The submissive pattern of postconflict affiliation in asymmetric relationships: a test in male and sexually coerced female baboons.

Alice Baniel, Christine Webb, Guy Cowlshaw, Elise Huchard

► To cite this version:

Alice Baniel, Christine Webb, Guy Cowlshaw, Elise Huchard. The submissive pattern of postconflict affiliation in asymmetric relationships: a test in male and sexually coerced female baboons.. *Animal Behaviour*, 2021, 175, pp.87-97. 10.1016/j.anbehav.2021.02.014 . hal-03192677

HAL Id: hal-03192677

<https://hal.science/hal-03192677>

Submitted on 10 Jun 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Published in final edited form as:

Animal Behaviour (2021), 175: 87-97. <https://doi.org/10.1016/j.anbehav.2021.02.014>

The submissive pattern of postconflict affiliation in asymmetric relationships: a test in male and sexually coerced female baboons

Alice Baniel^{1,2,6,*}, Christine E. Webb^{3,6}, Guy Cowlshaw⁴, Elise Huchard^{5,7}

¹ Institute for Advanced Study in Toulouse, Toulouse, France.

² Department of Anthropology, Stony Brook University, Stony Brook, NY, U.S.A.

³ Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.

⁴ Institute of Zoology, Zoological Society of London, London, U.K.

⁵ Institute of Evolutionary Biology of Montpellier (ISEM), UMR 5554, Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France

⁶ These authors contributed equally

***Corresponding author.**

E-mail: alice.baniel@gmail.com

ABSTRACT

Reconciliation, or postconflict (PC) affiliation between former opponents, is a widespread conflict management strategy in animal societies, so-named for its relationship–repair function. However, another possibility is that PC affiliation reflects a submissive response of victims towards aggressors to limit conflict escalation when the power imbalance between the opponents is large. Here we investigated this hypothesis in a highly asymmetric relationship context: heterosexual wild chacma baboon, *Papio ursinus*, dyads involving sexually receptive females, where sexual coercion by males is common. We found several lines of support for the submissive hypothesis in the context of sexual coercion. First, rates of sexual and nonsexual PC affiliative interactions in these dyads exhibited significant and comparable increases compared to baseline conditions (ca. three-fold). Second, the baseline strength of the heterosexual social bond (outside of an aggressive context) did not predict the likelihood of sexual and nonsexual PC affiliation. Third, mate-guarded females, which could not escape the proximity of their aggressor (and faced high risks of renewed aggression), exhibited the most PC affiliation with males. Finally, most PC affiliation sequences contained at least one sexual act, and the first sexual affiliative act was primarily initiated by females via presenting. This suggests that female victims affiliate in a submissive way by displaying sexual compliance to aggressive males. Nevertheless, we cannot exclude the co-occurrence of ‘true’ reconciliation: a quarter of PC affiliations between males and receptive females were exclusively nonsexual, and the first general affiliative act was equally initiated by males and females. Overall, our results suggest a mixed PC affiliation strategy in which submission may play an important role in highly asymmetric relationships and indicate the function of PC affiliation may vary from submission to reconciliation depending on the species, dyads, individuals and conflicts under consideration. Future research on PC interactions would usefully consider this full spectrum.

KEYWORDS

aggression, chacma baboon, male–female association, reconciliation, sexual coercion

INTRODUCTION

Two animals are said to have reconciled if, soon after an aggressive interaction between them, they engage in friendly contact (de Waal & van Roosmalen, 1979). Several nonexclusive hypotheses have been proposed to predict the distribution of reconciliation across opponent dyads (Arnold, Fraser, & Aureli, 2010), with proximate or ultimate explanations emphasizing its conciliatory nature (see Table 1). Friendly reunions following conflict may serve to repair mutually beneficial (i.e. fitness-enhancing) relationships (the ‘valuable relationship’ hypothesis: Kappeler and van Schaik 1992; de Waal and Aureli 1997), attenuate uncertainty or anxiety (the ‘uncertainty reduction’ hypothesis: Aureli, 1997; Aureli & van Schaik, 1991), or communicate peaceful intentions between former opponents (the ‘benign intent’ hypothesis: Silk 1996). The ‘integrated’ hypothesis combines the uncertainty reduction and valuable relationship hypotheses by proposing that disruptions to valuable bonds are particularly stressful for opponents, and therefore warrant stronger resolution attempts (Aureli, 1997). Although they occasionally generate different predictions, these hypotheses are generally treated as complementary, with expressions of benign intent serving to reduce uncertainty about the conflict and thereby restore valuable relationships (Aureli, Cords, & van Schaik, 2002; Cords & Aureli, 1996; Schaffner & Aureli, 2004). Tests of these hypotheses have commonly focused on primates, where the frequency and patterning of reconciliation vary according to the nature of the social systems and relationships under study (Arnold et al., 2010).

Theory and research on reconciliation have previously emphasized variation in postconflict (PC) behaviour across different levels of dominance asymmetry, with more

egalitarian species showing higher conciliatory tendencies than despotic ones (Thierry, 2000; Thierry et al., 2008). However, power imbalances have largely been considered at the level of the species or social organization rather than the dyadic level. In more hierarchical relationship contexts, two opponents may not ascribe equivalent fitness value to each other, and/or may not share equally in their uncertainty or anxiety about renewed aggression. These asymmetries highlight how the form, motive and function of PC behaviour may vary even within a dyad in ways not explicitly captured by existing reconciliation frameworks. Reflecting the full spectrum and complexity of primate social relationships, PC interactions can either be more reciprocal and conciliatory or hierarchical and coercive in nature.

One intriguing possibility is that, in the context of highly asymmetrical relationships, PC affiliation represents a submissive response by victims towards their recent aggressors (the ‘submissive’ hypothesis; de Waal, 1986; Kutsukake & Clutton-Brock, 2006). In other words, rather than expressing a motivation for peaceful and friendly interactions, victims of aggression may affiliate out of fear in order to accede to aggressors’ demands by displaying submission/compliance in an attempt to limit conflict escalation and injury. Several theoretical and experimental studies have emphasized the ubiquity of hidden threats and punishment in animal societies, and their role in enforcing cooperation across a range of contexts, particularly when the power imbalance between the opponents is pronounced (Cant, 2010; Clutton-Brock & Parker, 1995a). We propose here that prolonged intimidation and repeated aggression in a given dyad with high power asymmetry may yield PC interactions that are more characteristic of a submissive rather than conciliatory scenario, even if it takes the form of a typical affiliation (e.g. grooming).

At the ultimate level, the submissive hypothesis and the uncertainty reduction hypothesis may generate similar predictions, i.e. PC affiliation functions to limit renewed aggression and conflict escalation (Table 1). However, these hypotheses differ in at least

three important ways. First, at the proximate level, the underlying motivations for PC affiliation differ. In the uncertainty reduction hypothesis, both victims and aggressors affiliate to reduce physiological stress and anxiety about future interactions (the distress may come from the damage to a valuable relationship, or because opponents live in proximity and may incur future costs, for example of increased vigilance or decreased tolerance, if conflicts persist; Aureli et al., 2002). In contrast, the submissive hypothesis posits that victims submit to comply with aggressors out of fear, often conferring immediate social/sexual benefits upon aggressors. Second, the submissive hypothesis posits that victims affiliate to comply with their aggressor's demands, rather than to preserve a valuable relationship (as clarified by the integrated hypothesis). Consequently, the asymmetry of power between opponents rather than the strength of their social bond (relationship value) should predict the occurrence of PC affiliation. Third, the submissive hypothesis predicts that victims would be more likely to initiate PC affiliation, in contrast to the uncertainty reduction hypothesis, in which such distinctions are neither categorically made nor found (Arnold et al., 2010).

PC interactions among heterosexual pairs have rarely been studied in wild promiscuous primates but represent an ideal context in which to explore this submissive framework because of pronounced sexual dimorphism and power asymmetries between males and females. Recent work has highlighted a previously underappreciated density and complexity of primate heterosexual relationships (Archie, Tung, Clark, Altmann, & Alberts, 2014; Fürtbauer, Heistermann, Schülke, & Ostner, 2014; Machanda, Gilby, & Wrangham, 2013; Reddy & Mitani, 2020). On the one hand, males and females can form enduring bonds, which enhance individual survival and reproductive success (Archie et al., 2014; Campos et al., 2020; Palombit, 2000). On the other hand, heterosexual relationships can be violent since males commonly attack sexually receptive females to achieve mating benefits, either immediately (through forced copulation or sexual harassment) or subsequently (through

intimidation or punishment; Clutton-Brock & Parker, 1995b; Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007; Smuts & Smuts, 1993). Sexual coercion usually targets the most fertile females and can be costly in terms of stress and injury for the victims (Baniel, Cowlishaw, & Huchard, 2017; Colmenares, Polo, & Herna, 2014; Kitchen et al., 2009; Muller et al., 2007; Swedell et al., 2014). Females could thus benefit from evolving behavioural strategies to decrease the chances of escalated or renewed aggression from coercive males.

In the handful of studies that have investigated male–female PC affiliation, sexual behaviours have rarely been systematically analysed. Generally, whereas noncopulatory sexual behaviours (e.g. presenting and mounting) feature commonly in studies of reconciliation, copulations have been omitted as a form of PC affiliation for a number of potential reasons (e.g. they do not occur among same-sex dyads or they do occur but are not interpreted as affiliative acts). When sociosexual contacts are incorporated, they are often aggregated with other affiliative contacts, precluding formal tests between reconciliation and sexual coercion (but see Call et al. 1999). To our knowledge, bonobos, *Pan paniscus*, are the only species for which copulations and nonconceptive sexual behaviours are thought to play a key role in conciliatory reunions (Clay & de Waal, 2014; Palagi, Paoli, & Tarli, 2004). In less tolerant animal societies where aggression is more severe and asymmetric, it is possible that PC affiliations traditionally interpreted as conciliatory reunions in some cases represent submissive responses to sexual (or other forms of) coercion. In particular, sexual harassment, defined as repeated and costly aggressive mating attempts by males that induce females to mate (Clutton-Brock & Parker, 1995b), is operationally identified by increases in males' chances of mating with their victims immediately following aggression (compared to baseline chances). Thus, the conceptual frameworks supporting reconciliation and sexual harassment make overlapping predictions regarding increased rates of affiliation following conflicts,

provided sexual behaviours count as affiliative interactions. Yet the sexual coercion and reconciliation literatures rarely reference one another.

In this study, we investigated the form and function of PC affiliative interactions among males and sexually receptive (i.e. swollen) females in wild chacma baboons, *Papio ursinus*. Chacma baboons live in female-bonded societies, where immigrant males fight to achieve dominance and monopolize swollen females through long (i.e. several consecutive days) episodes of mate guarding around ovulation (Bulger, 1993; Weingrill, Lycett, Barrett, Hill, & Henzi, 2003). This mate guarding is coercive in the sense that females cannot escape male proximity, and males regularly herd their consort females away from rivals (Cheney & Seyfarth, 1977; Kitchen, Cheney, & Seyfarth, 2005; Kitchen et al., 2009). While reconciliation has been documented in this species, the focus has predominantly been on female–female dyads (Cheney, Seyfarth, & Silk, 1995; Silk, Cheney, & Seyfarth, 1996; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007). Only one study has focused on PC affiliation among heterosexual chacma baboon dyads, which found that reconciliation commonly occurs between males and pregnant/lactating females when they are involved in a ‘friendship’, a long-term heterosexual social bond formed around an infant (Webb, Baniel, Cowlshaw, & Huchard, 2019). Little is known about patterns of PC affiliation between males and swollen females. Male aggression towards swollen females is common in this species, inflicting frequent injuries to females (Baniel et al., 2017; Kitchen et al., 2009), and functions as a form of sexual intimidation, where repeated aggression throughout the cycle increases the aggressor’s chances of consorting with the female around ovulation (Baniel et al., 2017). There is, however, no evidence for sexual harassment, where males harass females until they accept matings, as there is no immediate increase in the rate of mating following male aggression (Baniel et al., 2017). On a spectrum ranging from submission to reconciliation, affiliation following conflicts between males and swollen females in this

coercive context may fall closer to the former. In this case, female victims would adopt a compliant strategy to reduce the costs of conflict escalation (e.g. injury), while male aggressors enact a coercive strategy to secure immediate or future mating opportunities (Table 1).

Here, we tested whether the pattern of PC affiliation between heterosexual pairs involving sexually receptive females could be explained by the submission hypothesis in the context of sexual coercion, via the following four predictions. First, we predicted that increases in PC affiliation between males and swollen females would involve both sexual and nonsexual affiliation (Prediction 1, P1), as intimidated females may use any behavioural strategy at their disposal, for example sexual solicitations or grooming, to appease coercive males. Second, we predicted that the rate of PC affiliation between a male and swollen female would not reflect the strength of their social bond in baseline conditions (i.e. outside an aggressive context; P2). Third, we predicted that the rate of PC affiliation would increase in more coercive contexts; namely, mate-guarded females should display a higher rate of PC affiliation than unguarded females, because they cannot escape the spatial proximity of their aggressor and thus have a higher incentive to de-escalate conflicts with him (P3). Lastly, we predicted asymmetrical patterns in who initiates PC affiliation, particularly when it comes to sexual affiliations, where females should be mostly responsible for initiating the first affiliative act (P4a) and/or the first sexual act of the PC affiliation sequence (P4b) in order to display submission and propose positive sociosexual contacts to coercive males following aggression.

This predictive framework differentiates itself from that generated by previous hypotheses to explain pos-conflict affiliation, including both the sexual harassment hypothesis, and the integrated hypothesis. According to the former, if patterns of affiliation solely reflected sexual harassment, we would expect no support for P1 (rather, we would

expect only sexual PC affiliation to increase) or P4 (we would expect males rather than females to initiate copulations). According to the latter, if patterns of affiliation solely reflected attempt to reduce anxiety and repair a valuable bond, we would expect no support for P2 or P3 (because we would expect baseline affiliation rather than the power asymmetry between opponents to predict PC affiliation).

METHODS

Data Collection

We studied two habituated groups of wild chacma baboons living at Tsaobis Nature Park, a semiarid environment in Namibia (Cowlshaw, 1997) over four field seasons (2005, 2006, 2013 and 2014) of variable length (5–9 months per year). Groups contained 3–11 adult males and 9–19 adult females according to the period of study. Dominance ranks of adult males and females were established using both ad libitum and focal observations of dyadic agonistic interactions (see Appendix 1)

The reproductive state of each adult female was monitored daily and categorized as pregnant, lactating, cycling swollen (i.e. sexually receptive with a perineal swelling) and cycling nonswollen (i.e. between two swelling phases). Mate-guarding episodes, defined as periods when swollen females were constantly followed by a male that mated exclusively with them and prevented others from doing so (Alberts, Altmann, & Wilson, 1996), were monitored ad libitum daily, and confirmed or updated accordingly for each focal observation. In the following analyses, we focused only on cycling swollen females and their interactions with adult males.

Observers followed groups on foot daily from dawn to dusk, conducting 1 h focal observations on all adult females and males, spread equally across the day. In total, we collected 1418 focal observations on 40 swollen females (mean $\pm$ SD: 35.5 $\pm$ 32.2 observations

per individual) and 524 observations on 25 males (21.0 ± 8.8 ; male focal observations were only collected in 2013–2014). During observations, we continuously recorded all occurrences of male–female agonistic and affiliative interactions involving the focal individual, including the partner’s identity and the direction of the interaction. Agonistic interactions comprised attacks (any aggressive physical contact), chases and physical threats (including staring, head bobbing and ground sweeping while oriented towards the targeted individual) and approach–avoid interactions (supplants, displacements). For the analysis of PC affiliation, we only used attacks, chases and physical threats because more subtle agonistic interactions such as displacements, supplants or vocal threats are less likely to be stressful for the victim. As expected on the basis of pronounced sexual dimorphism, 98% of aggression between males and swollen females (i.e. 92 of 94 observed conflicts) were directed from males to females. Affiliative interactions included grunts, positive facial expressions (come-here faces, lip-smacks, sniff-mouths), positive physical contacts (touching, embracing, grooming, sniffing or touching perineum, mounting, grasping pelvis) and sexual behaviour (presents, copulations). Note that swollen females in this species invite males to copulate by presenting, which can potentially directly lead to sex. A female’s presenting behaviour can be either followed by a copulation (in which case, observers only noted the copulation and indicated that the copulatory act was female initiated) or not followed by a copulation when the male ignores the female’s initiative (in which case, observers only recorded the presenting bout). For each copulation, we thus recorded whether it was initiated by the female (via presenting) or by the male (by approaching and usually grabbing the female’s hindquarters).

Statistical Analyses

Rate of sexual and nonsexual PC affiliation

We first tested whether swollen females and males exhibit higher rates of affiliation following male aggression (compared to baseline conditions), and whether any increase detected in PC affiliation is primarily attributable to increases in sexual versus nonsexual behaviours (P1). Using the collected focal observations of males and swollen females, and following a statistical methodology previously validated in our study system (Webb et al., 2019), we established the rate of (1) sexual affiliation (presenting and copulations) and (2) nonsexual affiliation (e.g. grunts, grooming, etc) between a given heterosexual dyad immediately after a conflict (i.e. the PC sexual and nonsexual affiliation rate) versus in the absence of an immediate conflict (i.e. the baseline sexual and nonsexual affiliation rate). Specifically, for each heterosexual dyad that exchanged at least one act of aggression, we first identified all focal observations that were conducted on both individuals in a given year and in which the female was swollen. Then, we split these observations into two categories.

First, the PC sample, in which we pooled all 15 min observations following a conflict between the same dyad together (i.e. dyads had between one to five conflicts, each of which generated a 15 min observation period, so we pooled the corresponding 15–75 min of PC observation to calculate the rate of PC affiliation of a given dyad). We chose a duration of 15 min following each conflict because our validation study identified this time window as the best trade-off between the number of available PC observations (which decreases as time period increases) and the strength of the reconciliation signal (which increases as time period increases; Webb et al., 2019). Incomplete PC observations (e.g. due to the focal individual going out of sight or the occurrence of another bout of aggression shortly after the first one) were retained only if they lasted for at least 9 min without interruption (mean $\pm$ SD=12.1 $\pm$ 1.6 min, $N=15$ incomplete PC of 94 total PC observations). This 9 min threshold was chosen because the mean latency between aggression and the first affiliative act was 4.5 $\pm$ 4.2 min (calculated over 37 occurrences of PC affiliation in complete PC observations). We thus

considered that 9 min would be enough time to capture, in most cases, the potential occurrence of PC affiliation acts.

Second, for the baseline sample, we pooled the rest of the focal observations of the dyad. To establish these baseline rates, we excluded each 15 min period following a conflict (i.e. the PC samples), as well as each 15 min period at the start of the focal observation or following its resumption after the focal individual briefly went out of sight (if an aggression occurred between the two members of the dyad when they were not visible). Third, we tabulated the number of times that the two individuals affiliated sexually or nonsexually in the PC and baseline samples, respectively, as well as the total observation time of the corresponding (i.e. PC or baseline) sample.

We compared the strength of the PC affiliation signal between males and swollen females when considering only sexual affiliations versus only nonsexual affiliations. We thus ran two negative binomial generalized linear mixed models (GLMMs) using the total number of affiliations exchanged between each male and swollen female dyad as the response variable and including (1) only sexual affiliations or (2) only nonsexual affiliations in the count. Fixed effects comprised the type of observation (PC versus baseline samples) and the dominance ranks of the female and male. The total observation time of the corresponding sample (PC or baseline) was log transformed and included as an offset variable. Random effects comprised the identity of the female and male.

Determinants of the occurrence of PC affiliation

We then investigated the determinants of the presence (versus absence) of PC affiliation in the subsequent 15 min following aggression ($N=94$ PC observations), namely with respect to the strength of the affiliative relationship of the dyad in baseline conditions (i.e. outside an aggressive context, P2) and female mate-guarding status (P3). We ran a binomial GLMM

using the occurrence of affiliation following an aggressive event (yes/no) as the response variable. Fixed effects comprised the mate-guarding status of the swollen female (unguarded versus mate-guarded by the aggressor), the dyad's baseline affiliation rate (calculated via the occurrence of sexual and nonsexual behaviours in swollen periods), female rank, male rank and the type of aggression (chase, attack, threat). For both models, random effects comprised the identities of the female and male. As supplementary analysis, we also calculated the dyad's baseline affiliation rate using focal observations where the female was nonswollen only.

Pattern of initiation of PC affiliation

We tested for asymmetry in the pattern of initiation of the first PC affiliative act (P4a) and of the first sexual act of a PC sequence (P4b) between male and female opponents using two-tailed exact binomial tests.

All GLMMs were run using the `glmer` function of the `lme4` package (Bates, Maechler, Bolker, & Walker, 2014) in R version 3.5.2 (R Core Team, 2018). The significance of the fixed factors was tested using a likelihood ratio test, LRT (assuming an asymptotic chi-square distribution of the test statistic) via the `drop1` function. We further computed the 95% parametric bootstrap confidence intervals of fixed factors (using `confint.merMod`) and checked that they did not cross zero. To validate models, we examined the distribution of residuals and confirmed the absence of overdispersion by using the `DHARMA` package (Hartig, 2018). Sample size is indicated for each model in the relevant output table.

Ethical Note

This study was strictly observational and relied on behavioural data collected noninvasively on animals well habituated to human observers. Our research procedures were evaluated and approved by the Ethics Committee of the Zoological Society of London and the Ministry of Environment and Tourism (MET), Namibia, and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. Our research was conducted under MET permit numbers 886/2005, 1039/2006, 1786/2013 and 1892/2014.

RESULTS

Rate of sexual and nonsexual PC affiliation

We observed 94 incidents of male aggression towards swollen females. Of these, 73 had a documented context (as inferred by the observer): 42% were unprovoked (no apparent reason for the male to attack the female), 25% were apparently triggered by the female leaving the male's spatial proximity and may represent herding, 15% involved redirected aggression to the female following aggression received from a rival male, 10% occurred during feeding bouts and 7% occurred during intragroup male display (wahoo bouts) or intergroup interactions. Of these 94 observed agonistic interactions, 43 (46%) were followed by at least one affiliative act between the male and swollen female in the following 15 min. The latency before the first affiliative act was 4.7 ± 4.2 min on average (range 0–13 min). As expected under P1, the observed rates of affiliation between males and swollen females following conflicts were significantly higher (about three times more) than in baseline samples when considering exclusively sexual behaviours (mean rate of affiliation $\pm$ SD in PC: 0.033 ± 0.054 events/min; in baseline: 0.010 ± 0.011 ; Table 2, Fig. 1a). The same was true when considering exclusively nonsexual behaviours (mean rate of affiliation $\pm$ SD in PC: 0.044 ± 0.069 events/min; in baseline: 0.013 ± 0.017 ; Table 2, Fig. 1a). Females were more likely to exhibit

sexual affiliations (but not more nonsexual affiliations) with high-ranking males in both PC and baseline conditions.

Determinants of the occurrence of PC affiliation

Heterosexual dyads with strong affiliative relationships in baseline conditions were not more likely to display affiliation following aggression (Table 3, Appendix 2, Table A1), consistent with P2. Nevertheless, there was a high uncertainty around this effect, with a lot of variation across dyads (Appendix 2, Fig. A1). According to P3, higher rates of PC affiliation are expected when females are confined in close proximity to mate-guarding males. The need for PC affiliation under these circumstances is highlighted by the finding that 38 of 41 recorded incidences of male aggression towards mate-guarded females came directly from their consort male. As predicted, males and swollen females involved in a mate-guarding consortship were more likely to exhibit PC affiliation than when they were not involved in a consortship (Table 3, Fig. 1b).

Pattern of initiation of PC affiliation

When PC affiliation occurred ($N=43$ cases), 32 (74%) cases involved at least one sexual behaviour and 11 (26%) involved exclusively nonsexual behaviours in the 15 min sequence following aggression. Among these 43 PC sequences, the first PC affiliative act was initiated equally by males and females, contrary to P4a: males initiated 23 PC affiliations and females initiated 20 PC affiliations (two-tailed exact binomial test: $P=0.761$; 95% confidence interval: 0.31–0.62; see Fig. 2a and Appendix 2, Table A2 for behavioural details on the first affiliative act). However, when focusing on those 30 PC affiliations that contained at least one sexual act (two sexual interactions had unknown initiators), the first sexual behaviour was initiated 21 times by the female, mostly via presenting, and nine times by the male, in

accordance with P4b (two-tailed exact binomial test: $P=0.043$; 95% confidence interval: 0.51–0.85; Appendix 2, Table A2, Fig. 2b). In the 11 PC affiliations that remained exclusively nonsexual, three were initiated by females and eight by males.

DISCUSSION

The present study reveals that in highly asymmetrical relationship context, like those characterizing heterosexual dyads in chacma baboons, PC affiliation may frequently correspond to a submissive response from victims to a powerful opponent, rather than reflecting a conciliatory pattern. The evidence for submission by sexually receptive females to aggressive males in chacma baboons in response to sexual coercion is fourfold. First, the frequency of sexual interactions increased three-fold following aggression, just like the frequency of nonsexual affiliation (compared to baseline conditions). Second, the baseline strength of the heterosexual social bond (i.e. the ‘value’ of their relationship) did not predict the likelihood of PC affiliation. Third, dyads involving males and mate-guarded females, who faced high risks of renewed aggression due to the permanent proximity of their aggressor, exhibited the highest rates of PC affiliation. Finally, most PC affiliation sequences (74%) contained at least one sexual act, and the first sexual affiliative act was primarily initiated by females via presenting. This suggests that receptive female victims often affiliate in a submissive way by displaying sexual compliance (i.e. proposing matings) to coercive males to limit the chances of escalated aggression.

PC Affiliation Reflects Female Submission to Male Intimidation

The observed pattern of PC affiliation between male and female baboons does not reflect a strict sexual harassment strategy, where males attack or persistently run after females until they accept mating, as reported in some ungulates (Clutton-Brock & Parker, 1995b) and

orangutans (Fox, 2002; Knott, 2009). Indeed, male baboons seldom initiated copulations following aggression (male-initiated copulations only represented 18% of the first affiliative act and 30% of the first sexual act; see Appendix 2, Table A2). Instead, females were mostly responsible for initiating PC sexual behaviour by presenting to the male. Furthermore, the observed increases in rates of nonsexual affiliation following conflicts were not expected under the sexual harassment hypothesis, which exclusively focuses on sexual behaviour.

The fact that female baboons are primarily responsible for initiating the first sexual act following aggression is more compatible with a scenario of long-term sexual intimidation, where females would express sexual compliance towards males to appease them and limit escalated aggression and future injuries. Males, on the other hand, may rarely pursue immediate mating opportunities following aggression (and female presenting) to avoid unnecessary matings, especially when the female is not in her ovulatory window (which can be costly, e.g. sperm depletion; Gesquiere, Wango, Alberts, & Altmann, 2007; Moscovice et al., 2010; Weingrill, Lycett, & Henzi, 2000). Instead, they seem to use repeated aggressive and affiliative behaviour to optimize their control of female spatial behaviour. In our population, 42% of male attacks towards swollen females are unprovoked, sudden and probably unpredictable. Such randomly timed attacks provide an effective means for the aggressor to generate continuous anxiety, vigilance and chronic stress in his victims (Silk, 2002). In line with this, half of our observed PC affiliation events happened in the context of mate guarding, where females have no choice but to stay in the proximity of their aggressor and are thus likely to face renewed aggression. Mate-guarding episodes are particularly long in chacma baboons (between 0.5 and 32 days, mean=9 days), and can last several consecutive cycles (Baniel, Cowlshaw, & Huchard, 2016). Females might particularly benefit from displaying their compliance in this context. Similar long-term sexual intimidation strategies are also thought to occur in some chimpanzee, *Pan troglodytes*, populations: males that are

repeatedly aggressive towards particular females are more likely to mate with them during ovulatory periods and more likely to sire their offspring (Feldblum et al., 2014; Muller, Emery Thompson, Kahlenberg, & Wrangham, 2011; Muller et al., 2007; Muller, Kahlenberg, & Wrangham, 2009).

The patterns of subordination observed in female chacma baboons immediately following male aggression also resemble those seen in hamadryas baboons, *Papio hamadryas*, where males use frequent aggression to enforce the spatial proximity of females that are newly incorporated into their harem. New females spend more time affiliating with their leader male than do resident females, and in particular groom him following aggression (Swedell, 2015; Swedell & Schreier, 2009). In the long term, the aggression they face from him decreases once their social bond is established and when females are ‘conditioned’ (or ‘abducted’) to follow their leader male (Polo & Colmenares, 2012; Swedell, 2015; Swedell & Schreier, 2009). Male aggression therefore specifically targets females that are weakly bonded to the aggressor, presumably to dissuade them from dispersing or leaving male proximity. The conditioning of female hamadryas baboons is probably similar to the pattern we report in chacma baboons, particularly for consorting partners, where males may seek to condition their female consorts to stay in proximity. It would be interesting to test whether male aggression towards female chacma baboons decreases once the mate-guarding episode is well established and as females become more compliant (the same heterosexual dyad often consort during the receptive phase across several consecutive cycles), and whether females’ propensity to propose sex following aggression decreases the chances of renewed aggression or conflict escalation.

Variation in the Function of PC Affiliation

The observed pattern of affiliation is not fully compatible with true conciliatory tendencies, under which we would expect an effect of relationship quality (i.e. baseline rates of affiliation) between the two opponents on the probability of PC affiliation. In addition, we would not expect any effect of mate-guarding episodes on the probability of PC affiliation. However, we cannot exclude the occasional occurrence of ‘true’ reconciliation, alongside submission. Specifically, 26% of affiliations following conflicts between males and sexually receptive females were exclusively nonsexual, with nonsexual affiliative behaviours occurring three times more frequently than expected in baseline contexts, and symmetry in initiation patterns (of the first general affiliative act) suggesting that males and females were equally motivated to reconcile. It is noteworthy that had we only tested for a reconciliation signal, following the conventions of the reconciliation literature, we would have interpreted these findings as evidence of a conciliatory tendency.

A subset of PC interactions may thus be conciliatory, an interpretation reinforced by the existence of true reconciliation between new mothers and their male friends in the same population (Webb et al., 2019), as well as among female–female dyads in this species (Cheney et al., 1995; Silk et al., 1996; Wittig et al., 2007). This may also explain the observed trend in the effect of baseline affiliation rates on rates of PC affiliation (Appendix 2, Fig. A1), which may reflect this minority of conciliatory PC affiliation. We might expect the occasional occurrence of reconciliation between swollen females and males on the basis that a given male and cycling female dyad occasionally maintains a preferential relationship (in terms of grooming or proximity) that may last across consecutive female cycles (Baniel et al., 2016) and that may become a friendship when they conceive an offspring together, therefore affording fitness benefits to both partners (Archie et al., 2014; Cheney, Silk, & Seyfarth, 2012). For a swollen female, reconciling with males may further enable immediate benefits such as spatial association and tolerance, access to better food patches, and provide a buffer

against other aggressive groupmates. For males, reconciliation may encourage swollen females to tolerate their proximity and therefore minimize the risk of extrapair matings or the loss of mate guarding to rivals (Bercovitch, 1995; Smuts, 1985).

Sex under Coercion or Affiliative ‘Make-up’ Sex?

The mixed function of PC affiliation observed in this study, encompassing both submissive and true conciliatory behaviour, raises an interesting possibility: that when female chacma baboons mate with males following aggression, this may occasionally reflect a voluntary choice of females to use sex to reconcile with males, rather than the submissive acceptance of the sexual advances of males under coercion. In bonobos, sociosexual behaviours also occur in socially tensed situations, and although their tension alleviation function remains unclear (Hohmann, Mundry, & Deschner, 2009) such sexual interactions in PC contexts are conventionally considered friendly and conciliatory (‘make-up sex’) (Clay & de Waal, 2014; de Waal, 1987; Palagi et al., 2004). Importantly, however, these interactions predominantly occur in the context of female–female bonds and have a variety of documented nonconceptive functions (Hohmann & Fruth, 2000).

While female chacma baboons may occasionally choose to use sexual affiliations to reconcile, such voluntary choice probably does not reflect the general pattern in our population, where sexual affiliations are more likely to reflect sexual appeasement under duress given the support we found for the submissive hypothesis. So overall, although sexual PC affiliation behaviour may appear similar in baboons and bonobos, the motivational and emotional basis of PC affiliation probably differs for the initiator in most cases: whereas female baboons may generally sexually submit out of fear, female bonobos may use sexual contacts in a more symmetric way, although observations suggest that such contacts are not necessarily always consensual (Z. Clay and M. Surbeck, personal communication).

Interpretations concerning both ultimate functions and proximate motivations for PC behaviours should thus reflect the broader social dynamics of a given social system (such as power asymmetries between males and females).

Wider Implications for the Reconciliation Literature

The idea that PC affiliative behaviour, whether sexual or not, serves a submissive function contrasts with previous hypotheses, which generally revolve around conciliatory explanations (see Table 1; Aureli & van Schaik, 1991; Kappeler & van Schaik, 1992; Silk, 1996). The uncertainty reduction and integrated hypotheses emphasize the symmetric function of PC affiliation to alleviate anxiety and restore a damaged, reciprocal and mutually beneficial bond, whereas the submission hypothesis highlights its asymmetry in dyads characterized by pronounced power imbalances. While the reconciliation literature has occasionally alluded to the submissive pattern of reconciliation (de Waal, 1986; Kutsukake & Clutton-Brock, 2006), our study is the first to formally test its predictions and emphasize the full spectrum of possible PC patterns. In this study, we tested the submissive hypothesis in the specific context of coercive relationships between males and fertile female baboons, but it may apply to any kind of asymmetric relationships, which are ubiquitous in animal societies. By (re)framing the study of PC behaviour in the context of hierarchical relationships, the submissive hypothesis generates unique predictions from existing reconciliatory frameworks but does not exclude other hypotheses previously proposed to explain the occurrence of PC affiliation; such hypotheses are complementary, rather than mutually exclusive, within a given species or even dyad.

Taken together, our results emphasize the diversity of relationships possible within and across dyads, where the function of PC affiliation may vary from reconciliation to submission depending on the context and quality of the social bond. Attempts to separate

these two hypotheses at the species level may be oversimplistic given the sophistication of social strategies and the individualized nature of social bonds within primate groups (Cheney & Seyfarth, 2007; Smuts & Smuts, 1993).

Conclusion

Primate societies are a mosaic of social bonds, ranging from the most coercive/hierarchical to the most egalitarian/reciprocal in nature (de Waal, 1986). Conflict resolution patterns reflect this spectrum, with a higher frequency of PC affiliation in more tolerant species compared to more despotic ones (Thierry, 2000; Thierry et al., 2008). Our results further suggest that, on top of its frequency, the very function of PC affiliation similarly varies across and within populations, and hypotheses pertaining to proximate and ultimate explanations for the observed behavioural patterns should account for such variation. On the egalitarian end of the spectrum, reconciliation may be required after conflicts to restore the relationship to baseline levels of tolerance and affiliation. On the hierarchical end, reconciliation may facilitate the avoidance of injury through submissive behaviour rather than repairing social bonds. Overall, a more balanced view of the functions of PC affiliation is warranted. Animal social relationships are multifaceted and involve a mixture of coercive and sociopositive interactions, a reality that research on PC behaviour should reflect.

Author Contributions

A.B., C.E.W. and E.H. designed the study and performed the analyses. A.B and E.H collected the data. All authors contributed to drafting the manuscript.

Data Availability

The data sets necessary to run the analyses included in this paper have been deposited in the public depository GitHub at <https://github.com/AliceBaniel/The-Submissive-hypothesis>.

Declaration of Interest

We have no competing interests.

Acknowledgments

We are very grateful to the Tsaobis Baboon Project volunteers (2005–2006 and 2013–2014) for help with data collection, the Tsaobis beneficiaries for permission to work at Tsaobis, the Gobabeb Research and Training Centre for affiliation, and the Snyman and Wittreich families for permission to work on their land. This paper is a publication of the ZSL Institute of Zoology's Tsaobis Baboon Project. Contribution ISEM 2020-339. A.B. was supported by the Agence Nationale de la Recherche Labex IAST and C.E.W was supported by a Fyssen Foundation postdoctoral fellowship.

REFERENCES

- Alberts, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging activity of male baboons. *Animal Behaviour*, 51(6), 1269–1277. Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters : both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 281(1793), 20141261.
- Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, 61(2), 489–495.
- Arnold, K., Fraser, O. N., & Aureli, F. (2010). Postconflict reconciliation. In C. J. Campbell,

563 A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in*
 564 *Perspective* (pp. 608–625). Oxford, U.K.: Oxford University Press.

565 Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: The mediating role of emotion
 566 in conflict resolution. *Aggressive Behavior*, 23(5), 315–328.

567 Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in
 568 gregarious animals: A predictive framework. *Animal Behaviour*, 64(3), 325–343.

569 Aureli, F., & van Schaik, C. P. (1991). Post-conflict behaviour in long-tailed macaques
 570 (*Macaca fascicularis*): II. Coping with the uncertainty. *Ethology*, 89(2), 101–114.

571 Baniel, A., Cowlishaw, G., & Huchard, E. (2017). Male violence and sexual intimidation in a
 572 wild primate society. *Current Biology*, 27(14), 2163–2168

573 Baniel, A., Cowlishaw, G., & Huchard, E. (2016). Stability and strength of male-female
 574 associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology*,
 575 70(5), 761–775.

576 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: linear mixed-effects models
 577 using Eigen and S4. R package version 1.1-7. *R Package Version 1.1-7*. [http://cran.r-](http://cran.r-project.org/package=lme4)
 578 [project.org/package=lme4](http://cran.r-project.org/package=lme4).

579 Bercovitch, F. B. (1995). Female cooperation, consortship maintenance, and male mating
 580 success in savanna baboons. *Animal Behaviour*, 50, 137–149.

581 Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna baboons.
 582 *Behaviour*, 127, 67–103.

583 Call, J., Aureli, F., & de Waal, F. B. M. (1999). Reconciliation patterns among stumptailed
 584 macaques: A multivariate approach. *Animal Behaviour*, 58(1), 165–172.

585 Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., Alberts, S. C., & Alberts, S. C.
 586 (2020). Social bonds , social status and survival in wild baboons: a tale of two sexes.
 587 *Philosophical Transactions of the Royal Society B*, 375, 20190621.

588 Cant, M. A. (2010). The role of threats in animal cooperation. *Proceedings of the Royal*
589 *Society B: Biological Sciences*, 278(1703), 170–178.

590 Cheney, D. L., & Seyfarth, R. M. (1977). Behavior of adult and immature male baboons
591 during intergroup encounters. *Nature*, 269, 404–406.

592 Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics—The evolution of a social*
593 *mind*. Chicago, IL: The University of Chicago Press.

594 Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling
595 opponents and facilitating interactions among adult female baboons. *Animal Behaviour*,
596 50, 249–257.

597 Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2012). Evidence for intrasexual selection in
598 wild female baboons. *Animal Behaviour*, 84, 21–27.

599 Clay, Z., & de Waal, F. B. M. (2014). Sex and strife: Post-conflict sexual contacts in
600 bonobos. *Behaviour*, 152, 313–334.

601 Clutton-Brock, T. H., & Parker, G. A. (1995a). Punishment in animal societies. *Nature*, 373,
602 209–216.

603 Clutton-Brock, T. H., & Parker, G. A. (1995b). Sexual coercion in animal societies. *Animal*
604 *Behaviour*, 49, 1345–1365.

605 Colmenares, F., Polo, P., & Herna, V. (2014). Male takeovers are reproductively costly to
606 females in hamadryas baboons: A test of the sexual coercion hypothesis. *PLoS One*,
607 9(3), e90996.

608 Cords, M., & Aureli, F. (1996). Reasons for reconciling. *Evolutionary Anthropology*, 2(5),
609 42–45.

610 Cowlishaw, G. (1997). Refuge use and predation risk in a desert baboon population. *Animal*
611 *Behaviour*, 54(2), 241–253.

612 de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *The*

613 *Quarterly Review of Biology*, 61(4), 459–479.

614 de Waal, F. B. M. (1987). Tension regulation and non-reproductive functions of sex in
615 captive bonobos. *National Geographic Research*, 3, 318–335.

616 de Waal, F. B. M., & Aureli, F. (1997). Conflict resolution and distress alleviation in
617 monkeys and apes. In C. S. Carter, B. Kirkpatrick, & I. Lenderhendler (Eds.), *The*
618 *Integrative Neurobiology of Affiliation* (Vol. 807, pp. 317–328). New York: Annals of
619 the New York Academy of Sciences.

620 de Waal, F., & van Roosmalen, A. (1979). Reconciliation and consolation among
621 chimpanzees. *Behavioral Ecology and Sociobiology*, 5(1), 55–66.

622 Feldblum, J. T., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Paiva, T., Cetinkaya-
623 Rundel, M., Pusey, A.E., Gilby, I. C. (2014). Sexually coercive male chimpanzees sire
624 more offspring. *Current Biology*, 24(23), 2855–2860.

625 Fox, E. A. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan
626 (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology*, 52(2), 93–101.

627 Fürtbauer, I., Heistermann, M., Schülke, O., & Ostner, J. (2014). Low female stress hormone
628 levels are predicted by same- or opposite-sex sociality depending on season in wild
629 Assamese macaques. *Psychoneuroendocrinology*, 48, 19–28.

630 Gesquiere, L. R., Wango, E. O., Alberts, S., & Altmann, J. (2007). Mechanisms of sexual
631 selection: sexual swellings and estrogen concentrations as fertility indicators and cues
632 for male consort decisions in wild baboons. *Hormones and Behavior*, 51, 114–125.

633 Hartig, F. (2018). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
634 Regression Models. R package version 0.2.0. [https://CRAN.R-](https://CRAN.R-project.org/package=DHARMA)
635 [project.org/package=DHARMA](https://CRAN.R-project.org/package=DHARMA).

636 Hohmann, G., & Fruth, B. (2000). Use and function of genital contacts among female
637 bonobos. *Animal Behaviour*, 60(1), 107–120.

638 Hohmann, G., Mundry, R., & Deschner, T. (2009). The relationship between socio-sexual
639 behavior and salivary cortisol in bonobos: Tests of the tension regulation hypothesis.
640 *American Journal of Primatology*, 71(3), 223–232.

641 Kappeler, P. M., & van Schaik, C. P. (1992). Methodological and evolutionary aspects of
642 reconciliation among primates. *Ethology*, 92(2), 51–69.

643 Kitchen, D. M., Beehner, J. C., Bergman, T. J., Cheney, D. L., Crockford, C., Engh, A. L.,
644 Fischer, J., Seyfart, R.M., Wittig, R. M. (2009). The causes and consequences of male
645 aggression directed at female chacma baboons. In M N Muller & R. W. Wrangham
646 (Eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male*
647 *aggression against females* (pp. 128–156). Cambridge, MA: Harvard University Press.

648 Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2005). Contextual factors mediating
649 contests between male chacma baboons in Botswana: effects of food, friends and
650 females. *International Journal of Primatology*, 26(1), 105–125.

651 Knott, C. D. (2009). Orangutans: sexual coercion without sexual violence. In M N Muller &
652 R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: an evolutionary*
653 *perspective on male aggression against females* (pp. 81–111). Cambridge, MA: Harvard
654 University Press.

655 Kutsukake, N., & Clutton-Brock, T. H. (2006). Aggression and submission reflect
656 reproductive conflict between females in cooperatively breeding meerkats *Suricata*
657 *suricatta*. *Behavioral Ecology and Sociobiology*, 59(4), 541–548.

658 Machanda, Z. P., Gilby, I. C., & Wrangham, R. W. (2013). Male-female association patterns
659 among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *International*
660 *Journal of Primatology*, 34(5), 917–938.

661 Moscovice, L. R., Di Fiore, A., Crockford, C., Kitchen, D. M., Wittig, R., Seyfarth, R. M., &
662 Cheney, D. L. (2010). Hedging their bets? Male and female chacma baboons form

663 friendships based on likelihood of paternity. *Animal Behaviour*, 79, 1007–1015.

664 Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male
665 coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of*
666 *the Royal Society B: Biological Sciences*, 274(1612), 1009–1014.

667 Muller, M. N., Emery Thompson, M., Kahlenberg, S., & Wrangham, R. (2011). Sexual
668 coercion by male chimpanzees shows that female choice may be more apparent than
669 real. *Behavioral Ecology and Sociobiology*, 65, 921–933.

670 Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009). Male aggression against
671 females and sexual coercion in chimpanzees. In M N Muller & R. W. Wrangham (Eds.),
672 *Sexual coercion in primates and humans: an evolutionary perspective on male*
673 *aggression against females* (pp. 184–217). Cambridge, MA: Harvard University Press.

674 Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdi, A.
675 Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of
676 progressive evaluation with Elo-rating. *Animal Behaviour*, 82, 911–921.

677 Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and consolation in captive bonobos
678 (*Pan paniscus*). *American Journal of Primatology*, 62(1), 15–30.

679 Palombit, R. A. (2000). Infanticide and the evolution of male-female bonds in animals. In C.
680 P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 239–
681 268). Cambridge, U.K.: Cambridge University Press.

682 Polo, P., & Colmenares, F. (2012). Behavioural processes in social context: female
683 abductions, male herding and female grooming in hamadryas baboons. *Behavioural*
684 *Processes*, 90(2), 238–245.

685 R Core Team. (2018). R: A language and environment for statistical computing. Vienna,
686 Austria: R Foundation for Statistical Computing.. <http://www.r-project.org/>

687 Reddy, R., & Mitani, J. (2020). Adolescent and young adult male chimpanzees form

688 affiliative, yet aggressive, relationships with females. *Journal of Human Evolution*, 144,
 689 102813.

690 Schaffner, C. M., & Aureli, F. (2004). Conflict resolution. *International Journal of*
 691 *Phytoremediation*, 21(1), 295–297.

692 Silk, J. B. (1996). Why do primates reconcile? *Evolutionary Anthropology*, 5(2), 39–42.

693 Silk, J. B. (2002). Practice random acts of aggression and senseless acts of intimidation: The
 694 logic of status contests in social groups. *Evolutionary Anthropology*, 11(6), 221–225.

695 Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (1996). The form and function of post-conflict
 696 interactions between female baboons. *Animal Behaviour*, 52, 259–268.

697 Smuts, B. B. (1985). *Sex and friendship in baboons*. Hawthorne, NY: Aldine Publishing.

698 Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in
 699 nonhuman primates and other mammals: evidence and theoretical implications.
 700 *Advances in the Study of Behavior*, 22, 1–63.

701 Swedell, L. (2015). *Strategies of sex and survival in female hamadryas baboons: Through a*
 702 *female lens*. Upper Saddle River, NJ: Pearson Prentice Hall.

703 Swedell, L., & Schreier, A. (2009). Male aggression towards females in hamadryas baboons:
 704 conditioning, coercion, and control. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual*
 705 *coercion in primates and humans: an evolutionary perspective on male aggression*
 706 *against females* (pp. 244–268). Cambridge, MA: Harvard University Press.

707 Swedell, L., Leedom, L., Saunders, J., Pines, M. (2014). Sexual conflict in a polygynous
 708 primate: Costs and benefits of a male-imposed mating system. *Behavioral Ecology and*
 709 *Sociobiology*, 68(2), 263–273.

710 Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In
 711 Filippo Aureli & F. B. M. de Waal (Eds.), *Natural Conflict Resolution* (pp. 106–128).
 712 Berkeley, CA: University of California Press.

- 713 Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & de Waal, F. B. M. (2008). A
 714 comparative study of conflict resolution in macaques: Insights into the nature of trait
 715 covariation. *Animal Behaviour*, 75(3), 847–860.
- 716 Webb, C. E., Baniel, A., Cowlshaw, G., & Huchard, E. (2019). Friend or foe: Reconciliation
 717 between males and females in wild chacma baboons. *Animal Behaviour*, 151, 145–155.
- 718 Weingrill, T., Lycett, J. E., Barrett, L., Hill, R. A., & Henzi, S. P. (2003). Male consortship
 719 behaviour in chacma baboons: the role of demographic factors and female conceptive
 720 probabilities. *Behaviour*, 140, 405–427.
- 721 Weingrill, T., Lycett, J. E., & Henzi, S. P. (2000). Consortship and mating success in chacma
 722 baboons (*Papio cynocephalus ursinus*). *Ethology*, 106(11), 1033–1044.
- 723 Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-
 724 mediated reconciliation substitutes for direct reconciliation in female baboons.
 725 *Proceedings of the Royal Society B: Biological Sciences*, 274(1613), 1109–1115.

726 **Table 1.** Summary of the main proximate and ultimate hypotheses proposed to explain postconflict affiliative behaviour.

Hypothesis	Explanation		Evidence (reviewed in Aureli et al. 2002; Arnold et al. 2010)
	Proximate	Ultimate	
Valuable relationships (de Waal & Aureli, 1997; Kappeler & van Schaik, 1992)	Usually not clarified	Repair valuable (i.e. fitness enhancing) social bond	Kin or close affiliates (e.g. as indexed by frequency of grooming, proximity, cooperation, agonistic support) more likely to reconcile than nonkin or nonaffiliates
Uncertainty reduction (Aureli & van Schaik, 1991)	Motivation to reduce stress/anxiety due to uncertainty about the social situation	Reduce risk of renewed aggression, alleviate more subtle social risks, prevent negative consequences of chronic stress	Elevated rates of self-directed behaviour (SDB) in victims and aggressors following conflicts are decreased following reconciliation
Integrated (Aureli, 1997)	Motivation to reduce stress/anxiety due to uncertainty about the social situation	Repair valuable social bond	Aggression between opponents with more valuable bonds results in higher SDB and reconciliation rates
Benign intent (Silk, 1996)	Signal friendly intentions (that the conflict has ended) in order to restore tolerance	Achieve benefits of resumed interaction (e.g. short-term objectives like grooming or access to resources)	Grunts between female–female baboons serve as signals of friendly intent and facilitate infant handling
Submissive (this study)	Victims: fear and/or stress/anxiety about conflict escalation Aggressors: motivation to obtain immediate social/sexual benefits, restore tolerance	Victims: reduce risks of renewed aggression and costs of conflict escalation (e.g. injury) Aggressors: reap the benefits of subordination/compliance of the victim (e.g. secure grooming or mating opportunities)	Present study

727 **Table 2.** Rate of postconflict (PC) and baseline affiliation between males and swollen females when considering only sexual behaviour or
728 nonsexual behaviour.

Fixed factor	Only sexual behaviour							Only nonsexual behaviour						
	Estimate	SE	95% confidence interval	LRT	df	P		Estimate	SE	95% confidence interval	LRT	df	P	
Intercept	-5.60	0.35	-	-	-	-		-5.9	0.71	-	-	-	-	
PC observation ^a	1.29	0.24	[0.78 ; 1.73]	27.1	1	<0.001		1.20	0.13	[0.98 ; 1.39]	68.3	1	<0.001	
Female rank	-0.20	0.33	[-0.84 ; 0.44]	0.31	1	0.580		0.69	0.97	[-1.29 ; 2.99]	0.49	1	0.480	
Male rank	1.59	0.44	[0.8 ; 2.57]	12.4	1	<0.001		0.77	0.64	[-0.53 ; 2.21]	1.44	1	0.230	

729 The response variable is number of affiliations exchanged between male–female dyads. The duration (min) of observations for each dyad (in PC or in
730 baseline) was fitted as an offset fixed factor, to control for variation in observation time across dyads. Parameters and tests are based on 29 females, 27 males,
731 61 dyads and 94 aggressive events. The negative binomial GLMMs were performed controlling for male and female identity. LRT: likelihood ratio test. The
732 95% confidence intervals that do not cross zero and *P* values of statistically significant results are highlighted in bold.

733 ^aReference category: baseline.

734 **Table 3.** Determinants of the occurrence of postconflict (PC) affiliation between males and swollen females.

Fixed factor	Level	Estimate	SE	95% confidence interval	LRT	df	P
Intercept		-1.73	0.85	-	-	-	-
Mate-guarding status	Mate guarded	1.55	0.63	[0.46 ; 3.82]	7.48	1	0.006
Baseline rate of affiliation		14.85	11.7	[-9.75 ; 53.98]	1.6	1	0.206
Female rank		-0.37	0.84	[-2.49 ; 1.47]	0.2	1	0.653
Male rank		0.47	0.81	[-1.54 ; 2.78]	0.34	1	0.563
Type of aggression	CH (ref: AT)	0.85	0.68	[-0.47 ; 2.83]	3.74	2	0.154
	TH (ref: AT)	-0.46	0.96	[-4.42 ; 1.65]			
	TH (ref: CH)	-1.31	0.84	[-9.89 ; 0.18]			

735 The response variable is the occurrence of PC affiliation between males and swollen females (yes/no). Parameters and tests are based on 28 females, 27
736 males, and 91 aggressive events (including 43 followed by PC affiliation). Of these aggressive events 53 involved unguarded swollen females, and 38
737 involved mate-guarded swollen females. For this model, we removed three observed aggressive events where mate-guarded females received aggression from
738 a nonconsort male. The baseline rate of affiliation of the dyad was calculated using focal observations collected when the female was swollen and outside an
739 aggressive context. Type of aggression refers to attack ('AT', $N=18$), chase ('CH', $N=58$), or threat ('TH', $N=15$). The binomial GLMM was performed
740 controlling for male and female identity. The 95% confidence intervals that do not cross zero and P values of statistically significant results are highlighted in
741 bold.

742 **Figure 1.** Pattern of postconflict (PC) affiliation between males and females. (a) Mean rate of affiliation between swollen females and males in
743 PC versus baseline observations according to whether only sexual affiliations (presenting and copulations) or only nonsexual affiliations are
744 included in the pool of affiliations. Error bars show the standard error of the distribution. (b) Percentage of aggressive events followed by
745 affiliation according to the mate-guarding status of swollen females (unguarded versus mate guarded by the aggressor). * $P < 0.05$.

747 **Figure 2.** Pattern of initiation of the first postconflict (PC) act and the first sexual PC act by females and males. (a) Percentage of the first PC
748 affiliative act (both sexual and nonsexual behaviour combined) of the PC sequence (lasting 15 min) initiated by females and males. (b)
749 Percentage of the first sexual PC affiliative act of the PC sequence initiated by females and males. * $P < 0.05$.

Appendix 1

Individual dominance ranks were assessed through focal and ad libitum observations of approach–avoid interactions (supplants, when one animal actively displaces another to take its place; displacements, when one animal passes close to another and makes it move away) and agonistic interactions (attacks, any agonistic physical contacts including hits, bites or grabbing movements; chases, when one animal chases another for a distance of at least 3 m; and threats, including staring, head bobbing and ground sweeping while oriented towards the targeted individual). Female dominance hierarchies were calculated separately in each year using Matman 1.1.4 (Noldus Information Technology, Wageningen, The Netherlands) and were always linear ($N_{2005} = 412$ interactions, $N_{2006} = 576$, $N_{2013} = 367$, $N_{2014} = 1259$ in group L; $N_{2005} = 184$, $N_{2006} = 460$, $N_{2013} = 590$, $N_{2014} = 978$ in group J, Landau's linearity index h : $P < 0.05$ in all cases). In the analyses, we used relative female rank to control for variation in group size, where absolute ranks were standardized to vary between 0 and 1 using the formula: $1 - ((1-r)/(1-N))$, where r is the absolute rank of an individual (ranging from 1 to the group size, N). In contrast to females, the male hierarchies were much less stable within a year (Baniel et al., 2016), so male ranks were established using an Elo-rating procedure implemented in the R package EloRating (version 0.43; Neumann et al., 2011). Compared to matrices of dyadic interactions where ranks are calculated over a given time period, an Elo-rating procedure continuously updates rankings according to the temporal sequence of interactions and is better adapted to situations of unstable social dominance (Albers & de Vries, 2001; Neumann et al., 2011). This gives a score for each individual on each day of observation. We derived a daily standardized rank by scaling the Elo-rating score of each individual proportionally between 0 (corresponding to the minimal score and thus the lowest ranking male) and 1 (corresponding to the maximal score and the highest-ranking male).

775 **Appendix 2**

776 **Table A1.** Determinants of the occurrence of postconflict (PC) affiliation between males and swollen females.

777

Fixed factor	Level	Estimate	SE	95% confidence interval	LRT	df	P
Intercept		-0.53	0.64	-	-	-	-
Mate-guarding status	Mate guarded	1.75	0.61	[0.71 ; 4.03]	9.26	1	0.002
Baseline rate of affiliation		-10.62	26.67	[-70.61 ; 47.62]	0.16	1	0.690
Female rank		-0.65	0.81	[-2.64 ; 1.1]	0.64	1	0.424
Male rank		0.73	0.8	[-1.12 ; 2.66]	0.84	1	0.360
Type of aggression	CH (ref: AT)	0.66	0.65	[-0.77 ; 2.37]	2.60	2	0.273
	TH (ref: AT)	-0.42	0.91	[-14.88 ; 1.73]			
	TH (ref: CH)	-1.08	0.78	[-3.39 ; 0.42]			

778 The response variable is the occurrence of PC affiliation between males and swollen females (yes/no). Parameters and tests are based on 25 females, 26
779 males, and 80 aggressive events (including 38 followed by PC affiliation). Type of aggression refers to attack ('AT', $N=18$), chase ('CH', $N=58$), or threat
780 ('TH', $N=15$). The binomial GLMM was performed controlling for male and female identity. In contrast to Table 3, the baseline rate of affiliation of the dyad
781 was calculated using focal observations collected when the female was nonswollen and outside an aggressive context. The 95% confidence intervals that do
782 not cross zero and P values of statistically significant results are highlighted in bold.

783 **Table A2.** Behavioural details on the first affiliative act and the first sexual affiliative act.

784

Behaviour	First affiliative act		First sexual act	
	Female initiates	Male initiates	Female initiates	Male initiates
Copulation	2	8	2 ^a	9 ^a
Presenting	11	NA	19	NA
Grooming	5	3		
Grunt	0	6		
Lip-smack	0	4		
Sniffing perineum	0	2		
Sniffing mouth	1	0		
Come-here face	1	0		
Total	20	23	21	9

785 NA: not applicable. The table shows the type and direction of the first postconflict (PC) affiliation act and the first sexual PC affiliation act of a PC sequence
 786 (lasting 15 min in total) between males and swollen females. There were 43 PC sequences containing at least one PC affiliative act and 32 PC sequences
 787 containing at least one sexual act.

788 ^aTwo copulations had unknown initiator and are not reported here.

789 **Fig. A1.** Occurrence of postconflict (PC) affiliation according to the baseline rate of affiliation (i.e. outside an aggressive context) of the
790 maleefemale dyad calculated over the (a) swollen or (b) nonswollen period. The violin plots (created using `geom_violin` from the `ggplot2`
791 package, cran.r-project.org/package=ggplot2) show the kernel probability density of the data at different y values.