FIRST EVIDENCE OF CONTAGIOUS YAWNING IN A WILD LEMUR

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ABSTRACT

Contrary to spontaneous yawning, yawn contagion occurs when yawning in a subject (responder) is elicited by the yawns of others (triggers). Yawn contagion has been associated with inter-individual synchronisation, activity coordination and possibly emotional contagion, based on the perception-action mechanism. We collected data on yawn contagion and grooming and verified - for the first time - yawn contagion presence and modulating factors in a wild strepsirhine. Specifically, we considered the diurnal lemur *Indri indri* (inhabiting Maromizaha rainforest, eastern Madagascar), which lives in socially cohesive family units. We recorded 613 yawning events involving 28 individuals and found that yawn contagion was present in the indris (with the best predictor for an individual to yawn at a given time of day was observing another group member yawning) and that it was positively influenced by grooming levels (but not by the spatial distance) between trigger and responder. Age and sex had no significant relationship with yawn contagion likelihood. Because yawn contagion has been found in different mammalian species regardless of their phylogenetic closeness, this study, reporting the phenomenon in a lemur species with highly cohesive behavioural pattern and able to emit coordinated vocal displays, adds a valuable piece to the investigation of the pressures that may have favoured yawning as a (possibly emotional) communicative cue during evolution.

KEYWORDS

Emotional contagion, primates, perception-action model, behavioural synchronisation

STATEMENTS AND DECLARATIONS

Competing Interests

The authors declare no conflict of interest.

Significance Statement

Yawn contagion is associated with inter-individual synchronisation and activity coordination. While this behaviour is often investigated in apes, its presence in lemurs is debated. Here, we explored presence and modulating factors of yawn contagion in *Indri indri*, a critically endangered primate living in small family units where individuals show coordinated circadian rhythms and a highly cohesive behavioural pattern. We first demonstrated the presence of yawn contagion in wild indris where, in line with the high degree of behavioural synchrony showed by the individuals within a group, it may possibly indicate a transmission of physiological states. We also demonstrated the association of contagion with grooming rates, but not with the spatial proximity between triggers and responders, nor with their sex and age, pointing at social closeness as the most likely modulating factor.

Author Contribution

IN, DV, VT conceived the study design and the methodology. Data collection was performed by DV, CDG, FP and FC. Formal analysis was conducted by DV. The first draft of the manuscript was written by IN and DV. All the authors read and approved the final version of the manuscript.

Ethics Approval

The research permit for this research has been granted from the Ministère de l'Environnement, de l'Écologie et des Forêts (MEEF) and Direction du Système des Aires Protégées (2018: 91/18/MEEF/SG/DGF/DSAP/SCB.Re). Since this study was observational and no animal manipulation was performed, we did not require a permit from our University. We also declare the data collection protocol conforming to the national legislation and international regulation concerning animal welfare.

Data availability

Data generated or analysed during this study are included in this published article (and its supplementary information files).

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INTRODUCTION

Spontaneous yawning is a common stereotyped behaviour (Guggisberg et al. 2011). Contagious yawning differs from spontaneous yawning in that it is induced by others' yawns (Provine 1989). Spontaneous yawning (or a yawning-like morphological pattern) appears to be phylogenetically widespread across vertebrates (Baenninger 1987) including humans (*Homo sapiens*) and non-human primates (Provine 1986, 2012; Anderson 2020). Among other functions (brain cooling, arousal, neurovascular circulation and behavioural state change: Guggisberg et al. 2011; Massen et al. 2014; Gallup 2022) spontaneous yawning under relaxed conditions appears to be related to the sleep-wake cycle (Provine 1986; Leone et al. 2014; Zannella et al. 2015). Therefore, individuals that share similar circadian rhythms and activity budgets may show a peak in yawning within the same time slot (Giganti and Zilli 2011; Zannella et al. 2015). However, yawning together does not equal yawning contagiously. For yawn contagion to occur, the yawn emitted by an individual (hereafter, trigger) must act as releasing stimulus (*sensu* Tinbergen and Perdeck 1950) and induce yawning in the individuals that detect such stimulus (hereafter, responders: Provine 1986, 2012; Demuru et al. 2022). Intraspecific contagious yawning has been described in different mammalian species: wolves (*Canis lupus*, Romero et al. 2014), sheep (*Ovis aries*, Yonezawa et al. 2017), elephant seals (*Mirounga leonina*, Wojczulanis-Jakubas et al. 2019), domestic pigs (*Sus scrofa*, Norscia et al. 2021b), lions (*Panthera leo*, Casetta et al. 2021), and one bird species (budgerigars, *Melopsittacus undulates*. Gallup et al. 2015) but not in another *(Corvus corax*. Gallup et al. 2022*)*. Overall, the presence of yawn contagion has not been detected in a phylogenetically consistent way (Palagi et al. 2020). Indeed, in haplorhine primates - the most investigated animal group - yawn contagion may be more linked to the type of sociality than to phylogenetic closeness (Palagi et al. 2020). Within hominids, yawn contagion has been described in highly social Hominini, including non-pathological humans (Provine 1986, 1989; Norscia and Palagi 2011; Bartholomew and Cirulli 2014; Chan and Tseng 2017; Norscia et al. 2021a), chimpanzees (Anderson et al. 2004; Campbell and Waal 2011; Campbell and Cox 2019), and the majority of bonobo colonies that have been investigated in this respect (Demuru and Palagi 2012; Tan et al. 2017; Norscia et al. 2022; but see Amici et al. 2014). Yawn contagion has not been observed in captive lowland gorillas (Amici et al. 2014; Palagi et al. 2019), but it has been recorded in orangutans (*Pongo* spp., van Berlo et al. 2020), which diverged from the human line earlier than gorillas (Groves 2018). Intriguingly, lowland gorillas generally show low affiliation levels (Palagi et al. 2019), whereas orangutans show a very dispersed sociality but might have been more social in the past when food availability was higher (Harrison and Chivers 2007; van Berlo et al. 2020). Within cercopithecids, yawn contagion has not been found in the despotic Japanese macaque (*Macaca fuscata*: Palagi and Norscia 2019). However, it has been observed in tolerant species, namely Tonkean macaque (*Macaca tonkeana*, Palagi and Norscia 2019) and geladas (*Theropithecus gelada*: Palagi et al. 2009; Gallo et al. 2021).

The link between the type of sociality and yawn contagion can have an adaptive value: yawn contagion may favour inter-individual synchronisation within social groups, may enhance group vigilance (Miller et al. 2012; Palagi et al. 2020; Casetta et al. 2021; Gallo et al. 2021; Gallup and Meyers 2021), and may reflect physiological resonance and emotional contagion, an important trigger of prosociality (Decety et al. 2016; de

Waal and Preston 2017; Prochazkova and Kret 2017). Hence, yawning might have been co-opted to become a triggering stimulus that elicits contagion and favours inter-individual synchronisation and - as a result - yawn contagion might have emerged at different times during evolution when particularly beneficial to group living (Palagi et al. 2020).

Although not consistently, yawn contagion can be influenced by individual and social factors (Palagi et al. 2020). In primates, it appears to increase with age or at least to be highest in adults in geladas (Palagi et al. 2009), bonobos (Norscia et al. 2022), chimpanzees (Madsen et al. 2013), and humans (Anderson and Meno 2003; Helt et al. 2010; Millen and Anderson 2011; Cordoni et al. 2021). On the other hand, yawn contagion can decrease with age in certain groups or cohorts, in humans and bonobos (Bartholomew and Cirulli 2014; Norscia et al. 2022). Sex can also influence yawn contagion, partly depending on the social role that each sex has in a given species and group (Palagi et al. 2020). Females may respond more to others' yawns in bonobos (Norscia et al. 2022), although not in all cohorts (Norscia and Palagi 2011; Demuru and Palagi 2012; Bartholomew and Cirulli 2014). A comparable pattern, with mixed evidence on the influence of sex on yawn contagion, has also been reported in humans (Gallup and Massen 2016; Norscia and Palagi 2016; Chan and Tseng 2017). In wild geladas - where many one-male/multi-female units form coordinated, large associations (teams and bands)- a previous study found the highest yawning responses in adult males, which lead unit movements within teams (Gallo et al. 2021). Adult females can preferentially trigger yawns in bonobos where they are central to the group social matrix (Demuru and Palagi 2012; Norscia et al. 2022) or in high-ranking male chimpanzees, a male-dominated society (Massen et al. 2012), at least under certain conditions, e.g. depending on the sex of the responder, presence of a swelling cycle (Massen et al. 2012; Norscia et al. 2022). Finally, intraspecific yawn contagion may increase as social bonding and kinship levels increase, as demonstrated in wolves (Romero et al. 2014), domestic pigs (Norscia et al. 2021b), geladas (Palagi et al. 2009), chimpanzees (Campbell and Waal 2011), bonobos (Demuru and Palagi 2012), and humans (Norscia and Palagi 2011), but see Bartholomew and Cirulli 2014; Tan et al. 2017; Norscia et al. 2022.

Because yawn contagion is a basic form of transfer of internal physiological states, it should not necessarily require particularly advanced cognitive abilities (de Waal and Preston 2017; Prochazkova and Kret 2017). Therefore, it is plausible to posit that yawn contagion can be present in primates -such as group-living strepsirhines- that retain several neuro-anatomical ancestral traits (Norscia and Palagi 2016). However, besides a study exploring different hypotheses on spontaneous yawning on wild lemurs, *Lemur catta* and *Propithecus verreauxi* (Zannella et al. 2015), the only study conducted so far on yawn contagion in strepsirhines showed no evidence for the presence of the phenomenon (Reddy et al. 2016). Indeed, the authors failed to detect a yawning response to life-size video projections of yawning stimuli from conspecifics in semi-free ranging ring-tailed (*Lemur catta*) and red-ruffed lemurs (*Varecia variegata rubra*).

Given the potential importance of species-specific social features in determining the presence of yawn contagion, for the first time we investigated the possible presence of yawn synchronisation and possibly contagion in another species of strepsirhine, the Indriid *Indri indri* (hereafter, indri), which can only be found in the wild. Indris live in socially monogamous family groups (Torti et al. 2017; Bonadonna et al. 2019) of two to six individuals (Torti et al. 2013), usually one adult pair and their offspring (Bonadonna et al. 2014). Indris are tolerant lemurs (Kavanagh et al. 2021) that defend stable and exclusive territories (Bonadonna et al. 2020) and show female dominance (Pollock 1979). Indris are the only lemur species able to emit songs in various contexts, for intra- and inter-group communication (Torti et al. 2013, 2018; De Gregorio et al. 2022a; Spezie et al. 2022). Songs are species-specific coordinated vocal displays (Gamba et al. 2011, 2016; Valente et al. 2022) usually given by two or more individuals either as duets or choruses (De Gregorio et al. 2022a). Both adult and immature individuals can participate in the songs (De Gregorio et al. 2021a, 2022b), which are sexually dimorphic (Zanoli et al. 2020; Valente et al. 2021) and show remarkable rhythmic features (De Gregorio et al. 2019, 2021b). Indris are diurnal, with an activity pattern concentrated during the first part of the day (Pollock 1975; Petter and Charles-dominique 1979). Social groups show a coordinated circadian rhythm and highly cohesive behaviour, with the individuals starting and performing the activity pattern with a high degree of behavioural synchrony (Pollock 1975) also mediated through short-distance communicative signals like contact calls (*hum*: Maretti et al. 2010; Valente et al. 2019). Thanks to their highly cohesive social behaviour and synchronised activity pattern, indris are an ideal model to investigate the presence of contagious yawning. To investigate the possible presence of the phenomenon, we formulated the following, sequential predictions.

Because -among others- spontaneous yawning is associated with the sleep-wake cycle (Gallup 2022) and indris are diurnal with synchronous behavioural activities (Pollock 1975) we expected spontaneous yawns in indris to be grouped in time (i.e. synchronised during the day) and primarily concentrated in the morning (**Prediction 1**). Even though yawn contagion seems not to be related to the phylogeny, and a previous study failed to find it in *Lemur catta* and *Varecia variegata rubra* by using video stimuli (Reddy et al. 2016), we nonetheless hypothesised that the phenomenon might be present in the indris, owing to their peculiar high level of synchronisation and coordination abilities (**Prediction 2a**). If so, we expected yawn contagion to be modulated by individual and social factors. Because yawn contagion in non-human primates can be higher in adults (Palagi et al. 2009; Madsen et al. 2013) and females are dominant in indris (Pollock 1979), we expected to detect yawn contagion especially in adults (**Prediction 2b**) and in females (**Prediction 2c**). Because in nonhuman primates, yawn contagion is also positively influenced by social bonding, e.g. informed by group membership, grooming rates, kinship (Palagi et al. 2009; Campbell and Waal 2011; Demuru and Palagi 2012), we expected that a similar effect might be present in indris (**Prediction 2d**).

METHODS

Data collection and operational definitions

We collected data from May 9th to October 25th 2018, from 28 individuals living in 7 habituated family groups inhabiting the Maromizaha New Protected Area, a montane rainforest in northeastern Madagascar (18° 56′ 49" S – 48° 27′ 33" E).

Indris are strictly diurnal, with a narrow active window limited to the first part of the day (Pollock 1975; Petter and Charles-Dominique 1979). For the purpose of this study we, therefore, followed the animals throughout their active period (i.e. we arrived at the sleeping site before they woke up and followed them until they became inactive, around 2pm). Previous analyses ascertained the genetic relationship between reproductive pairs and offspring involved in the study (Bonadonna et al. 2019). We used this information to compute the kinship degree of each dyad of indris. We distinguished among dyads composed of a parent and an offspring, of two siblings, or of two reproductive individuals. Group membership, identity, sex, age class, and social status of each individual are shown in Online Resource 1. Via all occurrences sampling method (Altmann 1974), we gathered 1580 total observation hours and recorded 613 yawning bouts (an example can be seen in Online Resource 2) emitted without external perturbing factors, eliciting alarm calls or displacement. For each yawning bout, we recorded the following data: i) time of the day; ii) identity, sex and age class (1: adults, individuals above six years of age; 2: juveniles, between 4 and 6 years of age, 3: yearlings, between 1 and 2 years of age, 4: infants, less than one year of age (defined following Rolle et al. 2021) of the subject that yawned first (hereafter, *trigger*); iii) identity, sex and age class of the subjects present within a range of 20m from the trigger (hereafter, *potential responders*); iv) which of the potential responders yawned or not within a three-minute time window from the trigger; v) kinship between the trigger and each potential responder; vi) visibility condition: whether each potential responder could see or not the triggering yawn. We considered that the potential responder could not see the triggering yawn when an obstacle (e.g. a tree) was present between the trigger and potential responder, preventing the latter from seeing the former, or when the potential responder's head was rotated by 180° to the trigger. We indicated the triggering yawn as visible to other subjects when it fell within its visual range (e.g., when the potential responder was frontal, diagonal or lateral to the trigger, thus 0-90° head rotation to reach the frontal vision of the trigger). We selected the three-min time window to allow comparison with previous studies (Anderson et al. 2004; Demuru and Palagi 2012; Gallo et al. 2021) and because this criterion reduces the probability of autocorrelation (a yawn emitted by a subject at t_0 can increase the probability to have another yawn by the same subject at $t_{(0+X)}$ where X is the increasing unit of time (Kapitány and Nielsen 2017).To further decrease the autocorrelation likelihood, in the case of a yawning chain (i.e., more yawns emitted in a row by the same subject during three-min, with no other subject yawning), we considered as a response only the first yawn emitted after the last triggering yawn (Norscia et al. 2022).

Via all occurrences sampling (Altmann 1974), we also collected data on social grooming bouts. We measured the observation time at both individual and dyadic levels. We then calculated the dyadic grooming rates by normalising the number of grooming bouts between each trigger and potential responder by the observation time of the dyad. Lastly, dyads were divided into two categories (low/high) depending on whether their grooming rates fell below the median frequency of grooming (low grooming dyads) or not (high grooming dyads). Since our study relied on observing wild animals in the field, it was not possible to record data blind.

Statistical Analyses

We first investigated differences in the individual yawning rates across different daily time slots (6:00-8:00, 8:01-10:00, 10:01-12:00, 12:01-14:00; we did not detect yawns before 6.10 am and after 12.20 pm). We built a Generalized Linear Mixed Model (R, *glmmTMB* package: Brooks et al. 2017) fitting a Poisson distribution and entering the number of individual yawns in each time slot as the response variable, time slot as fixed factor, individual ID as a random factor (GLMM$_1$; $N_{individual\_spontaneous\_yawns}$=53). To investigate the possible presence of yawn contagion in indris and its modulating factors, we built three more models fitting a binomial distribution. In all we entered the presence/absence of the yawning response as the binomial response variable. The first two included the dyad identity (trigger/potential responder) as a random factor. The last one included time slot and dyad identity as random factors. In all models, we entered all random factors as intercepts. As fixed factors, the first of these models (GLMM$_2$; $N_{yawning\_events}$=485) included the visibility condition (trigger's yawns visible or not visible to the potential responder), and the distance between trigger and potential responder. Then, to verify what individual factors could modulate the yawning response, we considered only the cases in which a previous yawn could be seen by the potential responders in the three-min time span and ran a second GLMM (GLMM$_3$; $_{Ncases\_visible\_yawns}$=108). We included the following fixed factors: sex and age class of both trigger and responder, and distance between trigger and receiver. $GLMM_3$ was restricted to the cases for which the distance between trigger and receiver was known. Lastly, to verify what social factors could modulate the yawning response, we run a further model ($GLMM_4$; $_{\mathrm{Ncases\_visible\_yawns}}$=130), entering kinship (siblings, parent-offspring, reproductive pair) and grooming level (low or high) as fixed factors. For each GLMM, we first verified whether the full model significantly differed from the null model (only including the random factor (Forstmeier and Schielzeth 2011) using a likelihood ratio test (ANOVA with argument 'Chisq', Dobson 2002). We reported the structure and results of all models in Table 1. We excluded collinearity among predictors by evaluating the Variance of Inflation Factors (VIF; Online Resource 1). through the *performance* package (Lüdecke et al. 2021a). Subsequently, we calculated the p-values for the individual predictors based on likelihood ratio tests between the full and the null model (Barr et al. 2013). We then used the Tukey post-hoc test (*multcomp* package: Hothorn et al. 2008) to perform the pairwise comparisons among the levels of four predictors: kinship, time slots, trigger, and responder age class.

RESULTS

We recorded 613 yawning events, mostly in the first two time slots (397 and 196 cases during the 6:00-8:00 and 8:01-10:00, respectively). The yawning events involved 28 individuals (13 females, 15 males) and 46 dyads, of which 11 were composed of siblings, 28 of a parent and an offspring, and seven of two reproductive individuals. We reported the number of times in which individuals of different sexes and age classes acted as either trigger or responder in Online Resource 1.

Yawn synchronisation

The results indicated that spontaneous yawning was concentrated in the morning (between 6:01 and 8:00 am). Indeed, individual spontaneous yawning frequencies varied across daily time slots (Table 1 $GLMM_1$; Fig. 1a), differing across time slots except for the comparison between the third and fourth slot (Tukey post-hoc test; Table 1 $GLMM_1$). These results suggest that yawning is synchronised across individuals.

Yawn contagion

We found that observing a yawn from a conspecific significantly increased the probability of detecting a yawning response in the observers in the successive three-minute slot (Table1 $GLMM_2$, $t=2.241$, $p=0.025$; Fig. 2a). Hence, yawn contagion was present in the indris under study. We also observed an inverse relationship between the yawning response and the distance between two individuals in a dyad (Table1 $GLMM_2$, $t=-3.310$, $p<0.001$; Fig. 1b).

Factors modulating yawn contagion

We found that neither individual factors (sex and age class of both responder and receiver) nor the distance between two individuals influenced the yawning response (the full model did not differ from the null model; $\chi^2 = 12.4339$, $p=0.189$; Table 1 $GLMM_3$). Lastly, yawning responses were higher for high-grooming dyads ($t=2.137$, $p=0.032$; Fig. 2b) but we found no difference in the presence of yawns among the three kinship levels (Tukey post hoc test; Table 1 $GLMM_4$; Fig. 2c).

DISCUSSION

In line with our first prediction, we found spontaneous yawning in indris to be concentrated in the first part of the morning (until 10 am with a peak between 6 and 8 am; Table 1, Fig. 1a), which is consistent with the association between yawning and sleep-wake cycle (Provine 1986; Leone et al. 2014; Massen et al. 2014). In two other lemur species (*Lemur catta* and *Propithecus verreauxi*) the peak of yawn contagion was detected from late morning to afternoon around a long phase of sleeping and resting associated with very high temperatures (Zannella et al. 2015). However, these lemurs were observed in the gallery forest of South Madagascar and their activity period usually lasts until 5 pm or more, especially for *L. catta* (Zannella et al. 2015). In contrast, indris live in the dense rainforests of eastern Madagascar, under completely different climate conditions and no such high temperatures. In particular, Maromizaha is a mountainous moist evergreen forest, with a tropical/subtropical climate and a daily average temperature of 15°C during the cool season (May-September) and 21°C during the warm season (October-April, Randrianarison et al. 2022). Moreover, although warmer days tend to be associated with a longer activity period, indris usually cease activities several hours before dusk (Pollock 1975). Still, indris do show occasional resting periods up to two hours, but these events are more common in non-habituated individuals (and apparently in response to potential predators) and are not temperature-related (Pollock 1975).

In line with our prediction 2a, we found that the indris were significantly more likely to yawn when they could potentially see a yawn from a conspecific, compared to when they could not, thus showing that yawn contagion was present in the indris under study (Table 1, Fig. 2a). This finding diverges from the result obtained in two other lemur species (*Lemur catta* and *Varecia variegata rubra*) where no yawn contagion was detected using video stimuli (Reddy et al. 2016). However, the overall variability in the presence of yawn contagion in lemurs reflects the variability observed in other primate groups (namely Old World Monkeys and apes) and in non-primate mammals where the occurrence of the phenomenon does not follow a phylogenetic pattern and appears to be more related to certain aspects of sociality (Palagi et al. 2020). The large majority of lemur species are solitary or pair-living (Kappeler and Fichtel 2015), which may make the presence or the expression of yawn contagion unlikely. Nonetheless, yawn contagion in lemurs might have emerged when particularly adaptive in social species, considering that group living has probably evolved independently in different lemur families with the change from nocturnal to (at least partly) diurnal activity patterns, requiring more cooperation, e.g. to reduce predation risks (Shultz et al. 2011; Kappeler 2014).

The emergence of yawn contagion in indris -where the synchronisation of individuals as a consequence of seeing a conspecific's yawn may drive an adjustment of physiological states and circadian rhythms- is in line with the especially high degree of behavioural synchrony showed by the individuals within a group (Pollock 1975), also expressed via their vocal coordination ability underlying the production of duets and choruses, rare among primates and unique among lemurs (De Gregorio et al. 2022a). Despite the uniqueness of indris' behaviour, previous evidence showing the lack of yawn contagion in captive lemurs (Reddy et al. 2016) calls for future studies to further explore the phenomenon. In this regard, we argue the combination of naturalistic and experimental studies to be vital. Indeed, studies in the wild allow for the measurement of ecologically valid responses whereas experimental studies can deal with a greater set of controlled variables. Concerning indris, being difficult to captive breed the species due to its ecological requirements, further investigation in the wild may indeed reveal whether the phenomenon of yawn contagion can enhance individual vigilance and motor synchrony among individuals (Casetta et al. 2021; Gallup 2022).

In contrast with prediction 2b and with findings on other primate and non-primate mammals, we found no differences in the level of yawn contagion across age classes. Previous studies showed that in primates yawn contagion can increase up to a certain age or be almost exclusively shown in adulthood (Anderson and Meno 2003; Palagi et al. 2009; Madsen et al. 2013; Norscia et al. 2022). In contrast with the prediction 2c, sex had no effect on the yawning response, with male and female indris equally likely to act as either responder or trigger. The influence of sex on yawn contagion -not consistently found across species- is puzzling because it may be related to different factors such as group composition, dominance, cooperative or attachment skills, individual sensitivity to stimuli, or social role (Demuru and Palagi 2012; Bartholomew and Cirulli 2014; Gallup and Massen 2016; Norscia et al. 2016, 2022; Chan and Tseng 2017; Gallo et al. 2021). Even if females are dominant in indris (Pollock 1979) and in other species of the indriid family, e.g. *Propithecus verreauxi*, *Avahi meridionalis* (Norscia and Palagi 2016), such dominance is mostly expressed as feeding priority and is not usually derived (*sensu* Lewis 2020) from in-group alliances, as it occurs for example among non-kin females in bonobos (Furuichi 2011).

In partial agreement with prediction 2d, grooming levels (but not kinship) positively influenced yawn contagion in indris (Fig. 2b, c), as observed in other primates (Palagi et al. 2009; Campbell and Waal 2011; Demuru and Palagi 2012) and in humans (Norscia and Palagi 2011). Social closeness (informed by grooming rates) can enhance the establishment of a physiological connection between individuals (Prochazkova and Kret 2017; Palagi et al. 2020). Moreover, yawn contagion expression may be influenced by both affective (Palagi et al. 2022) and selective attentional processes (Massen and Gallup 2017; Gallup 2021). In our case, the most parsimonious explanation may be that social closeness corresponded to spatial closeness leading to an enhanced perception of the triggering stimulus, as suggested by the significant effect of inter-individual distance in observing subsequent yawns from different subjects ($GLMM_2$). However, in the $GLMM_3$ including the distance between individuals as a predictor of yawning after perceiving others' yawns we found that the null and the full model were not significantly different. Thus, further investigation is necessary to detangle social closeness (measured via grooming) from spatial closeness (measured via inter-individual distance), and to address the interplay between social bonding and attention in shaping contagious yawning.

In conclusion, our work detected for the first time the presence of yawn contagion in a wild strepsirhine. Given the uniqueness of the present findings across lemurs, further studies may elucidate if the occurrence of the yawn contagion in basal primates is more widespread than previously thought and what individual, social and environmental factors may modulate it. On a broader perspective, this study can add a valuable piece to the comprehension of the yawn contagion and, more generally, to the investigation of the pressures that may have favoured the co-option of yawning as a communicative cue during evolution.

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Table 1 Structure and results of the four GLMM built through the package *glmmTMB* (Brooks et al. 2017). We computed the Tukey tests via the package *multcomp* (Hothorn et al. 2008). [a] Not shown as not having a meaningful interpretation; [b] This predictor was dummy-coded, with the 'Time slot (10:01-12:00)' being the reference category; [c] This predictor was dummy-coded, with the 'Sight (yawn not visible=0)' being the reference category; [d] This predictor was dummy-coded, with 'Kinship (sibling=0)' being the reference category; [e] This predictor was dummy-coded, with 'Grooming level (Low=0)' being the reference category. Statistically significant values are indicated in bold.

[GLMM_1] n ~ time_slot + (1|trigger) [**R Package** *glmmTMB*] null vs full model: df=4, χ² =85.4814**, p <0.001**

Predictor	*Estimate*	*SE*	*t*	*p*
Intercept^{a}	1.2395	0.5518	a	a
Time slot (8:01-10:00)^{b}	-0.5073	0.0917	-5.531	**<0.001**

[Tukey test: **R Package** *multcomp*]

Time slot	*Estimate*	*SE*	*z*	*p*
8:01-10:00 vs 06:00-08:00	-0.5028	0.0919	-5.471	**<0.001**
10:01:12:00 vs 06:00-08:00	-1.5822	0.2852	-5.549	**<0.001**
12:01:14 vs 06:00-08:00	-1.6943	0.4311	-3.930	**<0.001**
10:01:12:00 vs 8:01-10:00	-1.0794	0.2889	-3.737	**<0.001**
12:01:14 vs 8:01-10:00	-1.1916	0.4336	-2.748	**0.024**
12:01:14 vs10:01:12:00	-0.1121	0.5144	-0.218	0.996

[GLMM_2] yawn pres/abs ~ sight + distance + (1|dyad)

[**R Package** *glmmTMB*] null vs full model: df=2, χ² =25.172, **p <0.001**

Predictor	*Estimate*	*SE*	*t*	*p*
Intercept^{a}	-2.0176	0.3722	a	a
Sight (1)^{c}	0.8942	0.3990	2.241	**<0.001**
Distance	-0.1455	0.0468	-3.110	**0.001**

[GLMM_3] yawn pres/abs ~ trigger sex + responder sex + trigger class + responder class + distance + (1|dyad)

[**R Package** *glmmTMB*] null vs full model: df=9, χ² =12.4339, p=0.189

[GLMM_4] yawn pres/abs ~ grooming level + kinship + (1|dyad) + (1|time_slot)

[**R Package** *glmmTMB*] null vs full model: df=6, χ² =9.689, **p = 0.029**

Predictor	*Estimate*	*SE*	*t*	*p*
Intercept^{a}	-3.9634	1.1851	a	a
Kinship (Parent-offspring)^{d}	0.5569	0.7085	0.786	0.432

Grooming (High)[e]	2.3016	1.0770	2.137	**0.032**
[Tukey test: **R Package** *multcomp*]				
Kinship	*Estimate*	*SE*	*z*	*p*
Parent-offspring - siblings	0.5569	0.7085	0.786	0.698
Reproductive pair - siblings	1.8676	1.5917	1.173	0.451
Reproductive pair - Parent-offspring	1.3107	1.4789	0.886	0.634

Fig. 1 Predicted probabilities of the response variable in relation to two predictors: **(a)** Number of yawns in relation to the time slot (1=6:00-8:00, 2=8:01-10:00, 3=10:01-12:00, 4=12:01-14:00). **(b)** Distance in meters between two individuals trigger and receiver. For data visualisation, we used the package *sjPlot* 2.8.10 in R (Lüdecke et al. 2021b). The error bars and shaded area indicate confidence intervals

Fig. 2 Predicted probabilities of the yawn response in relation to three predictors. **(a)** Yawning response in relation to the visibility condition (0=not visible, 1=visible); **(b)** Grooming level (0=low-grooming dyads, 1=high-grooming dyads); **(c)** Kinship between the individuals within a dyad (0=siblings, 1=parent-offspring, 2=reproductive pair). For data visualisation, we used the package *sjPlot* 2.8.10 in R (Lüdecke et al. 2021b). Error bars indicate confidence interval

Fig.1

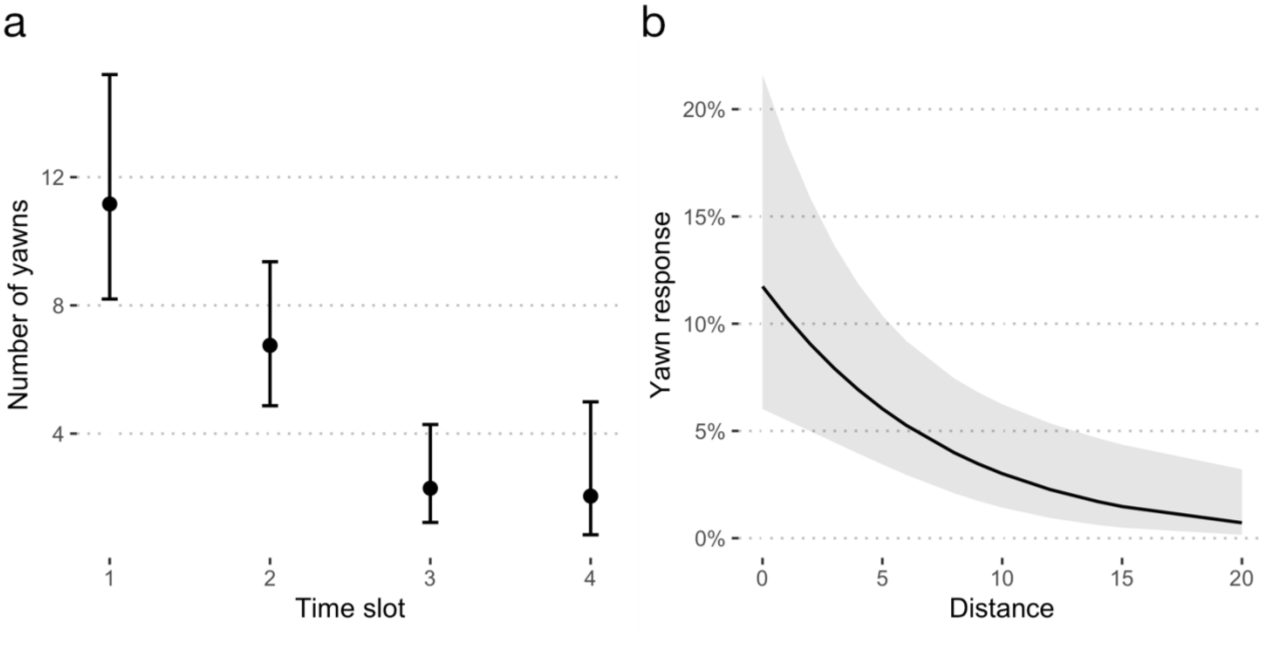
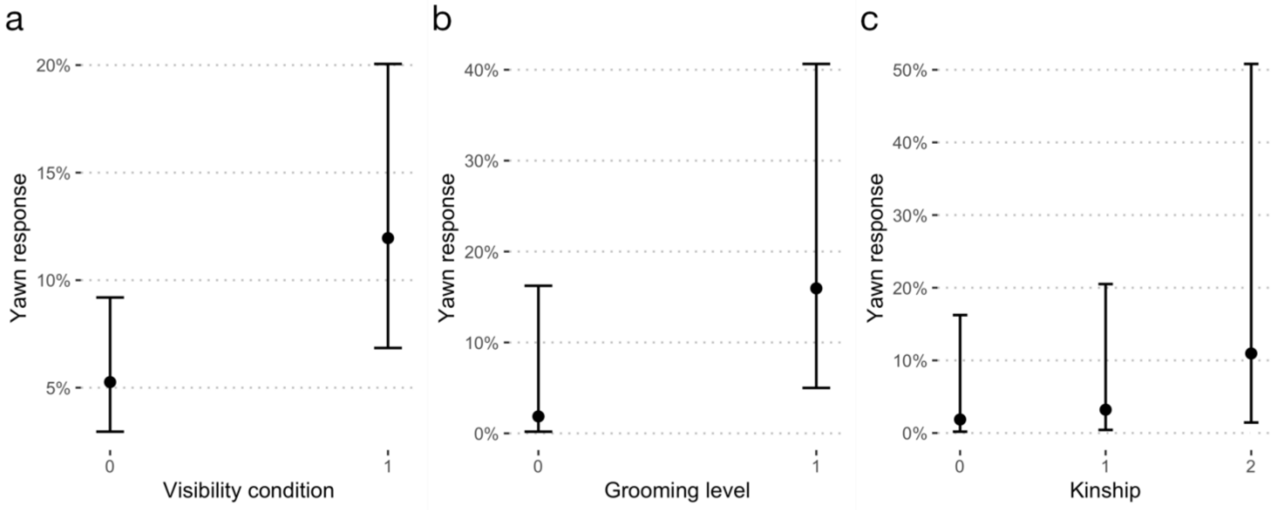


Fig.2


a
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