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**This is a pre print version of the following article:**

*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1884422> since 2025-01-23T09:41:02Z

*Published version:*

DOI:10.1007/s00265-022-03284-5

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1 **FIRST EVIDENCE OF CONTAGIOUS YAWNING IN A WILD LEMUR**

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30  
31  
32 **ABSTRACT**

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

51

## 52 **KEYWORDS**

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

54

55

## 56 **STATEMENTS AND DECLARATIONS**

57

## 58 **Competing Interests**

59 The authors declare no conflict of interest.

60

## 61 **Significance Statement**

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

## 73 **Author Contribution**

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

## 78 **Ethics Approval**

79 The research permit for this research has been granted from the Ministère de

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

#### 85 **Data availability**

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

#### 88 **ACKNOWLEDGMENTS**

89 We express our gratitude to Cesare Avesani Zaborra and Caterina Spiezio for their  
90 support. We also thank the field guides and assistants helping during the data  
91 collection and the GERP (Groupe d'Étude et de Recherche sur les Primates de  
92 Madagascar) for the field logistics organisation. We are grateful to two anonymous  
93 reviewers for their constructive recommendations to improve the manuscript.

94

#### 95 **Funding**

96 This research was supported by Università degli Studi di Torino and by grants from the  
97 Parco Natura Viva-Garda Zoological Park.

## 98 INTRODUCTION

99 Spontaneous yawning is a common stereotyped behaviour (Guggisberg et al. 2011).  
100 Contagious yawning differs from spontaneous yawning in that it is induced by others'  
101 yawns (Provine 1989). Spontaneous yawning (or a yawning-like morphological  
102 pattern) appears to be phylogenetically widespread across vertebrates (Baenninger  
103 1987) including humans (*Homo sapiens*) and non-human primates (Provine 1986, 2012;  
104 Anderson 2020). Among other functions (brain cooling, arousal, neurovascular  
105 circulation and behavioural state change: Guggisberg et al. 2011; Massen et al. 2014;  
106 Gallup 2022) spontaneous yawning under relaxed conditions appears to be related to  
107 the sleep-wake cycle (Provine 1986; Leone et al. 2014; Zannella et al. 2015). Therefore,  
108 individuals that share similar circadian rhythms and activity budgets may show a peak  
109 in yawning within the same time slot (Giganti and Zilli 2011; Zannella et al. 2015).  
110 However, yawning together does not equal yawning contagiously. For yawn contagion  
111 to occur, the yawn emitted by an individual (hereafter, trigger) must act as releasing  
112 stimulus (*sensu* Tinbergen and Perdeck 1950) and induce yawning in the individuals  
113 that detect such stimulus (hereafter, responders: Provine 1986, 2012; Demuru et al.  
114 2022). Intraspecific contagious yawning has been described in different mammalian  
115 species: wolves (*Canis lupus*, Romero et al. 2014), sheep (*Ovis aries*, Yonezawa et al.  
116 2017), elephant seals (*Mirounga leonina*, Wojczulanis-Jakubas et al. 2019), domestic  
117 pigs (*Sus scrofa*, Norscia et al. 2021b), lions (*Panthera leo*, Casetta et al. 2021), and one  
118 bird species (budgerigars, *Melopsittacus undulates*. Gallup et al. 2015) but not in  
119 another (*Corvus corax*. Gallup et al. 2022). Overall, the presence of yawn contagion has  
120 not been detected in a phylogenetically consistent way (Palagi et al. 2020). Indeed, in

121 haplorhine primates - the most investigated animal group - yawn contagion may be  
122 more linked to the type of sociality than to phylogenetic closeness (Palagi et al. 2020).  
123 Within hominids, yawn contagion has been described in highly social Hominini,  
124 including non-pathological humans (Provine 1986, 1989; Norscia and Palagi 2011;  
125 Bartholomew and Cirulli 2014; Chan and Tseng 2017; Norscia et al. 2021a),  
126 chimpanzees (Anderson et al. 2004; Campbell and Waal 2011; Campbell and Cox 2019),  
127 and the majority of bonobo colonies that have been investigated in this respect  
128 (Demuru and Palagi 2012; Tan et al. 2017; Norscia et al. 2022; but see Amici et al.  
129 2014). Yawn contagion has not been observed in captive lowland gorillas (Amici et al.  
130 2014; Palagi et al. 2019), but it has been recorded in orangutans (*Pongo* spp., van Berlo  
131 et al. 2020), which diverged from the human line earlier than gorillas (Groves 2018).  
132 Intriguingly, lowland gorillas generally show low affiliation levels (Palagi et al. 2019),  
133 whereas orangutans show a very dispersed sociality but might have been more social  
134 in the past when food availability was higher (Harrison and Chivers 2007; van Berlo et  
135 al. 2020). Within cercopithecids, yawn contagion has not been found in the despotic  
136 Japanese macaque (*Macaca fuscata*; Palagi and Norscia 2019). However, it has been  
137 observed in tolerant species, namely Tonkean macaque (*Macaca tonkeana*, Palagi and  
138 Norscia 2019) and geladas (*Theropithecus gelada*; Palagi et al. 2009; Gallo et al. 2021).

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

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

149         Although not consistently, yawn contagion can be influenced by individual and  
150 social factors (Palagi et al. 2020). In primates, it appears to increase with age or at least  
151 to be highest in adults in geladas (Palagi et al. 2009), bonobos (Norscia et al. 2022),  
152 chimpanzees (Madsen et al. 2013), and humans (Anderson and Meno 2003; Helt et al.  
153 2010; Millen and Anderson 2011; Cordoni et al. 2021). On the other hand, yawn  
154 contagion can decrease with age in certain groups or cohorts, in humans and bonobos  
155 (Bartholomew and Cirulli 2014; Norscia et al. 2022). Sex can also influence yawn  
156 contagion, partly depending on the social role that each sex has in a given species and  
157 group (Palagi et al. 2020). Females may respond more to others' yawns in bonobos  
158 (Norscia et al. 2022), although not in all cohorts (Norscia and Palagi 2011; Demuru and  
159 Palagi 2012; Bartholomew and Cirulli 2014). A comparable pattern, with mixed evidence  
160 on the influence of sex on yawn contagion, has also been reported in humans (Gallup  
161 and Massen 2016; Norscia and Palagi 2016; Chan and Tseng 2017). In wild geladas -  
162 where many one-male/multi-female units form coordinated, large associations (teams  
163 and bands)- a previous study found the highest yawning responses in adult males,  
164 which lead unit movements within teams (Gallo et al. 2021). Adult females can  
165 preferentially trigger yawns in bonobos where they are central to the group social  
166 matrix (Demuru and Palagi 2012; Norscia et al. 2022) or in high-ranking male



167 chimpanzees, a male-dominated society (Massen et al. 2012), at least under certain  
168 conditions, e.g. depending on the sex of the responder, presence of a swelling cycle  
169 (Massen et al. 2012; Norscia et al. 2022). Finally, intraspecific yawn contagion may  
170 increase as social bonding and kinship levels increase, as demonstrated in wolves  
171 (Romero et al. 2014), domestic pigs (Norscia et al. 2021b), geladas (Palagi et al. 2009),  
172 chimpanzees (Campbell and Waal 2011), bonobos (Demuru and Palagi 2012), and  
173 humans (Norscia and Palagi 2011), but see Bartholomew and Cirulli 2014; Tan et al.  
174 2017; Norscia et al. 2022.

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

187         Given the potential importance of species-specific social features in determining  
188 the presence of yawn contagion, for the first time we investigated the possible  
189 presence of yawn synchronisation and possibly contagion in another species of

190 strepsirhine, the Indriid *Indri indri* (hereafter, indri), which can only be found in the  
191 wild. Indris live in socially monogamous family groups (Torti et al. 2017; Bonadonna et  
192 al. 2019) of two to six individuals (Torti et al. 2013), usually one adult pair and their  
193 offspring (Bonadonna et al. 2014). Indris are tolerant lemurs (Kavanagh et al. 2021) that  
194 defend stable and exclusive territories (Bonadonna et al. 2020) and show female  
195 dominance (Pollock 1979). Indris are the only lemur species able to emit songs in  
196 various contexts, for intra- and inter-group communication (Torti et al. 2013, 2018; De  
197 Gregorio et al. 2022a; Spezie et al. 2022). Songs are species-specific coordinated vocal  
198 displays (Gamba et al. 2011, 2016; Valente et al. 2022) usually given by two or more  
199 individuals either as duets or choruses (De Gregorio et al. 2022a). Both adult and  
200 immature individuals can participate in the songs (De Gregorio et al. 2021a, 2022b),  
201 which are sexually dimorphic (Zanoli et al. 2020; Valente et al. 2021) and show  
202 remarkable rhythmic features (De Gregorio et al. 2019, 2021b). Indris are diurnal, with  
203 an activity pattern concentrated during the first part of the day (Pollock 1975; Petter  
204 and Charles-dominique 1979). Social groups show a coordinated circadian rhythm  
205 and highly cohesive behaviour, with the individuals starting and performing the activity  
206 pattern with a high degree of behavioural synchrony (Pollock 1975) also mediated  
207 through short-distance communicative signals like contact calls (*hum*: Maretti et al.  
208 2010; Valente et al. 2019). Thanks to their highly cohesive social behaviour and  
209 synchronised activity pattern, indris are an ideal model to investigate the presence of  
210 contagious yawning. To investigate the possible presence of the phenomenon, we  
211 formulated the following, sequential predictions.

212           Because -among others- spontaneous yawning is associated with the sleep-wake  
213 cycle (Gallup 2022) and indris are diurnal with synchronous behavioural activities  
214 (Pollock 1975) we expected spontaneous yawns in indris to be grouped in time (i.e.  
215 synchronised during the day) and primarily concentrated in the morning (**Prediction 1**).  
216 Even though yawn contagion seems not to be related to the phylogeny, and a  
217 previous study failed to find it in *Lemur catta* and *Varecia variegata rubra* by using  
218 video stimuli (Reddy et al. 2016), we nonetheless hypothesised that the phenomenon  
219 might be present in the indris, owing to their peculiar high level of synchronisation and  
220 coordination abilities (**Prediction 2a**). If so, we expected yawn contagion to be  
221 modulated by individual and social factors. Because yawn contagion in non-human  
222 primates can be higher in adults (Palagi et al. 2009; Madsen et al. 2013) and females  
223 are dominant in indris (Pollock 1979), we expected to detect yawn contagion especially  
224 in adults (**Prediction 2b**) and in females (**Prediction 2c**). Because in nonhuman  
225 primates, yawn contagion is also positively influenced by social bonding, e.g. informed  
226 by group membership, grooming rates, kinship (Palagi et al. 2009; Campbell and Waal  
227 2011; Demuru and Palagi 2012), we expected that a similar effect might be present in  
228 indris (**Prediction 2d**).

## 229 **METHODS**

### 230 **Data collection and operational definitions**

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

234 Indris are strictly diurnal, with a narrow active window limited to the first part of  
235 the day (Pollock 1975; Petter and Charles-Dominique 1979). For the purpose of this  
236 study we, therefore, followed the animals throughout their active period (i.e. we arrived  
237 at the sleeping site before they woke up and followed them until they became inactive,  
238 around 2pm). Previous analyses ascertained the genetic relationship between  
239 reproductive pairs and offspring involved in the study (Bonadonna et al. 2019). We  
240 used this information to compute the kinship degree of each dyad of indris. We  
241 distinguished among dyads composed of a parent and an offspring, of two siblings, or  
242 of two reproductive individuals. Group membership, identity, sex, age class, and social  
243 status of each individual are shown in Online Resource 1. Via all occurrences sampling  
244 method (Altmann 1974), we gathered 1580 total observation hours and recorded 613  
245 yawning bouts (an example can be seen in Online Resource 2) emitted without external  
246 perturbing factors, eliciting alarm calls or displacement. For each yawning bout, we  
247 recorded the following data: i) time of the day; ii) identity, sex and age class (1: adults,  
248 individuals above six years of age; 2: juveniles, between 4 and 6 years of age, 3:  
249 yearlings, between 1 and 2 years of age, 4: infants, less than one year of age (defined  
250 following Rolle et al. 2021) of the subject that yawned first (hereafter, *trigger*); iii)  
251 identity, sex and age class of the subjects present within a range of 20m from the

252 trigger (hereafter, *potential responders*); iv) which of the potential responders yawned  
253 or not within a three-minute time window from the trigger; v) kinship between the  
254 trigger and each potential responder; vi) visibility condition: whether each potential  
255 responder could see or not the triggering yawn. We considered that the potential  
256 responder could not see the triggering yawn when an obstacle (e.g. a tree) was present  
257 between the trigger and potential responder, preventing the latter from seeing the  
258 former, or when the potential responder's head was rotated by 180° to the trigger. We  
259 indicated the triggering yawn as visible to other subjects when it fell within its visual  
260 range (e.g., when the potential responder was frontal, diagonal or lateral to the trigger,  
261 thus 0-90° head rotation to reach the frontal vision of the trigger). We selected the  
262 three-min time window to allow comparison with previous studies (Anderson et al.  
263 2004; Demuru and Palagi 2012; Gallo et al. 2021) and because this criterion reduces  
264 the probability of autocorrelation (a yawn emitted by a subject at  $t_0$  can increase the  
265 probability to have another yawn by the same subject at  $t_{(0+X)}$  where X is the increasing  
266 unit of time (Kapitány and Nielsen 2017). To further decrease the autocorrelation  
267 likelihood, in the case of a yawning chain (i.e., more yawns emitted in a row by the  
268 same subject during three-min, with no other subject yawning), we considered as a  
269 response only the first yawn emitted after the last triggering yawn (Norscia et al. 2022).

270 Via all occurrences sampling (Altmann 1974), we also collected data on social  
271 grooming bouts. We measured the observation time at both individual and dyadic  
272 levels. We then calculated the dyadic grooming rates by normalising the number of  
273 grooming bouts between each trigger and potential responder by the observation time  
274 of the dyad. Lastly, dyads were divided into two categories (low/high) depending on

275 whether their grooming rates fell below the median frequency of grooming (low  
276 grooming dyads) or not (high grooming dyads). Since our study relied on observing  
277 wild animals in the field, it was not possible to record data blind.

278

## 279 **Statistical Analyses**

280 We first investigated differences in the individual yawning rates across different daily  
281 time slots (6:00-8:00, 8:01-10:00, 10:01-12:00, 12:01-14:00; we did not detect yawns  
282 before 6.10 am and after 12.20 pm). We built a Generalized Linear Mixed Model (R,  
283 *glmmTMB* package: Brooks et al. 2017) fitting a Poisson distribution and entering the  
284 number of individual yawns in each time slot as the response variable, time slot as  
285 fixed factor, individual ID as a random factor (GLMM<sub>1</sub>;  $N_{\text{individual\_spontaneous\_yawns}}=53$ ). To  
286 investigate the possible presence of yawn contagion in indris and its modulating  
287 factors, we built three more models fitting a binomial distribution. In all we entered the  
288 presence/absence of the yawning response as the binomial response variable. The first  
289 two included the dyad identity (trigger/potential responder) as a random factor. The  
290 last one included time slot and dyad identity as random factors. In all models, we  
291 entered all random factors as intercepts. As fixed factors, the first of these models  
292 (GLMM<sub>2</sub>;  $N_{\text{yawning\_events}}=485$ ) included the visibility condition (trigger's yawns visible or  
293 not visible to the potential responder), and the distance between trigger and potential  
294 responder. Then, to verify what individual factors could modulate the yawning  
295 response, we considered only the cases in which a previous yawn could be seen by the  
296 potential responders in the three-min time span and ran a second GLMM (GLMM<sub>3</sub>;  
297  $N_{\text{cases\_visible\_yawns}}=108$ ). We included the following fixed factors: sex and age class of both

298 trigger and responder, and distance between trigger and receiver. GLMM<sub>3</sub> was  
299 restricted to the cases for which the distance between trigger and receiver was known.  
300 Lastly, to verify what social factors could modulate the yawning response, we run a  
301 further model (GLMM<sub>4</sub>;  $N_{\text{cases\_visible\_yawns}}=130$ ), entering kinship (siblings, parent-offspring,  
302 reproductive pair) and grooming level (low or high) as fixed factors. For each GLMM,  
303 we first verified whether the full model significantly differed from the null model (only  
304 including the random factor (Forstmeier and Schielzeth 2011) using a likelihood ratio  
305 test (ANOVA with argument 'Chisq', Dobson 2002). We reported the structure and  
306 results of all models in Table 1. We excluded collinearity among predictors by  
307 evaluating the Variance of Inflation Factors (VIF; Online Resource 1). through the  
308 *performance* package (Lüdecke et al. 2021a). Subsequently, we calculated the p-values  
309 for the individual predictors based on likelihood ratio tests between the full and the  
310 null model (Barr et al. 2013). We then used the Tukey post-hoc test (*multcomp*  
311 package: Hothorn et al. 2008) to perform the pairwise comparisons among the levels  
312 of four predictors: kinship, time slots, trigger, and responder age class.

313

## 314 **RESULTS**

315 We recorded 613 yawning events, mostly in the first two time slots (397 and 196 cases  
316 during the 6:00-8:00 and 8:01-10:00, respectively). The yawning events involved 28  
317 individuals (13 females, 15 males) and 46 dyads, of which 11 were composed of  
318 siblings, 28 of a parent and an offspring, and seven of two reproductive individuals. We

319 reported the number of times in which individuals of different sexes and age classes  
320 acted as either trigger or responder in Online Resource 1.

321

### 322 *Yawn synchronisation*

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

329

### 330 *Yawn contagion*

331

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

338

### 339 *Factors modulating yawn contagion*

340 We found that neither individual factors (sex and age class of both responder  
341 and receiver) nor the distance between two individuals influenced the yawning



342 response (the full model did not differ from the null model;  $\chi^2 = 12.4339$ ,  $p = 0.189$ ;  
343 Table 1 GLMM<sub>3</sub>). Lastly, yawning responses were higher for high-grooming dyads  
344 ( $t = 2.137$ ,  $p = 0.032$ ; Fig. 2b) but we found no difference in the presence of yawns  
345 among the three kinship levels (Tukey post hoc test; Table 1 GLMM<sub>4</sub>; Fig. 2c).  
346

## 347 **DISCUSSION**

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

367 In line with our prediction 2a, we found that the indris were significantly more  
368 likely to yawn when they could potentially see a yawn from a conspecific, compared to  
369 when they could not, thus showing that yawn contagion was present in the indris

370 under study (Table 1, Fig. 2a). This finding diverges from the result obtained in two  
371 other lemur species (*Lemur catta* and *Varecia variegata rubra*) where no yawn  
372 contagion was detected using video stimuli (Reddy et al. 2016). However, the overall  
373 variability in the presence of yawn contagion in lemurs reflects the variability observed  
374 in other primate groups (namely Old World Monkeys and apes) and in non-primate  
375 mammals where the occurrence of the phenomenon does not follow a phylogenetic  
376 pattern and appears to be more related to certain aspects of sociality (Palagi et al.  
377 2020). The large majority of lemur species are solitary or pair-living (Kappeler and  
378 Fichtel 2015), which may make the presence or the expression of yawn contagion  
379 unlikely. Nonetheless, yawn contagion in lemurs might have emerged when particularly  
380 adaptive in social species, considering that group living has probably evolved  
381 independently in different lemur families with the change from nocturnal to (at least  
382 partly) diurnal activity patterns, requiring more cooperation, e.g. to reduce predation  
383 risks (Shultz et al. 2011; Kappeler 2014).

384 The emergence of yawn contagion in indris -where the synchronisation of  
385 individuals as a consequence of seeing a conspecific's yawn may drive an adjustment  
386 of physiological states and circadian rhythms- is in line with the especially high degree  
387 of behavioural synchrony showed by the individuals within a group (Pollock 1975), also  
388 expressed via their vocal coordination ability underlying the production of duets and  
389 choruses, rare among primates and unique among lemurs (De Gregorio et al. 2022a).  
390 Despite the uniqueness of indris' behaviour, previous evidence showing the lack of  
391 yawn contagion in captive lemurs (Reddy et al. 2016) calls for future studies to further  
392 explore the phenomenon. In this regard, we argue the combination of naturalistic and

393 experimental studies to be vital. Indeed, studies in the wild allow for the measurement  
394 of ecologically valid responses whereas experimental studies can deal with a greater  
395 set of controlled variables. Concerning indris, being difficult to captive breed the  
396 species due to its ecological requirements, further investigation in the wild may indeed  
397 reveal whether the phenomenon of yawn contagion can enhance individual vigilance  
398 and motor synchrony among individuals (Casetta et al. 2021; Gallup 2022).

399 In contrast with prediction 2b and with findings on other primate and non-  
400 primate mammals, we found no differences in the level of yawn contagion across age  
401 classes. Previous studies showed that in primates yawn contagion can increase up to a  
402 certain age or be almost exclusively shown in adulthood (Anderson and Meno 2003;  
403 Palagi et al. 2009; Madsen et al. 2013; Norscia et al. 2022). In contrast with the  
404 prediction 2c, sex had no effect on the yawning response, with male and female indris  
405 equally likely to act as either responder or trigger. The influence of sex on yawn  
406 contagion -not consistently found across species- is puzzling because it may be related  
407 to different factors such as group composition, dominance, cooperative or attachment  
408 skills, individual sensitivity to stimuli, or social role (Demuru and Palagi 2012;  
409 Bartholomew and Cirulli 2014; Gallup and Massen 2016; Norscia et al. 2016, 2022; Chan  
410 and Tseng 2017; Gallo et al. 2021). Even if females are dominant in indris (Pollock  
411 1979) and in other species of the indriid family, e.g. *Propithecus verreauxi*, *Avahi*  
412 *meridionalis* (Norscia and Palagi 2016), such dominance is mostly expressed as feeding  
413 priority and is not usually derived (*sensu* Lewis 2020) from in-group alliances, as it  
414 occurs for example among non-kin females in bonobos (Furuichi 2011).

415 In partial agreement with prediction 2d, grooming levels (but not kinship)  
416 positively influenced yawn contagion in indris (Fig. 2b, c), as observed in other primates  
417 (Palagi et al. 2009; Campbell and Waal 2011; Demuru and Palagi 2012) and in humans  
418 (Norscia and Palagi 2011). Social closeness (informed by grooming rates) can enhance  
419 the establishment of a physiological connection between individuals (Prochazkova and  
420 Kret 2017; Palagi et al. 2020). Moreover, yawn contagion expression may be influenced  
421 by both affective (Palagi et al. 2022) and selective attentional processes (Massen and  
422 Gallup 2017; Gallup 2021). In our case, the most parsimonious explanation may be that  
423 social closeness corresponded to spatial closeness leading to an enhanced perception  
424 of the triggering stimulus, as suggested by the significant effect of inter-individual  
425 distance in observing subsequent yawns from different subjects (GLMM<sub>2</sub>). However, in  
426 the GLMM<sub>3</sub> including the distance between individuals as a predictor of yawning after  
427 perceiving others' yawns we found that the null and the full model were not  
428 significantly different. Thus, further investigation is necessary to detangle social  
429 closeness (measured via grooming) from spatial closeness (measured via inter-  
430 individual distance), and to address the interplay between social bonding and attention  
431 in shaping contagious yawning.

432 In conclusion, our work detected for the first time the presence of yawn  
433 contagion in a wild strepsirhine. Given the uniqueness of the present findings across  
434 lemurs, further studies may elucidate if the occurrence of the yawn contagion in basal  
435 primates is more widespread than previously thought and what individual, social and  
436 environmental factors may modulate it. On a broader perspective, this study can add a  
437 valuable piece to the comprehension of the yawn contagion and, more generally, to

438 the investigation of the pressures that may have favoured the co-option of yawning as  
439 a communicative cue during evolution.

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719 indris (*Indri indri*). Am J Primatol 82:e23132. <https://doi.org/10.1002/ajp.23132>

720 Table 1 Structure and results of the four GLMM built through the package *glmmTMB* (Brooks et al.  
 721 2017). We computed the Tukey tests via the package *multcomp* (Hothorn et al. 2008). <sup>a</sup> Not shown as  
 722 not having a meaningful interpretation; <sup>b</sup> This predictor was dummy-coded, with the 'Time slot (10:01-  
 723 12:00)' being the reference category; <sup>c</sup> This predictor was dummy-coded, with the 'Sight (yawn not  
 724 visible=0)' being the reference category; <sup>d</sup> This predictor was dummy-coded, with 'Kinship (sibling=0)'  
 725 being the reference category; <sup>e</sup> This predictor was dummy-coded, with 'Grooming level (Low=0)' being  
 726 the reference category. Statistically significant values are indicated in bold.

[GLMM<sub>1</sub>]  $n \sim \text{time\_slot} + (1|\text{trigger})$  [R Package *glmmTMB*] null vs full model:  $df=4$ ,  $\chi^2 = 85.4814$ ,  $p < 0.001$

<i>Predictor</i>	<i>Estimate</i>	<i>SE</i>	<i>t</i>	<i>p</i>
<b>Intercept<sup>a</sup></b>	1.2395	0.5518	a	a
<b>Time slot (8:01-10:00)<sup>b</sup></b>	-0.5073	0.0917	-5.531	<b>&lt;0.001</b>

[Tukey test: R Package *multcomp*]

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

727

[GLMM<sub>2</sub>]  $\text{yawn pres/abs} \sim \text{sight} + \text{distance} + (1|\text{dyad})$

[R Package *glmmTMB*] null vs full model:  $df=2$ ,  $\chi^2 = 25.172$ ,  $p < 0.001$

<i>Predictor</i>	<i>Estimate</i>	<i>SE</i>	<i>t</i>	<i>p</i>
<b>Intercept<sup>a</sup></b>	-2.0176	0.3722	a	a
<b>Sight (1)<sup>c</sup></b>	0.8942	0.3990	2.241	<b>&lt;0.001</b>
<b>Distance</b>	-0.1455	0.0468	-3.110	<b>0.001</b>

728

[GLMM<sub>3</sub>]  $\text{yawn pres/abs} \sim \text{trigger sex} + \text{responder sex} + \text{trigger class} + \text{responder class} + \text{distance} + (1|\text{dyad})$

[R Package *glmmTMB*] null vs full model:  $df=9$ ,  $\chi^2 = 12.4339$ ,  $p=0.189$

729

[GLMM<sub>4</sub>]  $\text{yawn pres/abs} \sim \text{grooming level} + \text{kinship} + (1|\text{dyad}) + (1|\text{time\_slot})$

[R Package *glmmTMB*] null vs full model:  $df=6$ ,  $\chi^2 = 9.689$ ,  $p = 0.029$

<i>Predictor</i>	<i>Estimate</i>	<i>SE</i>	<i>t</i>	<i>p</i>
<b>Intercept<sup>a</sup></b>	-3.9634	1.1851	a	a
<b>Kinship (Parent-offspring)<sup>d</sup></b>	0.5569	0.7085	0.786	0.432

<b>Grooming (High)<sup>e</sup></b>	2.3016	1.0770	2.137	<b>0.032</b>
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[Tukey test: **R Package** *multcomp*]

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<i>Kinship</i>	<i>Estimate</i>	<i>SE</i>	<i>z</i>	<i>p</i>
<b>Parent-offspring - siblings</b>	0.5569	0.7085	0.786	0.698
<b>Reproductive pair - siblings</b>	1.8676	1.5917	1.173	0.451
<b>Reproductive pair - Parent-offspring</b>	1.3107	1.4789	0.886	0.634

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730

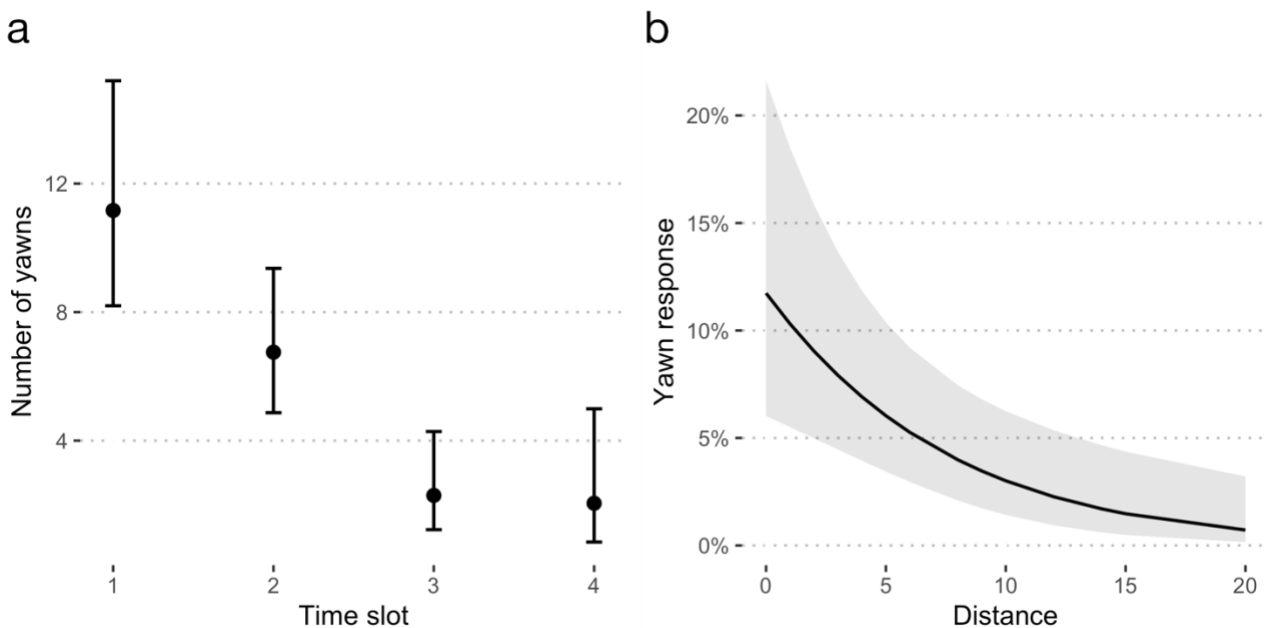
731

732 Fig. 1 Predicted probabilities of the response variable in relation to two predictors: **(a)** Number of yawns  
733 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  
734 meters between two individuals trigger and receiver. For data visualisation, we used the package *sjPlot*  
735 2.8.10 in R (Lüdecke et al. 2021b). The error bars and shaded area indicate confidence intervals  
736

737 Fig. 2 Predicted probabilities of the yawn response in relation to three predictors. **(a)** Yawning response  
738 in relation to the visibility condition (0=not visible, 1=visible); **(b)** Grooming level (0=low-grooming  
739 dyads, 1=high-grooming dyads); **(c)** Kinship between the individuals within a dyad (0=siblings,  
740 1=parent-offspring, 2=reproductive pair). For data visualisation, we used the package *sjPlot* 2.8.10 in R  
741 (Lüdecke et al. 2021b). Error bars indicate confidence interval

742

743 Fig.1

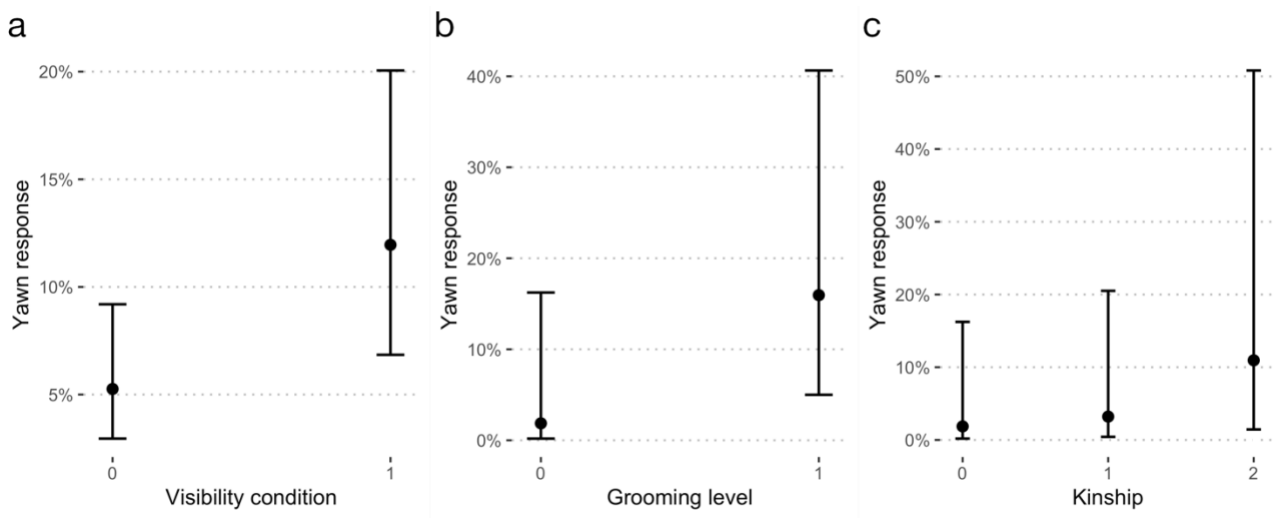


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745

746

747 Fig.2



748