



Beware! Different methods lead to divergent results on yawn contagion modulation in bonobos

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Abstract

Contagious yawning (CY)—linked to physiological synchronization and possibly emotional contagion—occurs when one individual's yawn induces yawning in others. CY was investigated over different time windows (minutes from the triggering stimulus) via naturalistic or experimental studies (using real and video yawns, respectively) with contrasting results, especially in bonobos. We verified whether in bonobos result divergences may derive from different methods. We gathered yawning data on 13 bonobos at Twycross Zoo (UK) via a naturalistic (all-occurrences observations) and experimental approach (by showing yawn/control video stimuli). Based on literature, we used 1- and 3-min windows to detect CY. Due to fission-fusion management, individuals could form permanent or non-permanent associations (more/less familiar subjects under naturalistic setting). Video yawn stimuli may come from group mates/stranger models (more/less familiar subjects under the experimental setting). Stimulus type and time window affected CY modulating factors but not CY detection. Familiarity and age effect on CY showed opposite trends in 3-min trials and 1-min observations. CY was highest in oldest, non-permanently (rather than permanently) associated subjects in the naturalistic setting, but in the youngest subjects and with ingroup (rather than outgroup) models in trials. The age effect differences on CY might be due to decontextualized yawns and immature subject curiosity toward videos. The reversed familiarity effect suggests CY's context-dependent function in promoting social synchronization with socially distant group mates, as failing to coordinate as a group may lead to social disruption. Complementary methods are needed to fully understand motor replication phenomena.

KEYWORDS

behavioral contagion, emotional contagion, methodology issue, motor contagion, synchronization

Abbreviations: CC, control condition; FM, female/male; GLMM, generalized linear mixed model; MC, matched control; MF, male/female; PC, post-conflict; PY, post yawning; YC, yawn condition; YCI, yawn contagion index.

Sara De Vittoris and Marta Caselli share the first authorship.

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1 | INTRODUCTION

Contrary to spontaneous yawning, contagious yawning occurs when the yawn of an individual (responder) is induced by the perceived yawn of another individual (trigger; [Provine, 1989]). In this respect the yawn of an individual acts as releasing stimulus (*sensu* Tinbergen, 1952). Yawn contagion has been investigated in various primate species spanning strepsirrhines and haplorrhines using naturalistic observations (with real yawn stimuli) for some species (e.g., Gallo et al., 2021; Palagi et al., 2009; Valdivieso-Cortadella et al., 2023; Valente et al., 2023) and an experimental trials with video stimuli for others (e.g., Palagi & Norscia, 2019; Paukner & Anderson, 2006; Pedruzzi et al., 2022; Reddy et al., 2016; van Berlo et al., 2020). Few species have been studied with both methods, and even fewer with both approaches in the same study (e.g., Norscia et al., 2021a; Palagi et al., 2019). The use of different types of stimuli (video vs. real yawns) has led (with one exception only) to generally consistent results with respect to the presence of yawn contagion in the few species where different types of stimuli were used (although rarely in the same study). Yawn contagion was not detected in gorillas (*Gorilla gorilla gorilla*) across methods (video stimuli: Amici et al., 2014; naturalistic observations: Palagi et al., 2019), yet was consistently observed in chimpanzees (*Pan troglodytes*) both experimentally (Anderson et al., 2004; Campbell & de Waal, 2011; Campbell et al., 2009) and under naturalistic conditions (Campbell & Cox, 2019). In bonobos (*Pan paniscus*), it was reported in two studies under naturalistic conditions (Demuru & Palagi, 2012; Norscia et al., 2022) and one experimental study (Tan et al., 2017), but not in another study (Amici et al., 2014). In humans (*Homo sapiens*), naturalistic observations (Norscia & Palagi, 2011; Norscia et al., 2021a) or video stimuli (Bartholomew & Cirulli, 2014; Chan & Tseng, 2017; Provine, 1986, 1989) have confirmed the presence of yawn contagion, originally described by Provine (1986, 1989) by using experimental trials.

As an automatic response that is not purely motoric but is also based on autonomic processes, yawn contagion may occur from immediately to several minutes after perceiving a yawn (Palagi et al., 2020; Prochazkova & Kret, 2017). Different time windows have been used to detect yawn contagion, spanning 20 s to several minutes after the triggering stimulus (Kapitány & Nielsen, 2017). The choice of the time window duration is a sensitive matter because it bears the risk of including either false positives (if the time window is too long)—that is yawns considered as induced by contagion when they are spontaneous—or false negatives (if the time window is too short)—that is yawns considered as spontaneous when they are elicited by contagion (Kapitány & Nielsen, 2017; Norscia & Palagi, 2011). Some studies used 5 min as a time latency (Palagi et al., 2009), but since autocorrelation (the fact that a yawn performed by a subject at t_0 may increase the likelihood of inducing another yawn by the same subject at t_{0+x}) can be highest at the fourth minute (Kapitány & Nielsen, 2017), most studies have settled on a time window of 3 min (naturalistic conditions; lions, *Panthera leo*: Casetta et al., 2021; pigs, *Sus scrofa*: Norscia et al., 2021b; indri, *Indri indri*: Valente et al., 2023; spider monkeys, *Ateles geoffroyi*: Valdivieso-Cortadella et al., 2023; geladas,

Theropithecus gelada: Gallo et al., 2021; bonobos: Demuru & Palagi, 2012; Norscia et al., 2022; humans: Norscia & Palagi, 2011; bonobos/humans: Palagi et al., 2014; video stimuli; red-capped mangabeys, *Cercocebus torquatus*: Pedruzzi et al., 2022; stump-tail macaques, *Macaca arctoides*: Paukner & Anderson, 2006; chimpanzees: Anderson et al., 2004). Hence, the 3-min time range may reduce the probability of autocorrelation (Kapitány & Nielsen, 2017) and the likelihood of considering a spontaneous yawn as one resulting from contagion. Indeed, in hominins yawn contagion has been mostly detected in the 3-min time window, with a pick in the first minute (chimpanzees: Campbell & de Waal, 2011; humans: Norscia & Palagi, 2011; bonobos/humans: Palagi et al., 2014) and in one case for chimpanzees within 3.5 min with a pick at 1.5 min (over a longer time slot; Campbell & Cox, 2019). The situation in bonobos is particularly tricky, because one study reported a pick of yawn contagion in the first minute (Demuru & Palagi, 2012) and another that yawn contagion *only* occurred within 1 min (Norscia et al., 2022). In light of the above, and because this study is focused on bonobos, we used both the 3- and 1-min time windows to understand whether the use of different time windows can lead to divergent results regarding yawn contagion.

Besides the presence/absence of yawn contagion, the use of different approaches may affect the amount of detected contagion, which in turn can lead to differences in the detection of modulating factors. In humans, an effect of familiarity has been verified only via naturalistic observations (with yawn contagion increasing as familiarity increases; Norscia & Palagi, 2011; Norscia et al., 2020; Norscia et al., 2021a). However, the general yawning response in humans (along with other motor mimicry responses) to prerecorded video stimuli can be weaker than the response observed in real, face-to-face interactions (Diana et al., 2023). Because the modulating factors precisely act on the amount of yawn contagion (by increasing or decreasing it), possible differences may emerge when comparing the results obtained from video and real stimuli in humans. In bonobos, the results coming from video and naturalistic studies reported either no differences or stronger contagion between more familiar subjects (Demuru & Palagi, 2012; Norscia et al., 2022; Tan et al., 2017). To our knowledge no other species have been studied with respect to modulating factors (e.g., familiarity, age, sex) by using both naturalistic observations and video-stimuli.

A critical point is that what we know about yawn contagion in different species is based on single or very few case studies, and on the use of either method (naturalistic observations or experimental trials), with rare exceptions (Palagi et al., 2020). This study is not as much focused on the phenomenon of yawn contagion per se. Rather, it is focused on whether the diverging results can actually be ascribed to different methodological approaches and on how to interpret the possible result differences. To this purpose, we carried out both experimental trials (by showing yawn/control video stimuli) and observational data collection (involving the display of real yawns) on the same individuals of a bonobo colony housed at Twycross Zoo (UK). Bonobos are a good model to investigate this aspect because there are enough studies on yawn contagion that suggest that some apparently contrasting results may derive from the use of different methodological approaches (Amici et al., 2014; Demuru & Palagi, 2012; Norscia et al., 2022; Palagi et al., 2014;

Tan et al., 2017). Such studies are enough to allow general predictions, which are listed here below.

Presence of yawn contagion. Because in bonobos yawn contagion has been found in both experimental and naturalistic studies using different time windows (Demuru & Palagi, 2012; Norscia et al., 2022; Tan et al., 2017), we expected that the phenomenon could be detected with both naturalistic and experimental settings (Prediction 1a), and different time windows (Prediction 1b).

Modulation of yawn contagion. Video and naturalistic studies apparently report contrasting results on the effect of familiarity on yawn contagion in bonobos (Demuru & Palagi, 2012; Norscia et al., 2022; Tan et al., 2017). However, familiarity determination had a different basis in video and naturalistic studies. In experimental video studies, familiarity level was based on whether the video shows group-mate or stranger models (Tan et al., 2017). In the naturalistic approach, familiarity level was based on the level of association (e.g., affiliation) between group members (no strangers were present in the group, only more or less familiar subjects; Demuru & Palagi, 2012; Norscia et al., 2022). No information is available on possible differences in the effect of age or sex because only naturalistic studies considered these variables (Demuru & Palagi, 2012; Norscia et al., 2022). However, yawn contagion can be affected by the method in humans (prerecorded video stimuli/real yawns; Diana et al., 2023) and by the time elapsed from the yawning stimulus in great apes and humans (Campbell & Cox, 2019; Demuru & Palagi, 2012; Norscia & Palagi, 2011; Norscia et al., 2022). Because modulation acts on the amount of yawn contagion, we expected that the yawn contagion rates within different time window would not necessarily correlate between methods (Prediction 2a), and to find differences in the factors that can influence yawn contagion when considering different methods (Prediction 2b) and time windows (Prediction 2c). However, it was not possible to predict any specific direction.

2 | METHODS

2.1 | Ethical statement

This study was totally noninvasive and purely observational. Individuals would spontaneously approach to watch videos on the tablet for experimental trials and were not separated from the group. No element of their environment was modified for this study. This study was approved by the Bioethics Committee of the University of Torino (approval #0272400). This research complies with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

2.2 | Study site, period, and colony

The study was conducted over the period May 2021–July 2022 on a colony of bonobos housed at Twycross Zoo (Atherstone, UK). The colony was managed using a fission-fusion approach, involving the occasional transfer of individuals between two subgroups under the supervision of

keepers. Initially the two subgroups were housed in an enclosure with indoor spaces (52.8 m²/per group) and an outdoor space (547 m²)—that the two subgroups would use alternatively every other day—to be then moved (in September 2021) to another enclosure with two outdoor spaces (211 m² and 433 m²; one per subgroup) and indoor spaces (54.3 m²/per group). The colony consisted of 13 individuals (age range: 2–44 years old; group composition is fully described in Table 1). Some individuals always stayed together in the same subgroup, namely Lina and her offspring (Rubani, Louisoko, and Lucuma) in one group, Diatou and offspring (Keke) in another. Cheka with offspring (Ndeko) and Likemba with offspring (Lola) would always stay together but could switch subgroups.

2.3 | Data collection

2.3.1 | Naturalistic data collection

After an identification period (2 weeks), behavioral data were collected over 4 days per week from 9 a.m. to 5 p.m. on the interactions between the bonobos of the colony. Via audio recordings during live observations (Fsdhn recorder; MP3 audio, 8 GB) and—in case of various animals to be checked—with the support of video recordings of live interactions (Panasonic HC-V180, Full HD). Observational data on yawning were gathered in absence of any perturbing event (e.g., aggressions, feeding contexts, moments before and after fission-fusion) via the all-occurrences sampling method (Altmann, 1974) for approximately 350 h of observations. Data on yawning were collected when the individuals of a subgroup were close and all easily observable (within 10 m). For each yawn, the following data

TABLE 1 Colony housed at Twycross Zoo during the study period.

Name	Sex	Age
Cheka	Female	25
Diatou	Female	44
Keke	Male	27
Likemba	Female	11
Lina	Female	36
Lola	Female	2
Lopori	Female	9
Louisoko	Male	23
Lucuma	Male	18
Malaika	Female	11
Maringa	Female	23
Ndeko	Male	6
Rubani	Male	5

Note: The table includes identity, sex, and age of individuals.

were recorded: (i) sex, age, and identity of both the trigger and the potential responders (individuals present in the group); (ii) the distance between all the potential responders from the trigger (in proximity: 1 m; out of proximity: 1–10 m); (iii) time of the yawn, considering the last yawn if more than one was emitted in a row; (iv) if the potential responder could see or not the triggers' yawn. Figure 1a shows the situation of a triggering yawning and a response in the study bonobos. In this research, the Post-Conflict/Matched Control method (PC-MC) that was designed by de Waal and Yoshihara (1983) to shed light on reconciliation strategies that animals use after an aggressive event, has been readjusted to see whether the probability of yawning was higher after perceiving a yawn (here called Post-Yawning, PY) compared to a control observation (MC). PY refers to the minutes following the triggering yawn, when other individuals were observed to verify if there was a yawning response. A posteriori we extracted data on the possible yawning response over two different time windows: 1 or 3 min. MC (same duration as PY, 1 min or 3 min) was carried out: (i) on the first possible day at around the same time as PY; (ii) under similar social and environmental conditions; and (iii) without any triggering yawn in the previous 3 or 1 min depending on the time window (3 or 1 min, respectively). The presence or absence of yawning response was recorded in both PY and MC. A posteriori we also determined two categories of familiarity based on whether the individuals had formed permanent associations (always together) or not (not always together).

2.3.2 | Experimental trials and video analysis

The experimental trials were carried out 4 days per week from around 9 a.m. to 6 p.m. The procedure involved the use of a tablet (Lenovo, A7600-H 10.1") to show a video sequence. The video sequence (1 min in total) consisted of 4 s of blue screen with a beep sound (1 s) at the beginning of the video—marking the exact moment the test started—and 3–7 s clips (530 × 610 pixel) repeatedly showing faces of bonobo models, and specifically a male and a female in an alternate way. We prepared videos under two main conditions, yawn (YC) and control condition (CC): YC videos showed the conspecifics yawning whereas CC videos showed the same conspecifics (in the same sequence as the yawning condition) moving their mouths. One adult male and one adult female—in either YC or CC. Each control clip was extracted from the same video as the yawning clips, either after or before the yawning. For each one of the two main conditions (yawn/control) we had the following subconditions: (i) Male–female (MF)/female–male (FM): first yawn stimulus was the male in MF and a female in FM; (ii) stranger (outgroup)/familiar (same group) condition, depending on whether the bonobos showed on videos were total strangers (individuals never met before by the experimental subject, with clips selected from www.youtube.com) or in-group members (pre-recorded yawning clips). Two sample clips of a familiar individual are shown in Video S1 (YC) and Video S2 (CC).

The tests were conducted only during relaxed situations (i.e., resting) when a bonobo voluntarily approached the experimenter.



FIGURE 1 (a) Top—Trigger yawn by an individual (left) and response by another individual (right) in the naturalistic setting; (b) Bottom—Yawning sequence of a male.

Each subject would watch the video from the enclosure glass and was exposed to a total of eight trials covering all condition/subcondition combinations, for a total of 104 tests. Video conditions and subconditions were shown in a randomized order. The experimenter was always the same (Sara De Vittoris) and she showed the videos on the tablet using a special support (Ulanzi, 7.9"–12.9") that allowed the simultaneous filming of the individuals tested on a camcorder (Panasonic HC-V180, Full HD). The tests were not considered valid if any other individual in the group yawned during the experiment. After each trial, the tested individuals were followed by video–audio recordings for 3 min from the first stimulus so as to record possible yawning responses. The same individual could be exposed to multiple tests (for a maximum of 3–4/day) but a minimum time of 5 min had to pass between one test and the other. All videos were analyzed frame by frame via PotPlayer (64 bit) by two observers (Sara De Vittoris and Marta Caselli) with an agreement of 100% (Cohen's $K = 1$; level of agreement: perfect, *sensu* McHugh, 2012) on the presence/absence of yawning response. Data were extracted over two different time windows that 1 and 3 min from the beginning of the video stimulus. Figure 1b shows yawning sequence.

2.4 | Statistical elaboration

We first checked for the presence/absence of yawn contagion in the naturalistic and experimental settings. As concerns the naturalistic setting we ran two models considering either a 3 min (GLMM_{1a}; $N = 672$) or a 1 min (GLMM_{1b}; $N = 760$) time window after the triggering stimulus. We included the presence/absence of a yawning response as binary target variable and the yawning and matched-control conditions (PY/MC) as binary fixed factors. We mirrored the same analyses on experimental data. Hence, we ran two models to check for the presence of yawn contagion on either a 3 min (GLMM_{2a}; $N = 104$) or a 1 min (GLMM_{2b}; $N = 104$) time window. We included the presence/absence of a yawning response as binary target variable and the yawning and control video conditions (YC/CC) as binary fixed factors.

We then assessed the possible modulation effect of perceptual, individual, and social factors on yawn contagion. To this purpose, in the naturalistic setting we considered the condition PY (i.e., retaining yawn resulting from contagion and not spontaneous ones) and the cases where the stimulus came from a single trigger because we needed to determine the relationship between trigger and potential responder with certainty. We ran two GLMMs by using 3 min (GLMM_{3a}; $N = 307$) and 1 min (GLMM_{3b}; $N = 430$) time windows. In both models we included the presence/absence of yawning response as binary target variable and the following fixed factors: (i) trigger and potential responder sex (binomial variable; male/female); (ii) potential responder age (numeric variable); (iii) familiarity between trigger and potential responder (binomial variable; not always together in a subgroup = 0; always together in a subgroup = 1); (iv) distance between trigger and potential responder (binomial variable; within 1 m = 1; between 1 and 10 m = 2). We mirrored the analyses in the

experimental setting. We restricted the database to the YC, and we ran two models with 3 min (GLMM_{4a}; $N = 52$) and 1 min (GLMM_{4b}; $N = 52$) time windows. We included the presence/absence of yawning response as binary target variable and the following fixed factors: (i) responder sex (binomial variable; male/female); (ii) potential responder age (numeric variable); (iii) familiarity between the bonobo models shown in the video and the potential responder (binomial variable; same-group/stranger); (iv) number seconds during which the subject watched the screen showing the video (numeric variable); and (v) whether the conditions was MF or FM (binomial variable).

For all the GLMMs we included the responder's identity and the group membership of the responder as random factors. All GLMMs were fitted using the function "glmer" of the package "lme4" (Bates et al., 2015) of the statistic program R (R Core Team, 2022; version 4.2.1). We proceeded with the likelihood ratio test (Dobson & Barnett, 2018) to compare the full model (including all the considered fixed factors) and the null model (including only the random factors), making the analysis of variance with argument "Chisq." If the difference between the full and the null model was significant, we used the R-function "drop1" to extract the p values for each predictor included in the full model (Barr et al., 2013). Then, we calculated the effect size of each variable included in the full model via the package "effect," with the function "allEffects," and the confidence interval of each predictor using the function "Confint."

We calculated the Yawn Contagion Index (YCI) for either naturalistic and experimental setting by considering, at the individual level, the number of responses after the yawning stimulus (PY in the naturalistic setting and YC in the experimental setting), the number of responses under CCs (MC in the naturalistic setting and CC in the experimental setting), and the total number of occasions (observation bouts in the naturalistic and tablet trials in the experimental setting). We applied the following formula: $YCI = [(number\ of\ responses\ after\ the\ yawning\ stimulus - number\ of\ responses\ in\ the\ CC) / (number\ of\ occasions)]$. Owing to the non-normal distribution of YCIs in the experimental setting (Kolmogorov–Smirnov: $p < 0.05$), we ran a Spearman's rank test to correlate individual YCIs between naturalistic and experimental setting in the 1- and 3-min time windows.

3 | RESULTS

3.1 | Presence of yawn contagion

3.1.1 | Naturalistic setting

As concerns the 3-min time window model (GLMM_{1a}) with presence/absence of yawning response as target variable, we found that the full model including the fixed factor (PY/MC condition) significantly differed from the null model including random factors only (responder identity and group membership; likelihood ratio test: $\chi^2 = 36.272$, $df = 1$, $p < 0.001$). Thus, we proceeded with the drop1 procedure. We found that the response probability was higher in PY condition than in the MC condition (Table 2 and Figure 2a). Similarly,

TABLE 2 Results of: (i) GLMM_{1a} on the presence of yawn contagion in the naturalistic setting within the 3-min time window ($N = 672$); (ii) GLMM_{1b} on the presence of yawn contagion in the naturalistic setting within the 1-min time window ($N = 760$); (iii) GLMM_{2a} on the presence of yawn contagion in the experimental setting within the 3-min time window ($N = 104$); and (iv) GLMM_{2b} on the presence of yawn contagion in the experimental setting within the 1-min time window ($N = 104$).

Predictors	Estimates	SEM	CI ₉₅	Effect size	χ^2	p
GLMM _{1a}	Full versus null model: $\chi^2 = 36.272$; $df = 1$; $p < 0.001$					
(Intercept) ^a	-4.738	0.577	-5.868; -3.607	a	a	a
Condition (PY) ^b	2.469	0.523	1.444; 3.494	0.094	4.722	<0.001
GLMM _{1b}	Full versus null model: $\chi^2 = 33.261$; $df = 1$; $p < 0.001$					
(Intercept) ^a	-6.276	1.058	-8.350; -4.202	a	a	a
Condition (PY) ^b	3.467	1.023	1.461; 5.472	0.057	3.388	0.001
GLMM _{2a}	Full versus null model: $\chi^2 = 4.178$; $df = 1$; $p = 0.041$					
(Intercept) ^a	-2.126	0.487	-3.081; -1.171	a	a	a
Condition (PY) ^b	1.073	0.545	0.004; 2.142	0.259	1.969	0.049
GLMM _{2b}	Full versus null model: $\chi^2 = 5.514$; $df = 1$; $p = 0.019$					
(Intercept) ^a	-3.421	0.832	-5.051; -1.791	a	a	a
Condition (PY) ^b	1.711	0.825	0.094; 3.328	0.153	2.074	0.038

Note: For all models, responder identity and group membership were included as random factors. Bold indicates significant values.

^aNot shown as not having a meaningful interpretation.

^bThese predictors were dummy-coded, with the reference category as MC.

via the 1 min time window model (GLMM_{1b}) with the same target variable as the previous model (presence/absence of yawning response), we found a significant difference between the full model (including the fixed factor PY/MC condition) and the null model including the random factors only: (responder's identity and group membership; likelihood ratio test: $\chi^2 = 33.261$, $df = 1$, $p < 0.001$). Hence, via the drop1 procedure we found that the higher response levels occurred in the PY condition than in the MC condition (Table 2 and Figure 2b).

3.1.2 | Experimental trials

We ran the 3-min time window model (GLMM_{2a}) with presence/absence of yawning response as target variable. We found that the full model (including the fixed factor YC/CC) significantly differed from the null model, including only the random factors (responder's identity and group membership; likelihood ratio test: $\chi^2 = 4.178$, $df = 1$, $p = 0.041$). The drop1 procedure revealed a significant effect of the condition, with the highest probability of yawning response recorded in the YC (Table 2 and Figure 3a). We then ran the 1-min time window model (GLMM_{2b}) with the same target variable (presence/absence of yawning response). We found that the full model (including the fixed factor YC/CC) significantly differed from the null model including the random factors only (responder's identity and group membership; likelihood ratio test: $\chi^2 = 5.514$, $df = 1$, $p = 0.019$). Via the drop1 procedure we detected a significant effect of the

condition, with the highest probability of yawning response recorded in the YC (Table 2 and Figure 3b). In sum, yawn contagion was detected via both naturalistic data and experimental data, with both 3- and 1-min time windows.

3.2 | Factors modulating yawn contagion

As a preliminary analysis, we found no significant correlation in the individual YCIs between settings in the 1-min time window (Spearman's test: $\rho = -0.427$, $N_{\text{individuals}} = 13$, $p = 0.146$) and, in 3-min time window (Spearman's test: $\rho = -0.530$, $N_{\text{individuals}} = 13$, $p = 0.062$).

3.2.1 | Naturalistic setting

We ran a model on the PY cases (GLMM_{3a}) using a 3-min time window and including presence/absence of a yawning response as target variable. We found that the full model including all fixed factors (distance between the trigger and the potential responder; trigger and responder sex and age; familiarity between trigger and potential responder) did not differ from the null model including only the random factors (responder's identity and group membership), (likelihood ratio test: $\chi^2 = 7.579$, $df = 5$, $p = 0.181$). Therefore, none of the tested variables had an effect on the phenomenon over the 3-min time window. We also ran a model on PY cases (GLMM_{3b}), with the same target variable as the previous model (presence/absence of a

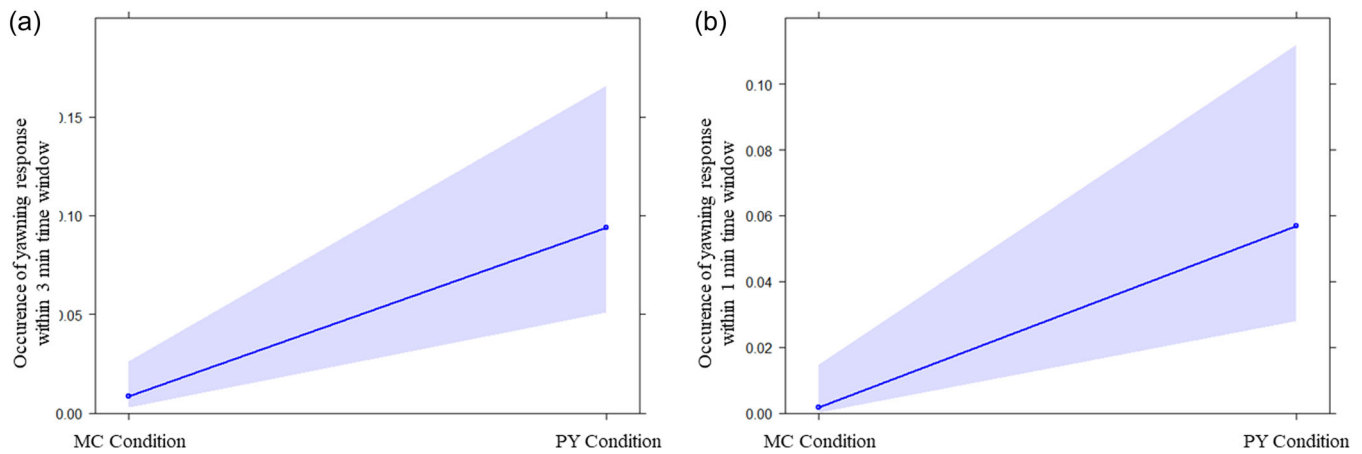


FIGURE 2 Presence of yawn contagion within different time windows in the naturalistic setting (Table 2). Yawning response occurrence (y-axis) increased in the YC (x-axis) in (a) 3-min time window and (b) 1-min time window. The confidence interval is represented by the band. YC, Yawn Condition.

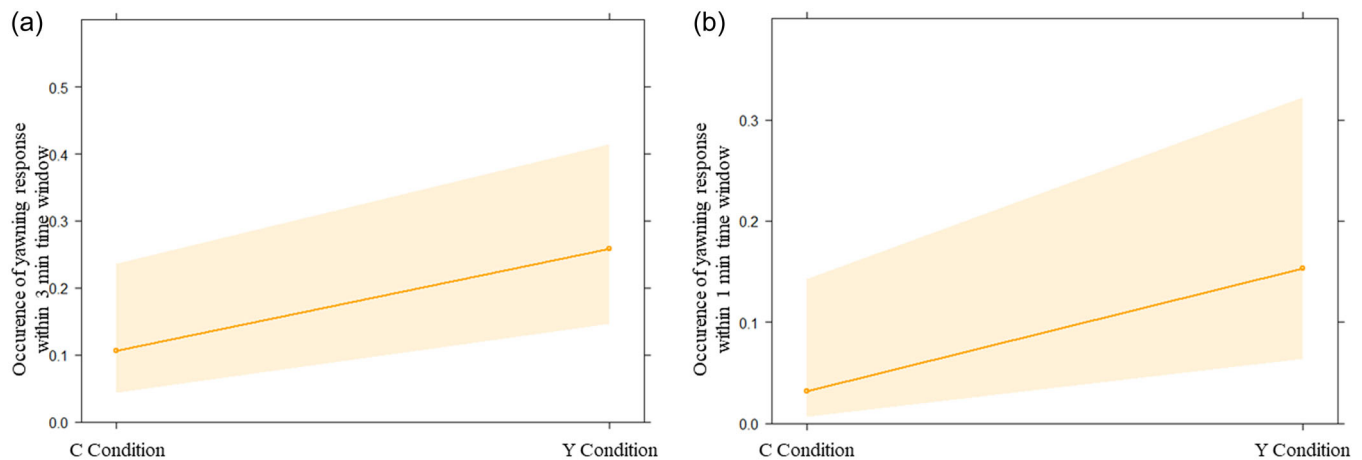


FIGURE 3 Presence of yawn contagion within different time windows in the experimental setting (Table 2). Yawning response occurrence (y-axis) increased in the YC (x-axis) in (a) 3-min time window and (b) 1-min time window. The confidence interval is represented by the band. YC, yawn condition.

yawning response), this time using a 1-min time window. We found a significant difference between the full model including all fixed factors and the null model including random factors only (same factors as the previous model; likelihood ratio test: $\chi^2 = 14.039$, $df = 5$, $p = 0.015$). Via the drop1 procedure, we found a significant effect of two variables: responder age and familiarity (always/not-always together) between trigger and responder (Table 3). In particular, the yawning response was higher as the responder age increased (Figure 4a) and between less familiar (rather than more familiar) subjects (Figure 4b).

3.2.2 | Experimental setting

We ran a model on YC cases (GLMM_{4a})—using a 3-min time window—with the presence/absence of the yawning response as target

variable. We found that the full model including all fixed factors (responder sex and age; familiarity between model and potential responder; seconds watching the screen; MF/FM condition) significantly differed from the null model including only the random factors (responder's identity and group membership; likelihood ratio test: $\chi^2 = 14.023$, $df = 5$, $p = 0.015$). Thus, we proceeded with the drop1 procedure, and we found a significant effect of the variable responder's age and the variable familiarity (Table 3). Specifically, the probability of yawn contagion decreased as the age of the responder increased (Figure 5a) and was higher with the stranger than the in-group model (Figure 5b). We then ran a model similar to the previous one (GLMM_{4b}) but considering a 1-min time window. The full model including all the fixed factors did not significantly differ from the null model including the random factors only (same factors as previous model; likelihood ratio test: $\chi^2 = 8.623$, $df = 5$, $p = 0.125$). Hence, none of the tested variables had a significant influence on yawn contagion.

TABLE 3 Results of GLMMs on the effect of modulating factors on yawn contagion: (i) GLMM_{3a}: naturalistic setting within 3 min ($N = 307$); (ii) GLMM_{3b}: naturalistic setting within 1 min ($N = 430$); (iii) GLMM_{4a}: experimental setting within 3 min ($N = 52$); and (iv) GLMM_{4b}: experimental setting within 1 min ($N = 52$).

Predictors	Estimates	SEM	CI ₉₅	Effect size	χ^2	p
GLMM _{3a}	Full versus null model: $\chi^2 = 7.579$; $df = 5$; $p = 0.181$					
GLMM _{3b}	Full versus null model: $\chi^2 = 14.039$; $df = 5$; $p = 0.015$					
(Intercept) ^a	-3.265	0.685	-4.608; -1.922	a	a	a
Distance (between 1 and 10 m) ^b	-0.414	0.460	-1.312; 0.488	0.063	-0.900	0.368
Trigger sex (male) ^b	0.817	0.471	-0.106; 1.174	0.086	1.735	0.083
Responder sex (male) ^b	0.074	0.545	-0.994; 1.143	0.050	0.137	0.891
Responder age	0.053	0.022	0.010; 0.096	0.152	2.419	0.016
Familiarity (always together) ^b	-1.326	0.528	-2.361; -0.291	0.078	-2.511	0.012
GLMM _{4a}	Full versus null model: $\chi^2 = 14.023$; $df = 5$; $p = 0.015$					
(Intercept) ^a	0.186	1.179	-1.495; 3.128	a	a	a
Order (MF) ^c	1.051	0.753	-0.424; 2.526	0.296	1.396	0.163
Responder sex (male) ^c	-1.011	0.805	-2.588; 0.567	0.268	-1.256	0.209
Responder age	-0.068	0.034	-0.135; -0.001	0.431	-1.983	0.047
Familiarity (stranger) ^c	-2.018	0.818	-3.621; -0.415	0.405	-2.467	0.014
Seconds of attention	-0.003	0.026	-0.054; 0.048	0.209	-0.112	0.911
GLMM _{4b}	Full versus null model: $\chi^2 = 8.623$; $df = 5$; $p = 0.125$					

Note: For all models, responder identity, and group membership were included as random factors. Bold indicates significant values.

^aNot shown as not having a meaningful interpretation.

^bDummy coded predictors, reference category: Distance: "within 1 m"; trigger sex: "female"; responder sex: "female"; familiarity: "not always together."

^cDummy coded predictors, reference category order: "FM"; responder sex: "female"; familiarity: "same group."

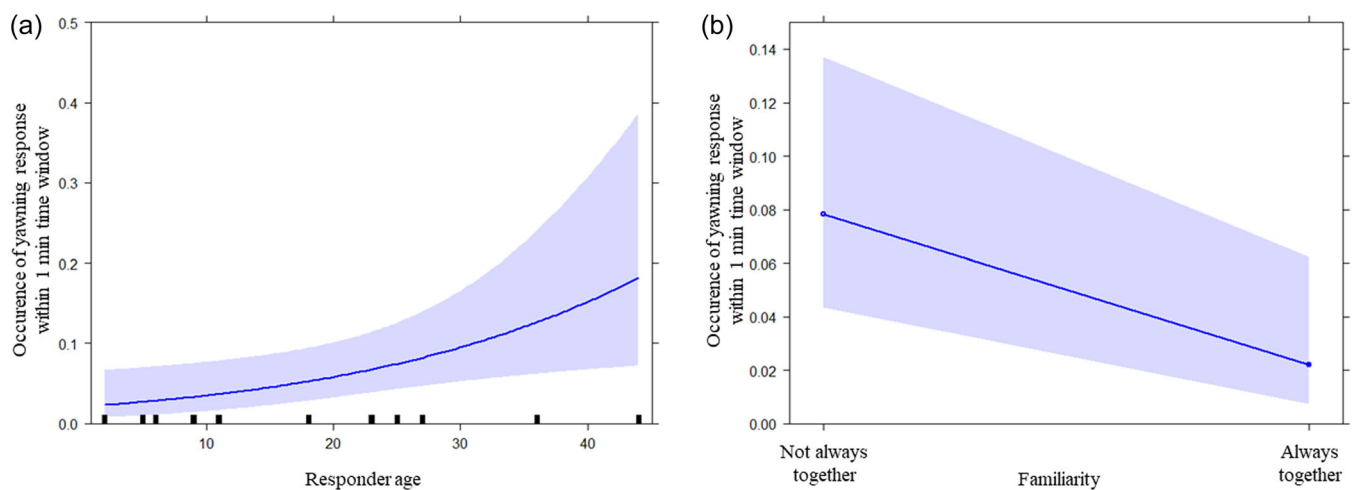


FIGURE 4 Influence of individual and social factors on yawning response occurrence within 1-min time in the naturalistic setting (Table 3). The yawning response occurrence (y-axis) was higher: (a) as the responder age (x-axis) increased and (b) between less familiar subjects (x-axis). The confidence interval is represented by the band.

In sum, none of the tested perceptive, individual, and social factors affected yawn contagion in the naturalistic setting over a 3-min time window and in the experimental setting over a 1-min time window. However, familiarity and age showed opposite

trends on yawn contagion with different methods and time windows in that yawn contagion was highest in older and less familiar subjects in the naturalistic setting (1-min time window) whereas it was highest in younger subjects and in response to in-group

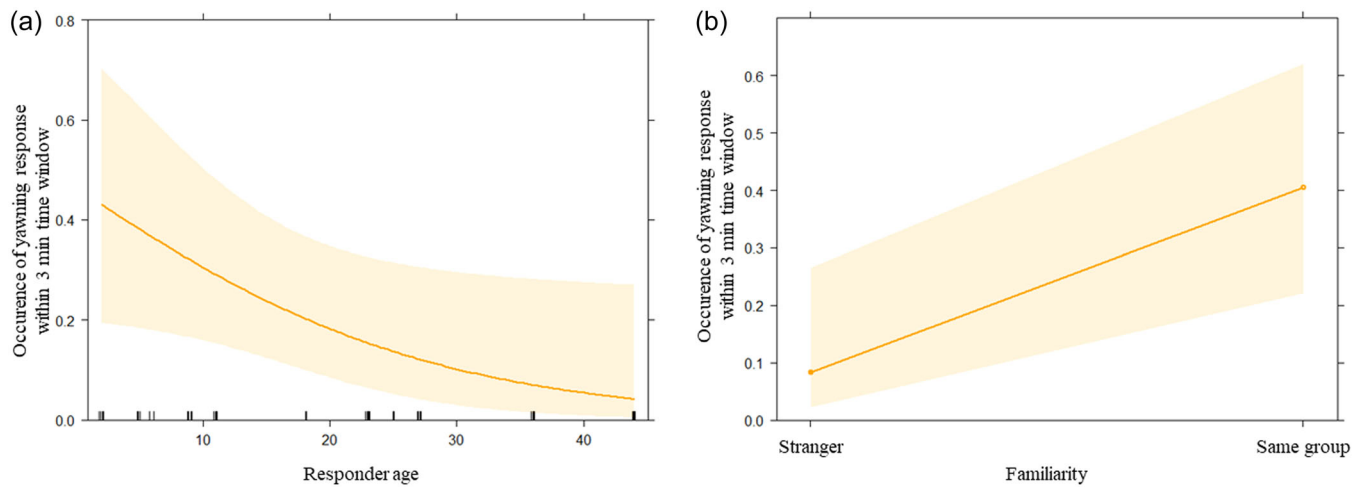


FIGURE 5 Influence of individual and social factors on the yawning response occurrence within 3 min in the experimental setting (Table 3). The occurrence of yawning response (y-axis) was higher: (a) as the responder age (x-axis) decreased and (b) between more familiar subjects (x-axis). The confidence interval is represented by the band.

members (rather than strangers) in the experimental setting (3-min time window).

4 | DISCUSSION

Our study shows that the use of different methodological approaches— involving real vs. video stimuli and checking for yawning responses over different time windows (1 or 3 min from the triggering stimulus)— can indeed lead to diverging results. We considered the same subjects, in the same location and with the same data collector/experimenter for both the naturalistic setting where yawning responses to others' yawns were recorded and the experimental trials where bonobos watched yawn/control video stimuli. Here we discuss whether the detected differences can be considered as actually contradictory or—rather—can be complemented into a comprehensive picture on the phenomenon of yawn contagion in bonobos.

4.1 | Presence of yawn contagion

Our study confirms that yawn contagion in bonobos can be detected via both naturalistic behavioral collection and experimental trial methods (Prediction 1a confirmed; Figures 2 and 3), as it was expected considering that most of the previous literature described the phenomenon in bonobos by using either method (naturalistic conditions: Demuru & Palagi, 2012; Norscia et al., 2022; video stimuli: Tan et al., 2017; but see Amici et al., 2014). Similarly, in the two other extant hominin species (humans and chimpanzees) yawn contagion was consistently found by using either an experimental approach (e.g., Bartholomew & Cirulli, 2014; Campbell & de Waal, 2011; Provine, 1986, 1989) or naturalistic observations (e.g., Norscia & Palagi, 2011; Norscia et al., 2016) and in humans when using both methods (Norscia et al., 2021a).

In both naturalistic and experimental settings, we detected yawn contagion within both 1 and 3 min from the triggering stimulus (Prediction 1b confirmed; Figures 2 and 3). This result is in line with the fact that in bonobos the phenomenon has been found by using different time windows, e.g., 10 min video stimuli (Tan et al., 2017 via video trials) or 3 min (Demuru & Palagi, 2012 under naturalistic conditions). In other hominins, namely chimpanzees and humans, yawn contagion has been found within 3.5 and 3 min respectively, with pick observed around 1.5 and 1 min, respectively (Campbell & Cox, 2019; Campbell & de Waal, 2011; Norscia & Palagi, 2011; Palagi et al., 2014). Hence, it is possible that in hominins the time windows within 3 min do not much affect the likelihood of detecting contagion. Because this time window may decrease the autocorrelation likelihood (Kapitány & Nielsen, 2017), the variability in yawn contagion detection probability may also be reduced. However, in a study of bonobos, Norscia et al. (2022) observed yawn contagion only in the first out of 3 min and Amici et al. (2014) detected no yawn contagion in four bonobos over a 3-min span. This variability, as noted by Norscia et al. (2022), may arise from significant inter-individual differences, with not all individuals showing contagion. Thus, individual characteristics and group composition could affect the detection of this phenomenon, suggesting that this aspect deserves further research.

4.2 | Factors modulating yawn contagion

While the presence of yawn contagion in bonobos could be consistently detected between naturalistic and experimental setting, regardless of the time-window, we found no correlation in the individual yawn contagion rates (measured via YCIs; Prediction 2a confirmed). Consistently, the factors that can modulate yawn contagion levels differed across the methods and time windows considered. Although sex had no effect— possibly due to variability across

bonobo groups and individuals, which makes it hard to find consistent results (Demuru & Palagi, 2012; Norscia et al., 2022) other modulating factors were influenced by method and time window (Prediction 2b-c confirmed). We found that in naturalistic conditions, an effect of familiarity (individual staying always or not always together) and age were detected only in the 1-min time window (Figure 4). This result may be due to the fact that—precisely under naturalistic conditions—yawn contagion in bonobos has been found to peak or be only present in the first minute (Demuru & Palagi, 2012; Norscia et al., 2022). Similarly, under naturalistic conditions a peak of yawn contagion was observed after 1.5 min after the triggering stimulus in chimpanzees (Campbell & Cox, 2019) and in the first minute in humans (Norscia & Palagi, 2011). Because yawn contagion rates plummet after the first minute, it is possible that in later minutes low contagion levels leave little margin for modulating factors to effectively act in increasing or decreasing the amount of yawn contagion. Although in a different way, this issue also affected video trials. We found that in experimental trials, the factors that influence yawn contagion emerged only using the 3-min time (Figure 5). In humans, Diana et al. (2023) observed that video stimuli induced yawn contagion at lower rates than real stimuli. More minutes may be necessary under video conditions to record yawn contagion at sufficiently high rates that allow the modulating factors to intervene. This aspect may be related to the fact video stimuli - even if repeatedly shown to the experimental subjects - are possibly more effective in inducing yawn contagion over a longer period of time, which results in the increased latency in the yawning response onset. In bonobos, yawn contagion elicitation may require longer time with non-real, video stimuli (e.g., 10 min: Tan et al., 2017 vs. 3 min: Amici et al., 2014) but also this aspect requires further investigation.

The crucial point of this study is that—when detected—the yawn contagion factors modulating were similar (age and familiarity) but had apparently opposite effects on the phenomenon. Yawn contagion was highest in older bonobos and between less familiar individuals in the naturalistic setting (1-min time window) whereas it was highest in younger bonobos and in response to in-group members (rather than strangers) in the experimental setting (3-min time window).

As concerns age, the increase of yawn contagion with age observed in naturalistic conditions is not in contrast with literature. Indeed, yawn contagion tends to be absent or be present at low rates in immature humans (Anderson & Meno, 2003; Cordoni et al., 2021; Helt et al., 2010; Millen & Anderson, 2011) and has not been detected so far in infant bonobos and chimpanzees (Madsen et al., 2013; Norscia et al., 2022). In human and nonhuman mammals, the increase of yawn contagion with age can be possibly linked with the maturation of neurobiological substrates underlying the ability to decode social cues and identify the internal states of others (Cordoni et al., 2021; Norscia et al., 2021b). On the other hand, also the decrease of yawn contagion with age observed in the experimental setting is not inconsistent with previous studies, as yawn contagion has been observed to decrease with aging in certain cohorts of humans (people over 40; Bartholomew & Cirulli, 2014) and bonobos (Norscia et al., 2022). This trend might be linked to decreased

sensitivity to others' states and in humans to increased replacement of bottom-up with top-down processes in emotional appraisal (Norscia et al., 2022; Petro et al., 2021; Reed & Carstensen, 2012). Either way (increasing or decreasing yawn contagion rates as age increases), the main point here is that two different methods led to divergent results with respect to the same modulating factor. The number of seconds that individuals watched the screen in the experimental trials did not influence the likelihood of yawn contagion in our study, but it is also true that eye-tracking techniques may better reveal to what extent the stimulus has been or not observed. The number of previously observed yawns can influence yawn contagion in bonobos (Norscia et al., 2022) and it is not possible to exclude that the stimulus was more effective in triggering the response in immature subjects owing to their increased curiosity toward the videos or the tablet used to show them. Indeed, immature subjects of bonobos, chimpanzees, and humans can be more keen to explore and interact with new objects, including technological devices (Gruber & Fandakova, 2021; Kalan et al., 2019). In autistic children, yawn contagion increases when the subjects are induced to redirect toward the video stimulus during experimental trials (Usui et al., 2013). Further investigation is necessary to investigate this aspect.

Finally, another interesting aspect that emerged from the use of two methods is that familiarity had an apparently opposite effect on yawn contagion in the two different settings (naturalistic vs. experimental). An issue that is relevant to interpret our findings is that we did not test identical familiarity factors in the two conditions. Via experimental trials we were able to test whether yawn contagion was elicited more by video yawn stimuli coming from complete strangers (beyond the colony) or by colony mates whereas via naturalistic data we could verify—within the colony—whether the yawning responses varied between “real” individuals that formed permanent association (always together) or not (not-always together). While yawn contagion was enhanced in response to own-colony models compared to strangers (experimental trials), within the colony it was highest between individuals that spent less time together (naturalistic data). These divergent results are critical, as the effect of familiarity on yawn contagion is debated (Palagi et al., 2020). In humans, yawn contagion is highest in individuals that are socially closer than others, which may suggest underlying emotional contagion (Norscia & Palagi, 2011; Norscia et al., 2016; Norscia et al., 2020; Norscia et al., 2021a). In chimpanzees, video trials showed increased response toward in-group than out-group members (Campbell & de Waal, 2011) but to our knowledge the effect of social bond on yawn contagion within the same group has not been tested. In bonobos, one naturalistic study found that socially closer individuals showed highest levels of yawn contagion (Demuru & Palagi, 2012) whereas no such effect was found in another naturalistic study (Norscia et al., 2022). Moreover, no effect was found when comparing yawning responses to strangers and familiar models in an experimental study using video stimuli (Tan et al., 2017). As explained above with respect to the detection of yawn contagion over different time windows, also in this case the high interindividual variability in yawn contagion presence and rates may in part explain why results

on different bonobo cohorts are not consistent (Norscia et al., 2022). The increased yawn contagion between less familiar bonobo group mates fits with previous findings on the species. Weakly bonded bonobo females can engage in the longest socio-sexual contacts (Annicchiarico et al., 2020) and they can most likely synchronize on their maximum sexual swelling (possibly underlying autonomic contagion), thus enhancing socio-sexual contacts (Demuru et al., 2022). Finally, the attention of bonobos is biased toward emotional scenes depicting unfamiliar bonobos rather than groupmates (van Berlo et al., 2023). In bonobos the social system combines clear in-group/out-group distinction but also out-group tolerance (Samuni et al., 2022). Indeed, bonobos react more to calls from familiar than stranger conspecifics (Keenan et al., 2016) but during intergroup encounters certain individuals can socialize with outgroup members (Cheng et al., 2022). Additionally, the individuals that cooperate more with in-group members are also more cooperative with out-groups (Samuni & Surbeck, 2023). Interacting with complete strangers versus less familiar group members is a completely different experience for bonobos and, in this respect, our results on familiarity deriving from the naturalistic and experimental setting are to be considered as complementary.

The above results prompt interesting considerations on the relationship among the motor replication of facial expressions, socio-emotional cohesion, and ecological context. Firstly, individuals responded differently to the same facial expression (yawning) depending on its contextualization within the social fabric (naturalistic setting) versus its absence (experimental setting), emphasizing the pivotal role of context. The social intelligence hypothesis contends that facial expression phenotypes and functions are tightly connected to socio-ecological context (Schmidt & Cohn, 2001). Moreover, context may determine the emotional valence of expressions that are not inherently negative and the corresponding response (Kret & Akyüz, 2022). Yawning in humans is not inherently negative as it can be associated with mild stress but also with neutral behavioral transitions related to the circadian rhythm (Zilli et al., 2007). From a biological perspective, we posit that the concept of valence may not be relevant in relation to facial expressions per se, as natural selection favors the most suitable responses in strict relation with the environment and external conditions, which influence its nature (Bijlsma & Loeschcke, 2005). Secondly, the fact that in the social environment bonobo showed yawn contagion more frequently between weakly bonded individuals aligns with the hypothesis that motor mimicry may reduce prediction errors on others' behavior (Kret & Akyüz, 2022). Because the prediction error is supposedly higher between weakly bonded individuals, its reduction may be relevant in facilitating the development of social relationships via synchronization. Depending on the circumstances, yawning in response to the yawn of less familiar individuals may also serve to interrupt, rather than facilitate, an interaction, as it has been posited for motor mimicry (Kret & Akyüz, 2022). Supporting this hypothesis is the fact that yawning—as said above—can be enhanced by anxiety, stress, and behavioral transitions, which involve the interruption of

one activity to commence another (e.g., resting to moving, sleep to wake; Gallup, 2022; Thompson, 2014; Zannella et al., 2015). In humans, for example, mimicry can lead to lower levels of trust thus favoring social disruption (Diana et al., 2023).

In summary, this study cautions against using singular methods to draw general conclusions about motor replication phenomena and suggests that, under certain circumstances, such phenomena, including yawn contagion, may promote emotional state synchronization. Synchronizing with other group members, especially less familiar ones, is adaptive as failing to predict others' behaviors and to coordinate can threaten the survival of both the group and its members.

AUTHOR CONTRIBUTIONS

Sara De Vittoris collected data, sorted out data, and wrote the manuscript; Marta Caselli students' training for data collection, analyzed data, wrote the manuscript, and revised the manuscript; Elisa Demuru carried out initial training on bonobo behavior and revised the manuscript; Lisa Gillespie provided access to resources and facilities; Ivan Norscia conceived the manuscript, carried out training on yawning data collection, analyzed data, wrote the manuscript and revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available on a Google Drive folder and access will be given under reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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