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Bared-teeth displays in bonobos (*Pan paniscus*): An assessment of the power asymmetry hypothesis

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Abstract

Facial expressions are key to navigating social group life. The *Power Asymmetry Hypothesis of Motivational Emancipation* predicts that the type of social organization shapes the meaning of communicative displays in relation to an individual's dominance rank. The bared-teeth (BT) display represents one of the most widely observed communicative signals across primate species. Studies in macaques indicate that the BT display in despotic species is often performed unidirectionally, from low- to high-ranking individuals (signaling submission), whereas the BT display in egalitarian species is usually produced irrespective of dominance (mainly signaling affiliation and appeasement). Despite its widespread presence, research connecting BT displays to the power asymmetry hypothesis outside the *Macaca* genus remains scarce. To extend this knowledge, we investigated the production of BT in relation to social dominance in dyadic interactions ($N = 11{,}377$ events) of 11 captive bonobos (*Pan paniscus*). Although adult bonobos were more despotic than previously suggested in the literature, BT displays were produced irrespective of dominance rank. Moreover, while adults produced the BT exclusively during socio-sexual interactions, especially during periods of social tension, immature bonobos produced the BT in a wider number of contexts. As such, the results indicate that the communicative meaning of the BT display is consistent with signaling appeasement, especially in periods of social tension. Moreover, the BT display does not seem to signal social status, supporting the prediction for species with a high degree of social tolerance. These results advance our understanding of the origins of communicative signals and their relation to species' social systems.

KEYWORDS
bared-teeth display, bonobo, facial expression, power asymmetry hypothesis

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Abbreviations: BORIS, behavioral observation research interactive software; BT, bared-teeth; Bulk_ESS, estimate bulk effective sample size; CI, credible interval; FACS, facial action coding system; GG-rubbing, genito-genital rubbing; MCMC, Markov chain monte carlo; SBT, silent bared-teeth; Tail_ESS, estimated tail effective sample size; VBT, vocalized bared-teeth.

1 | INTRODUCTION

Communication is an essential tool for any social species. It occurs through various sensory channels, including acoustic, tactile, olfactory, and/or visual paths. Within the visual domain, facial displays are central to primate communication (Waller et al., 2022) and are proposed to convey important information about the signaler's motivation, intentions, and emotions (Ekman & Keltner, 1997; Flack et al., 2004; Parr & Waller, 2006; Van Hooff, 1967). For example, individuals should respond to situations based on conspecific facial expressions (e.g., Morimoto & Fujita, 2011), and adjust their behaviors accordingly. As such, accurately interpreting conspecific facial expressions and responding to them appropriately seems to be a crucial ability for an individual's successful regulation of social group life (Parr et al., 2005).

Humans have, to some extent, control over their facial expressions (Ekman & Keltner, 1997; Fridlund, 1991). While the traditional view has been that nonhuman primate (henceforth primate) facial expressions are innate and fixed behavioral action patterns (for a review, see Kret et al. [2020] and Heesen et al. [2021]), studies on chimpanzees (*Pan troglodytes*) have challenged this view by demonstrating that they also have some degree of voluntary control over their facial movements (Florkiewicz & Campbell, 2021; Hopkins et al., 2011; Reynolds Losin et al., 2008). Studies on other great apes, such as bonobos (*Pan paniscus*) and orangutans (*Pongo* sp.), strengthen the argument that at least great apes have greater control over their facial expressions than has been previously assumed (Clay & Zuberbühler, 2012; Waller et al., 2015). For example, bonobos produce play faces in a selective manner based on whom they play with (Palagi, 2008). Such play faces are used more frequently during social play compared to solitary play, most often when the interactant is facing and seeing the other individual (Demuru et al., 2015); orangutans produce play faces more intensely, by using more movements, when their partner is facing them (Waller et al., 2015); and chimpanzees can be selective as to which facial expression to mimic and which not (Davila-Ross et al., 2011). Although these examples could reflect a difference in the producers' underlying valence/arousal states (elicited by the nature of the play interaction or partner), these examples also suggest that facial expressions may be used with intention, where patterns in performance fulfill some intentionality criteria regarding social use, and sensitivity to the receivers' attentive states (e.g., Florkiewicz & Campbell, 2021; Graham et al., 2020).

Morphological characteristics of facial expressions appear relatively conserved across primates, which may be indicative of their homology (Burrows, 2008; Diogo et al., 2009). One of the most stereotyped and highly conspicuous facial expressions reported in most primate species is the silent-bared teeth display (hereafter SBT; De Waal & Luttrell, 1985; Van Hooff, 1967). The SBT display resembles the vocalized-bared teeth in its appearance, which has been hypothesized to originate from a function to defend oneself by preparing to bite (Van Hooff, 1962). Through the process of ritualization—where an unspecialized but formerly adaptive behavior becomes separated from its original context to evolve a communicative meaning (Preuschoft & van Hooff, 1995)—the SBT display has evolved into a communicative signal with its meaning ranging from fear or submission to affiliative intent, depending on species' sociality, all of which ultimately function to reduce aggression and increase affinitive contact (Bout & Thierry, 2005; De Waal & Luttrell, 1985; Flack & De Waal, 2007; Waller & Dunbar, 2005).

Given its morphological and functional similarities with the human smile, the SBT display has been proposed to be a primate homolog of the human smile (Preuschoft & van Hooff, 1995; Van Hooff, 1967). In humans, smiles are used in multiple contexts, ranging from affiliative to submissive situations (Ekman & Friesen, 1982; J. Martin et al., 2017; Rychlowska et al., 2017). Pleasure smiles reinforce desired behaviors, affiliation smiles invite and maintain social bonds, and dominance smiles are used to manage hierarchical relationships (J. Martin et al., 2017; Niedenthal et al., 2010), all of which play an important role in social relationships. Smiles also convey information about social status between interacting partners. For example, different smiles are observed depending on who the receiver is: men are more likely to show *deliberate smiles*—a fake smile that is believed to communicate a positive feeling that is not felt (Ekman & Keltner, 1997)—when interacting with older people compared to their peers, which may indicate a signal for submission by the younger men. The authors argued that this could indicate the role of smiles in regulating social relationships in men, especially when a hierarchy is present (for a review on social smiles in humans, see Hess & Fischer, 2013).

Although the SBT display in primates was primarily considered a signal of submission (Van Hooff, 1967), systematic investigations have revealed a considerable variation in its use and meaning across closely related species, some of which were similar to the use of the human smile (e.g., Petit & Thierry, 1992; Thierry et al., 1989). Importantly, the use and function of the SBT display was found to be closely linked to a species' social structure (Preuschoft & van Hooff, 1997). This was later formulated as the *Power Asymmetry Hypothesis of Motivational Emancipation* (hereafter Power Asymmetry Hypothesis; Preuschoft & van Hooff, 1997), which predicts that distinct displays of submission and appeasement are expected among despotic species, whose social system is characterized by strong asymmetrical relationship and steep linear hierarchies, where usually one dominates all. Subordinates in intolerant groups usually respond to aggression by fleeing or showing signals of submission (De Waal & Luttrell, 1985). In steep dominance hierarchies, often low conciliatory tendencies are observed, and a bias toward kin might be present (Aureli et al., 1997). Thus, the outcome of any given interaction is mainly determined by rank and/or kinship (Dobson, 2012). Indeed, in rhesus macaques (*Macaca mulatta*)—a despotic species with a steep dominance hierarchy (De Waal & Luttrell, 1985)—the SBT display is a signal of submission, but also a formal expression of a dominance relationship. It is thus produced unidirectionally from subordinates to dominants, acknowledging the lower status (De Waal & Luttrell, 1985). In contrast, in more tolerant species, where relationships are more equal and where the dominance gradient is lower, the

SBT is used in a variety of social affiliative contexts (Duboscq et al., 2013; Petit & Thierry, 1992; Preuschoft & van Hooff, 1997; Thierry, 2002; Thierry et al., 1989). In these societies, high rates of counter-aggression (Petit et al., 1997; Thierry, 1986, 2002), as well as high rates of reconciliation are also found, and a bias toward kin is usually absent (Thierry, 2002). Thus, the outcome of any given interaction is open to negotiation (Silk, 1997) Indeed, in Tonkean macaques (*Macaca tonkeana*), a species characterized as egalitarian (Thierry, 2007; Thierry et al., 1989), the SBT display is used flexibly, irrespective of dominance status, supposedly serving to signal general appeasement and to increase social attraction and affiliation (Preuschoft & van Hooff, 1995, 1997). In this sense, rather than signaling submission, the SBT display may stress a signaler's benign intent, mitigating the risk of aggression (Van Hooff, 1967).

While research into social signaling among the *Macaca* genus has provided important contributions to our understanding of the evolution of primate facial expressions, systematic investigations of the SBT display and its relation to social dominance structures are lacking in other primate species, notably the great apes. In chimpanzees—our closest living relative along with bonobos (Prüfer et al., 2012), it has been suggested that SBT displays are not necessarily restricted as a response to aggression, and that its function may depend on context (Waller & Dunbar, 2005). It has also been found that SBT displays are performed by subordinate chimpanzees when threatened, but also by dominant individuals to reassure subordinates (Van Hooff, 1972), and that they are usually directed to the same age-class individuals as the signaler (Waller & Dunbar, 2005). In contrast, most research on bonobo facial expressions has focused on the play face (relaxed-open mouth display or full play face; Demuru et al., 2015; Palagi, 2008; Palagi & Mancini, 2011), whereas the SBT display remains less explored. The SBT display has been described in a limited number of studies, but only as part of an ethogram, without a focus on the association of the display with the species' social characteristics (Palagi et al., 2004; Paoli et al., 2006; Vervaecke et al., 2000).

de Waal (1988) was the first to describe the SBT display within the behavioral ethogram established for a group of captive bonobos. He found the SBT display to be present during affiliative contexts, such as during sexual solicitations and reconciliations, and concluded that it indicates affiliative tendencies. Though the SBT display was not a focus of investigation, other studies focusing on bonobo socio-sexual behaviors have reported the SBT display to be the most common facial expression during sexual contacts (Clay & Zuberbühler, 2011, 2012; Palagi et al., 2020). These lines of findings suggest that SBT display in bonobos serves affiliative purposes; yet, thorough investigation of the SBT display in this species under the power asymmetry hypothesis framework (i.e., the use of the SBT with regard to rank relationship and its communicative meaning, given the social structure of bonobos) remains to be conducted.

As such, to advance our understanding of the meaning of the SBT among primates, this study examined the validity of the power asymmetry hypothesis in bonobos. For a number of reasons, bonobos are a relevant species to study the SBT display and its relation to social structure. Most research indicates that bonobos have relatively high levels of social tolerance and prosociality as a species (Furuichi, 2011; Hare et al., 2007, 2012; Hohmann, 2001; Idani, 1991). Females are central to group social networks, particularly due to their gregariousness (Nurmi et al., 2018) and strong intra-sexual bonds (Hare et al., 2012; Hohmann, 2001; Moscovice et al., 2015, 2019). Compared to chimpanzees, bonobos also show reduced levels of physical aggression, with no conclusive reports of lethal aggression in the wild (Furuichi, 2011; Hohmann, 2001; Tokuyama et al., 2019; Wilson et al., 2014). In both wild and captive settings, bonobo intergroup interactions are relatively peaceful and they are willing to share food with nongroup members (Tan et al., 2017), without signs of aggression (Fruth & Hohmann, 2018; Hare & Kwetuenda, 2010). Related to their enhanced social tolerance and reduced aggression, bonobos appear to show heightened social sensitivity; they show an extensive repertoire of play behaviors, including into adulthood (Palagi et al., 2006), and offer consolation to victims in distress, potentially indicative of their empathic nature (Clay & de Waal, 2013; Palagi et al., 2004). When tension is high, such as during food competition, bonobos have evolved elaborate adaptations to conflict resolution: socio-sexual behaviors—consisting of rubbing genitals together—even with strangers (Furuichi, 2011; Hare et al., 2012), which they use in the wild (Aureli et al., 2008; Hohmann & Fruth, 1996; Moscovice et al., 2015) and in captivity (Paoli et al., 2007).

However, in captivity, results regarding their social tolerance and dominance structure are contradictory, suggesting that bonobos might be less egalitarian than commonly assumed (Cronin et al., 2015; Jaeggi et al., 2010; Vervaecke et al., 2000). For example, when testing the degree of reciprocity and influence of dominance in a captive food sharing experiment, bonobos were less likely to share, and less tolerant than predicted (Jaeggi et al., 2010). In a similar setup, bonobos were found to have lower social tolerance levels than assumed (Cronin et al., 2015). Given their flexibility in the dominance style across populations and the wide use of the SBT display as a communicative signal (de Waal, 1988), the bonobo is a good model to test the power asymmetry hypothesis.

Age is also an important factor to take into account when studying communication systems, as young individuals still develop their repertoire and may explore which signals are most effective and in which contexts they are used (Byrne et al., 2017). Recent research into the use of gestures has indeed shown that as signalers mature, signals are used in more specific ways and contexts (Genty, 2019; Hobaiter & Byrne, 2011). However, despite the acknowledgment of the importance of facial communication, limited information is available on the specific functions of the bared-teeth (BT) display in bonobos, and how this facial expression is influenced by age.

Thus, the overall aim of this study was to investigate the contextual use of the SBT display in a species for which variation of dominance styles are found across populations. To address the power asymmetry hypothesis, we investigated the role of dominance rank on the use of the SBT display, and the general flexibility by which the display is used across social contexts. First, we assessed the group's dominance style by analyzing the outcomes of social dominance interactions. Next, we explored in which social contexts the SBT display was likely to occur in adult bonobos, and whether the dyadic rank relationship influenced patterns in the occurrence of this facial expression (*Model 1*). We further examined the difference in the use of the silent bared-teeth (SBT) and vocalized bared-teeth (VBT) displays, as the context in which both displays are produced is known to differ in closely related species (the chimpanzee; Van Hooff, 1967, 1973). Given that socio-sexual behaviors in bonobos appear to function in social tension regulation (de Waal, 1988), especially during feeding events in captive settings (Aureli et al., 2008; Hohmann & Fruth, 1996; Moscovice et al., 2015; Paoli et al., 2006, 2007), we analyzed whether SBT displays during socio-sexual interactions were influenced by the level of social tension (*Model 2*). We predicted that, if the SBT display during socio-sexual interactions signals appeasement, it should occur more frequently in the high-tension situations compared to the low-tension situations. Finally, we explored how the SBT display was used in immature bonobos (*Model 3*).

2 | METHODS

2.1 | Study subjects and site

This study was conducted at Apenheul Primate Park, Apeldoorn, the Netherlands. One group of bonobos, consisting of 11 individuals in total (five adult females, three adult males, one juvenile female, and two infants males; Supporting Information: Table S1) were housed in an enclosure with indoor (total 158 m^2) and outdoor access (total 2,812 m^2). The indoor enclosure included three compartments (left, middle, and right), connected to each other by hatches, which could be open or closed. Each compartment had an upper part which was fully visible from the visitor area where the observations took place, whereas the bottom part was either partly visible (the middle compartment) or hidden from the visitors' view. Apenheul aims to recreate the fission-fusion lifestyle of wild bonobos and does so by splitting the main group in two separate groups, varying in group composition (on average 5 individuals in a given group, ranging from minimum 2 to maximum 9) and enclosure when necessary. The groups had auditory and some visual contact with each other, but no physical contact. When the temperature was above 5°C, the bonobos had access to the outdoor exhibit. However, due to construction work in Apenheul, the bonobos did not have access outside during the study period. For these reasons, as well as due to visibility and practicality constraints, the observations were done in the indoor compartments. The bonobos were fed approximately five times a day. They were also provided with food and nonfood enrichment items—such as blankets, drapes, plastic bottles filled with food, and so on. Water was available ad libitum.

2.2 | Data collection

Data collection took place between January and March 2020. Observations were carried out by JMRV four days a week, from 9:30 to 16:00, with breaks from 12:00 to 13:30. All occurrence sampling (Altmann, 1974; P. Martin & Bateson, 1993) was chosen over focal animal sampling to ensure sufficient number of facial expressions collected for the statistical analyses. A SONY HDR-CX560V camera was used to record social interactions between individuals in both groups, defined as when 2 or more individuals approached within 3 m, given limited space in the enclosure (Graham et al., 2018). Social interactions consisted of affiliative, aggressive, neutral, sexual, submissive, and play behaviors (for a detailed description, see Table 1 and Supporting Information: Table S2). Data were collected through approximately 20-min video recordings to facilitate coding afterward, with a break of 5 min in between, while speaking into the camera for information that was not visible in the recordings. To ensure all animals and groups were observed at the same rate, a flexible schedule was made at the beginning of the day when it was known which group would be in what enclosure, and observation times of the groups from the previous day were considered. Due to cleaning, only one group was usually visible during the first 3–4 recordings. In total, 106 h of video material was recorded for the whole group. BT displays were recorded during social interactions when visible. To ensure visibility of facial expressions, most social interactions were zoomed in on, unless the behaviors took place all around the enclosure and certain facial expressions or individuals would have been missed on screen. If multiple social interactions and the faces of individuals engaging in social interactions were visible on the same screen, it was not zoomed in upon. When the social interaction of a target dyad stopped, we switched to another dyad engaging in a social interaction. Information that was not visible in the recordings (e.g., tension conditions, caretaker movements, behaviors from the other group, etc.) was expressed in the camera. If one group was *out of sight* for more than 10 min and the other group was engaging in social interactions, the other 10 min were allocated to the group being social. The observer stood in the public area, with a glass window separating the animals and the observer, which made it impractical to hear most vocalizations, except for loud screams. Therefore, it was possible that mild vocalizations accompanying SBT displays might have been misclassified (but see below). Due to the structure of the enclosure, the bonobos could easily hide from the public viewing area, making it impossible to record all interactions.

2.3 | Video coding

Video recordings were analyzed with the program BORIS (Behavioral Observation Research Interactive Software; Friard & Gamba, 2016), following the ethogram created based on previously established studies (Cronin et al., 2015; de Waal, 1988; Palagi, 2008; Parr et al., 2005; Pollick & De Waal, 2007; Vervaecke et al., 2000) and modified for the purpose of this study (see Supporting Information: Table S2 for details). Every social interaction with one or more recipients was coded as an event.

For each social interaction, the behavior of the bonobos involved were scored, indicating the initiator and recipient, and the presence or

TABLE 1 Grouped behavioral contexts and tension conditions

Social contexts	
Affiliative	Affiliative touch; buddy walk; follow; lateral embrace; kiss; invitation; support; grooming; sit together; being carried; peering; nursing
Sexual	Mounting; nonreproductive genito-genital rubbing; rump contact; hand touch genital; genital rub; copulation; smell genitals
Social play	Airplane; grab gentle; play push; play bite; play recovering a thing; play slap; tickle; pirouetting; acrobatic play; play run; play stamping; rough and tumble; play brusque rush; play retrieve
Aggressive	Directed display; quasi-aggression; pestering; pestering aggression; aggression with attack; aggressive intention; charge; displacement; forced claim
Submissive	Flee; yielding; distress
Neutral	Pass-by; approach; move away
Tension conditions	
Neutral	Nonfeeding, nonfeeding and interaction inside and outside
Anticipation	Anticipation for:
	Feeding, change group, change enclosure, change group and enclosure
Feeding	Feeding, feeding hand-given, feeding and interaction inside and outside
Fission-Fusion (Nonfeeding)	Change group, change enclosure, change group and enclosure without feeding
Fission-Fusion (Feeding)	Change group, change enclosure, change group and enclosure with feeding

Note: Fission-Fusion with feeding are the conditions where food was involved. Definitions can be found in the Supporting Information: Table S2 (Cronin et al., 2015, de Waal, 1988, Palagi, 2008; Parr et al., 2005; Pollick & De Waal, 2007; Vervaecke et al., 2000).

absence of the BT display for the initiator was coded (silent or vocalized; see Supporting Information: Figure S1 for details). If the recipient was indistinguishable, it was scored as "unspecified." When a recipient made a facial expression but did not perform any behavior—for example, individual A approaches individual B, individual B performs a BT display but does not move—it was noted in the comments. When a recipient responded to the behavior of the initiator with another behavior, the recipient became the initiator, and a new event was created (Supporting Information: Figure S1). For example, individual A chasing individual B was coded as one event. If individual B fled from individual A, this was coded as a different event (Event 1 = A chases B, Event 2 = B flees from A). Bonobo faces were often not or only partially visible, and those cases were coded as face not visible (*Out of sight*).

2.3.1 | Facial expression coding

SBTs were coded by following the definitions created by de Waal (1988): "Retraction of the lips, resulting in partial or complete exposure of the teeth and gums, with mouth practically closed and without vocalizations. The face is usually oriented toward the partner, but the eyes may make evasive movements." However, as this facial expression can also occur with vocalizations, we additionally coded when vocalizations accompanied this facial expression (VBT) to further explore the difference in the use of silent vs vocalized BTs. All BTs without audible vocalizations were categorized into the SBT.

2.3.2 | Tension conditions

For each social interaction, we also scored external conditions (hereafter Tension Conditions) which could potentially influence group social tension to test the association between the BT display and social tension. Tension conditions were grouped into five categories, namely *neutral*, *anticipation*, *feeding*, *fission-fusion (non-feeding)*, and *fission-fusion (feeding)* (Table 1) based on its characteristics and the degree of tension involved. It should be noted that the categorization was made a priori based on previous findings that uncertainty and competition over food are likely to lead to social tension in bonobos (Aureli et al., 2008; Hohmann & Fruth, 1996; Moscovice et al., 2015; Paoli et al., 2006), which corroborates with the hormonal data, where changes in salivary cortisol were observed when anticipating competition over food (Hohmann et al., 2009). We also verified our categorization by testing the association between the likelihood of aggression and tension conditions (please see Supporting Information: Section S2).

The *neutral* condition, where less tension was expected, consisted of conditions where no food or enrichments were present in the enclosures.

The *anticipation* condition included anticipation for feeding, anticipation for enclosure swapping, and anticipation for group composition change (for definitions see Supporting Information: Table S3). This condition was only scored based on the outcome. For example, *feeding anticipation* was only scored if the other bonobo group was already getting food, or when the caretakers walked by with food, and thus the bonobos could see or hear that they were about to receive food. Similarly, based on the restless behaviors of the bonobos, anticipation to change enclosures was scored if the bonobos eventually changed enclosures. If they did not change enclosures, but received food in their own enclosure, feeding anticipation was scored instead.

The *feeding* condition included conditions when food and enrichments were given, either by being placed in the enclosure, or hand given through the mesh. The start was set when the food was provisioned and ended when all the provisioned food was consumed. This did not include branches, nor hanging enrichments, as those were available all day long.

The *fission-fusion* conditions occurred when the bonobos actually changed enclosures, group compositions, or both simultaneously, and were scored once the anticipation for the respective conditions were done (e.g., when the hatch to a new enclosure opened, or when a new individual received access to the other group). Feeding has been shown to be a stressful factor in captive bonobos (Paoli et al., 2007), thus the fission-fusion condition was split into two categories: if food was present during fission-fusion conditions, the events were scored as *fission-fusion (feeding)*, whereas when no food was present, the events were scored as *fission-fusion (nonfeeding)*. Conditions were scored for 10 min after they first happened, to ensure all behaviors related to this condition were scored. Usually, during enclosure swapping behaviors, infants were carried by their mothers, and thus infants were not often considered initiators during these conditions.

2.4 | Statistical analyses

For the purpose of this study, only dyadic events with known initiators and recipients were included ($N = 2{,}139$ events excluded, which included multiple or unspecified recipients). Only facial expressions of the initiator were included in the analyses, as records of the recipient's facial expressions was relatively rare (*Adult recipients*: BT = 32; *Immature recipients*: BT = 31). Additionally, as no BT display was found during social play contexts, we did not include those in the analysis ($N = 2{,}617$ events excluded). Thus, the final data set consisted of 11,377 social events between 54 dyads (34.5% of adult-adult events, ranging from 4.6% to 23.64% across adults, and 65.5% of immature-adult/immature events, ranging from 29.31% to 35.58% across immatures; Supporting Information: Table S5).

2.4.1 | Interrater reliability

A randomly selected subset of the videos was coded by a second coder (SK), who was blind to the hypothesis: 16 videos of 20 min were coded, which included all bonobo individuals, in which 456 events were coded, amounting to 5.7% of all videos in which behaviors occurred. A detailed and comprehensive instruction was provided: SK coded *tension conditions*, *behavioral contexts*, *presence of BT display* and *recipient*, already as grouped behaviors (Table 1). Interrater reliability was assessed by calculating Cohen's Kappa and weighted Kappa, using the “kappa2” function in the *irr* package in R (Gamer et al., 2019). The agreement between the two coders was 0.765, which is considered substantial (Landis & Koch, 1977).

2.4.2 | Dominance rank analysis

For the social hierarchy rank analysis, we excluded immatures from the analysis, as immatures only enter the dominance hierarchy when they approach adult size and reproductive age (Davies et al., 2012; Pereboom & Stevens, 2008). Therefore, dyadic aggressive and submissive interactions among adults only were used (above 7 years of age, when they become socially and sexually mature; Pereboom & Stevens, 2008), including both sexes. Aggressive behaviors included *directed display*, *quasi-aggression*, *pestering*, *pestering aggression*, *aggression with attack*, *aggressive intention*, and *charge* were used, and submissive behaviors included *Fleeing* and *Yielding*, based on the definitions by Vervaecke et al. (2000) (Supporting Information: Table S2). There were no instances of *pestering*, nor *pestering aggression* between adults, thus these were not considered. It is important to note that the BT display was not considered a submissive indicator in our study. For the analysis, only dyadic interactions with a clear winner and a clear loser were used, which included submissive behaviors upon aggression, displacement, and yielding upon approach. We produced a dominance interaction matrix, and performed subsequent analysis with MatMan (de Vries et al., 1993). The improved index of linearity (h_0) was calculated with MatMan (de Vries et al., 1993), as it allows for the possibility of tied and unknown relationships. To indicate a clear linear hierarchy, the index of linearity should be greater than 0.90 (de Vries, 1998). As linearity and steepness are complementary measures to characterize a dominance hierarchy, indicating how linear and steep/shallow a population is (de Vries, 1995, 1998; de Vries et al., 2006), the steepness of hierarchy based on the normalized David's score was also calculated, using the “steeptest” function in the *steepness* package in R. By using the Dij values, a difference in interactions between individuals is taken into account. The steepness of dominance results in an index ranging from 0 to 1, where 0 represents an egalitarian dominance hierarchy, in which rank differences are small and where 1 indicates a despotic hierarchy.

2.4.3 | Bared teeth facial expression

We ran three models to investigate the use of the BT display in bonobos. We first tested the use of the BT display according to social contexts and dominance rank in adults (Model 1). Additionally, we subdivided the BT display into silent bared-teeth and VBT and ran two separate models to explore whether the effect of social contexts and dominance rank differs between the SBT (Model 1a) and VBT (Model 1b). Second, given that socio-sexual behaviors are commonly associated with social tension contexts in bonobos, we tested whether the BT display during socio-sexual interactions was also used as a signal to mitigate social tension, by examining its association with external tension conditions which are known to elicit tension in bonobos (Model 2). Finally, to understand the developmental trajectories of the BT display, we additionally explored the use of the BT display in immature bonobos in a separate model (Model 3). For social contexts, only the categories where the facial expressions were present were used in the analysis. For all the analyses, we used Bayesian generalized mixed models, using the Stan computational framework (http://mc-stan.org/). Bayesian statistics can inform about the reliability of the data of the parameters used, given the data observed (Kruschke et al., 2012; McElreath, 2018). Unlike the conventional null hypothesis testing, which assumes no prior knowledge or relationship with regard to the variables of interest, Bayesian methods allow the inclusion of background knowledge into the model which helps the estimation of the parameters. More practically, it can reliably model data with small data sets without losing their power and are better at controlling type 1 error (Hox et al., 2012; Lee & Song, 2004; Makowski et al., 2019; Van De Schoot et al., 2015), thus making it a particularly useful approach for our study.

All models were fitted in R (version 4.0.2; R Core Team, 2020) using the "brm" function in the *brms* package (Bürkner, 2017). For inference, we checked whether 0 was included in the 90% credible intervals, which were calculated from the posterior distributions. All models included four MCMC chains, with 4000 iterations per chain. To ensure sampling calibration, 1000 iterations were specified as warm-up, resulting in a total of 16,000 posterior samples. For all models, weakly informative priors on the intercept $\alpha \sim$ Normal (0, 1), fixed effects $\beta \sim$ Normal (0, 1), and random effects $\sigma \sim$ Cauchy (0, 1) were set to reduce inferential error and discourage overfitting 2018. The model diagnostics disclosed that the posterior distributions mirrored the original observations of response, with no divergent transitions in the MCMC chains, with all R-hat statistics <1.05, and with all effective samples >100 (see Supporting Information: Figures S2 and S3 for details).

Model specificities

Model 1—Influence of context and social rank on the use of the BT display in adult bonobos. The first model was fitted to the Bernoulli response of the BT display (binary coded as yes or no) with social context (five categorical levels: affiliative, sexual, aggressive, submissive, and neutral), relative dominance rank (two levels: to dominant, to subordinate), and sex of initiator and receiver (two levels: female, male) as fixed effects. Considering rank and sex could interact due to bonobo societies being female dominated, we first included the interaction sex and rank. We also tested for an interaction between rank and social contexts. However, none of these interactions had an effect, and therefore, such interactions were excluded from the final model. To avoid pseudoreplication, group compositions and the identity of the initiator, receiver, and their interaction were included as random intercepts, accounting for individual, as well as, dyad variation. The sample for this model consisted of dyadic interactions between nonkin adult bonobos only ($N = 8$). The models for the SBT displays (Model 1a) and the VBT displays (Model 1b) were essentially the same as the first model, except for the outcome variable (Model 1a: the SBT as yes or no, Model 1b: the VBT as yes or no).

Model 2—Influence of presumably high-tension conditions (measured during socio-sexual interactions) on the use of the BT display in adult bonobos. In bonobos, there is a well-established association between social tension and the performance of socio-sexual behaviors (Paoli et al., 2007). Although BT displays are known to occur during socio-sexual contacts in bonobos (Clay & Zuberbühler, 2011, 2012; Palagi et al., 2020), it is unclear whether this association is driven by the fact that sex is associated with social tension (i.e., BT display reflect social tension) or whether BT displays are more generally associated with socio-sexual contexts, regardless of whether tension is present. To verify that potential tension conditions (five levels: anticipation, neutral, feeding, fission-fusion [nonfeeding], and fission-fusion [feeding]) actually increase social tension in the group, we first checked the likelihood of aggression associated with tension conditions (Model 2a). We also checked whether socio-sexual behaviors were also associated with tension conditions in this group of bonobos (Model 2b). After confirming that most aggression occurred during the anticipation, holding procedure (nonfeeding) and holding procedure (feeding) conditions, and that all sexual behaviors were likely to be found in all tension conditions (please see Supporting Information: Section 2), we ran the model (Model 2) to test whether BT displays emitted during socio-sexual behaviors were more likely to occur during periods of social tension. Using a subset of the data, which only contained nonreproductive sexual behaviors, a similar analysis as in Model 1 was performed, by fitting the second model to the Bernoulli response of the BT display (binary coded yes or no), with the tension conditions (five levels: anticipation, neutral, feeding, fission-fusion [nonfeeding], and fission-fusion [feeding]) and rank (two levels: to dominant, to subordinate) as fixed effects. Same as the Model 1, Model 2 consisted of dyadic interactions between nonkin adult bonobos only ($N = 8$).

Model 3—Influence of context on the use of the BT display in immature bonobos. Further, we explored the association between the use of the BT display and social context in immature bonobos. Considering their exclusion in the dominance rank analysis, we could only investigate the influence of social contexts on BT displays, but not rank. A similar analysis as in Model 1 was performed, using social context (five levels: affiliative, sexual, aggressive, submissive, and neutral) as a predictor variable. Tension condition (four levels: anticipation, neutral, feeding, and fission-fusion [feeding]) was included as a control variable, to account for the fact that mothers carried infants in tension situations. The data set for this model consisted of only immature bonobo individuals as initiators ($N = 3$). Therefore, the random intercepts consisted of group compositions and only the interaction term between initiator and receiver, to account for dyadic variability.

3 | RESULTS

3.1 | Dominance style

The matrix of dominance interactions ($N = 591$, between 28 dyads) showed a good measure for this group's dominance hierarchy (significant linearity index $h' = 0.714$, $p = 0.015$). As the h' index was less than 0.90, the dominance hierarchy cannot be considered strictly linear; however, the slope steepness of 0.67 ($p < 0.001$) suggests that this group of bonobos was leaning toward a despotic dominance hierarchy. Individuals were therefore ordered into a linear dominance hierarchy, ranging from highest to lowest ranking (Jill > Bonnie > Kumbuka > Pangi > Besede > Kindu > Bolombo > Makasi; Figure 1). All females in this group dominated all the males. It is important to note that two males had very similar values, as well as two females (see Supporting Information: Table S4A,B). The relative rank relationships (to dominant vs. to subordinate) of each dyad was used for the subsequent analyses.

3.2 | Facial expressions

From the analyzed data set, 245 BT displays (BT; Figure 2) were observed between dyads: 144 BT displays were performed by adults and 101 by immatures (Table 2). All bonobos, including the alpha female, Jill, showed the BT display, in all contexts but social play (Table 2). Interestingly, the alpha female produced the BT display most often during sociosexual contexts (nine BT displays in total, eight [89%] during socio-sexual behaviors, mainly toward three other subordinate females). For adults, the BT display occurred in all tension conditions, whereas for immatures, the BT display never occurred in the fission-fusion (no feeding) condition (Table 2). Additionally, the two dyads that had similar values in the dominance hierarchy never performed the BT display toward each other.

3.2.1 | Model 1—Influence of context and social rank on the use of the BT display in adult bonobos

Our model showed that the BT displays were more likely to be produced during sexual contexts ($b = 4.33$ SD = 0.27, 90% CI [3.89, 4.79]) compared to the neutral context. However, BTs were not more likely to be used in any other social contexts compared to the neutral context (Figure 3a; see Supporting Information: Table S6 for details).

Moreover, the likelihood of BT displays was not higher when directed toward dominant individuals than toward subordinate individuals ($b = 0.00$ SD = 0.49, 90% CI [−0.81, 0.80]), and thus it was performed irrespectively of rank (Figure 3b). Additionally, sex of initiators and receivers had no association with the use of the BT display (*sex initiator*: $b = 0.20$ SD = 0.70, 90% CI [−1.00, 1.29]; *sex receiver*: $b = -0.32$ SD = 0.54, 90% CI [−1.20, 0.58]; see Supporting Information: Table S6 for details).

FIGURE 2 Bared teeth display in an adult bonobo during genito-genital rubbing, while just having received food

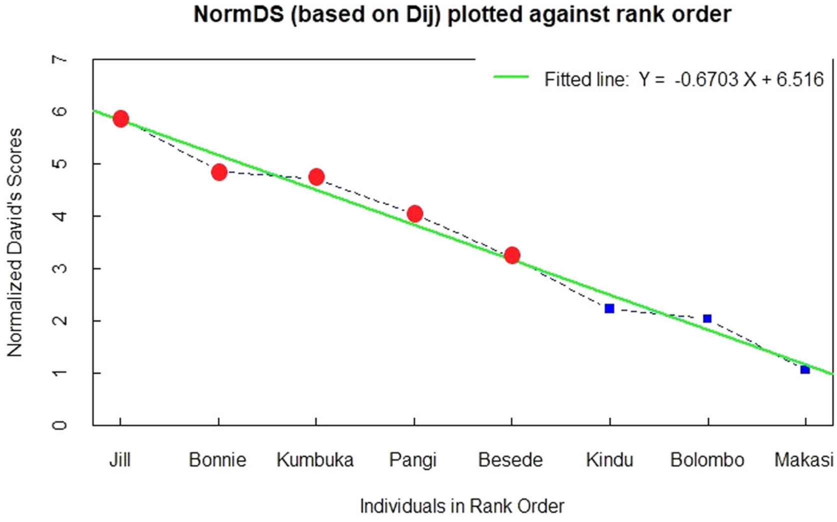

FIGURE 1 Steepness of rank order, based on only dyadic interactions with a clear winner and a clear loser were used, which included submissive behaviors upon aggression, displacement, and yielding upon approach. The normalized David's scores (NormDS based on Dij) plotted against rank of eight adult bonobos, ranked from Jill (alpha female) to Makasi (lowest in rank). Red circles represent females, blue squares represent males.

TABLE 2 Percentages of bared-teeth displays found in each social context and tension condition, for adult and immature bonobos

Social contexts	Adults		Immatures		Tension conditions	Adults		Immatures	
	SBT (%)	VBT (%)	SBT (%)	VBT (%)		SBT (%)	VBT (%)	SBT (%)	VBT (%)
Affiliative	1.4	9.7	18.8	18.8	Neutral	3.5	3.5	31.7	15.8
Sexual	17.4	48.6	22.8	8.9	Anticipation	7.6	11.1	6.9	8.9
Social play	0	0	0	0	Feeding	2.8	12.5	14.9	6.9
Aggressive	0	0.7	0	1.9	Fission-Fusion (Nonfeeding)	1.3	2.1	0	0
Submissive	3.5	6.9	11	5	Fission-Fusion (Feeding)	12.5	43.1	5.9	8.9
Neutral	5.6	6.2	6.9	5.9					

Abbreviations: SBT, silent bared-teeth; VBT, vocalized bared-teeth.

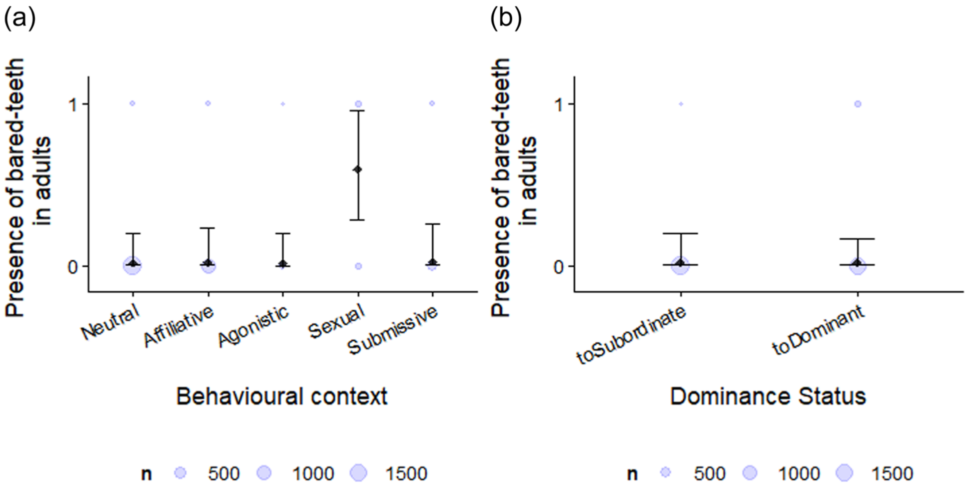

FIGURE 3 Plots depict the predicted probability of outcome variables for the marginal effects of the complete Bayesian generalized linear mixed model 1. (a) Influence of context on the use of the bared-teeth (BT) display in adult bonobos (*N* = 8). (b) Influence social rank on the use of the BT display in adult bonobos (*N* = 8). The upper and lower vertical lines correspond to the upper and lower 90% credible intervals and the diamonds represent the posterior means. Circles represent the frequency of the observations.

Additional investigation of the use of the SBT and VBT revealed that the SBT and VBT are essentially produced in the same context (during sexual interactions) and the rank did not influence the likelihood of the both displays (for detailed information, please see the Supporting Information: Section 2, Tables S1 and S2).

3.2.2 | Model 2—Influence of presumably high-tension conditions (measured during socio-sexual interactions) on the use of the BT display in adult bonobos

The likelihood of BT displays was higher during the fission-fusion with feeding condition ($b = 1.51$ SD $= 0.54$, 90% CI [0.62, 2.42]), where social tension was presumed to be highest of all tension conditions, compared to the neutral condition (Figure 4). There was no association between BT displays and the other social tension conditions, when compared to the neutral condition (*Anticipation*: $b = 0.24$ SD $= 0.60$, 90% CI [−0.75, 1.21]; *Fission-Fusion (Nonfeeding)*: $b = 0.54$ SD $= 0.83$, 90% CI [−0.81, 1.94]; *Feeding*: $b = -0.53$ SD $= 0.57$, 90% CI [−1.46, 0.41]; see Supporting Information: Table S6 for details).

Similar to Model 1, BT displays during socio-sexual interactions were performed irrespectively of rank ($b = 0.23$ SD $= 0.58$, 90% CI [−0.75, 1.17]), and sex had no influence on the likelihood of BT displays (*sex initiator*: $b = -0.10$ SD $= 0.68$, 90% CI [−1.23, 1.02]; *sex receiver*: $b = -0.23$ SD $= 0.70$, 90% CI [−1.38, 0.93]; see Supporting Information: Table S6 for details).

3.2.3 | Model 3—Influence of context on the use of the BT display in immature bonobos

BT displays in immatures were more likely to occur in sexual ($b = 3.86$ SD $= 0.35$, 90% CI [3.29, 4.43]), submissive ($b = 1.68$ SD $= 0.35$, 90% CI [1.10, 2.25]), and affiliative contexts ($b = 0.58$ SD $= 0.27$,

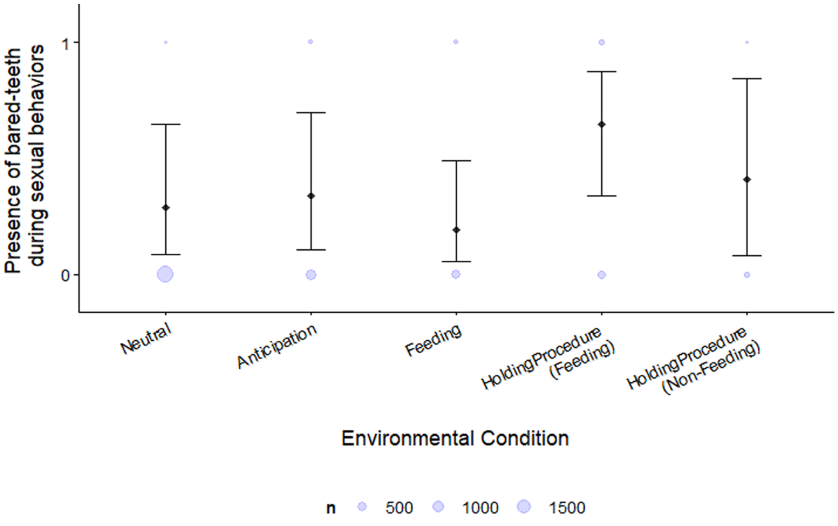

FIGURE 4 Plots depict the predicted probability of outcome variables for the marginal effects of the complete Bayesian generalized linear mixed **model 2**: Influence of presumably high-tension conditions (measured during socio-sexual interactions) on the use of the bared-teeth display in adult bonobos (*N* = 8). The upper and lower vertical lines correspond to the upper and lower 90% credible intervals and the diamonds represent the posterior means. Circles represent the frequency of the observations.

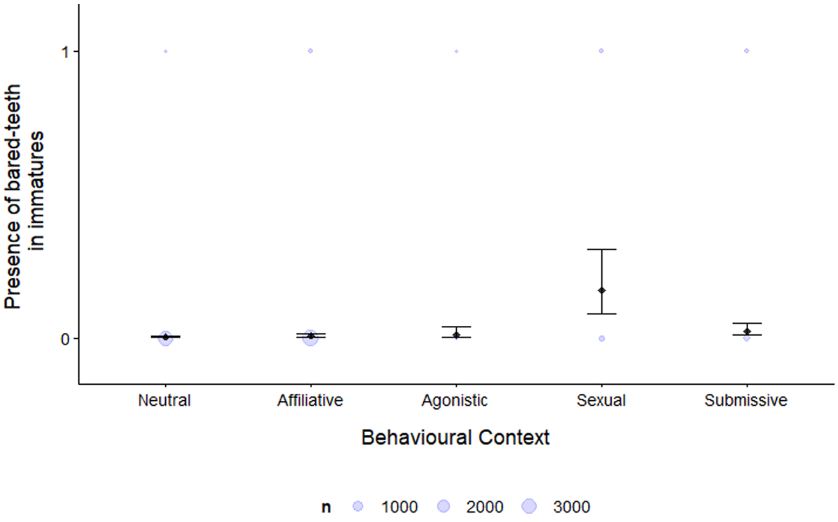

FIGURE 5 Plots depict the predicted probability of outcome variables for the marginal effects of the complete Bayesian generalized linear mixed **model 3**: Influence of the context on the sue of the bared-teeth display in immatures (*N* = 3). The upper and lower vertical lines correspond to the upper and lower 90% credible intervals and the diamonds represent the posterior means. Circles represent the frequency of the observations.

90% CI [0.14, 1.02]), compared to the neutral context (Figure 5). Only the aggressive context had no influence on the likelihood of BT displays (*b* = 0.76 SD = 0.76, 90% CI [−0.52, 1.99]; see Supporting Information: Table S6 for details) when compared to the neutral context.

4 | DISCUSSION

This study investigated the use of BT displays in a group of 11 captive bonobos to test the Power Asymmetry Hypothesis (Preuschoft & van Hooff, 1997). The social dominance analysis for this group revealed a relatively linear female biased dominance hierarchy (h'index [0.714] lower than a threshold of 0.90, indicating strongly linear hierarchy; P. Martin & Bateson, 1993), leaning more toward a despotic rather than egalitarian society. It should be noted though that the relatively despotic nature of this group of bonobos is not comparable with what has been found in rhesus macaque groups, which show clear linearity and strong power asymmetry between adjacently ranked individuals (e.g., Balasubramaniam et al., 2012; Beisner et al., 2016; Dobson, 2012). Interestingly, even in this relatively despotic bonobo population, the BT display was produced irrespective of dominance rank and mainly in the sexual context for tension regulation. This suggests that the BT display is best explained by their tolerant species characteristics, rather than their current despotic social environments. An additional investigation revealed that immature bonobos performed BT displays in a wide range of contexts, contrasting to the adults, suggesting a potential role of learning in the communicative development of the BT display. In the following sections, we will discuss the results in more detail.

Unlike our prediction that bonobos would have a shallow dominance hierarchy, the bonobos in this study exhibited a rather steep dominance hierarchy, with all females occupying higher ranks than all adult males (Figure 1). Although contradicting studies of wild population (Hare et al., 2012; Hohmann, 2001; Idani, 1991), this finding is in line with most captive studies, where female despotism in bonobos has been reported (Cronin et al., 2015; Jaeggi et al., 2010; Stevens et al., 2007; Vervaecke et al., 2000). It is also common to find variation in the dominance style across populations of the same species (de Vries et al., 2006) and study periods of the same population (Paoli & Palagi, 2008). There could be a number of aspects potentially influencing this variation, but the ratio of females to males (Hemelrijk et al., 2008) and the methods and behaviors to evaluate dominance (Vervaecke et al., 2000) were found to play a role. Interestingly, studies on multiple populations of captive bonobos have reported either a similar or even a stronger linearity and steepness than what has been found in the current study group (Jaeggi et al., 2010; Stevens et al., 2007). Whereas bonobos in the wild experience high levels of fission-fusion dynamics, with frequent intergroup interactions (Furuichi, 1997, 2011), bonobo groups in captivity often consist of long-term stable group members with access to monopolizable resources; this facilitates dominant individuals to exercise power to control subordinates (Stevens et al., 2008). The low level of aggression and high level of submissive displays found in this group are indeed one of the characteristics of long-term stable primate groups (see Preuschoft & van Schaik, 2000, for a review). Therefore, it is not uncommon to expect a strong difference in the dominance style between captive and wild populations (Furuichi, 2011; Surbeck & Hohmann, 2013), and describe captive bonobos as semidespotic (Stevens et al., 2007).

Interestingly, the semidespotic dominance hierarchy we observed did not seem to have a greater impact on their use of communicative signals, as the BT display was produced irrespective of dominance rank and mostly during sexual interactions. In fact, 33% of BT displays were produced by dominant individuals to subordinate individuals (see Supporting Information: Figure S4), and the alpha female also performed the BT display herself. The same female also produced the BT display toward a subordinate female when she was hesitant to enter a newly open enclosure, potentially reflecting nervousness and asking for reassurance from the subordinate female (Kim, personal observation). Therefore, our results are more in line with what the power asymmetry hypothesis predicts for tolerant or egalitarian societies (Preuschoft & van Hooff, 1997). Comparably, in other captive populations that were found to have similar semidespotic hierarchies, the BT display was not performed unidirectionally either (de Waal, 1988; Vervaecke et al., 2000). Accordingly, even though bonobos have some flexibility in their dominance styles across wild and captive populations, the use of the communicative BT signal seems to be less prone to changes in their current social environments.

It is, however, important to note that the use of the BT display in this group is highly variable across individuals, with one individual producing a high amount of BT displays (the lowest ranking female; see Supporting Information: Figure S4), and only one individual performing the BT display consistently toward dominant individuals. These findings could be due to several factors, such as personality (e.g., Dimberg et al., 2011; Staebler et al., 2011), prior rearing history, or different levels of sensitivity to social signals, with certain individuals being more sensitive to social signals than others. However, we would need more data to support our claim regarding the association between the use of BT display and individual differences. The power asymmetry hypothesis does not predict tolerant species to *never* use the BT as a signal of submission, rather, it predicts the meaning of the BT to be broadened, and thus to be used in a wide range of social contexts. A recent study on crested macaques indeed showed that the SBT is used in submissive context as well, although it was most frequently used during affiliative interactions (Clark et al., 2020).

The fact that the BT display in this group of bonobos is not unidirectional suggests that it cannot be classified as a formal status indicator, compared to pant grunt vocalizations in chimpanzees, which are produced unidirectionally and reliably indicate an individual's social subordination toward another (Noë et al., 1980; Sakamaki, 2011). Although in the original article of the PAH the authors suggests the BT display in intolerant societies to be a *distinct* signal of submission, potentially indicating an internal state of fear (Preuschoft & van Hooff, 1997), it is still largely debatable whether the BT accompanied with submissive behaviors actually reflects the signaler's internal state of fear, due to limited methods to correctly measure *emotions* in animals (Nieuwburg et al., 2021). In our study, around 10% of the BT display were produced by adults in the submissive context and it was not more likely than in the neutral context (12%). Although it is hard to tell what would be the internal state of the signaler producing the BT, given the limitations stated above and the current data set, it is unlikely that the BT display in bonobos is used to soley signal submission. The context where the BT display was most likely to occur was the sexual context.

Several possible explanations have been proposed for the significance of the BT display during sexual contexts in bonobos. de Waal (1988) has proposed that the BT display during sexual behaviors in bonobos may indicate arousal or pleasure. This seemed to be further supported by a recent study demonstrating Rapid Facial Mimicry (RFM) of the SBT during face-to-face sexual interactions in captive bonobos (Palagi et al., 2020). The authors in this study argued that the positive effect of the RFM in prolonging the duration of the sexual interaction is an indirect evidence of the SBT as a communicative expression of sexual arousal. However, the authors did not rule out the possibility of the RFM communicating (potentially without conscious awareness) nervousness caused by high tension during sexual interactions, which is also possible according to the Perception Action Model (Preston & De Waal, 2002). Moreover, their finding that the duration of sexual contacts had no effect on the likelihood of the SBT mimicry made it harder to support the arousal explanation, as it is expected to have the arousal expression in the late, not in the initial, phase of sexual interaction (de Waal, 1988). Therefore, given that socio-sexual behaviors in bonobos are used as a means to regulate tension (Aureli et al., 2008; Hohmann & Fruth, 1996; Moscovice et al., 2015; Paoli et al., 2006, 2007), and that the BT display during sexual contexts was associated with the highest tension condition in our study, the explanation of internal pleasure seems unlikely. Future research should test the arousal hypothesis by investigating the timing of the BT display during such sexual behaviors or masturbation.

An alternative explanation is that the BT display during sexual behaviors may reflect nervousness and signal appeasement, especially considering their socio-emotional sensitivity (Clay & de Waal, 2013). In captivity, feeding, as well as changing enclosures which may or may not contain food, changing groups, and the anticipation of these situations can be stressful. Previous research found that bonobos used nonreproductive genito-genital rubbing more frequently during feeding times, compared to the baseline, both in captivity (Paoli et al., 2007) and in the wild (Fruth & Hohmann, 2006; Hohmann et al., 2009). Similar results were also found in the current study, where BT displays were also most often found during high tension conditions, when uncertainty and competition over food was high. Additionally, BT displays in the sexual context were produced mostly likely in the condition with the highest likelihood of tension (*Fission-Fusion with feeding*), measured by likelihood of aggression. Thus, similar to the function of genito-genital rubbing, the BT display in the socio-sexual context seems to convey appeasement.

Even though the bonobos were most likely to show the BT display during sexual contexts, they still performed the BT display in different contexts as well (Table 2). This could potentially resemble the multi-contextual use of the smile in humans (Mehu & Dunbar, 2008). Especially, the BT display in the sexual context reflecting nervousness can be comparable to the nervous smile in humans (Mehu & Dunbar, 2008). In fact, human smiles have subtle morphological variations, with each variant having a different meaning (J. Martin et al., 2017; Rychlowska et al., 2017). Recently, similar patterns have been found for SBT displays in crested macaques (*Macaca nigra*; Clark et al., 2020), one of the most socially tolerant macaque species. It was found that the SBT display differed subtly in appearance in different social contexts. For example, during submissive behaviors, a higher intensity in movement was observed (Clark et al., 2020). This is also very likely to have been the case of the bonobos in this group, had we examined the subtle differences in the morphology of the BT display in the different social contexts. In costly situations, avoiding any miscommunication is rather important (Johnstone, 1997), and therefore facial expressions are expected to be highly intense or conspicuous in its appearance. Future research would benefit from incorporating the FACS (Facial Action Coding System; Ekman, 2002) to further investigate the contextual variation in the use of BT displays in bonobos. Furthermore, considering that social signals are very complex, and combined with gestures and vocalizations, it would be beneficial to investigate the possibility that due to our coding method, certain complex signals or cues were clear to the bonobos, but simplified in this study.

From a developmental stance, our results suggest that immature bonobos performed the BT display across a wide range of social contexts, including affiliative, submissive, and sexual contexts. Yet, the highest likelihood of the use of the BT display was found in the sexual context for both adults and immatures, even though immatures were less likely to engage in sexual behaviors as adults were. Given that the adult bonobos produced the BT display mostly in the sexual context, our results may suggest that immature bonobos become competent in their use of the BT display in proper contexts throughout the development via social learning (Pika et al., 2005), similar to the "Repertoire Tuning" hypothesis in gestural communication (Bard et al., 2014; Hobaiter & Byrne, 2011; Pika & Fröhlich, 2019). In this scenario, older individuals may have learned by experience which signals—facial expressions in this case—to use to amplify their communication capacity. On the other hand, immatures may use a "fail-safe" strategy: they are able to produce a large and redundant repertoire, but still lack the knowledge of which one is the most efficient (Hobaiter & Byrne, 2011). Infants, therefore, need to learn how to effectively use the BT display and refine the signal production through multiple and different social interactions with all members of the group (Genty, 2019). In this case, communicative repertoire is progressively tuned down to the most effective signals (Genty, 2019). However, it could also be that the BT in a wide range of contexts may simply reflect greater underlying arousal or uncertainty of immatures driven by less social security and potentially enhanced risk of aggression due to their unstable social position in the group. It is also important to note, that similar to the adults, individual variation was rather high, and skewed toward the juvenile individual, whereas the infants had similar frequencies of BT displays. As such, it would be important to directly compare different age classes, as well as conducting a longitudinal study to further elucidate the developmental trajectories of the BT display in bonobos. This line of research would allow us to answer at what age the BT display is fully adapted to using it in proper contexts.

Taken together, although the dominance style of this group of bonobos found to be more despotic than previously assumed, the meaning of the BT display seems to be in line with the power asymmetry hypothesis for species with a high degree of social tolerance (Preuschoft & van Hooff, 1997). Further studies should follow to replicate our findings in other groups of bonobos, as well as to disentangle the influence of dominance styles (i.e., species vs. environmental aspects) on the use of the BT display. This could be achieved by studying captive populations with different levels of social tolerance (especially populations with stronger despotic characteristics), as well as by studying wild bonobo populations. Moreover, studying the extent to which the environment influences the use of BT displays in different bonobo populations should highlight whether the BT display in this species is genetically inherited (has a fixed form) or whether it is largely influenced by environmental components; such evidence would further inform on the signaling flexibility in bonobos. For example, in capuchin monkeys (*Cebus apella*), the BT display has been suggested to have different meanings across populations, presumably due to different levels of dominance hierarchy. Whereas the BT display signaled submission when there was a pronounced hierarchy, it signaled affiliation when the hierarchy was not that pronounced (Visalberghi et al., 2006). Therefore, our findings as well could be only specific to this group of bonobos, and should not be generalized to the species' characteristics.

5 | CONCLUSION

Taken together, in line with wild bonobo studies (Hare et al., 2012; Hohmann, 2001; Idani, 1991), the captive bonobos in this study had a female-dominated hierarchy, but with a steeper dominance hierarchy than expected based on the previous literature (Cronin et al., 2015; Jaeggi et al., 2010; Vervaecke et al., 2000). The use of BT display in this semidespotic population of bonobos however is best explained by their egalitarian species characteristics, rather than the despotic dominance style of the current population, as it was produced regardless of rank and most likely in the sexual context. The BT display during socio-sexual interactions appears best described as signaling appeasement or reassurance, as it was tightly associated with the condition of the highest tension and uncertainty. Hence, these results are in line with what the power asymmetry hypothesis predicts for species with a high degree of social tolerance (Preuschoft & van Hooff, 1997). Finally, results from immature bonobos potentially suggest that the communicative meaning of the BT display is being tuned throughout the development, similar to the development of the gestural communication (Bard et al., 2014; Genty, 2019; Hobaiter & Byrne, 2011; Oña et al., 2019; Pika & Fröhlich, 2019). Future research should aim at replicating these results on a larger scale across species and populations, not only focusing on the BT display but also on other communicative signals, such as gestures and vocalizations. Studies on the potential effects facial expressions may have on the recipients should also follow to better understand the function of the expressions. To conclude, this study is the first to systematically investigate the BT display in a great ape species. By doing so, it can help to better understand the evolutionary origins of communicative signals in relation to a species' social system.

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AUTHOR CONTRIBUTIONS

Jolinde M. R. Vlaeyen: Conceptualization; data collection; data analysis; visualization; writing original draft; writing review and editing. **Raphaela Heesen**: Data analysis/validation; assistance with coding of behaviors and communication; writing review and editing. **Mariska E. Kret**: Funding acquisition; writing review and editing. **Zanna Clay**: Funding acquisition; writing review and editing. **Thomas Bionda**: writing review and editing. **Yena Kim**: Conceptualization; data analysis/validation; project administration; supervision; writing review and editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at 10.6084/m9.figshare.16782925.

ETHICS STATEMENT

Permission to conduct this study was granted by Apenheul Primate Park. It was a purely observational study involving nonhuman animals, where no invasive procedures were conducted. The care of the bonobos adhered to the guidelines of the European Endangered Species Program, developed by the European Association and Zoos and Aquaria (EAZA). Due to the absence of any potential discomfort for the bonobos and due to the noninvasive nature of this study, it did not meet the definition of *animal test* as mentioned in Article 1 of the Dutch "Experiments on Animals Act." Thus, the Apenheul Ethics Committee waived the need for approval. This study adhered to the American Society of Primatologists Principles for the Ethical Treatment of nonhuman Primates.

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SUPPORTING INFORMATION

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