YAWN CONTAGION PROMOTES MOTOR SYNCHRONY IN WILD LIONS (*PANTHERA LEO*)

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Yawning, a fixed action pattern, is widespread in almost all vertebrate taxa. Several hypotheses have been proposed to explain the functions of yawning. These hypotheses, not mutually exclusive, can be conventionally arranged according to both Physiological (e.g., Drowsiness Hypothesis - sleeping *vs* awaking states and viceversa, Arousal Hypothesis - contexts of high social tension) and Social Communicative domains (e.g., Contagion Hypothesis, Activity Synchronization Hypothesis). Due to their high social cohesion and group activity synchronization, wild lions (*Panthera leo*) are a good model to investigate both spontaneous yawning from the physiological domain and, possibly, contagious yawning, from the social communicative domain. Spontaneous yawning was particularly frequent during the relaxing context and, in agreement with the 24-h activity cycle typical of the species, was similarly distributed over night and day. These findings support the Drowsiness Hypothesis predicting that yawning is linked to the shift between sleeping vs awaking states (and viceversa). Lions did not show high levels of yawning under contexts of high-tension provoked by the competition over clumped food (e.g., carcass) (Arousal Hypothesis not supported). We found that yawn contagion is present in wild lions (Contagion Hypothesis supported). The presence of yawn contagion favoured the convergence of subsequent motor behaviours between the trigger and the responder thus favouring the synchronization of group activities (Activity Synchronization Hypothesis supported). Our findings suggest that the phenomenon of motor convergence triggered by yawn contagion (to our knowledge never explored in any other species) could represent an important tool to shed light on the adaptive and immediate benefits at the basis of the evolution of the yawn contagion phenomenon in human and nonhuman animals.

Keywords - Group cohesion and synchrony; immediate benefits; motor convergence; spontaneous yawning; yawn contagion

In memory of Robert Provine, an inspiring and authentic mentor

Yawning is a ubiquitous behaviour which is present in many taxa including fish, reptiles, birds and mammals (Baenninger, 1997). Yawning is described as a fixed action pattern which is stereotyped and often repetitive. It is characterized by mouth gaping that is accompanied by a long breath inspiration followed by a brief apnoea and then by a quick expiration (Walusinski & Deputte, 2004). Many hypotheses have been proposed to explain proximate and ultimate factors of spontaneous yawning. These hypotheses can fall into two main conventional domains: the Physiological (non-directed yawns, sensu Moyaho, Flores Urbina, Monjaraz Guzmán & Walusinski, 2017) and the Social Communicative one (directed yawn, sensu Moyaho et al., 2017).

The cluster of Physiological Hypotheses predicts that some internal factors, such as drowsiness, arousal, thermoregulation, or brain oxygenation can modulate the occurrence and frequency of yawning (Gallup, 2010, 2011, 2014; Giganti & Zilli, 2011; Guggisberg, Mathis, Schnider & Hess, 2010; Krestel, Bassetti & Walusinski, 2018; Walusinski, 2014). According to the Drowsiness Hypothesis, spontaneous yawning often occurs during resting periods (Provine, Hamernik & Curchack, 1987; Provine & Hamernik, 1986) and is performed when animals shift from an awake to a sleep phase and viceversa (*Struthio camelus australis*, Sauer & Sauer, 1967; *Loxodonta africana*, Rossman et al., 2017; *Otaria flavescens*, Palagi, Guillén-Salazar, & Llamazares-Martín, 2019; *Homo sapiens*, Giganti, Zilli, Aboudan & Salzarulo, 2010, Greco, Baenninger & Govern, 1993, Provine, 2005). In such behavioural transitions, the role of yawning is to increase the alertness state, thus making human and non-human animals able to properly adjust their behaviour in response to sudden and unexpected situations (Provine, 2005).

Spontaneous yawning can also vary as a function of the stimuli an animal receives from its social environment (Baenninger, 1997; Deputte, 1994; Greco et al., 1993; Guggisberg et al., 2010; Provine 1997). The Arousal Hypothesis predicts that anxiogenic events (e.g., competition over food, agonistic contacts, predation attacks) can lead to an increase of yawning. This has been reported in many different taxa such as birds (*Sula granti*, Liang, Grace, Tompkins & Anderson, 2015; *Melopsittacus undulatus*, Miller, Gallup, Vogel & Clark, 2010), rats (*Rattus norvegicus*, Moyaho & Valencia, 2002), sea lions (*Otaria flavescens*, Palagi, Guillén-Salazar & Llamazares-Martín, 2019a) and primates (*Lemur catta, Propithecus verreauxi*, Zannella, Norscia, Stanyon & Palagi, 2015; *Theropithecus gelada*, Leone, Ferrari & Palagi, 2014; *Macaca fascicularis*, Schino, Maestripieri, Scucchi & Turillazzi, 1990; *Macaca fuscata, Macaca tonkeana,* Zannella, Stanyon & Palagi, 2017). In accordance with the Arousal Hypothesis, Baker & Aureli (1997) showed that chimpanzees (*Pan troglodytes*) yawned more frequently after periods of high social tension that induced an arousal state in the subjects. In South American sea lions (*Otaria flavescens*), yawning peaked immediately after an aggressive conflict both in aggressors and victims (Palagi et al., 2019a). Several studies indicate that, under such circumstances, yawning can function as a stress-releaser mechanism by facilitating the restoration of the physiological/emotional homeostasis (Eldakar et al., 2017; Liang et al., 2015; Miller et al., 2010; Miller, Gallup, Vogel & Clark, 2012; Moyaho et al., 2017; Walusinski, 2006, 2010).

The cluster of Social Communicative Hypothesis claims that yawns, a physiological response, can nonetheless convey information about the internal/affective state (e.g., threat yawns) of the yawner that can be used by group members to adjust their behavioural response according to specific contexts (Deputte, 1994; Guggisberg et al., 2010; Leone et al., 2014; Zannella et al., 2015). One of the phenomena which seems to support the Social Communicative Hypothesis of yawning is its contagious nature (Provine, 1986). Contagious yawning, a behavioural response provoked automatically by viewing/listening others' yawns (Provine, 2005), has been demonstrated in humans and several non-human species (*Homo sapiens*, Anderson, 2020; Chan & Tseng, 2017; Cooper et al., 2012; Franzen, Mader & Winter, 2018; Giganti & Esposito Ziello, 2009; Giganti & Zilli, 2011; Norscia & Palagi, 2011; Platek, Critton, Myers & Gallup, 2003; Provine, 1986, 1989; *Pan troglodytes*, Amici, Aureli & Call, 2014; Anderson, Myowa-Yamakoshi & Matsuzawa, 2004; Campbell, Carter, Proctor, Eisenberg & de Waal, 2009; Campbell & de Waal, 2011, 2014; Madsen, Persson, Sayehli, Lenninger, & Sonesson, 2013; Massen Vermunt & Sterck, 2012; *Pan paniscus*, Demuru & Palagi, 2012; Tan, Ariely & Hare, 2017; *Theropithecus gelada*, Palagi, Leone, Mancini & Ferrari, 2009; *Canis lupus lupus*, Romero, Ito, Saito & Hasegawa, 2014; *Canis lupus familiaris,* Neilands et al., 2020, Romero, Konno & Hasegawa, 2013; *Ovis aries*, Yonezawa, Sato, Uchida, Matsuki, & Yamazaki, 2016; *Melopsittacus undulates*, Miller et al., 2012; *Loxodonta africana*, Rossman, Padfield, Young, Hart & Hart, 2020). Although the issue is still under debate (Adriaense, Koski, Huber, & Lamm, 2020; Massen & Gallup, 2017; Neilands et al., 2020; Gallup & Massen, 2020; Kis et al., 2020), yawn contagion is considered as a proxy of emotional contagion since the phenomenon has been found to be modulated by the level of social attachment between the interacting partners (Campbell & de Waal, 2011; Norscia, Zanoli, Gamba, & Palagi, 2020; Palagi, Celeghin, Tamietto, Winkielman & Norscia, 2020; Romero et al., 2013, 2014; Tan et al., 2017).

One of the most parsimonious explanations at the basis of yawn contagion is the so-called ‘chameleon effect’ (Chartrand & Bargh, 1999). The ‘chameleon effect’ predicts that the perception of a behaviour leads to unconscious imitation by the observer that in turn provokes an alignment of representations, also known as behavioural convergence (Arnott, Singhal & Goodale, 2009; Lakin & Chartrand 2003; Palagi & Cordoni, 2020). This convergence is highly adaptive because it can foster social cohesion, coordination and synchrony between subjects which do not necessarily share strong affiliation (Clay & de Waal, 2013; Lakin, Jefferis, Cheng & Chartrand, 2003; Palagi et al., 2020; Preston & de Waal, 2002; Prochazkova & Kret, 2017). For example, the synchronization in movements and vigilance activities in a group can increase the effectiveness in the resource exploitation (e.g., hunting) and defence from predators (Duranton & Gaunet, 2016).

Lions are a good model to explore the yawning phenomenon. Among felids, lions are the most social species (Bertram, 1975) whose social structure is characterized by fission-fusion dynamics (Mosser & Packer, 2009; Packer, Pusey & Eberly, 2001). Moreover, a recent social network analysis revealed that cohesion and convergent activities are fundamental for the success of a group (Dunston et al., 2016).

Here, we try to identify the contexts in which spontaneous yawning occurs and the possible presence of yawn contagion in a wild population of lions (*Panthera leo*). To accomplish our goal, we tested the following hypotheses that, due to the versatile nature of yawning, are not necessarily mutually exclusive.

The Drowsiness Hypothesis

Rudnai (2012) observed that most of the yawning events in wild lions occurred during the resting periods and, particularly, during the transitional phase from a sleep to an awake state. This finding suggests that in lions yawning can be linked to changes in the mood/states (e.g., from sleep to awake state or viceversa; from laying down to licking a group mate). If yawning, like in other mammal species (Guggisberg, Mathis, Herrmann & Hess, 2007, Guggisberg et al., 2010, *Theropithecus gelada,* Leone et al., 2014; *Propithecus verreauxi* and *Lemur catta*, Zannella et al., 2015; *Otaria flavescens*, Palagi et al., 2019a), is a mechanism signalling the shift between different moods/states, we expect it to be significantly more frequent during relaxed contexts, characterized by a fluctuation of resting/sleeping/affiliative behavioural patterns, than during contexts characterized by motor activity such as moving or hunting (Prediction 1a).

In macaques (*Macaca fascicularis*) and mangabeys (*Cercocebus albigena*), Deputte (1994, p. 238) found that “yawn duration was influenced by the activity or emotional level of the yawner”; yawns with a long duration were significantly more frequent during periods of relaxation compared to periods of locomotor activity or other physiologically arousing contexts (e.g., agonistic context). If relaxation is one of the main proximate factors (sensu Tinbergen, 1963) at the basis of the duration of the yawning event, we expect animals to perform long-lasting yawns during the relaxing contexts (Prediction 1b).

Since lions are active throughout the 24-h daily cycle and engage in relaxing activities both during the night and the day (Hayward & Hayward, 2006; Schaller, 1972), we expect no difference in the frequency and duration of spontaneous yawning between night and day (Prediction 2).

The Arousal Hypothesis

In a study on a captive group of lions, Baenninger (1987) reported that subjects increased their level of yawning just before food provisioning and that the yawning frequency tended to decrease in the post-feeding period "[…]. During the morning there were relatively few yawns (0.8/lion-hour), but there was a progressive increase before feeding time (to 1.8 yawns/lion hour between 1:00 and 2:00 p.m.). During and after feeding there was a sharp decline in the frequency of yawns (0.35 yawn/lion-hour)" (Baenninger, 1987, p. 351). In agreement with Deputte's findings (1994), in Sulawesi macaques short yawns were observed in aroused individuals during tension situations such as immediately after object shaking or stamping, two behavioural patterns characterized by high levels of locomotor/arousal activity (Thierry et al., 2000). If yawning is a behavioural response linked to the arousal state of the subjects, we expect that spontaneous yawning increases during contexts characterized by high social tension such as when animals are competing for the access to a clumped food resource (e.g., carcass) (Prediction 3a). Moreover, we expect that those yawning events occurring under such arousing circumstances are shorter in their duration compared to yawning events occurring during relaxed circumstances (Prediction 3b)

The Social Communicative Hypothesis

Yawn Contagion - Compared to other carnivore taxa, data show that felids tend to yawn at a higher frequency (Leyhausen, 1956). Rudnai (2012) observed that wild lions tend to yawn in chorus with two or more individuals yawning within 14 minutes after viewing others' yawns. In agreement with

Rudnai’s anecdotic observations and due to the social cohesion characterizing the groups of wild lions, we expected that yawn contagion is present in the species (Prediction 4).

Effect of Yawn Contagion on Motor Convergence - If yawn contagion has a role in the social alignment of animals’ activities (Vick & Paukner, 2010), we expect that those subjects that respond with a yawn to a first yawner will also show behavioural convergence by replicating the same motor pattern exhibited by the first yawner immediately after yawning (Prediction 5).

Methods

Ethical Note

The research was purely observational and non-invasive and it complies with the ASAB/ABS Guidelines for the Use of Animals in Research, the current South African and Italian law and University regulations. Thus, no permit from the Bio-Ethical Committee of the University of Pisa (Italy) was needed.

The Species and the Reserve

Data were collected from June to October 2019 at the research camp Siyafunda Wildlife & Conservation located in the Greater Makalali Private Game Reserve (GMPGR). The GMPGR is a fenced reserve covering 25,000 hectares and located in the Limpopo Province, South Africa (29º09'S, 30º42'E). The area is dominated by a savannah-semi arid ecosystem and the dominant vegetation types are characterized by mixed lowveld, bushveld, and mopane bushveld (Low & Rebelo, 1996). The monthly mean temperatures are reported in Table A1.

The Selati River and Makhutswi River, a perennial tributary of the Olifants River, run through the GMPGR. The reserve is punctuated by several artificial waterpoints, which are provided with water during the driest months in winter. The reserve hosts many large mammals such as *Hippopotamus* *amphibius*, *Giraffa camelopardalis*, various species of antelope (duiker genus *Cephalophus*, steenbok *Raphicerus campestris*, impala *Aepyceros melampus*, kudu *Tragelaphus strepsiceros*), brown hyenas (*Parahyaena brunnea*) and spotted hyenas (*Crocuta crocuta*), wild dogs (*Lycaon pictus*), including also the "Big Five": elephants (*Loxodonta africana*), lions (*Panthera leo*), buffalos (*Syncerus caffer*), rhinos (white rhinos *Ceratotherium simum* and black rhinos *Diceros bicornis*) and leopards (*Panthera pardus pardus*).

An estimated population of 31 lions with three reproductive and two bachelor groups can be found in the GMPGR. Lions were introduced in the reserve at the beginning of 1990s from a pride coming from the Kruger National Park (Druce et al., 2004b; Slotow & Hunter, 2009). Management interventions allow the introductions of new genes and prevent lions from inbreeding (Druce et al., 2004a). The GMPGR adopts a strategy of contraception, which consists of a hormonal implant, as part of the lion management regime. Lionesses are allowed breeding on a rotational basis, so that rate of reproduction slows down, and the genetic diversity is guaranteed.

Composition of the Study Groups and Data Collection

Data were collected on 19 lions divided into two social groups. The Tembe group included two adult females (>4 yrs), one sub-adult female (2-4 years), one sub-adult male (2-4 years), three juvenile females (1-2 yrs) and one juvenile male (1-2 yrs). The Garonga group included two adult females, one sub-adult male, and six juveniles whose sex was unknown. Data were also collected on two adult males (>4 yrs) which frequently roamed and visited the two groups. This group formation is similar to that reported for other study sites (Serengeti National Park, Tanzania, Schaller, 1972; Nairobi National Park, Kenia, Rudnai, 2012) in which females form permanent groups and coalition of males can associate with them. For the age classification we followed the descriptions of the morphological keys used by Schaller (1972) and Rudnai (2012). All the subjects were individually recognized thanks to several distinctive features (including sex, size, permanent scars, deformations, and shape of the mane).

Animals were well habituated to humans sitting in the vehicles (Hayward & Hayward, 2009). Since animals were not radio-collared, the two observers (G.C. & A.P.N.) and an expert ranger from the Siyafunda reserve searched for animals by tracking and with the aid of binoculars. Once one pride was detected, the observers monitored the animals until the group moved out of sight. The data collection was not carried out during bad weather conditions.

Observations were conducted both in the night (after dusk, 06.00-10.00 pm) and the day (after the dawn, 05.00-11.00 am and 03.00-06.00 pm). To limit disturbances as much as possible, nocturnal data collections were carried out with the aid of red illumination that was never directed towards animals but on the ground around them (Finley, 1959; Spoelstra et al., 2017). Every time the observers encountered one of the two groups (Tembe or Garonga), all the activities of the visible animals were video-recorded by a camera (Full HD Canon EOS® 1100D). In case of group splitting and formation of subgroups, the use of a second camera (Full HD Panasonic Lumix DC-FZ82) permitted continued video-recording of the entire group. The use of 50x optical zooms and a tripod allowed accurate video-data also at long distances (up to 50 meters). The concurrent use of the two cameras permitted continuous video-recording of all the activities of the subjects and to quantify the exact amount of time each subject was present in each video. Only those subjects (eight from Tembe, five from Garonga, and the two males) with at least one hour of high-quality video-recording (the animal had to be perfectly visible), were included in the analyses (individual mean hours of video-recordings = 4.8 ±0.9SE). Since in some cases some individuals went out of sight, it was not possible to film all the subjects for the same amount of time. For this reason, the number of subjects in the analyses can change as a function of these limitations.

Video Analysis

Videos were analysed by VLC 2.1.5 Rincewind software and Jump-to-Time extension with an accuracy of 0.02 seconds. We used all-occurrence sampling in order to obtain all yawning events from the videos. Following the Schaller's description (1972), we defined a yawning event as follows. A yawn starts when a subject opens its mouth and protrudes its tongue, while simultaneously inhaling deeply, until its mouth opens to its maximum. At this time, the lips are retracted and the teeth exposed. Tongue retraction, mouth closing and air exhalation are faster than the mouth opening phase and inhalation. The yawning events are silent (sounds were never detected during yawns) (Baenninger, 1987), often accompanied by eye closing and rarely by pandiculation, only 4.5 % of yawning were associated to stretching in the Baenninger's study (1987). There was a strong uniformity in the execution of yawning in terms of the degree of mouth opening and the exposure of the teeth (Figure 1). When a yawn occurred, we registered i) the identity of the yawner, ii) the exact time and duration of the yawning event (0.02 sec accuracy), iii) the yawner's posture (defined as laying, sitting or walking), iv) the individual/s who could detect the yawn (condition Y seen), and v) individual/s who could not detect the yawn (condition Y not seen).

To measure the duration of each yawning event, we made a frame-by-frame analysis on the 252 yawns which were fully visible in each phase of their motor sequence. A yawn event started with the first frame in which the lips appeared parted and ended with the frame in which the lips appeared closed (Figure 1).

G.C. and A.P.N. performed the video analysis and, before starting the analysis, underwent a training period to learn how to analyse videos frame-by-frame (the trainer was E.P.). Inter-observer reliability in characterizing and scoring the behavioural patterns was tested by E.P., who randomly selected parts of the dataset and checked whether the behavioural categories/patterns were correctly classified from the videos. Such checking was carried out every two hours of videos analysed (8 checks of 20 min randomly selected videos). The Cohen's kappa values for each of the behavioural categories used for the analyses (yawning, sitting, standing, laying down, walking, feeding) were never below 0.89.

Operational definitions

Yawns and Contexts - Yawns were classified as occurring in three types of contexts: relaxing, arousal/feeding and moving. For the relaxing context, the animal often remained laying down, shifting from an awake to a sleeping phase and viceversa, sometimes it was involved in affiliative behaviours with groupmates (e.g., muzzle licking). If the subject was involved in a feeding session, the context was labelled as arousal/feeding (e.g., around carcass). Finally, when the subject moved from one site to another for more than three minutes, the context was labelled as moving.

The contexts at group level were defined by following the rule of 50%. The group was considered to be in relaxing context if more than 50% of the visible subjects were laying down and/or shifting from an awake to a sleeping phase (and viceversa) and were not involved in any social interaction. The group was considered to be in arousal/feeding if more than 50% of the visible subjects were feeding on a carcass. The group was in moving when more than 50% of the visible subjects were walking from one site to another for at least three minutes (Rudnai, 2012; Schaller, 1972). The exact amount of time that animals spent in each of the contexts was calculated.

Contagious Yawning - For the analysis of yawn contagion, we considered a yawn as not seen when i) the head of the potential receiver was rotated by 180° with respect to the first yawner or ii) a visual obstacle (e.g., vegetation, rocks) was present between the first yawner and the potential receiver. All the yawns performed by subjects without seeing a yawn performed by a first yawner were considered to be spontaneous. A yawn was considered to be seen when i) the receiver had its eyes open and was positioned to see the head of the first yawner, and ii) there were no visual obstacles separating the receiver and the first yawner. All yawns performed by the receiver after seeing the yawn performed by the first yawner were considered to be contagious (yawn contagion). The probability of miscoding a yawning response (coding a spontaneous yawn as contagious yawn) is lower in the first three minutes after the perception of the yawning stimulus than later, when autocorrelation is more likely (the presence of a yawn performed by a subject at t_0 increases the probability to have another yawn by the same subject at $t_{(0+X)}$ where X is the increasing unit of time) (Campbell & Cox, 2019). For this reason and following the previous ethological studies on contagious yawning, we adopted the 3-min time window criterion to record the yawn responses (*Ovis aries*, Yonezawa et al., 2016; *Canis lupus*, Romero et al., 2014; *Gorilla gorilla gorilla,* Palagi, Norscia & Cordoni, 2019b; *Pan troglodytes*, Campbell & Cox, 2019; *Pan paniscus* and *Homo sapiens*, Palagi, Norscia & Demuru, 2014).

Yawn Contagion and Motor Convergence - The trigger was defined as the first subject of the group that changed his/her behavioural status by shifting from moving to resting (moving→resting) and viceversa (resting→moving). To evaluate if the response to others' yawns (yawn contagion) increased the probability of motor convergence between two subjects (the trigger and the observer), we recorded each time (within 3-min time window) an observer matched his/her motor activity with that of the trigger in the following conditions: 1) the trigger changed his/her status (moving→resting; resting→moving) without emitting any yawn (NO_yawn); 2) the trigger changed his/her status after emitting a yawn that did not elicit any response in the observer (YES_yawn_NO_yawn contagion) and 3) the trigger yawned, changed his/her status and elicited a yawn response in the observer (YES_yawn contagion) (Figure 2).

Statistics

The analyses of spontaneous yawns were performed at individual levels and due to the non-normality of the data distributions (Kruskal-Wallis test for normality, $p<0.05$) we applied non-parametric tests.

To compare the frequency and duration of spontaneous yawning between the two different age classes (adult vs juveniles), we applied the Exact Mann-Whitney U test. The Exact Wilcoxon Signed Rank test was used to contrast the frequency and duration of spontaneous yawning between day and night. To compare the frequency and duration of spontaneous yawning across the three different contexts (relaxing, feeding, moving), we applied the Exact Friedman Test (only the subjects with at least 30-min of video recording for each context were included in the analysis). The post-hoc pairwise comparisons were performed via the Bonferroni-Dunnett test. The non-parametric tests were performed via SPSS 20.0 and the level of significance was set at 0.05.

To check for the presence of contagious yawning and to evaluate whether its presence increased the probability of motor convergence between subjects, we ran two Generalized Linear Mixed Models (GLMM) with a binomial error distribution by using the R-package glmmTMB 1.2.5042 (Brooks et al., 2017).

Contagious Yawning MODEL - In this model the response variable was the presence/absence of the yawning response in the observer. The fixed factors were: Yawn seen/Yawn not seen (Y_{seen}/Y_{not_seen}), day/night, contexts (relaxing, feeding, moving), the sex class combination of the trigger and the receiver (male-male, male-female, female-male, female-female), and the age class combination of the trigger and the receiver (juvenile-juvenile, adult-juvenile, juvenile-adult, adult-adult). The trigger/receiver dyad identities were entered as random factors.

Motor Convergence MODEL - In this model the response variable was the presence/absence of motor convergence. The fixed factors were: trigger's changing status (move→rest; rest→move), yawn contagion condition (NO_yawn; YES_yawn_NO_yawn contagion; YES_yawn contagion), the sex class combination of the trigger and the receiver (male-male, male-female, female-male, female-female), and the age class combination of the trigger and the receiver (juvenile-juvenile, adult-juvenile, juvenile-adult, adult-adult). The trigger/receiver dyad identities were entered as random factors.

For both models the Likelihood Ratio Test (LRT; Dobson, 2002) was applied to compare the full model (including all the fixed factors and the random factors) with the null model (including only the random effects) (Forstmeier & Schielzeth, 2011). The LRT was also employed to test the significance of the fixed factors by using the function Anova (R-package car 3.0-10) (Fox and Weisberg 2019). To exclude the occurrence of collinearity among predictors, we examined the variance inflation factors (VIF; X Fox 2015) by the R-package performance 0.4.4 (Lüdecke et al. 2020). Model fit and overdispersion were verified by using the R-package DHARMa 0.3.3.0 (X Hartig 2020). The marginal R^2 (representing the variance explained by fixed factors only) and the conditional R^2 (representing the variance explained by the entire model including both fixed and random factors) (Nakagawa et al. 2017), were calculated via the R-package MuMIn 1.43.17 (Bartoń 2020). Then, we used the "confint(x)" function to interpret the estimated effects as relative odds ratios. Relative odds ratio (i.e. the expected odds change for one unit increase in the explanatory variable when the remaining variables are set to their reference category) were used to evaluate the magnitude of the estimated effects. All analyses were performed using R 4.0.3 (R Core Team 2020).

Results

Spontaneous Yawning

Age Class - To calculate the hourly frequency of yawns per subject, we divided the number of yawning events performed by each subject by the number of hours of observation gathered for that subject (i.e., the time during which each subject was present in the videos). Adults and juveniles yawned with a similar hourly frequency (Exact Mann-Whitney test; U=18.00, $N_{\text{adults}}=9$; $N_{\text{juveniles}}=6$; $P=0.328$; $\text{mean}_{\text{adults}}=2.341 \pm 0.649$SE; $\text{mean}_{\text{juveniles}} = 3.370 \pm 0.585$SE). We did not find any differences in the mean duration (seconds) of the yawning events between adult and juvenile subjects (U=26.00, $N_{\text{adults}}=9$; $N_{\text{juveniles}}=6$; $P=0.955$; $\text{mean}_{\text{adults}}=2.576 \pm 0.571$SE; $\text{mean}_{\text{juveniles}}=2.350 \pm 0.141$SE).

Since adults and juveniles show similar frequency and durations of yawning, in the following analyses age was not included as a factor.

Yawning Frequency and Duration across Different Contexts (Prediction 1 – Drowsiness Hypothesis and Prediction 3 – Arousal Hypothesis) - To calculate the hourly frequency of yawns per subject, we divided the number of yawning events performed by each subject during the three contexts (relaxing, feeding, moving) by the number of hours of observation gathered for each subject during each context. 46 out of 47 agonistic interactions (including the following patterns: dismissing, attempt to bite/bite, aggressive paw, aggressive chasing) occurred in the feeding context (eight feeding slots) thus indicating that the presence of a carcass induced an arousal state in the subjects (all the subjects engaged in aggressive interactions). The distribution of the hourly yawn frequency weakly differed across the three contexts (relaxing, feeding, moving*:* Exact Friedman Test $\chi^2 = 1.167$, $N = 9$, df = 2, $P = 0.040$) (Figure 3).

Specifically, yawning in the relaxing context was more frequent compared to the feeding context (post-hoc Bonferroni-Dunnett test, q=1.167, *P*=0.04); while there was no evidence for a difference between the remaining pairwise comparisons ($q_{\text{feeding vs moving}}=0.667$, $P=0.472$; $q_{\text{relaxing vs moving}}=0.500$, $P=0.867$) (Prediction 1 Drowsiness Hypothesis not fully supported; Prediction 3 Arousal Hypothesis not supported). This analysis included only those individuals (*N*=9, including subjects of both sex and age classes) with at least 30 minutes of video-recordings in each of the three contexts.

The Friedman test provided no evidence for a difference in the median duration of the yawning events across the three contexts (Exact Friedman Test $\chi 2 = 3.250$, $N = 8$, df = 2, $P = 0.236$) (Prediction 1b and 3b not supported). These analyses included only those individuals (*N*=8, including subjects of both sex and age classes) with at least 30 minutes of video-recordings in each of the three contexts and who yawned at least once in each context.

Yawning Frequency and Duration in the Night and Day (Prediction 2 – Drowsiness Hypothesis) - To calculate the hourly frequency of yawns per subject in the night and day period, we divided the number of yawns performed by each subject during the night and the day by the number of hours of observation gathered for that subject during the night and day. There was no significant difference in the frequency of yawns between night (06.00pm – 10.00pm) and day (05.00–11.00am and 03.00-06.00pm) (Exact Wilcoxon Signed Rank test; T=14.00; ties=0; N=9; P=0.359; $\text{mean}_{\text{night}}$ = 3.669 ±0.408SE; mean_{day} = 2.975 ±0.606SE). The yawns performed during the night and the day did not differ in their duration (seconds) (T=14.00; ties=0; N=8; P=0.641; $\text{mean}_{\text{night}}$ = 2.543 ±0.474SE; mean_{day} = 2.652 ±0.140SE) (Prediction 2 Drowsiness Hypothesis supported). This last analysis included only those individuals (N=8; including subjects of both sex and age classes) that yawned at least once in each time period (night and day).

Social Communicative Hypothesis (Prediction 4 Contagious Yawning) - There was compelling statistical evidence for a difference between the full including all the fixed factors (see Methods for the definitions of each factor) and the null model comprising only the random factors (likelihood ratio test: χ^2 = 117.120, df = 10, P < 0.0001). No collinearity was found between the fixed factors (range VIF_{min}=1.00; VIF_{max}=1.14). The model was not overdispersed (P=0.912, dispersion parameter=1.003).

The only fixed factor that had a strong significant effect on the yawning response was the '$\text{Yawn}_{\text{seen}}$/$\text{Yawn}_{\text{notseen}}$' variable (Table 1; Figure 4). The likelihood of the occurrence of the yawning response was > 139 times (odds ratio = 1.39e+13) higher in the seen compared to not seen condition. The result indicates that seeing a previous yawning significantly increased the probability to yawn within 3-min time window thus supporting the Prediction 4, which stated that yawn contagion is present in wild lions. In 75.47% of cases, the yawn responses occurred within the first minute after seen the triggering yawn.

Social Communicative Hypothesis (Prediction 5 Effect of Yawn Contagion on Motor Convergence). There was convincing statistical evidence for a difference between the full model, including all the fixed factors (see Methods for the definitions), and the null model, comprising only the random factors (likelihood ratio test: $\chi^2 = 35.576$, df = 9, $P < 0.0001$). No collinearity was found between the fixed factors (range $\mathrm{VIF}_{\mathrm{min}}=1.26$; $\mathrm{VIF}_{\mathrm{max}}=1.96$). The model was not overdispersed ($P=0.504$, dispersion parameter=1.049). The fixed factor "yawn contagion condition" (NO_yawn; YES_yawn_NO_yawn contagion; YES_yawn contagion) had a strong significant effect on the motor convergence (Table 2; Figure 5). The likelihood of the motor convergence was about 11 times (odds ratio = 11.379) higher in presence of a yawn contagion event compared to its absence. The randomization pairwise comparisons revealed significant differences between NO_yawn and YES_yawn contagion (t=-3.037; $P=0.004$) and between YES_yawn_NO_yawn contagion and YES_yawn contagion (t=-5.337; $P=0.0001$). No difference was found between NO_yawn and YES_yawn_NO_yawn contagion (t=1.967; $P=0.070$). Bonferroni correction p-level=0.017. The result indicates that the presence of yawn contagion positively affects the probability that the observers replicate the same motor pattern of the triggers thus supporting the Prediction 5, which stated that yawn contagion can favour motor convergence in wild lions.

Discussion

This is the first systematic study on the yawning activity in wild lions. Yawning tended to be frequent during relaxing and moving, two activities that often involved all the subjects of the group concurrently (Prediction 1a Drowsiness Hypothesis partially supported) (Figure 3). Moreover, we found that the frequency of the yawns and their duration did not differ between the day and night in agreement with the 24-h resting cycle of lions (Hayward & Hayward, 2006; Schaller, 1972) (Prediction 2 Drowsiness Hypothesis supported).

In wild lions, spontaneous yawning punctuated the shifts between sleeping vs awaking / laying vs sitting / sitting vs standing and viceversa, being particularly frequent during the relaxing contexts which involved many of these shifts. Since relaxing contexts occurred both during the day and the night, the similar distribution of yawning in these periods supports the Drowsiness Hypothesis (Guggisberg et al., 2007, 2010). This is in line with previous descriptions provided by Rudnai (2012) on the presence of yawning in this species. The author affirmed that "[…] All yawning observed (ninety-five individual observations) occurred between 1530 and 1830 hours, indicating that lions […], do not usually yawn before sleeping but only after resting" (Rudnai, 2012, p. 45). In our case, it was not possible to determine whether the animals were sleeping; however, the lions alternated periods of total inactivity (laying down) with periods of low activity (slightly moving, changing position, sometimes sitting and engaging in affiliative interactions). Moreover, Baenninger (1987) observed that lions often yawned when they were laying down thus suggesting that the behaviour was linked to a relaxed state. The linkage between yawning and periods of relaxation has been found in several mammalian species, including humans (Zilli, Giganti & Salzarulo, 2007). In geladas (*Theropithecus gelada*), yawning is a context-dependant phenomenon. During the relaxing periods and their affiliative interactions, geladas emit small yawns during which the teeth and gums are covered (Leone et al., 2014). In sifakas (*Propithecus verreauxi*) and ringtailed lemurs (*Lemur catta*), Zannella and colleague (2015) demonstrated that yawning was particularly frequent during the behavioural shifting during relaxed contexts (e.g., sleep/awake, sitting/laying).

Our data show that in wild lions, yawning was also linked to the moving context, another activity that mostly involves all the subjects of the group that frequently alternated walking and standing phases. Since our observations were not uniformly distributed over the 24-hour cycle, it would be interesting to expand the data collection to additional time-windows (e.g., 10.00 pm – 05.00 am) to draw a more precise daily fluctuation of spontaneous yawning across the different contexts.

We did not find any empirical evidence in support of the Arousal Hypothesis. Indeed, yawning frequency did not peak during one of the most aroused contexts of social interaction such as competition over clumped food (Prediction 3a Arousal Hypothesis not supported) (Figure 3). The high frequency of agonistic contacts we recorded in wild lions indicates that this context was actually characterized by a high level of social tension. The low frequency of yawning we recorded in this context cannot be due to the fact that animals have their mouths engaged. The carcass (clumped food) did not allow all the animals feeding at the same time. If yawning is a sign of arousal/frustration, we would expect to find a peak frequency in the subjects that had to wait or fight to have access to the carcass. Our finding is not in agreement with the captive data obtained by Baenninger (1987) who reported that lions increased their level of yawning just before food provisioning (at 03.00 pm) and that the yawning frequency tended to decrease in the post-feeding period. It is possible that the distribution of food under limited spatial conditions and escape opportunities could determine higher levels of anxiety in animals thus stimulating their yawn activity. Due to the polyfunctional nature of yawning, additional data, both in wild and captive conditions, would help us understand if this phenomenon can function as an indicator of anxiety in lions similar to other species (*Macaca tonkeana*, Zannella et al., 2017; *Melopsittacus undulatus*, Miller et al., 2010; *Otaria flavescens*, Palagi et al., 2019a; *Rattus norvegicus*, Kubota, Amemiya, Yanagita, Nishijima & Kita, 2014; *Sula granti*, Liang et al., 2015).

Different from some primate species, who engage in shorter yawns during periods of high social tension and arousal (*Macaca fascicularis, Cercocebus albigena* Deputte, 1994; Sulawesi macaques, Thierry et al., 2000), in wild lions we did not find any difference in the mean duration of the yawning events across the three contexts considered (relaxing, feeding, moving). This basic uniformity in the duration and execution of the behaviour (Figure 1) makes the interpretation of yawning even more difficult in this species.

Yawning seems to have an important social communicative role in wild lions (Social Communicative Hypothesis, Guggisberg et al., 2010). We found that contagious yawning was present in this species (Prediction 4 Contagious Yawning supported) (Figure 2 and 4) and that, after being infected by others' yawns, both juveniles and adults tended to align their subsequent motor actions (Figure 2 and 5) thus suggesting that yawn contagion can have a role in promoting the synchronization of the group activity (Prediction 5 Effect of Yawn Contagion on Motor Convergence supported). This is in agreement with the hypothesis proposed by Vick and Paukner (2010) predicting that yawning can be a reliable indicator of change in the activity state and may help synchronize group behaviours.

The yawning response mostly occurred within the first minute (75.47%) after the perception of the yawning stimulus. The short latency in the response appears to be particularly adaptive if animals need to coordinate their movements in the minutes immediately following the yawn contagion event. This response latency is similar to that observed in human (Norscia & Palagi, 2011) and nonhuman primates (*Pan paniscus*, Demuru & Palagi, 2012; *Pan troglodytes*, Campbell & Cox, 2019; *Theropithecus gelada*, Palagi et al., 2009), in which yawn contagion typically peaked within the second minute after the triggering stimulus.

In lions, most of the maintenance activities are collectively performed by engaging in cooperative behaviours (Borrego, 2019; Packer & Ruttan, 1988; Rudnai, 2012; Schaller, 1972). Lions engage in cooperative hunting (Packer & Pusey 1997), territory defence (Grinnell, 2002; Heinsohn, Packer & Pusey, 1996; Heinsohn & Packer 1995; McComb, Packer & Pusey, 1994; Mosser & Packer 2009) and collectively rear their offspring (Packer & Pusey 1994). Since lion society is free from the tolerance constraints imposed by rigid dominance hierarchies, the species has been defined egalitarian (Borrego, 2019; Packer et al. 2001). Rudnai (2012) stated that the utilitarian interactions, which are strongly evolutionary adaptive, can also serve to strengthen the bond between group members. Through an elegant social network analysis, Dunston et al. (2016) demonstrated that the social cohesion and stability are central to the success of a lion group. The presence of yawn contagion and its effect on the subsequent behaviours by the interacting subjects can foster the synchronization of motor activity, thus leading to group coordination, stability, and cohesion.

Yawn contagion and its short latency in the response have been often interpreted in the light of emotional contagion, a basic-building block of empathy (Palagi et al., 2009, 2020; Preston and de Waal, 2002; Romero et al., 2013, 2014). However, this issue is still under strong debate not only in nonhuman animals (canids, monkeys, great apes), but also in humans (Adriaense et al., 2020; Neilands et al., 2020; Massen & Gallup, 2017). To our knowledge, in none of the species studied before, motor convergence following episodes of contagious yawning has ever been explored. Yet, focusing on the immediate effects of yawn contagion could represent an important step to shed light on the adaptive and short-term benefits at the basis of the evolution of yawn contagion and, possibly, emotional contagion.

References

Adriaense, J. E. C., Koski, S. E., Huber, L., & Lamm, C. (2020). Challenges in the comparative study of empathy and related phenomena in animals. *Neuroscience & Biobehavioral Reviews*, 112, 62-82. https://doi.org/10.1016/j.neubiorev.2020.01.021

Altmann, S. (1967). *Social communication among primates*. Chicago: University of Chicago Press.

Amici, F., Aureli, F., & Call, J. (2014). Response facilitation in the four great apes: is there a role for empathy? *Primates*, 55, 113–118, https://doi.org/10.1007/s10329-013-0375-1

Anderson, J. R. (2020). Anderson, J.R. One thousand yawns. *Primates*, https://doi.org/10.1007/s10329-020-00869-4

Anderson, J. R., Myowa-Yamakoshi, M., Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 271, S468–S470. https://doi.org/10.1098/rsbl.2004.0224

Arnott, S. R., Singhal, A., & Goodale, M. A. (2009). An investigation of auditory contagious yawning. *Cognitive, Affective, & Behavioral Neuroscience*, 9, 335–342. https://doi.org/10.3758/CABN.9.3.335

Baenninger, R., (1987). Some comparative aspects of yawning in *Betta splendens, Homo sapiens*, *Panthera leo* and *Papio sphinx*. Journal of Comparative Psychology, 101(4), 349-354. https://doi.org/10.1037/0735-7036.101.4.349

Baenninger, R. (1997). On yawning and its functions. *Psychonomic Bulletin and Review*. *4(2)*, 198-207. https://doi.org/10.3758/BF03209394

Baker, K. C., & Aureli, F. (1997). Behavioural indicators of anxiety: an empirical test in chimpanzees. *Behaviour*, 134, 1031-1050.

Bartoń, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bertram, B. C. R. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology*, London, 177(4), 463-482. https://doi.org/10.1111/j.1469-7998.1975.tb02246.x

Borrego, N. (2019). Socially tolerant lions (*Panthera leo*) solve a novel cooperative problem. *Animal Cognition,* 23**,** 327–336. https://doi.org/10.1007/s10071-019-01336-4

Campbell, M.W., & Cox C.R. (2019). Observational data reveal evidence and parameters of contagious yawning in the behavioral repertoire of captive-reared chimpanzees (*Pan troglodytes*). *Scientific Reports*, 9:13271. https://doi.org/10.1371/journal.pone.0018283

Campbell, M. W., & de Waal F. B. M. (2011). Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS One*, 6(4):e18283. https://doi.org/10.1371/journal.pone.0018283

Campbell, M. W. & de Waal, F. B. M. (2014). Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 281: 20140013. https://doi.org/10.1098/rspb.2014.0013

Campbell, M. W., Carter, J. D., Proctor, D., Eisenberg, M. L. & de Waal, F. B. M. (2009). Computer animations stimulate contagious yawning in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* , 276, 4255–4259. https://doi.org/10.1098/rspb.2009.1087.

Chan, M. H. M., & Tseng, C. H. (2017). Yawning detection sensitivity and yawning contagion. *i-Perception,* 8(4), 2041669517726797. https://doi.org/10.1177/2041669517726797

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: the perception–behavior link and social interaction. *Journal of Personality and Social Psychology*, 76, 893–910. https://doi.org/10.1037/0022-3514.76.6.893

Clay, Z., & de Waal F. B. M. (2013). Bonobos respond to distress in others: consolation across the age spectrum. *PLoS One*, 8(1):e55206. doi:10.1371/ journal.pone.0055206

Cooper, N. R., Puzzo, I., Pawley, A. D., Bowes-Mulligan, R. A., Kirkpatrick, E. V., Antoniou, P. A., Kennett, S. (2012). Bridging a yawning chasm: EEG investigations into the debate concerning the role of the human mirror neuron system in contagious yawning. *Cognitive, Affective & Behavioral Neuroscience*, 12, 393–405. https://doi.org/10.3758/s13415-011-0081-7

Demuru, E. & Palagi, E. (2012). In bonobos yawn contagion is higher among kin and friends. *PLoS One*, 7(11), e49613. https://doi.org/10.1371/journal.pone.0049613

Deputte, B. L. (1994). Ethological study of yawning in primates. I. Quantitative analysis and study of causation in two species of Old World monkeys (*Cercocebus albigena* and *Macaca fascicularis*). *Ethology*, 98, 221–245. https://doi.org/10.1111/j.1439-0310.1994.tb01073.x

Dobson, A. J. (2002). *An Introduction to Generalized Linear Models*. (2nd ed.). Boca Raton, FL: Chapman and Hall/CRC Press.

Druce, D., Genis, H., Braak, J., Greatwood, S., Delsink, A., Kettles, R., Hunter, L. & Slotow, R. (2004a). Prey selection by a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *African Zoology*, 39, 273-284. https://doi.org/10.1080/15627020.2004.11657223

Druce, D., Genis, H., Braak, J., Greatwood, S., Delsink, A., Kettles, R., Hunter, L. & Slotow, R. (2004b). Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Koedoe*, 47, 103–118. https://doi.org/10.4102/koedoe.v47i1.64

Dunston, E. J., Abell, J., Doyle, R. E., Kirk, J., Hilley, V. B., Forsyth A., Jenkins E. & Freire R. (2016). An assessment of African lion *Panthera leo* sociality via social network analysis: prerelease monitoring for an ex situ reintroduction program. *Current Zoology*, 63(3), 301–312. https://doi.org/10.1093/cz/zow012

Duranton, C., & Gaunet, F. (2016). Behavioural synchronization from an ethological perspective: Overview of its adaptive value. *Adaptive Behavior*, 24, 181–191. https://doi.org/10.1177/1059712316644966

Eldakar, O. T., Tartar, J. L., Garcia, D., Ramirez, V., Dauzonne, M., Armani, Y., & Gallup, A. C. (2017). Acute physical stress modulates the temporal expression of self-reported contagious yawning in humans. *Adaptive Human Behavior and Physiology*, 3, 156–170. https://doi.org/10.1007/s40750-017-0060-5

Finley, R. B. (1959). Observation of nocturnal animals by red light. *Journal of Mammalogy*, 40(4), 591-594. https://doi.org/10.2307/1376280

Fox, J. (2015). *Applied Regression Analysis and Generalized Linear Models*. Thousand Oaks, CA: SAGE Publications, Inc.

Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression*. (2nd ed.). Thousand Oaks, CA: SAGE Publications, Inc.

Franzen, A., Mader, S. & Winter, F. (2018). Contagious yawning, empathy, and their relation to prosocial behavior. *Journal of Experimental Psychology: General*, 147, 1950–1958. https://doi.org/10.1037/xge0000422.

Gallup, A. C., (2010). A thermoregulatory behavior. *Frontiers of Neurology and Neuroscience*, 28, 84-89. https://doi.org/10.1159/000307084

Gallup, A. C. (2011). Why do we yawn? Primitive versus derived features. *Neuroscience and Biobehavioral Reviews*, 35(3), 765–769. https://doi. org/10.1016/j.neubiorev.2010.09.009

Gallup, A. C. (2014). Abnormal yawning in stroke patients: the role of brain thermoregulation. *Frontiers in Neuroscience,* 8, 300. https://doi.org/10.3389/fnins.2014.00300

Gallup, A.G. & Massen, J.J.M. (2020). Intranasal oxytocin, empathy, and contagious yawning in dogs and humans. *Applied Animal Behaviour Science*, 224, 104971. https://doi.org/10.1016/j.applanim.2020.104971

Giganti, F. & Esposito Ziello, M. (2009). Contagious and spontaneous yawning in autistic and typically developing children. *Current Psychology Letters*, 25, 1–11.

Giganti, F. & Zilli, I. (2011). The daily time course of contagious and spontaneous yawning among humans. *Journal of Ethology*, 29, 215–219. https://doi.org/10.1007/s10164-010-0242-0

Giganti, F., Zilli, I., Aboudan, S., & Salzarulo, P. (2010). Sleep, sleepiness and yawning. *Frontiers of Neurology and Neuroscience*, Basel, Karger, 28, 42–46.

Greco, M., Baenninger, R., & Govern, J., (1993). On the context of yawning: when, where, and why? *The Psychological Record*, 43, 175–183.

Grinnell, J. (2002). Modes of cooperation during territorial defense by African lions. *Human Nature*, 13, 85–104. https://doi.org/10.1007/s12110-002-1015-4

Guggisberg, A. G., Mathis, J., Herrmann, U. S. & Hess, C. W. (2007). The functional relationship between yawning and vigilance. *Behavioral Brain Research*, 179, 159–166. https://doi.org/10.1016/j.bbr.2007.01.027

Guggisberg, A. G., Mathis, J., Schnider, A., & Hess, C. W. (2010). Why do we yawn? *Neuroscience & Biobehavioral Reviews*, 34, 1267–1276. https://doi.org/10.1016/j.neubiorev.2010.03.008

Hartig, F. (2020). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa

Hayward, M.W., & Hayward, G. J. (2006). Activity patterns of reintroduced lion *Panthera leo* and spotted hyaena *Crocuta crocuta* in Addo Elephant National Park, South Africa. *African Journal of Ecology*, 45(2), 135–141. https://doi.org/10.1111/j.1365-2028.2006.00686.x

Hayward, M. W., & Hayward, G. J. (2009). The impact of tourists on lion *Panthera leo* behavior, stress and energetics. *Acta Theriologica*. 54, 219-224. https://doi.org/10.4098/j.at.0001-7051.074.2008

Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science,* 269, 1260–1262.

Heinsohn, R., Packer, C. & Pusey, A. (1996). Development of cooperative territoriality in juvenile lions. *Proceedings of the Royal Society B: Biological Sciences*, 263, 475–479.

Kis, A., Tóth, K., Kanizsár, O., & Topál, J., (2020). The effect of oxytocin on yawning by dogs (*Canis familiaris*) exposed to human yawns. Applied Animal Behavior Science, 104916. https://doi.org/10.1016/j.applanim.2019.104916.

Krestel, H., Bassetti, C. L., & Walusinski, O. (2018). Yawning-Its anatomy, chemistry, role, and pathological considerations. *Progress in Neurobiology*, 161, 61-78 https://doi.org/10.1016/j.pneurobio.2017.11.003

Kubota, N., Amemiya, S., Yanagita, S., Nishijima, T., & Kita, I. (2014). Emotional stress evoked by classical fear conditioning induces yawning behavior in rats. *Neuroscience Letters*, 566, 182–187. https://doi.org/ 10.1016/j.neulet.2014.02.064

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science*, 14 (4), 334-339. https://doi.org/10.1111/1467-9280.14481

Lakin, J.L., Jefferis, V.E., Cheng, C.M., & Chartrand, T.L. (2003). The chameleon effect as social glue: evidence for the evolutionary significance of nonconscious mimicry. *Journal of Nonverbal Behavior*, 27, 145–162. doi:10.1023/A:1025389814290.

Leyhausen, P. (1956). Über die unterschiedliche Entwicklung einiger Verhaltensweisen bei den Feliden. *Säugetierk Mitt* 4 (3), 123-125.

Leone, A., Ferrari, P., & Palagi, E. (2014). Different yawns, different functions? Testing social hypotheses on spontaneous yawning in *Theropithecus gelada*. *Scientific Reports*, 4, 4010. https://doi.org/10.1038/srep04010

Liang, A. C., Grace, J. K., Tompkins, E. M. & Anderson, D. J. (2015). Yawning, acute stressors, and arousal reduction in Nazca booby adults and nestlings. *Physiology and Behavior*, 140, 38–43. https://doi.org/10.1016/j.physbeh.2014.11.029

Low, A. B., & Rebelo, A. G. (1996). Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Lüdecke, D. (2020). The Comprehensive R Archive Network. sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.4. URL: https://CRAN.R-project.org/package=sjPlot>.

Lüdecke, D., Makowski, D., & Waggoner, P. (2020). Performance: Assessment of Regression Models Performance. R package version 0.4.4. https://CRAN.R-project.org/package=performance.

Madsen, E. A., Persson, T., Sayehli, S., Lenninger, S. & Sonesson, G. (2013). Chimpanzees show a developmental increase in susceptibility to contagious yawning: A test of the effect of ontogeny and emotional closeness on yawn contagion. *PLoS One*, 8, e76266, https://doi.org/10.1371/journal.pone.0076266.

Massen, J. J. M., & Gallup, A. C. (2017). Why contagious yawning does not (yet) equate to empathy. *Neuroscience and Biobehavioral Reviews*, 80, 573–585. https://doi.org/10.1016/j.neubiorev.2017.07.006

Massen, J. J., Vermunt, D. A., & Sterck, E. H. (2012). Male yawning is more contagious than female yawning among chimpanzees (*Pan troglodytes*). *PLoS One*, 7(7), e40697. https://doi.org/10.1371/journal.pone.0040697

McComb, K., Packer, C., Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behavior*, 47, 379–387

Miller, M. L., Gallup, A. C., Vogel, A. R., & Clark, A. B. (2010). Handling stress initially inhibits, but then potentiates yawning in budgerigars (*Melopsittacus undulatus*). *Animal Behavior*, 80, 615–619. https://doi.org/10.1016/j.anbehav.2010.05.018

Miller, M. L., Gallup, A. C., Vogel, A. R. & Clark, A. B. (2012). Auditory disturbances promote temporal clustering of yawning and stretching in small groups of budgerigars (*Melopsittacus undulatus*). *Journal of Comparative Psychology*, 126(3), 324–328. https://doi.org/10.1037/a0026520

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behavior*, 78(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Moyaho, A., & Valencia, J. (2002). Grooming and yawning trace adjustment to unfamiliar environments in laboratory Sprague-Dawley rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, 116, 263–269. https://doi.org/10.1037/0735-7036.116.3.263

Moyaho, A., Flores Urbina, A., Monjaraz Guzmán, E., & Walusinski, O. (2017). Yawning: a cue and a signal. *Heliyon* 3: e00437. https://doi.org/10.1016/j.heliyon.2017.e00437

Nakagawa, S., Johnson, P.C.D., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, 14:20170213.

Neilands, P., Claessens, S., Ren, I., Hassall, R., Bastos, A. P. M., & Taylor, A. H. (2020). Contagious yawning is not a signal of empathy: no evidence of familiarity, gender or prosociality biases in dogs. *Proceedings of the Royal Society B: Biological Sciences*, 287(1920):20192236. https://doi.org/10.1098/rspb.2019.2236

Norscia, I., Zanoli, A., Gamba, M., & Palagi, E. (2020). Auditory contagious yawning is highest between friends and family members: support to the emotional bias hypothesis. *Frontiers in Psychology*, 11:442. doi: 10.3389/fpsyg.2020.00442

Norscia, I., & Palagi, E. (2011). Yawn contagion and empathy in *Homo sapiens*. *PLoS One*, 6(12):e28472. https://doi.org/10.1371/journal.pone.0028472

Packer, C., & Pusey, A. (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behavioral Ecology*, 5, 363–374

Packer, C., & Pusey, A. (1997). Divided we fall: cooperation among lions. *Scientific American*, 276, 32–39.

Packer, C., & Ruttan, L. (1988). The evolution of cooperative hunting. *The American Natutalist*, 132, 159-198.

Packer, C., Pusey, A. E. & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science*. 293, 690–693. https://doi.org/10.1126/science.1062320

Palagi, E., Leone, A., Mancini, G. & Ferrari, P. F. (2009). Contagious yawning in gelada baboons as a possible expression of empathy. *Proceedings of the National Academy of Sciences USA*, 106, 19262–19267. https://doi.org/10.1073/pnas.0910891106

Palagi, E., Norscia, I., & Demuru, E. (2014). Yawn contagion in humans and bonobos: Emotional affinity matters more than species. *PeerJ*, 2, e519. https://doi.org/10.7717/peerj.519

Palagi, E., Guillén-Salazar, F., & Llamazares-Martín, C. (2019a). Spontaneous yawning and its potential functions in South American sea lions (*Otaria flavescens)*. *Scientific Reports,* 9, 17226. https://doi.org/10.1038/s41598-019-53613-4

Palagi, E., Norscia, I., & Cordoni, G. (2019b). Lowland gorillas (*Gorilla gorilla gorilla*) failed to respond to others' yawn: experimental and naturalistic evidence. *Journal of Comparative Psychology*, 133, 406–416. https://doi.org/10.1037/com0000175

Palagi, E., & Cordoni, G. (2020). Intraspecific motor and emotional alignment in dogs and wolves: the basic building blocks of dog–human affective connectedness. *Animals*, 10, 241. https://doi.org/10.3390/ani10020241

Palagi, E., Celeghin, A., Tamietto, M., Winkielman, P., & Norscia, I. (2020). The neuroethology of spontaneous mimicry and emotional contagion in human and non-human animals. *Neuroscience and Behavioral Reviews,* 111, 149-165. https://doi.org/10.1016/j.neubiorev.2020.01.020

Platek, S. M., Critton, S. R., Myers, T. E., & Gallup, G. G. (2003). Contagious yawning: The role of self-awareness and mental state attribution. *Cognitive Brain Research*, 17(2), 223–227. https://doi.org/10.1016/S0926-6410(03)00109-5

Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, 25, 1-72. https://doi.org/10.1017/s0140525x02000018

Prochazkova, E., & Kret, M. E. (2017). Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion. *Neuroscience and Biobehavioral Reviews*, 80, 99–114. https://doi.org/10.1016/j.neubiorev.2017.05.013

Provine, R. R. (1986). Yawning as a stereotyped action pattern and releasing stimulus. *Ethology*, 72, 109–122. https://doi.org/10.1111/j.1439-0310.1986.tb00611.x

Provine, R. R. (1989). Faces as releasers of contagious yawning: An approach to face detection using normal human subjects. *Bulletin of the Psychonomic Society* **27**, 211–214. https://doi.org/10.3758/BF03334587

Provine, R. R. (1997). Yawns, laughs, smiles, tickles, and talking: naturalistic and laboratory studies of facial action and social communication. In Russell JA, Fernández Dols JM (eds), *The psychology of facial expression*. Cambridge University, Cambridge

Provine, R. R. (2005). Yawning. *American Scientist*, 93, 532–539. https://doi.org/10.1511/2005.56.980

Provine, R. R., & Hamernik, H. B. (1986). Yawning: effects of stimulus interest. *Bulletin of the Psychonomic Society*, 24, 437–438.

Provine, R. R., Hamernik, H. B., & Curchack, B. B. (1987). Yawning: relation to sleeping and stretching in humans. *Ethology*, 76, 152–160. https://doi.org/10.1111/j.1439-0310.1987.tb00680.x

Romero, T., Konno, A., & Hasegawa, T. (2013). Familiarity bias and physiological responses in contagious yawning by dogs support link to empathy. *PLoS One,* 8(8): e71365. https://doi.org/10.1371/journal.pone.0071365

Romero, T., Ito, M., Saito, A., & Hasegawa, T. (2014). Social modulation of contagious yawning in wolves. *PLoS One,* 9, e105963. https://doi.org/10.1371/journal.pone.0105963

Rossman, Z. T., Hart, B. L., Greco, B. J., Young, D., Padfield, C., Weidner, L., Gates J., & Hart L. A. (2017). When yawning occurs in elephants. *Frontiers in Veterinary Science*, 4, 1-7. https://doi.org/10.3389/fvets.2017.00022

Rossman, Z. T., Padfield, C., Young, D., Hart, B. L. & Hart, L. A. (2020) Contagious yawning in African elephants (*Loxodonta africana*): responses to other elephants and familiar humans. *Frontiers in Veterinary Science*, 7:252. https://doi.org/10.3389/fvets.2020.00252

Rudnai, J.A. (2012). *The Social Life of the Lion: A Study of the Behaviour of Wild Lions (Panthera leo massaica [Newmann]In the Nairobi National Park*. Springer Science & Business Media, Kenya.

Sauer, E. G., & Sauer, E. M. (1967). Yawning and other maintenance activities in the South African ostrich. *The Auk*, 84, 571-587.

Schaller, G. (1972). *The Serengeti lion: a study in predator-prey relations*. Chicago: University of Chicago Press.

Schino, G., Maestripieri, D., Scucchi, S., & Turillazzi, P. G. (1990). Social tension in familiar and unfamiliar pairs of long-tailed macaques. *Behaviour,* 113, 264–272. https://doi.org/10.1163/156853990X00518

Slotow, R., & Hunter, L.T.B., (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: African lion in South Africa., In: Hayward, M.W., Somers, M.J., (Eds.), *The Reintroduction of Top-order Predators*. Blackwell Publishing, Oxford, UK

Spoelstra, K., van Grunsven, R. H. A., Ramakers, J. J. C., Ferguson, K. B., Raap, T., Donners, M., & Visser, M. E. (2017). Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20170075. https://doi.org/10.1098/rspb.2017.0075

Tan, J. Z., Ariely, D., & Hare, B. (2017). Bonobos respond prosocially toward members of other groups. *Scientific Reports*, 7, 14733. https://doi.org/10.1038/s41598-017-15320-w

Thierry, B., Bynum, E. L., Baker, S., Kinnaird, M. F., Matsumura, S., *et al*. (2000). The social repertoire of Sulawesi macaques. *Primate Research*, 16(3), 203–226. https://doi.org/10.2354/psj.16.203

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für tierpsychologie*, 20, 410–433.

Vick, S. J., & Paukner, A. (2010). Variation and context of yawns in captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 72, 262–269. https://doi.org/ 10.1002/ajp.20781

Walusinski, O. (2006). Yawning: Unsuspected avenue for a better understanding of arousal and interoception. *Medical Hypotheses*, 67, 6-14. https://doi.org/10.1016/j.mehy.2006.01.020

Walusinski, O. (2010). The mystery of yawning in physiology and disease. *Frontiers of Neurology and Neuroscience*, Basel, Karger, 28, 1-21. https://doi.org/10.1159/000307069

Walusinski, O. (2014). How yawning switches the default-mode network to the attentional network by activating the cerebrospinal fluid flow. *Clinical Anatomy*, 27, 201-209. https:// doi:10.1002/ca.22280

Walusinski, O., & Deputte, B. L. (2004). The phylogeny, ethology and nosology of yawning. *Revue Neurologique (Paris)*, *160*, 1011–1021. https://doi.org/10.1016/S0035-3787(04)71138-8

Yonezawa, T., Sato, K., Uchida, M., Matsuki, N., & Yamazaki, A. (2016). Presence of contagious yawning in sheep. *Animal Science Journal*, 88(1), 195–200. doi:10.1111/asj.12681

Zannella, A., Norscia, I., Stanyon, R., & Palagi, E. (2015). Testing yawning hypotheses in wild populations of two strepsirrhine species: *Propithecus verreauxi* and *Lemur catta*. *American Journal of Primatology*, 77, 1207–1215. https://doi.org/10.1002/ajp.22459

Zannella, A., Stanyon, R., & Palagi, E. (2017). Yawning and social styles: different functions in tolerant and despotic macaques (*Macaca tonkeana* and *Macaca fuscata*). *Journal of Comparative Psychology*, 131, 179–188. https://doi.org/10.1037/com0000062

Zilli, I., Giganti, F. & Salzarulo, P. (2007). Yawning in morning and evening types. *Physiology & Behavior*, 91, 218–222. https://doi.org/10.1016/j.physbeh.2007.02.015

Table 1 - Results of the best Generalized Linear Mixed Model (response variable ‘yawn contagion’)

Fixed Effects	**Coeff**	**SE**	**2.5% CI**	**97.5% CI**	χ^2	**df**	***P***
Intercept	-3.040	0.284	-5.555	5.554			
$Y_{seen}/Y_{notseen}$	3.027	0.283	-5.554	5.555	104.864	1	**0.0001**
Day/Night	-0.472	0.402	-1.126	0.316	1.402	1	0.236
Contexts					1.077	2	0.584
Context [feeding][b,c]	-0.060	0.567	-1.052	1.172			
Context [moving][b,c]	0.399	0.455	0.493	1.291			
Sex Combination					3.661	3	0.301
Sex Combination [male-female][b,d]	-1.294	0.759	-2.782	0.193			
Sex Combination [female-male][b,d]	-0.615	0.703	-1.992	0.763			
Sex Combination [female-female][b,d]	-0.999	0.655	-2.284	0.285			
Age Combination					1.270	3	0.736
Age Combination [adult-juvenile][b,e]	0.214	0.450	-0.676	1.104			
Age Combination [juvenile-adult][b,e]	-0.311	0.501	-1.292	0.670			
Age Combination [adult-adult][b,e]	0.181	0.510	-0.819	1.181			

Estimated parameters (Coeff), Standard Error (SE), 95% Confidence intervals (2.5% - 97.5% CI), and results of the likelihood ratio tests (LRT) of the best Generalized Linear Mixed Model (with a binomial error distribution) investigating the effect of the following variables on the presence/absence of yawning response (yawn contagion): yawn seen/yawn not-seen (Yseen/Ynot-seen), day/night, contexts (relaxing, feeding, moving), trigger and observer’s sex class combination (male-male; male-female; female-male; female-female), trigger and observer’s age class combination (juvenile/juvenile; adult/juvenile; juvenile/adult; adult/adult). Marginal R^2=0.985; delta marginal R^2= 0.957; Conditional R^2=0.985; delta conditional R^2= 0.957). N_{cases} = 453; N_{dyads}=65. Variance for the random factor DYAD = 1.12e-07 (±0.00034 SD)

[b] Estimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

[c] These predictors were dummy coded, with the “Context [relaxing]” being the reference category.

[d] These predictors were dummy coded, with the “Sex Combination [male-male]” being the reference category.

[e] These predictors were dummy coded, with the “Age Combination [juvenile-juvenile]” being the reference category.

Table 2 - Results of the best Generalized Linear Mixed Model (response variable ‘motor convergence’)

Fixed Effects	**Coeff**	**SE**	**2.5% CI**	**97.5% CI**	χ^2	**df**	***P***
Intercept	-0.992	1.589	-4.106	2.122			
Trigger’s changing status	-1.188	1.251	-3.639	1.263	1.029	1	0.310
YC condition					24.045	2	**0.0001**
YC condition [YES_yawn_NO_yawn contagion][b,c]	-2.282	1.129	-4.494	-0.070			
YC condition [YES_yawn contagion][b,c]	1.749	0.791	0.199	3.299			
Sex Combination					0.484	3	0.922
Sex Combination [male-female][b,d]	0.395	1.549	-2.641	3.430			
Sex Combination [female-male][b,d]	-0.261	1.534	-3.268	2.745			
Sex Combination [female-female][b,d]	0.135	1.513	-2.830	3.099			
Age Combination					7.774	3	0.051
Age Combination [adult-juvenile][b,e]	2.023	1.049	-0.034	4.080			
Age Combination [juvenile-adult][b,e]	-0.835	1.124	-3.039	1.368			
Age Combination [adult-adult][b,e]	0.801	0.952	-1.066	2.668			

Estimated parameters (Coeff), Standard Error (SE), 95% Confidence intervals (2.5% - 97.5% CI), and results of the likelihood ratio tests (LRT) of the best Generalized Linear Mixed Model (with a binomial error distribution) investigating the effect of the following variables on the motor convergence: trigger changing status (move→rest; rest→move), yawn contagion (YC) condition (NO_yawn; YES_yawn_NO_yawn contagion; YES_yawn contagion), trigger and observer’s sex class combination (male-male; male-female; female-male; female-female), trigger and the observer’s age class combination (juvenile/juvenile; adult/juvenile; juvenile/adult; adult/adult). Marginal R^2=0.505; delta marginal R^2= 0.0.463; Conditional R^2=0.600; delta conditional R^2= 0.550). N_{cases} = 85; N_{dyads}=36. Variance for the random factor dyads = 0.787 (±0.887 SD).

[b] Estimate parameters ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

[c] These predictors were dummy coded, with the “YC condition [NO_yawn]” being the reference category.

[d] These predictors were dummy coded, with the “Sex Combination [male-male]” being the reference category.

[e] These predictors were dummy coded, with the “Age Combination [juvenile-juvenile]” being the reference category.

Table A1. Monthly data on temperatures for the Limpopo Region (https://www.meteoblue.com/it/tempo/historyclimate/climatemodelled/limpopo-highlands_sudafrica_982749)

MONTH		
June	Mean daily MAXIMUM	18°C
	Mean daily MINIMUM	5°C
	Hottest day	22°C
	Coldest night	1°C
July	Mean daily MAXIMUM	18°C
	Mean daily MINIMUM	5°C
	Hottest day	23°C
	Coldest night	0°C
August	Mean daily MAXIMUM	21°C
	Mean daily MINIMUM	7°C
	Hottest day	27°C
	Coldest night	1°C
September	Mean daily MAXIMUM	25°C
	Mean daily MINIMUM	10°C
	Hottest day	31°C
	Coldest night	4°C
October	Mean daily MAXIMUM	26°C
	Mean daily MINIMUM	12°C
	Hottest day	32°C
	Coldest night	7°C

Figure legends

Figure 1 - The picture shows a motor sequence of yawning in an adult female of lions (the time interval between two consecutive shoots is 35 csec). The inspiration phase starts at 00:00:00.00 (hh:mm:ss.00) and ends at 00:00:02.80 (the maximum mouth opening). The exhalation phase starts at 00:00:03.15 and ends at 00:03.85.

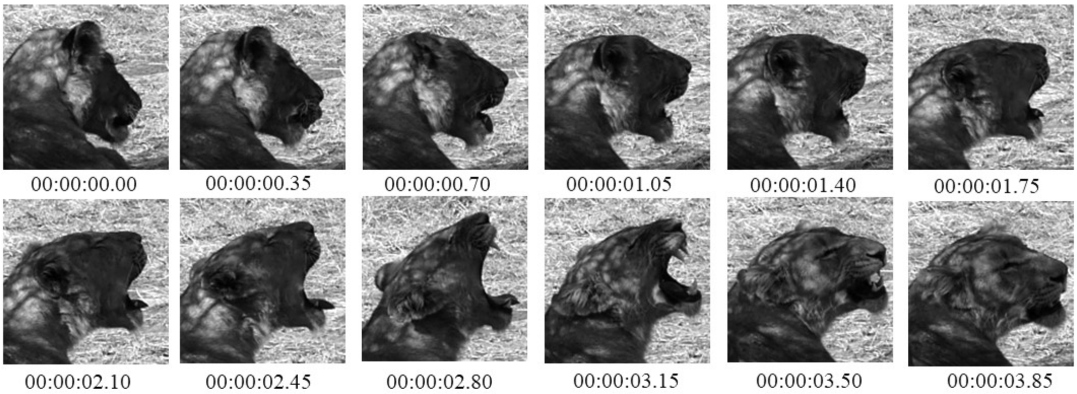

Figure 2 - In the picture are present three subjects (from left to right: a subadult female, a subadult male, a juvenile male). At 00:00:.00 (hh:mm:ss.00) the subadult female yawns (hereafter, the trigger), at 00:00:30.23 the subadult male responds to the trigger (here after, the observer). After the yawn contagion event, at 00:00:56.44 the trigger stands up and at 00:01:05.36 the observer stands up. At 00:01:12.13 the observer follows the trigger.

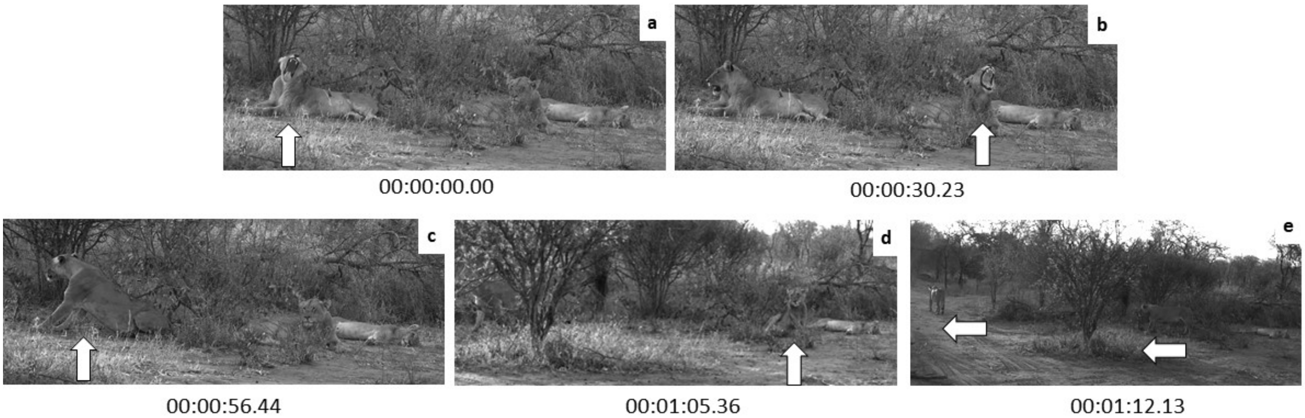

Figure 3 - Yawning hourly frequency in the three different contexts analysed. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the inter-quartile range, IQR. The open dots indicate outliers more than 1.5 IQR from the rest of the scores. The asterisk indicates an outlier more than 3.0 IQR from the rest of the scores.

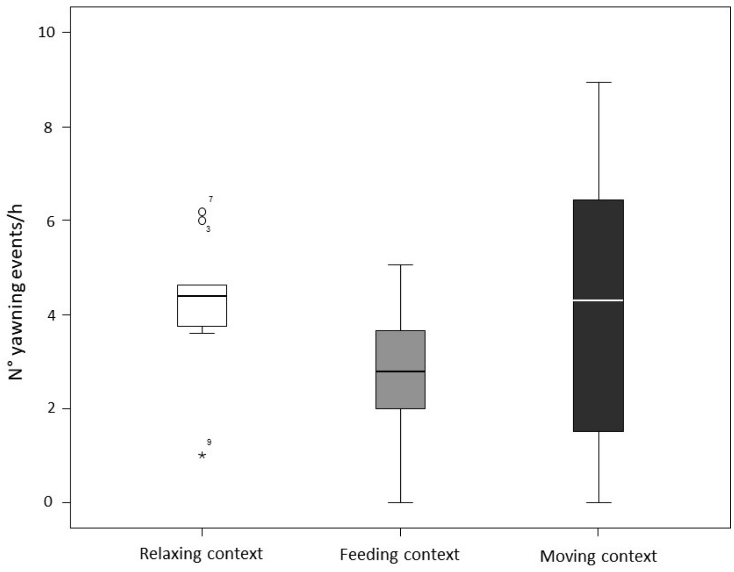

Figure 4 – Mean ±SE of the number of yawns performed in the NOT SEEN and SEEN condition

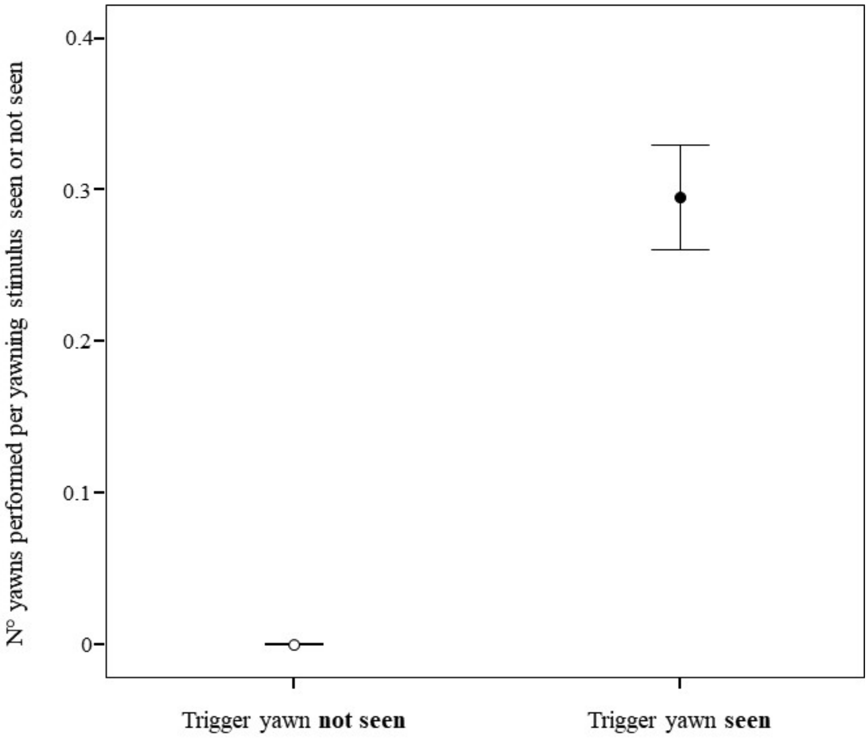

Figure 5 – Mean ±SE of the number of motor convergence events after a trigger status change in the three conditions (NO yawn; NO yawn contagion; YES yawn contagion).