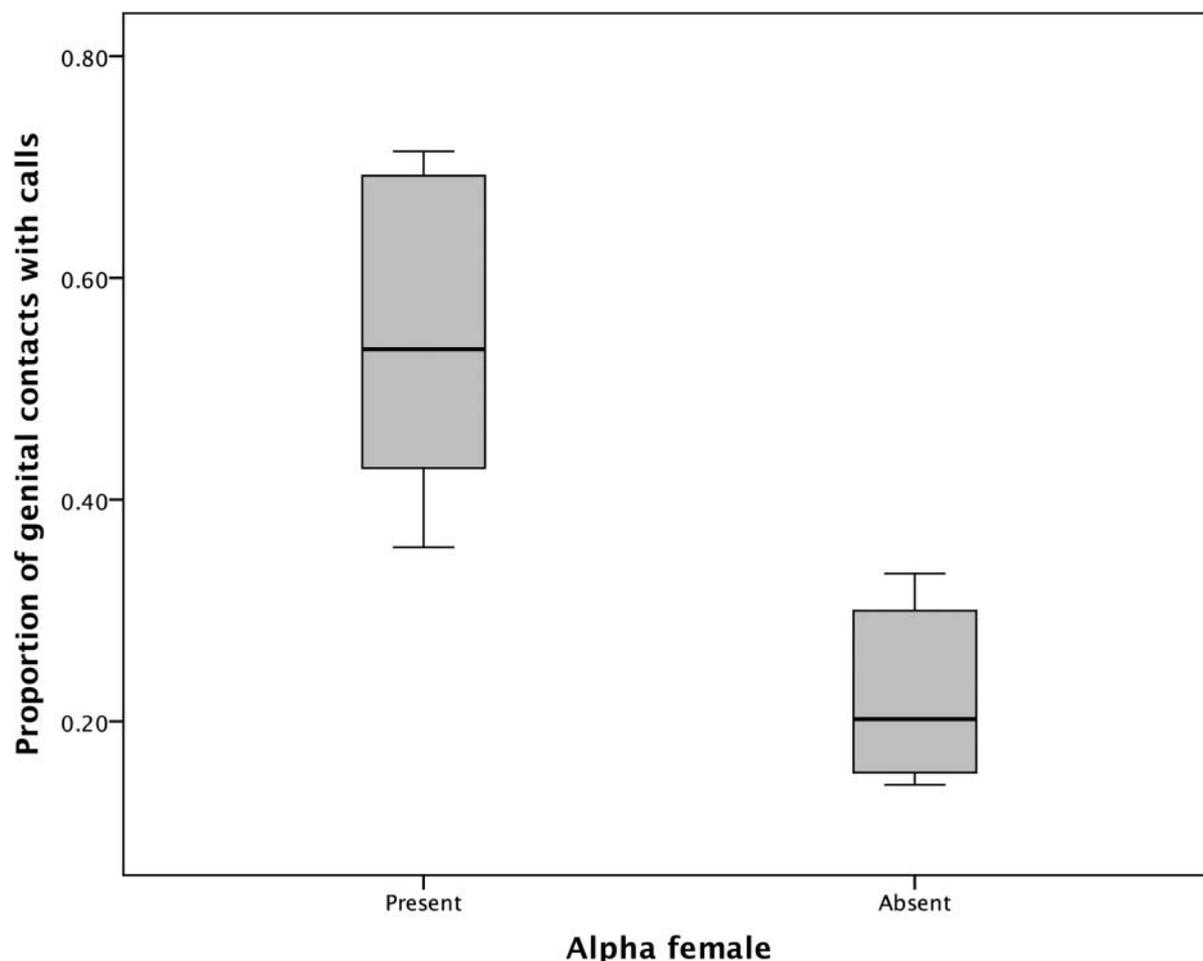


Figure 4 | Boxplot indicating the proportion of genital contacts accompanied by copulation calls ($N = 6$ females) in which the alpha female was present in the audience versus absent. Thick black lines represent medians; box edges represent the upper and lower hinges of the H-spread, which generally matches the upper and lower quartiles; whiskers represent the adjacent values, which are the most extreme values still lying within hinges and the normal distribution of the sample.

previous work showing that bonobo copulation calls share the same acoustic structure and are used in similar ways, regardless of whether females interact sexually with a male or female partner^{33,34}. Overall, results indicate that sexual interactions are an important social mechanism for female bonobos. For low-ranked females, they can provide a means to develop associations and alliances with more dominant females, which can subsequently strengthen their social position within the group. For high-ranked females, interested in sexual interactions for other reasons, they may provide a means to assert their social position, develop new alliances and control the formation of others' social bonds³⁰.

We also found strong rank effects in call production, with low-ranking females most likely to call especially when interacting with high-ranked females. The presence of the alpha female in the audience further enhanced call production. In contrast, variables related to the physical nature of the sexual interaction (spatial position and contact duration) had no influence. Rather than a product of physical stimulation, copulation calls are significantly driven by the social factors experienced by the caller, including their own rank relative to their partner's, the direction of solicitation and the presence of a socially important bystander. Although copulation calls in bonobos most likely evolved within the reproductive context, they have

Table 1 | Influence of audience on calling during female genital contacts (GCs). The top half indicates mean number of bystanders (\pm SD) for vocal vs. silent GCs ($N = 6$ females). The bottom half indicates proportion of GCs with calls in which the given audience member was present vs. absent. An asterisk indicates significant effect.

Audience variable	Vocal GCs	Silent GCs
Group size	8.51 (2.23)	6.52 (0.59)
N females	2.95 (1.01)	2.60 (0.55)
N males	5.55 (1.43)	3.91 (0.55)
	Proportion GCs with calls when present	Proportion GCs with calls when absent
*Alpha female	0.54 (0.14)	0.22 (0.08)
Alpha male	0.34 (0.26)	0.27 (0.16)
Dominant females	0.35 (0.19)	0.36 (0.33)
Subordinate females	0.35 (0.18)	0.20 (0.19)



become ritualised into broader, more flexible signals, used in both social and reproductive contexts.

As in previous studies with chimpanzees^{35–37}, we found evidence of audience effects, in this case particularly driven by the alpha female's presence. In contrast to chimpanzees, however, the presence of this socially most important individual had an enhancing rather than inhibiting effect on call production³⁵. While chimpanzee females were presumed to inhibit call production as a means to reduce risks of sexual competition from dominant females, the increase in calling in the alpha female's presence indicated the potential function of these calls for advertising successful socio-sexual interactions with dominant females towards a socially important bystander.

Why was calling most likely observed when females were solicited by high-ranked partners? Developing affiliations with dominant group members is critical to a female bonobo's own social position³⁸ and having been chosen by a higher-ranking partner may enhance a female's general social standing in a group. Thus, low-ranked females, presumably in need of social recognition, may want to advertise the fact of having been selected for sex by a socially more established female. Being solicited by a high-ranking partner may be judged as a social success, and advertising this to bystanders may accrue benefits to the signaller, particularly when the alpha female is nearby.

We were able to replicate our observational data with an experimental study, in which audience and dyad composition were more systematically controlled. To further test the hypothesis that bonobo copulation calls are social signals, we excluded the males from these experiments, but continued to find the same, albeit enhanced effects. Sexual interactions and calling were strongly biased towards low-ranked females with an enhancing effect of the alpha female, suggesting that call production was a female-driven affair that has become partly ritualised away from its original reproductive function. Although low-ranking females generally remained silent during interactions with other low-ranking females, they responded strongly to solicitation by a high-ranking female. High-ranking females during the same interaction remained silent. Overall, these results indicated that even if two females engaged in the same physical interaction, their experience was largely determined by their own and their partner's social position and that of the audience.

In contrast to another study³⁰, we were unable to find rank-related spatial effects during genital contacts²⁵, with high-ranking females exhibiting consistent individual preferences for one or the other spatial position, suggesting that they may exert their social power in this way (fig. S1).

Differences in the initiation of sexual interactions were strongest between females of high and low rank classes, with high-ranking females being more likely to initiate sex than low-ranking females, despite the fact that low-ranked females were sexually much more active. However, our general impression was that low-ranked females often attempted to initiate genital contacts with high-ranked females, but were typically ignored by them. More work will be required to address this aspect of female sexual behaviour, including the gestural and vocal signals involved in expressing sexual intention.

Our results are generally consistent with the main hypothesis that genital contacts are used as a means to express social dominance relationships, via asymmetric patterns in performance, initiation and calling behaviour. Unlike chimpanzees, bonobos appear to lack a formal vocal signal of submission, greeting and willingness to interact^{36,39,40}. Copulations calls may provide a means for females to exert some of these functions.

In wild populations, newly arriving immigrant females (presumed to be low-ranking) spend much time trying to develop bonds with older and more dominant females and frequently engage in genital contacts with them³¹. A bonobo female's social status (and presumably reproductive success) may thus crucially depend on developing and maintaining bonds with other females^{12,17}. Our results are consistent with the hypothesis that homosexual interactions may

facilitate the formation and consolidation of affiliation between unrelated females. Through intra-sexual tolerance and the development of female-female affiliations, female bonobos are able to form alliances and exert considerable power in their social groups^{13–17}.

It is difficult to be explicit about the nature of the psychological experiences responsible for call production. Social variables, such as partner rank or audience composition, are likely to influence a caller's motivational and arousal state, which in turn may drive call production. For example, call production by low-ranking females could be explained by raised levels of arousal when interacting with high-ranking females, especially when the alpha female is nearby. Interactions with high-ranked females can be dangerous as aggression typically occurs down the female hierarchy^{41,42}. Along similar lines, Wrangham¹⁶ suggested that genital contacts represent a means of testing the willingness of another individual to interact fairly, by exposing a vulnerable part of their body.

Whatever the nature of the mediating psychological forces, the overall patterns of calling cannot be explained as a simple response to physical stimulation, but is based on various judgements relating to the identity of the partner, the initiator, and the audience members. Female-female copulation calls, like the genital contacts they accompany, represent an example of an animal communication behaviour that has been influenced by social life, becoming partly divorced from a purely reproductive function to acquire a broader social significance. These results highlight the impact that social life can have on shaping the evolution of communication systems.

Methods

Study site. We conducted observations of three bonobo groups at Lola Ya Bonobo Sanctuary, Kinshasa, DR Congo, between September and November 2008 and between August and November 2009. Individuals spent their days ranging outdoors in one of three naturalistic forest enclosures (15–20 ha). Their daily routines remained the same throughout observation periods. More detail is provided in supplementary information.

In 2008, we carried out observations at enclosure 1 (henceforth 'Group 1a'). In 2009, we collected data from two groups housed in the same and the adjacent enclosure 2, (henceforth Group 1b and Group 2). Due to transfers, group composition in enclosure 1 changed between the two periods (Group 1a: $N = 9$ females, $N = 9$ males, $N = 4$ infants; Group 1b: $N = 7$ females, $N = 9$ males, $N = 4$ infants; Group 2: $N = 5$ females, $N = 11$ males, $N = 3$ infants; see Table S3). We pooled data across groups and combined data for dyads that met each other again in the second year ($N = 9$ dyads). This generated 58 dyads and $N = 14$ females available for analysis.

Data collection. We recorded female-female sexual interactions and accompanying vocalisations that occurred during physical contact of the genitals. Female genital contacts were defined as a ventro-ventral embrace with physical contact of the vulva and lateral hip swinging^{23,29}. Bonobo copulation calls typically consist of a single or succession of high-frequency squeaks and screams^{24,32}. They were acoustically distinct vocalisations, which were not observed in other interactions. We conducted observations ($N = 1,093$ hours) using ad-libitum and focal sampling, balanced across individuals⁴³. We recorded vocalisations at distances of 3–20 m using a SENNEHEISER MKH816T directional microphone and MARANTZ PMD660 solid-state recorder (sampling rate 44.1 kHz, 16 bits accuracy). Any verbal comments were later transcribed.

For each female-female genital contact, we recorded the following: identity of partners; call production; spatial positions of partners (top or bottom); identity of bystanders within a 15 m radius; and the identity of the initiating individual. Females used a diverse range of signals to initiate genital contacts, ranging from single behavioural actions or body postures to a more elaborate sequence of signals. Vocalisations sometimes occurred, though not reliably and unambiguously enough to be included as definitive behaviour. To assign solicitor identity, we relied on the occurrence of a key indicator (see ethogram table S4). Initiators were identified based on the presence of at least one directed bodily action or posture directed at the target. The individual producing the first directed action/posture was coded as the initiator. Interactions in which the identity of the initiator was either ambiguous or mutual were excluded ($N = 24$). The social status of the interacting individuals was unknown to the observer during data collection.

Although non-reproductive genital contacts between males and females did occasionally occur, this was mostly during episodes of high group tension. In the typical case, a male tried to briefly mount a female, while she showed no signs of sexual interest nor did she reciprocate with mating behaviour. Due to low sample size, we excluded such heterosexual genital contacts from our analyses.

Dominance. In order to assess the effect of social dominance on copulation calls, we focussed on the outcome of dyadic agonistic interactions³³, by using 'fleeing upon



aggression' as a behavioural marker for dominance^{20,44}. Dominance relationships and linearity were calculated using Matman (Noldus, version 1.1) in each study group. We then calculated the adjusted linearity index (h'), corrected for the number of unknown relationships and the direction consistency index (see supplementary information). For significantly linear hierarchies, we calculated individual cardinal rank scores using normalised David's Scores, corrected for chance⁴⁴. Using regression plots of these scores, we divided females into either high or low rank clusters, based on their position in the hierarchies (fig. S2, see³³).

Genital contact interactions. For comparisons of dyadic interactions, we used randomization-based statistical procedures, which addressed the problems of pseudo-replication and dependent data due to the fact that same individual could participate in several dyads. Randomization tests were employed using the 10,000 permutations-based Resampling Procedures algorithm developed by David Howell⁴⁵, which has been successfully used in other dyadic comparison studies with bonobos^{21,22}. This procedure provides a t -value (difference between the sample means, standardized by the standard error) for comparing two independent or paired groups with the probability of obtaining these values by chance.

In terms of spatial position, we examined whether high-ranked females ($N = 6$) were more likely to take the 'top' position than low-rank females ($N = 8$)²⁹. To explore rank asymmetries in the direction of initiation, we compared the rates of initiation by high and low-ranked females during their interactions with one another. In addition, we used the cardinal rank scores (David's Scores) to compare frequencies of initiations for the higher and lower ranked females within dyads composed of females from the same absolute rank class (i.e. the higher and lower-ranked of two females, both belonging to the low or high-ranked class).

To explore the effect of social rank, we examined observed vs. expected frequencies of genital contacts for symmetric dyads (low-ranked females or two high-ranked females) and asymmetric dyads (high- and low-ranked female). Calculations of expected frequencies were based on the total number of dyads possible for each dyad type (low-ranked dyads: $N = 17$; high-ranked dyads: $N = 9$; asymmetric dyads: $N = 32$).

Copulation calls. Previously, we found that partner rank (male or female) influenced copulation call production³³. To investigate whether the caller's rank also influenced calling, we conducted a Spearman's correlation to compare each female's dominance score (normalised David's Scores, corrected for chance) against the proportion of genital contacts in which she called. As David's Scores are an absolute value for a given time period, we only entered data for each female once, to avoid pseudo-replication (David's Score taken from her first data entry year, $N = 14$ females).

To investigate the effect of spatial position, we used the randomization procedure, described above, to analyse the proportion of genital contacts accompanied by calling when the female took the top versus the bottom position ($N = 13$ females). We excluded ambiguous cases where the females were in more equal/upright positions. To investigate the effect of direction of initiation, we conducted a two-way ANOVA based on the factors of 'initiation' (initiate vs. target) and 'partner rank' (high vs. low) on the proportion of genital contacts accompanied by calls ($N = 9$ females).

To examine whether the presence of bystanders influenced call production, whilst controlling for the effects of dyadic dominance rank, we analysed interactions between low- and high-ranked females (this represented the dyad type in which calling was most likely). As each interaction could only be entered once, to avoid pseudoreplication, and preliminary analyses indicated low-ranked females were more likely to call, we took the perspective of the low-ranked caller in each interaction and randomly selected a balanced number of sexual interactions for six focal females (LK, LI, IS, NO, KL; $N = 20$ interactions each; and KS: $N = 18$; $N = 118$ events in total). We compared the audience composition for silent and vocal sexual interactions for the following variables ($N = 118$ events): (a) total audience size; (b) female audience size; (c) male audience size. To investigate the influence of the social rank of the audience, we analysed the proportion of genital contacts accompanied by calls in which the following audience members were present compared to absent: (d) dominant female/s (one or more high-rank female/s present but alpha female absent); (e) subordinate females (one or more low-ranked female/s present but dominant/alpha females absent); (f) alpha female; (g) alpha male. In order to assess the influence of the alpha female as a bystander, we excluded all events in which she participated. To examine which audience variable most strongly predicted call production if all variables were combined in one model, we conducted a Generalized Linear Model analysis (binomial-logit) on the dependent variable of calling with the above-mentioned predictor variables. We were able to enter data for all low-ranked females ($N = 8$) and accounted for identity by entering it as a random factor. In order to analyse the effect of alpha female presence, we excluded all cases in which the alpha female was involved, which resulted in $N = 206$ interactions available for analysis.

Experimental manipulation of group composition. To control for the influence of partner identity and audience composition we carried out a behavioural experiment with female-only audiences. This was because male bonobos are notoriously difficult to separate in the indoor facility, and because we were especially interested in the hypothesis that copulation calls can be a female-directed behaviour to express social status.

Data were collected inside the dormitory facility (15 m² divided into 9 sub-rooms) connected to enclosure 1 over a 30-day period. The experimental rooms were separated by metal bar partitions with interconnecting tunnels, but all events were visible and audible to individuals kept inside (see supplementary information for more

detail; fig. S3). In each trial, we recorded the genital contact behaviours and copulation calls occurring between a focal dyad. All females of group 1b participated, acting both and audience members and as part of a focal dyad ($N = 7$ females). Five females were present in each trial; three as audience members, each housed in a separately, and two females as the focal dyad, in one compartment. A trial began by letting the two partners enter the compartment. We recorded interactions using a camcorder and professional sound equipment, as described earlier, supplemented by verbal commentaries. Although females frequently performed numerous sexual interactions over the trial, we only considered calls that occurred during the first genital contact (see Supplementary Information).

We analysed call production as a function of social rank of partners, spatial position, direction of initiation, and audience composition. Audience effects were analysed at three levels: (1) low-ranked females present; (2) high-ranked female/s present but alpha female absent (3) alpha female present (with 2 other females present).

We conducted 90 trials, balanced across females, with every dyad represented at least once (19/21 dyads met at least twice) on separate days (mean: 4 trials per dyad). Every female met every other female at least twice and interactions with partners of the same or different rank class were approximately balanced according to the number of possible dyads ($N = 43$ trials for twelve low-high dyads, $N = 37$ trials for six low-low dyads, $N = 10$ trials for three high-high dyads). Due to the low-sample sizes, we conducted non-parametric statistics throughout.

Genital contact duration. To further address whether physical stimulation influenced call production, we compared the genital contact duration (s) for vocal and silent interactions per focal female, using the video-footage in the indoor study. Due to a rank bias in caller identity (all callers were low-ranking), we were only able to examine data from low-ranked females. This resulted in a balanced sample of $N = 6$ call and $N = 6$ silent events for 3 females (KS, LI, NO), with a given genital contact event entered only once (female SL was excluded owing to inadequate sample size). Due to the low number of subjects, we conducted separate Wilcoxon signed-ranks tests (exact, two-tailed) per individual.

Statistical analyses. All statistical analyses were conducted using SPSS (v. 17.0 and v. 19.0). Randomization tests were conducted using the 'Resampling Procedure' program, developed by David Howell⁴⁵. For proportional data, $x = 1$ was replaced with $x = 1 - (1/4N)$ while $x = 0$ was replaced with $x = 1/4N$ before carrying out an arcsine transformation across the entire data set. These steps improved the homogeneity of variance distribution and rendered the data suitable for parametric analyses. All tests were two-tailed and significance levels were set at $\alpha = 0.05$. For small sample sizes, we used exact tests, as recommended by Mundry & Fischer (1998).

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Author contributions

Both authors contributed to the content of this paper. ZC and KZ conceived and designed the study. ZC collected the data and conducted the analyses. ZC and KZ co-wrote the main manuscript and ZC prepared figures and tables.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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