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http://researchonline.ljmu.ac.uk/id/eprint/12039/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

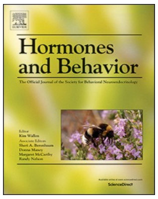
Moscovice, LR, Surbeck, M, Fruth, B, Hohmann, G, Jaeggi, AV and Deschner, T (2019) The cooperative sex: Sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. Hormones and Behavior. 116. ISSN 0018-506X

Hormones and Behavior 116 (2019) 104581

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh



The cooperative sex: Sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions

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ARTICLE INFO

Keywords:
Pan paniscus
Socio-sexual behavior
Copulations
Genito-genital rubbing
Oxytocin

ABSTRACT

In some species habitual same-sex sexual behavior co-occurs with high levels of intra-sexual alliance formation, suggesting that these behaviors may be linked. We tested for such a link by comparing behavioral and physiological outcomes of sex with unrelated same- and opposite-sex partners in female bonobos (*Pan paniscus*). We analyzed behavioral outcomes following 971 sexual events involving $n = 19$ female and $n = 8$ male adult and sub-adult members of a wild, habituated bonobo community. We additionally collected $n = 143$ urine samples before and after sexual interactions to non-invasively measure oxytocin (OT), which modulates female sexual behavior and facilitates cooperation in other species. The majority of sexual events (65%) consisted of female same-sex genito-genital rubbing (or GG-rubbing). Female dyads engaged in significantly more sexual interactions than did inter-sexual dyads, and females were more likely to remain within close proximity to their partners following GG-rubbing. Females also exhibited greater increases in urinary OT following GG-rubbing compared with copulations, indicating a physiological basis for increased motivation to cooperate among females. The frequency of coalitionary support among non-kin was positively predicted by the frequency of sexual interactions for female as well opposite-sex dyads, although coalitionary support tended to be more frequent among females. The emergence of habitual same-sex sexual behavior may have been an important step in the evolution of cooperation outside of kinship and pair-bonds in one of our closest phylogenetic relatives.

1. Introduction

Same-sex sexual behavior, referring to sexual solicitations, mounting or other genital contact between same-sex partners, occurs across a wide range of animal taxa under free-ranging conditions, though with much variation in form and frequency (reviewed in: Bailey and Zuk, 2009). In many species, same-sex sexual interactions are rare events that may represent redirected sexual behavior when suitable opposite-sex partners are absent (Bailey and Zuk, 2009). However, there are other taxa where a subset of the population exhibits same-sex preferences even when viable opposite-sex partners are available (e.g. Japanese macaques (*Macaca fuscata*), Vasey and Duckworth, 2006). In rarer cases, all adult members of one sex exhibit habitual same-sex sexual interactions that can occur at similar frequencies as opposite-sex sexual interactions (e.g. male bottlenose dolphins (*Tursiops* sp.): Mann, 2006; female bonobos (*Pan paniscus*): Hohmann and Fruth, 2000; Idani, 1991; Ryu et al., 2015). The extent of variation across species in the contexts that elicit same-sex sexual behavior and how widespread it is within a population suggest that its functions may be diverse and species-specific.

The adaptive hypotheses that have been proposed to explain same-sex sexual behavior more generally (reviewed in Bailey and Zuk, 2009) include: i) Establishing or maintaining cooperative social relationships (e.g. Japanese macaques (*Macaca fuscata*), Vasey, 1996); ii) Reducing social conflict, either by reducing social tension, or as a form of

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https://doi.org/10.1016/j.yhbeh.2019.104581
Received 27 March 2019; Received in revised form 15 July 2019; Accepted 20 August 2019

reconciliation following conflict (e.g. bonobos, de Waal, 1987, 1990); iii) As a form of intra-sexual competition, either by attracting members of the opposite sex for mating or by preventing members of the same sex from mating (e.g. tropical fish (*Poecilia mexicana),* Bierbach et al., 2012*)* or iv) As a form of practice for adult sexual behavior (e.g. fruit flies (*Drosophila melanogaster*), Dukas, 2010). The first two hypotheses both suggest a role of same-sex sexual behavior in promoting cooperative social outcomes. In dolphins and bonobos, members of the sex that engage in habitual same-sex sexual behavior are also noteworthy for their high levels of intra-sexual cooperation among unrelated individuals (Connor and Krützen, 2015; Furuichi, 2011; Tokuyama and Furuichi, 2016). This suggests that habitual same-sex sexual interactions may play a role in facilitating additional cooperation in these species, although the exact mechanisms by which this may occur remain unclear. Our goals were to test for evidence that habitual same-sex sexual behavior facilitates cooperative social outcomes, and to identify mechanisms by which this may occur, in female bonobos.

One way to infer potential functions of sexual behavior is by characterizing the social contexts and social configurations in which the behavior mainly occurs. In several species, same-sex sexual behavior occurs in contexts that are associated with additional behavioral coordination and cooperation between participants. In female Japanese macaques, same-sex sexual behavior occurs exclusively within short-term consortships in which dyads also engage in high levels of coordinated travel, feeding and grooming (Vasey, 2002). In dolphins, simultaneous same-sex sexual behavior is frequently observed among triads of primarily unrelated males and this is also the most frequent social configuration for cooperative alliances (Mann, 2006). In other species, same-sex sexual behavior mainly occurs when competition between participants is high, and it is used to attract opposite sex mates rather than to strengthen same-sex relationships (e.g. tropical fish (*Poecilia mexicana),* Bierbach et al., 2012).

In addition to behavioral data, measures of physiological changes associated with sexual behavior provide further insights into likely functions. Of particular interest in the context of cooperation is the neuropeptide hormone oxytocin (OT), which mediates many aspects of female sexual, reproductive and social behavior (reviewed in Borrow and Cameron, 2012). OT is released centrally from hypothalamic nuclei in response to salient social stimuli, including sexual behavior (rats: Nyuyki et al., 2011; voles: Ross et al., 2009). Centrally, OT activation in social brain circuitry results in enhanced social memory, reduced fear and anxiety and activation of neural reward pathways, all of which are related to fostering selective social bonds that promote cooperation (reviewed in Gangestad and Grebe, 2017). OT can also be released peripherally via the posterior pituitary, facilitating non-invasive measurement (Crockford et al., 2014). In several species, measures of peripheral OT correlate positively with the extent of behavioral coordination and cooperation within selective social relationships, such as between mothers and offspring (humans: Feldman, 2012), monogamous mates (humans: Grewen et al., 2005; Schneiderman et al., 2012; cotton-top tamarins (*Saguinus oedipus*): Snowdon et al., 2010) and stable alliance partners (chimpanzees (*Pan troglodytes*): Crockford et al., 2013). In humans (De Dreu, 2012; Nagasawa et al., 2009) and chimpanzees (Samuni et al., 2017), there is evidence that the OT system has been co-opted outside of maternal and reproductive contexts to facilitate cooperation with a broader range of social partners (reviewed in Trumble et al., 2015). Based on this combined evidence, the link between sexual behavior and OT system activation may be strongest related to sexual behavior that facilitates additional trust and cooperation, whether this occurs within or outside of monogamous pair-bonds. We were interested in whether unrelated female bonobos exhibit increases in peripheral oxytocin associated with sexual interactions, as this may explain their unusual extent of cooperation.

Bonobos are a particularly promising model for investigating different functions of sexual behavior, given that all adult females engage in same-sex sexual behavior that occurs at similar or higher rates as copulations (Hohmann and Fruth, 2000, 2003a; Ryu et al., 2015). In contrast, same-sex sexual interactions among male bonobos are relatively rare (Fruth and Hohmann, 2006; Kano, 1980; Surbeck et al., 2017b). Bonobos live in multi-male, multi-female communities characterized by fission-fusion social dynamics, female-biased dispersal and a promiscuous mating system notable for a relative lack of male coercion and a high degree of female control over sexual partners (Furuichi, 2011; Surbeck and Hohmann, 2013). For female bonobos, their strongest and most cooperative inter-sexual social relationships occur with their adult sons (Surbeck et al., 2011, 2017a). Females also cooperate preferentially with other unrelated females within their community in several contexts, including by sharing monopolizeable foods (Fruth and Hohmann, 2002; Yamamoto, 2015), co-defending access to food resources (White and Wood, 2007) and participating in coalitionary aggression, which frequently targets males (Nurmi et al., 2018; Surbeck and Hohmann, 2013; Tokuyama and Furuichi, 2016).

As in all anthropoid primates, female bonobos exhibit extended sexuality, characterized by sexual proceptivity and receptivity that is not limited to the fertile period (Wallen and Zehr, 2004). Bonobos also share with chimpanzees and some old world monkeys ‘exaggerated sexual swellings’, referring to conspicuous fluctuations in the size, firmness and color of their perineal sex skin across their menstrual cycles (Nunn, 1999). However, relative to other primates, their sexual swellings are less reliable indicators of ovulation (Douglas et al., 2016; Furuichi, 1987), and they exhibit higher levels of proceptive and receptive sexual behavior during anovulatory periods, including during pregnancy and lactational amenorrhea (Furuichi et al., 2014). Thus the majority of copulations in bonobos are unlikely to serve a reproductive function. In contrast with evidence in humans (Chapais, 2013) and other socially-monogamous primates (Snowdon et al., 2010), in bonobos non-reproductive sex between females and males does not appear to increase pair-bonding or other forms of male investment (Goldstone et al., 2016; Yamamoto, 2015). Rather, the high frequency of nonconceptive copulations may help to reduce male harassment and increase paternity confusion, which may contribute to the lack of evidence for infanticide in bonobos (reviewed in Furuichi et al., 2014).

Habitual same-sex sexual behavior among female bonobos primarily consists of genito-genital rubbing (or GG-rubbing), in which females embrace ventro-ventrally and use rapid lateral hip movements to rub their genital swellings together (Hohmann and Fruth, 2000). Females appear to use GG-rubbing flexibly as a quick and efficient means to signal trust and social tolerance with a broad range of partners (Moscovice et al., 2017), which may promote various forms of cooperation. Previous studies provide indirect evidence that GG-rubbing may facilitate cooperation by: i) helping recent female immigrants to initiate social relationships with other young females and with long-term residents of higher social status (Idani, 1991; Sakamaki et al., 2015); and by ii) increasing tolerance and reducing tension in potentially tense social contexts, including during fusions when members of a community reunite after associating in different sub-groups (Moscovice et al., 2015) and in competitive feeding contexts (de Waal, 1987; Douglas and Moscovice, 2015; Fruth and Hohmann, 2006; Hohmann et al., 2009).

In the current study we investigate behavioral and physiological outcomes of same-sex sexual behavior in female bonobos in comparison with outcomes related to sexual interactions with males, the majority of which are unlikely to result in insemination (Douglas et al., 2016). While previous studies have sometimes combined intra- and inter-sexual interactions when examining non-reproductive functions of sexual behavior more generally (de Waal, 1990; Hohmann et al., 2009), here we evaluate the evidence for GG-rubbing and copulations separately, in order to test for a unique role of habitual same-sex sexual behavior in facilitating female-biased cooperation in bonobos. In this case, we predict that in potentially competitive contexts in which cooperation is especially beneficial, i) females will be more likely to engage in GG-rubbing than in copulations (Sex preference hypothesis), ii) GG-rubbing, but not copulations, will lead to increases in close proximity between partners

(Post-sex behavior hypothesis) and iii) peripheral OT concentrations will increase in females following GG-rubbing but not after copulations (Post-sex physiology hypothesis). Finally, if female same-sex sexual interactions are associated with increases in close proximity and oxytocin, then iv) female dyads who have more frequent sexual interactions will also have more opportunities and motivation to participate in other forms of cooperation, such as coalitionary alliances (Coalitionary support hypothesis). Alternatively, it is possible that sexual behavior in bonobos helps to maintain cooperative relationships with a subset of unrelated male and female partners, analogous to the role of grooming in chimpanzees and other primate species (Mitani, 2009). In this case, females will exhibit higher frequencies of sexual behavior and greater post-sex maintenance of close proximity with a subset of unrelated females and males who are more preferred partners for other forms of affiliation and cooperation. Changes in uOT concentrations following sexual interactions will be predicted by the strength of the social relationship between partners, and the amount of joint coalitionary support among female-female as well as inter-sexual dyads will be predicted by their frequency of sexual interactions.

2. Material and methods

We conducted this study on the wild, habituated Bompusa bonobo community at LuiKotale, Democratic Republic of Congo (DRC) (Hohmann and Fruth, 2003b) during 1483 observation hours between January 2013 – May 2014. All research adhered to the legal requirements of the DRC and the Institut Congolais pour la Conservation de la Nature (ICCN). Methods for data and sample collection were non-invasive and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. The community consisted of between 36 and 40 individuals, including $n = 13$ parous, resident females along with their juvenile and infant offspring, $n = 7$ mature males estimated to be >10 years of age based on body size and dentition, $n = 4$ natal sub-adults (3 F, 1 M) between 7 and 8 years of age and $n = 3$ nulliparous female immigrants who associated with the community for at least six months during the study period and were considered as subadults in analyses. Among adults and sub-adults, close relatives, defined as parents and offspring ($n = 9$ dyads) or maternal siblings ($n = 6$ dyads) were known based on previous parentage analyses (Moscovice et al., 2017; Surbeck et al., 2017b). All other adult and sub-adult dyads were classified as non-kin. We collected behavioral data and urine samples during half-day focal follows of the thirteen parous females and seven mature males (mean (x ± SD) = 31.5 (± 15.1) h per subject). At five-minute intervals we recorded the behavior of the focal subject and the identity of any social partners for grooming. At fifteen-minute intervals we recorded the identity of all partners within close proximity (≤ 1 m). At 30-min intervals we recorded cumulative party compositions that included all individuals observed in the previous 29 min. We also recorded all occurrences of sexual behavior between focal subjects and other mature or sub-adult partners, including copulations and any non-penetrative genital contact. For each independent sexual event (separated by >1 min or involving a new partner), we recorded the identity of the partner and additional information when possible on the duration of the sexual event, the context(s) in which the sexual event occurred and maintenance of post-sex proximity between former sexual partners following the sexual interaction. Individuals were considered to remain within close proximity when they engaged in their next non-sexual activity (e.g. feeding, resting, traveling) while maintaining a distance of ≤ 1 m (within arm's reach) of their previous sexual partner. We did not systematically record the duration of post-sex time in close proximity, but rather considered the initial decision to remain within close proximity or not following sex as a sign of social tolerance, as such close proximity is rare in primates apart from a subset of preferred associates (Dubuc et al., 2012). We recorded all occurrences of food sharing, which was defined whenever a possessor shared some part of a preferred, monopolizeable food item (primarily meat or the large fruits of *Treculia africana* or *Anonidium mannii*) with a bystander, either by passively allowing a bystander to take pieces of the food, or in rarer cases by actively transferring part of the food item to a bystander. We also recorded all occurrences of aggression, which was defined as charging, chasing and/or contact aggression, including holding, hitting, or biting, where the intended target was clearly identifiable. Coalitionary aggression was recorded whenever two or more individuals directed any aggressive behaviors in a coordinated fashion against a third party. In the case of polyadic coalitions, we considered as coalition partners all combinations of dyads that directed aggression towards the same target during an aggressive event.

2.1. Characterizing relationships between individuals

We calculated dyadic Composite Relationship Indices (dyaCRIs) modified from Crockford et al. (2013) for $n = 146$ inter-sexual and $n = 156$ female dyads, representing all focal subjects with each other or with sub-adults (excluding male-male dyads since they were not the focus of analyses). We first determined directional CRIs (dirCRI) for each individual within a dyad based on: 1) The proportion of focal scans during which an individual was involved in common socio-positive behaviors (SPcommon; giving grooming or staying in close proximity) with each partner, 2) The frequency with which individuals directed rare socio-positive behaviors (SPrare; giving support in coalitions or food sharing) to each partner; and 3) The frequency with which individuals directed aggression to each partner, as a socio-negative (SN) score. The dirCRI for actor (A_i) and recipient (B_j) was calculated as: (SPcommon A_iB_j $_+$ SPrare AiBj) / 2 – SN A_iB_j. Each dirCRI was divided by the mean dirCRI for the given sex class (FF or FM), to correct for differences in the frequencies of these behaviors across sex-classes. The dyaCRI was calculated by summing the dirCRIs for partners. Positive values indicate relationships characterized by net socio-positive interactions.

2.2. Hormone collection, analyses and validations

We collected $n = 55$ urine samples from $n = 13$ female subjects between 15 and 60 min following either GG-rubbing events ($n = 35$ samples, 2.7 (± 1.5) per subject) or copulations ($n = 20$ samples, 1.5 (± 1.7) per subject) with seven male and eighteen female partners. We assumed a clearance time of uOT in bonobos of 15–60 min after secretion, based on a human clearance study (Amico et al., 1987) as well as several studies in chimpanzees indicating changes in uOT concentrations following biologically-relevant social interactions that occurred within this time window (Crockford et al., 2013; Samuni et al., 2017; Wittig et al., 2014). We included in the analyses n = 13 post-sex samples (1 (± 0.70) per subject) following multiple, independent sexual events (with the same or with different partners), as long as the events included only one type of sexual interaction (either copulations or GG-rubbing). Post-copulation urine samples represented mean (± SD) = 1.5 (± 0.70) copulation events, totalling 20 (± 12.8) s of sexual interactions. Only one post-copulation sample (0.05%) occurred following copulations with more than one partner. Post-GG-rubbing samples represented 1.6 (± 0.82) GG-rubbing events, totalling 21.5 (± 19.0) s and 34.3% of samples ($n = 12$) involved GG-rubbing events with more than one partner (mean (± SD) = 1.44 (± 0.66) partners per sample). We only included post-sex samples when subjects did not engage in any other direct affiliative or aggressive interactions in the intervening period between the sexual interaction(s) and sample collection. For comparison, we collected $n = 88$ baseline urine samples from the same females (6.8 (± 5.2) per female) following a period of >60 mn during which the subjects were not involved in any direct affiliative, sexual or aggressive interactions with other adults or sub-adults. Although samples were often collected in feeding contexts, we excluded from analyses any post-sex or baseline urine samples that occurred in food sharing contexts (while feeding on meat or highly preferred, monopolizeable fruits) due to evidence that food sharing is associated with elevated oxytocin in other species (e.g. Wittig et al., 2014). Samples were collected either in plastic bags or on leaves, pipetted into cryo vials and kept in a cooled thermos until arrival in camp, when they were transferred into liquid nitrogen.

Urine samples were transported frozen from the field site to the Endocrine Laboratory at the Max Planck Institute for Evolutionary Anthropology, where they were kept frozen at −20 °C until extraction following a modified protocol from Assay Designs. In brief, thawed samples were vortexed and centrifuged at 4 °C (5 min, 3000 rpm). 500 μl of urine were loaded on 30 mg Sep-Pak HR-X 1 ml cartridges (Macherey and Nagel), primed with 1 ml methanol and 1 ml HPLC water. Samples were washed with a 10% acetonitrile/1% trifluoroacetic-acid solution. Samples were eluted in an 80/20% acetonitrile solution. Samples were evaporated with air stream and then resuspended in 300 μl ethanol in a final precipitation step, in order to minimize any additional cross-reactivity. Samples were kept at 4 °C for 30 min, then re-evaporated and either frozen overnight or measured immediately. uOT was measured using an Enzyme Immuno-Assay (EIA, Assay Designs; catalogue no. ADI-901-153). The assay standard curve ranged from 15.62 to 1000 pg/ml and assay sensitivity was 15 pg/ml. Final uOT concentrations were calculated as pg OT per mg creatinine to compensate for variation in sample concentrations. Inter-assay coefficients of variation of low- (62.5 pg ml^{-1}) and high- (250 pg ml^{-1}) value quality controls were 27.7 and 18.1% respectively ($n = 48$). Intra-assay coefficients of variation of low- and high-value quality controls were 9.2% and 6.8% respectively. We performed a series of validations to confirm that the assay captures the majority of OT and its metabolites and is suitable for measuring OT secretion in bonobo urine (see also supplementary data and Fig. S1). Tests of parallelism revealed no differences in the slopes between the standard curve and a serial dilution of pooled bonobo urine spiked with concentrated standard (10,000 pg ml^{-1}) from the ELISA kit ($t = 0.724$, $p = 0.491$, $n = 6$). Recovery of OT in urine samples spiked with OT standards at three different concentrations spanning the linear range (4500 pg ml^{-1}, 1500 pg ml^{-1}, 500 pg ml^{-1}) was 87.6 (±16.0)% (n = 6 standard curve points).

2.3. Statistical analyses

We fit mixed models in R (version 3.5.1, R Core Team, 2018) using the packages ‘lme4’ (Bates et al., 2014) and ‘glmmADMB’ (Fournier et al., 2012). To test whether females preferentially engage in sex with members of the more cooperative sex (Sex preference hypothesis), we fit a zero-inflated poisson generalized linear mixed model (GLMM), with the number of times dyads engaged in sexual behavior in feeding contexts as the response. We included as the predictor an interaction between the dyadic sex combination and the dyaCRI score, since the influence of relationship quality on the likelihood of having sex may differ based on the sex of the partner. However, the interaction term was not significant (est ± SE = −0.07 ± 0.11, $p = 0.48$) and was removed from the final model. We included total dyadic observation time in the same party as an offset term, subject a and b within the dyad as random effects, and included random slopes of dyadic sex combination within subject. To test whether remaining in close proximity following sexual interactions was predicted by the sex of the partner (Post-sex behavior hypothesis), we fit a binomial GLMM with the post-sex distance ($\leq$ 1 m or > 1 m) between individuals as the response. This model included the subset of $n = 333$ GG-rubbing events and $n = 122$ copulations in feeding contexts for which we also had data on the distance between individuals during their first post-sex activities. We again included as the predictor an interaction between dyadic sex combination and dyaCRI score, but the interaction term was not significant (est ± SE = 0.22 ± 0.34, $p = 0.53$) and was removed from the final model. We controlled in the model for contexts that occurred together with feeding and that may have had additional influences on sexual behavior, including aggression, changes in party composition or sharing of highly preferred, monopolizeable foods (see Table 2 and Table S1). We included each subject, the dyad and each feeding bout (defined as the period of time while located in the same feeding tree, or in the same food patch if feeding on the ground) as random effects, and included random slopes of all predictors within subject and dyadic CRI score within feeding bout.

To test for a differentiated physiological response to sexual behavior according to the sex of the partner (Post-sex physiology hypothesis), we ran a gaussian LMM in which we paired each subjects' post-GG-rubbing or post-copulation urine sample with one baseline non-sexual sample that was collected as close in time to the sexual event as possible (mean (±SD) = 5.9 (±8.7) days between paired samples). This provided a precise measure of short-term changes in uOT associated with each sexual event. We tested whether uOT concentrations were influenced by an interaction between type of sample (baseline vs post-sex, representing relative changes in uOT) and type of sexual event (copulation vs GG-rubbing). We also interacted type of sample with the dyaCRI score between sexual partners. For one copulation and twelve GG-rubbing samples that occurred after sexual events with multiple partners of the same sex, we used the largest dyaCRI score from among the previous partners to represent the maximal strength of social relationships. We controlled in the model for the effect of having sex with more than one partner and for the time lag from the initiation of the sexual interaction until sample collection on uOT concentrations. We also controlled for stage of sexual swelling, since it tended to influence uOT in a preliminary model testing whether uOT increases following any sexual event compared to baseline (see supplementary data and Table S4). We included random effects for subject, feeding bout and to account for the pairing of each pre- and post-sex sample. We included random slopes of test predictors within subject. We also conducted planned comparisons of estimated marginal means (emm) using the Bonferroni adjustment of *p*-values in the package “em means” (Lenth, 2018) to compare uOT between post-GG-rubbing and post-copulation samples, as well as between each type of post-sex sample and baseline.

Although we did not analyze any urine samples that were collected in food sharing contexts, both post-sex and baseline urine samples were often collected in feeding contexts, and it is possible that feeding alone may induce changes in OT (Sabatier et al., 2013). We tested for any possible effects of feeding on OT by comparing uOT from the subset of baseline samples that were collected following feeding while alone ($n = 16$), feeding with a partner in close proximity ($n = 5$) or without any feeding in the previous hour ($n = 19$ samples). We also tested whether uOT was higher in samples that occurred following feeding with GG-rubbing ($n = 22$) vs feeding without GG-rubbing ($n = 21$). In both models we controlled for fluctuations in sexual swelling size and included random effects of subject and random slopes of swelling and sampling context (feeding alone, feeding near partner, no feeding) within subject.

To test whether the amount of joint coalitionary support between unrelated dyads was predicted by their frequency of sexual interactions (Coalitionary support hypothesis), we fit a poisson GLMM, with the number of times each dyad engaged in joint coalitionary aggression as the response. We included as the predictor an interaction between the dyadic sex combination (FF vs FM) and the frequency of sexual interactions, since we predicted that the impact of sexual interactions on the likelihood of additional cooperation would differ based on the sex of the partner. However, the interaction term was not significant (est ± SE = −0.30 ± 0.52, $p = 0.57$) and was removed from the final model. We included dyadic observation time in the same party as an offset term. We included each subject within the dyad as random effects, and included random slopes of frequency of sexual interactions within subject A and dyadic sex combination within subject B.

In all models, continuous predictors were log transformed when necessary to achieve normal distributions and were also normalized to a mean of zero and a standard deviation of 1 using a z-transformation. We confirmed that the models were stable by comparing the estimates derived from a model based on the full data set with those obtained from a model with each subject excluded one by one. We also used the “vif” function in the package “car” (Fox and Weisberg, 2011), to test for variance inflation and found no evidence for collinearity of the predictors (max VIF = 1.77). For GLMMs, we confirmed that the models were not overdispersed (chi-sq = 113.13–431.18, p = 0.13–1, dispersion parameters = 0.50–1.09). We used likelihood ratio tests to compare each model to a null model excluding the test predictors and present results of models that differed significantly from the null model. Unless otherwise noted, results are presented as mean (± SD).

3. Results

We observed $n = 971$ independent sexual events (0.65 per h) involving the $n = 20$ focal subjects, either with each other or with the $n = 7$ sub-adults. The distribution of sexual interactions among different dyadic sex combinations reflects their different propensities for cooperation. The majority (65%, $n = 627$, 0.42 per hour), involved sexual interactions among $n = 105$ unrelated female dyads, representing 70.1% of all unrelated female dyads. All but nine of these interactions (98.6%) involved GG-rubbing. Ten female sexual interactions between close relatives (one mother-adult daughter and two sister dyads) were excluded from further analyses. An additional 34% of events ($n = 330$, 0.22 per hour) involved inter-sexual interactions among $n = 79$ inter-sexual dyads, representing 56.4% of all unrelated inter-sexual dyads. The majority of these interactions (83.5%) consisted of copulations. Sexual interactions between males, the dyadic sex combination with the lowest levels of cooperation, occurred among two dyads, representing 7.7% of unrelated male dyads and accounted for $< 1\%$ of observations ($n = 4$, 0.002 per hour). The relative number of dyads of each sex combination that were observed having sex at least once during the study period differed significantly from expected (chi-square = 190.67, df = 2, $p < 0.001$). This was due to more female-female dyads and fewer male-male dyads engaging in sexual interactions than predicted, based on their relative frequencies in the community (see Fig. S2).

The majority of GG-rubbing ($n = 513$, 91.9%) and copulations ($n = 195$, 84.1%) occurred in feeding contexts (see Table S1), where females frequently form alliances that aggressively exclude males (Nurmi et al., 2018; Surbeck and Hohmann, 2013), while often feeding in close proximity or sharing monopolizeable foods with other females (Douglas and Moscovice, 2015; Yamamoto, 2015). Consistent with the sex preference hypothesis, female dyads engaged in significantly more sexual interactions in feeding contexts than did inter-sexual dyads (GLMM, likelihood ratio text, chi-sq = 23.34, df = 3, $p < 0.001$, est. ± SE = 1.10 ± 0.17, $p < 0.001$, see Table 1 and Table S2). Relationship quality measured by the dyaCRI did not influence dyadic frequencies of sexual interactions (see Table 1).

Consistent with the post-sex behavior hypothesis, females were more likely to remain within close proximity to their partners following GG-rubbing compared with copulations (56% of GG-rubbing events vs 35% of copulations, GLMM, likelihood ratio test, chi-sq = 8.74, df = 3, $p = 0.03$, est. ± SE = 0.72 ± 0.27, $p = 0.01$, see Fig. 1 and Table 2). The sex of the partner remained a significant predictor of staying in close proximity after controlling for sex that occurred in food sharing contexts, which also increased the likelihood of staying in close proximity (see Table 2). As in the sex preference model, the measure of relationship quality did not influence the outcome (see Table 2). To examine whether this result merely reflects a more general tendency for females to remain in closer spatial proximity with other females than with males, we also tested whether GG-rubbing or copulations influenced the likelihood of remaining in close proximity following sex for the subset of $n = 302$ events where partners were not in close proximity before their sexual interaction. Partners who were initially > 1 m apart were more likely to remain in close proximity after GG-rubbing ($n = 93$ events (48%) than after copulations (n = 30 events (28%), GLMM, likelihood ratio test, chi-sq = 4.23, df = 1, $p = 0.04$, est. ± SE = 0.71 ± 0.31, p = 0.04, see Table S3), suggesting that GG-rubbing is more effective than copulations in establishing proximity.

Table 1
Results of a GLMM predicting the effects of dyadic sex combination (relative to FM) and Composite Relationship Index (CRI) on frequencies of sex in feeding contexts (sex preference model). Statistically significant predictors ($p < 0.05$) are indicated in bold.

Term	est ± SE	chi-sq	df	p value
(Intercept)	0.47 ± 0.17			
Test predictors:				
Dyadic sex combination (FF)	**1.10 ± 0.17**	**6.27**	**1**	**< 0.001**
Dyadic CRI	0.02 ± 0.06	0.29	1	0.77

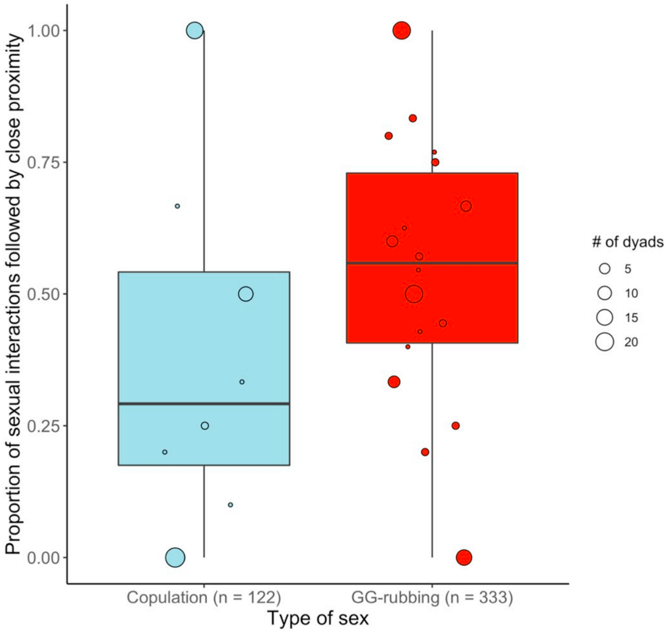

Fig. 1. Influence of different types of sex on the likelihood that partners remain within arm's reach during their subsequent post-sex activity. Box plots indicate medians and 25–75% interquartile ranges. The Tukey-style whiskers extend to a maximum of 1.5 × IQR beyond the box. For full model results see Table 2.

Table 2
Results of a GLMM predicting the effects of dyadic sex combination (relative to FM) and Composite Relationship Index (CRI) on the likelihood of staying in close proximity after sex (post-sex behavior model). Statistically significant predictors (p < 0.05) are indicated in bold.

Term	est ± SE	chi-sq	df	p value
(Intercept)	−0.76 ± 0.24			
Test predictors:				
Dyadic sex combination (FF)	**0.72 ± 0.27**	**6.25**	**1**	**0.01**
Dyadic CRI	−0.21 ± 0.14	1.83	1	0.18
Control predictors:				
Context: Feed + food sharing[a]	**1.64 ± 0.57**	**9.09**	**3**	**0.03**
Context: Feed + aggression[a]	**−0.17 ± 0.52**			
Context: Feed + change in party[a]	**0.58 ± 0.46**			

[a] Chi-square, df and p values refer to comparison with reference category: Feeding without additional contexts.

As expected based on the central role of OT in mediating female reproductive behavior more generally, female uOT concentrations tended to be higher following any sexual events ($n = 55$) compared to baseline ($n = 89$ samples, LMM, likelihood ratio test, chi-sq = 3.7, df = 1, $p = 0.05$, est. ± SE = 0.31 ± 0.15, p = 0.05, see supplementary data and Table S4). However, consistent with the post-sex

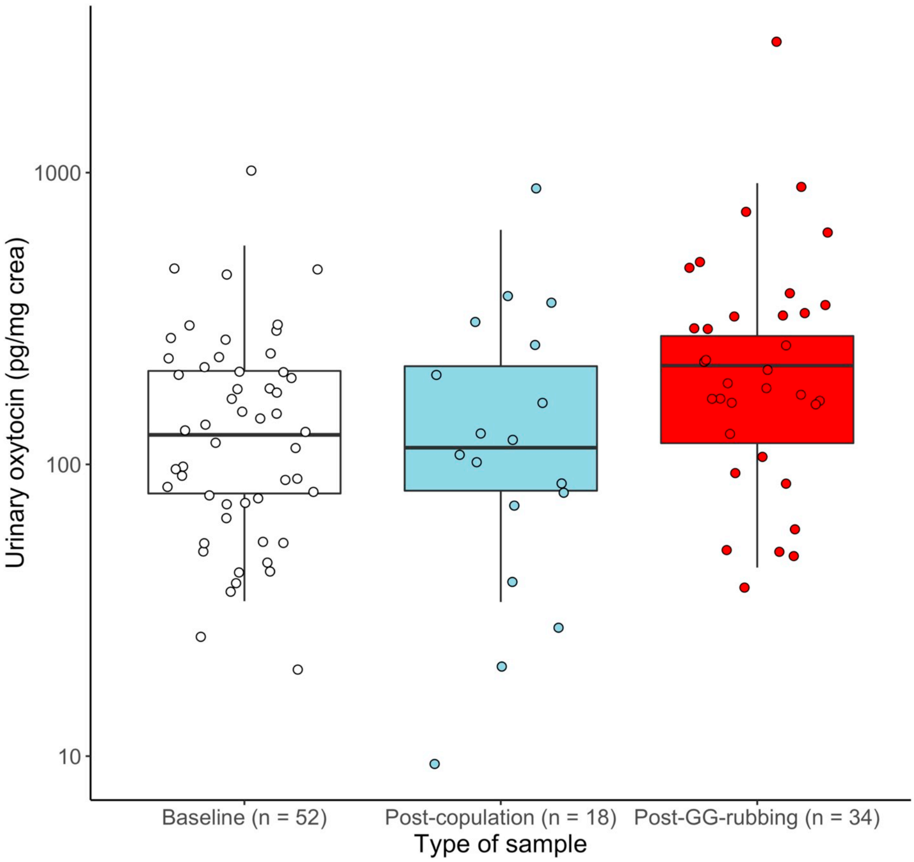

Fig. 2. Comparison of uOT concentrations (log transformed) between paired baseline and post-sex samples collected within similar time frames. Box plots indicate medians and 25–75% interquartile ranges. The Tukey-style whiskers extend to a maximum of 1.5 × IQR beyond the box. For full model results see Table 3.

Table 3
Results of a LMM predicting the effects of dyadic sex combination (relative to FM) and composite relationship index (CRI) on relative changes in uOT (log transformed) from pre- to post-sex samples (post-sex physiology model). Statistically significant predictors ($p < 0.05$) are indicated in bold.

Term	est ± SE	chi-sq	df	p value
Intercept	5.46 ± 0.26			
Test predictors:				
Sample type(post-sex) : Sex combination (FF)[*]	**0.65 ± 0.30**	**4.55**	**1**	**0.03**
Sample type(post-sex) : Dyadic CRI	−0.05 ± 0.14	0.11	1	0.74
Control predictors:				
Sample type (post-sex) : > 1 partner[†]	0.29 ± 0.34	0.71	1	0.40
Sample type (post-sex) : Time between event and sample	0.05 ± 0.14	0.16	1	0.69
Swelling score 1[‡]	**0.73 ± 0.26**	**8.99**	**3**	**0.03**
Swelling score 2[‡]	**0.07 ± 0.25**			
Swelling score 3[‡]	**−0.09 ± 0.20**			

[*,†,‡] Chi-square, df and p values refer to comparison with reference categories: *Changes in uOT from baseline to post-sex following sex with males; [†]Changes in uOT from baseline to post-sex following sex with only one partner, [‡]Relative to swelling score 4 (most tumescent).

physiology hypothesis, females also exhibited differentiated physiological responses following different types of sexual interactions (LMM, likelihood ratio test, chi-sq = 14.8, df = 7, p = 0.04, est. ± SE = 0.65 ± 0.30, p = 0.03, see Fig. 2 and Table 3). Planned comparisons indicated that log uOT concentrations rose significantly from baseline following GG-rubbing (emm ± SE = 5.45 ± 0.19, vs 4.85 ± 0.21, z = 2.96, adj. *p* = 0.02), but did not differ from baseline following copulations (emm ± SE = 4.81 ± 0.27 vs 4.86 ± 0.27, z = −0.17, adj. *p* = 0.98). Post-GG-rubbing samples also tended to be higher than post-copulation samples (z = 2.28, adj. p = 0.05, see Table S5). Post-sex changes in uOT concentrations were not influenced by the quality of the relationship with the sexual partner (see Table 3).

Consistent with the prevalence of sexual interactions in feeding contexts, the majority of post-copulation (75%, *n* = 15), as well as post-GG-rubbing (86%, n = 30) urine samples were collected in feeding contexts, and thus also represent post-feeding samples on one of over sixteen different food types that were consumed across the sampling period. An additional 24% (*n* = 21) of baseline samples were also collected within an hour following feeding events. We found no differences in uOT between baseline samples collected in feeding vs non-feeding contexts (GLMM, likelihood ratio test, chi-sq = 0.04, df = 2, p = 0.98). Females had higher uOT concentrations after feeding and engaging in GG-rubbing, compared with post-feeding samples without any sexual interactions (likelihood ratio test, chi-square = 10.63, df = 1, *p* = 0.001, est. ± SE = 0.95 ± 0.10, $p < 0.001$, see Table S6). These combined results suggest that the link between specific sexual interactions and elevated uOT is independent of feeding behavior.

We observed *n* = 38 independent coalitions (0.03 per hour), of which 24% (n = 9) involved more than two coalition partners, and 71% (*n* = 27) included unrelated coalition partners. Consistent with sex differences in cooperation more generally, the majority of non-kin coalitions occurred among females (73%, *n* = 37 dyads), while 24% of coalitions (*n* = 12 dyads) involved opposite-sex partners and only 5% of coalitions occurred among males (n = 2 dyads). Unrelated dyads who had more sexual interactions also participated in more joint coalitionary aggression (GLMM, likelihood ratio test, chi-sq = 12.42, df = 3, *p* = 0.006, est. ± SE = 0.66 ± 0.26, *p* = 0.01, see Fig. 3 and Table 4). In contrast with predictions from the coalitionary support hypothesis, this effect was similar for intra- as well as inter-sexual dyads. However, female dyads tended to engage in more joint

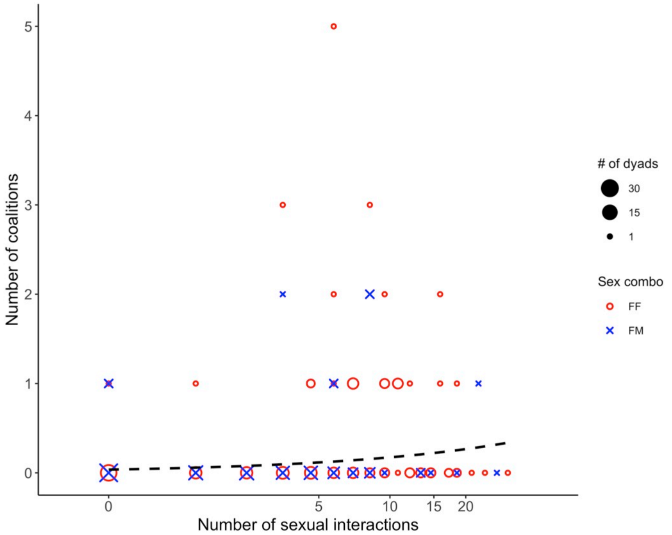

Fig. 3. Relationship between dyadic frequency of sexual interactions (log transformed) and participation in joint coalitionary aggression. The size of the shapes indicates the number of dyads receiving each score. For full model results see Table 4.

Table 4

Results of a GLMM measuring how the number of sexual interactions between partners (corrected for observation time), and the sex of the partner impact on the amount of coalitionary support between partners. Statistically significant predictors ($p < 0.05$) are indicated in bold.

Term	est ± SE	chi-sq	df	p value
Intercept	−2.9 ± 0.50			
Number of sexual interactions	**0.66 ± 0.26**	**7.12**	**1**	**0.01**
Dyadic sex combination (FF)	0.82 ± 0.50	2.71	1	0.10

coalitionary aggression than did inter-sexual dyads (see Fig. 3 and Table 4).

4. Discussion

Results of this study support a link between habitual same-sex sexual behavior and cooperation and suggest a novel mechanism by which such sexual behavior may promote additional cooperation in female bonobos, via oxytocinergic effects. Female preferences for female over male sexual partners in feeding contexts are reflected in an increase in close proximity and uOT following same-sex but not opposite-sex sexual interactions. Furthermore, female dyads that have higher frequencies of sexual interactions also support each other more often in intra-sexual coalitions, which reinforce female priority of access to preferred resources (Nurmi et al., 2018) and may reduce male harassment (Tokuyama and Furuichi, 2016). Future efforts will focus on increasing the number of physiological samples to measure changes in uOT following sexual interactions that co-occur with additional cooperation, such as coalitionary support or food sharing, in comparison with sexual interactions without any additional cooperation. This will help to further clarify the role of oxytocin and sexual interactions in facilitating cooperation among female bonobos.

Among non-kin, both intra- and inter-sexual dyads who engaged in more frequent sexual interactions were more likely to engage in joint coalitionary aggression against third parties. These results are interesting, given that previous investigations considering only female dyads have failed to find a link between GG-rubbing and coalitionary support (Moscovice et al., 2017; Tokuyama and Furuichi, 2016). In addition to including data from inter-sexual dyads, our analysis also differs from a previous study at this site (Moscovice et al., 2017) in that we included data from polyadic coalitions, which increased our sample size and allowed us to test whether dyads who exhibit more sexual behavior also engage in a greater number of coalitions, rather than merely measuring coalitionary support as present or absent in dyads. This distinction is important because effects of socio-positive interactions on associated oxytocin release and subsequent motivations to cooperate are likely to be cumulative, becoming stronger in dyads who have more opportunities to engage in emotionally-rewarding sexual interactions (Grewen et al., 2005).

Planned comparisons of the significant test predictors in the post-sex physiology model indicate that post-copulation uOT samples did not consistently differ from baseline. Vagino-cervical stimulation is considered a potent trigger of OT release in females more generally (Borrow and Cameron, 2012), but there are also a range of contextual factors that can influence OT responses to sexual stimuli, including the intensity of orgasm (humans: Carmichael et al., 1994; rabbits: Todd and Lightman, 1986), and the extent to which females have control over their sexual interactions (rats: Nyuyki et al., 2011). Our results suggest that in bonobos as well, oxytocinergic responses to sexual interactions are mediated by additional contextual factors.

Behaviorally, there are important distinctions between GG-rubbing and copulations that may help to explain the differences in underlying physiology. While copulations among wild bonobos most frequently occur in a ventro-dorsal position (Furuichi, 1987; Thompson-Handler et al., 1984, see Fig. S3a), GG-rubbing requires face-to-face contact, often involving mutual gaze, as well as a high degree of coordination of body movements to achieve and maintain genital stimulation (see Fig. S3b). In humans, mutual gaze and behavioral coordination are important for the formation of various social attachments and increases in these behaviors are associated with increases in peripheral OT across a range of relationships, including between mothers and infants (Feldman, 2012), romantic partners (Grewen et al., 2005; Schneiderman et al., 2012) and between dog owners and their pets (Nagasawa et al., 2009). GG-rubbing may thus be an especially effective means of communicating about trust and motivations to cooperate (Wrangham, 1993), which may also correspond with increases in peripheral OT. There is also anatomical and behavioral evidence that GG-rubbing provides direct clitoral stimulation, and is likely to be associated with orgasm in female bonobos (Blount, 1990; Dahl, 1985). The observed increases in uOT specifically in response to GG-rubbing provides further support for a link between GG-rubbing and orgasm.

We did not directly test whether GG-rubbing contributes to cooperation by promoting the establishment and maintenance of selective social relationships (e.g. Idani, 1991) or by reducing social conflict among partners who may not otherwise be strong associates (e.g. de Waal, 1987; Moscovice et al., 2017). However, our measure of dyadic relationship quality, which was weighted to reflect stronger or weaker social preferences than on average for each sex combination, did not predict any of the behavioral or physiological outcomes. Thus our results are more consistent with the 'reductions in social conflict' hypothesis to explain how habitual same-sex sexual interactions influence cooperative outcomes for female bonobos. Same-sex sexual behavior may reduce social conflict in part by promoting close proximity between partners, which may lead to additional mutually-beneficial cooperation such as co-defending access to food (Nurmi et al., 2018). In a captive study, females faced with a potentially competitive feeding task exhibited increases in same-sex but not opposite-sex sexual behavior and then shared access to a monopolizeable food exclusively with other females (Hohmann et al., 2009). These females also exhibited decreases in concentrations of the stress hormone cortisol during the feeding task, suggesting a possible physiological link between increased GG-rubbing and reductions in social tension.

Among chimpanzees, same-sex sexual interactions are sometimes observed in socially-tense situations, especially among males (e.g. Romero et al., 2011). However, such behavior is infrequent in comparison to the frequencies observed among female bonobos (reviewed in Gruber and Clay, 2016). Chimpanzees do engage in frequent social grooming and exhibit selective increases in uOT following grooming, but in this case increases in uOT concentrations are predicted by the strength of the dyadic social relationship, and not by the sex of the grooming partner (Crockford et al., 2013). While these results appear to contrast with our findings, they make sense in light of the differences in social dynamics between these two close phylogenetic relatives (Surbeck et al., 2017a). In chimpanzees cooperation is mainly dyadic and is largely predicted by the strength and stability of grooming relationships between kin and a subset of non-kin bond partners (reviewed in Mitani, 2009). In contrast in bonobos cooperation occurs among a wide range of primarily female social partners (Moscovice et al., 2017; Yamamoto, 2015), is frequently polyadic (Nurmi et al., 2018; Tokuyama and Furuichi, 2016) and is not linked to measures of association and grooming (Moscovice et al., 2017; Tokuyama and Furuichi, 2016). Thus, in both *Pan* species, individuals exhibit selective changes in uOT following socio-positive interactions with partners who are more likely to cooperate in other contexts.

5. Conclusions

Although same-sex sexual interactions have been reported across a wide range of animal taxa (Bailey and Zuk, 2009), they occur as frequently as opposite-sex sexual interactions in only a few species and sex combinations, including male dolphins and female bonobos. In humans, cross-culturally and historically a proportion of the population engages in habitual or exclusive same-sex sexual interactions (reviewed in Kirkpatrick, 2000; Sommer and Lowe, 2018). Research on the evolution of non-reproductive sexual behavior in humans often emphasizes its role in maintaining stable opposite-sex pair bonds that improve access to resources for females and paternity certainty for males (Chapais, 2013; Gangestad and Grebe, 2017). However, the alliance theory of homosexual behavior (Kirkpatrick, 2000; Muscarella, 2005) emphasizes the importance of stable same-sex alliances that are often reinforced through sexual interactions in providing benefits such as social support, resource sharing and mutual defense (Kirkpatrick, 2000; Sommer and Lowe, 2018). Comparative evidence suggests that this theory may also be relevant for explaining the evolution of habitual same-sex sexual behavior in species such as dolphins and bonobos that share with humans complex fission-fusion social systems, high levels of social cognition and extensive cooperation outside of kinship.

In contrast with evidence in humans and dolphins, in bonobos females do not restrict same-sex sexual interactions to a subset of preferred partners (Hohmann and Fruth, 2000; Moscovice et al., 2017). Rather, females use sexual interactions flexibly to signal social tolerance and promote close proximity with a wide range of female partners. Female sexual interactions are associated with OT release that may facilitate additional female-biased cooperation. These results provide a novel example of the co-option of the oxytocinergic system outside of kinship and selective pair bonds to facilitate flexible cooperation in a close phylogenetic relative of humans.

CRediT authorship contribution statement

Liza R. Moscovice: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Funding acquisition. **Martin Surbeck:** Conceptualization, Methodology, Investigation, Writing - review & editing, Funding acquisition. **Barbara Fruth:** Writing - review & editing, Funding acquisition. **Gottfried Hohmann:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Adrian V. Jaeggi:** Writing - review & editing, Funding acquisition. **Tobias Deschner:** Conceptualization, Methodology, Writing - review & editing, Resources, Funding acquisition.

Declaration of competing interest

None.

Acknowledgements

This research was supported by the Max Planck Society and by additional funding from the Leakey Foundation, the Wenner-Gren Foundation (grant no. 8450 to L.R.M and grant no. 8914 to M.S.), the National Geographic Society (GEFNE119-14 to M.S.) and the VolkswagenStiftung (Grant No. 86048 to L.R.M.). In addition, L.R.M. was supported by Emory University and M.S. was supported by the SNSF. We thank the Institut Congolais pour la Conservation de la Nature (ICCN) for permission to work in the Democratic Republic of Congo, and the people of the village of Lompole for granting access to their forest. Laura Martinéz-Inigo, Pamela Heidi Douglas, Lucas Goldstone, Max Kölbl and Luis Férnandez assisted with field data and sample collection. Vera Schmeling and Roisin Murtagh provided important assistance in sample analysis and in validation of the EIA. Franka Simea Schaebs and Verena Behringer provided helpful input on laboratory methods. Frieder Hadlich provided help with figures. We thank Kim Wallen and two anonymous reviewers for their helpful feedback that led to several improvements to the original manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2019.104581.

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