One thousand yawns

James R. Anderson¹

Published online: 22 October 2020
© Japan Monkey Centre and Springer Japan KK, part of Springer Nature 2020

Yawning: a short introduction

I expect many people to yawn as they read this editorial. Not because they are bored (although some might be), but because even just reading about the topic I am going to discuss—yawning—can often cause us to yawn. Many people also yawn when they see somebody else yawning (so-called contagious yawning), sometimes even if that “somebody” belongs to another species. Many primatologists working in laboratories and the field have described yawning in their study groups, along with associated activities and contexts, but fewer have explicitly addressed possible functions of this behaviour or its underlying mechanisms and development. Here, I review some of the experimental and observational research that has been done on yawning and contagious yawning in primates—human and nonhuman—and to a lesser extent in other species. I also present a detailed case study of yawning in one primate individual: myself.

First, a few introductory comments about yawning, a ubiquitous behaviour among vertebrates, recorded in many aquatic, terrestrial and avian species (Baenninger 1987, 1997; Walusinski 2010a). Almost everyone can recognize the act of yawning: a typical human yawn starts with the mouth opening and a deep inhalation that can last several seconds; if the yawner is sitting, the neck may stretch and the head tilt back with the mouth opening widely until the end of the inhalation (the acme of the yawn); the head then returns to its normal position during a shorter exhalation and the mouth closes. Some people vocalize during the exhalation phase. The average yawn lasts around 6 s (Provine 1986).

Although most people might notice changes in inner ear pressure and their eyes watering when they yawn, most

are unaware of the myriad neurological, physiological, and neurochemical changes that accompany yawning, affecting the cardiovascular and pulmonary systems, the brain, and eye pressure, among others (Corey et al. 2012; Krestel et al. 2018). Many people might also be surprised at the overall lack of consensus among scientists about why yawning originally evolved and what its primary function(s) might be. Research on yawning often throws up unexpected findings, such as yawning being largely unaffected by elevated CO₂ or low levels of O₂ when concentrations of these gases were experimentally manipulated (Provine et al. 1987a, b). This finding, along with fetuses yawning despite being in a fluid-filled environment, rules out any simple relationship between oxygenation and yawning (Walusinski 2010b). One recent hypothesis that has been gathering empirical support focuses on the thermoregulatory effects of yawning; more specifically: yawning can reduce cortical brain temperature (Gallup and Gallup 2007; Gallup and Eldakar 2013; Massen et al. 2014; Eguibar et al. 2017). The literature on the ontogeny and phylogeny of yawning leaves open the possibility of different functions at different life stages or in different species. Some examples of this literature are described below.

From seeing yawns to counting yawns

One morning in the mid 1980s, as I walked toward the captive group of capuchin monkeys that I was then studying, I noticed a young adult male Tonkean macaque in a nearby enclosure. He was yawning frequently and looking toward a large outdoor park about 25 m away. I knew that this male should be in the park, in the group in which he was born and grew up, but earlier that morning he had escaped, yet again. A caretaker had lured him with fruit into the enclosure where he now was and where he would stay until it was decided what to do with him. The young male's rapid rate of yawning is what had especially caught my attention. So, in an example of cross-species gaze following (before it became a research topic), I turned around

✉ James R. Anderson
j.r.anderson@psy.bun.kyoto-u.ac.jp

¹ Department of Psychology, Graduate School of Letters, Kyoto University, Yoshida-honamichi, Sakyo-ku, Kyoto 606-8501, Japan

Fig. 1 An adult male *Macaca tonkeana* yawns Photo: Bernard Thierry

to see what he was looking at. There it was: the dominant adult male of the group, in a tree in the park, yawning back at the escapee. Those flashes of long, white canine teeth (Fig. 1) as the two males yawned back and forth at each other impressed me. They clearly also impress monkeys: the visual scanpaths of rhesus monkeys presented with pictures of adult males either yawning or open-mouth threatening revealed frequent first saccades to the canines in the yawning pictures; open-mouth threats elicited less specific saccades to the mouth area (Gothard et al. 2004).

The exchange of yawns that I saw that morning sparked my interest in yawning, and started me on a series of studies aimed at better understanding this behaviour in both nonhuman primates and humans. At that time my knowledge about yawning in other primates amounted to little more than this: adult males of some species, particularly Old World monkeys such as baboons and macaques, yawn in tense, agonistic or potentially agonistic situations (Bertrand 1969; Redican 1975; Hadidian 1980). The combination of contexts, exposed canines, and the distinction between “directed” and “undirected” yawns pointed toward yawns functioning as a threat signal [although clearly not all yawns are threat related (Deputte 1994)]. Altmann (1967) had suggested that, with experience, adolescent males got better at directing threat yawns toward their intended targets. I also started wondering about a possible role for learning in yawning, but more in relation to the high rates of yawning by adult males in socially tense situations, as in the two Tonkean males. If male monkeys increased their frequency of yawning to intimidate others, did that mean that they could voluntarily produce and inhibit yawns? [Humans can do this; see Baenninger and Greco (1991).]

Conditioning a communicatory act

Previous studies had used positive reinforcement to operantly condition vocalizations in primates (Pierce 1985), but no one had tried anything similar for yawning. So, we made a first attempt, with the help of two adult male pigtailed macaques. The study consisted of a series of 1-h baseline sessions with or without 20 pieces of banana being given to the monkey at irregular intervals, followed by conditioning sessions in which a piece of banana was given to the monkey as a reward after every yawn. In the first session one monkey received a reward immediately after every spontaneous yawn, while the other was trained through successive approximations—at first, he received a reward every time he opened his mouth, but by the end of the first session only full yawns were accepted as correct responses. Each male received five “reinforcement” sessions (every yawn rewarded), two “extinction” sessions (no rewards given), another reinforcement session, and finally three extinction sessions.

It proved surprisingly easy to increase these monkeys’ rates of yawning with positive reinforcement (Louboungou and Anderson 1987); by contrast, another natural behaviour, namely the “protruded lips” facial expression, proved extremely resistant to conditioning in the same study. In baseline sessions each male yawned fewer than 20 times, but in reinforcement sessions this rose to 60–70 and 80–150 times, and during extinction sessions their yawning rates fell back to baseline levels. The yawns they produced during reinforcement sessions appeared to be authentic, full yawns, including eyes closed and head tilted head back during the climactic phase (or acme). Furthermore, the males tried to make themselves yawn as humans sometimes do, by opening the mouth and inhaling deeply; sometimes this triggered a yawn, sometimes the attempt was abandoned. A follow-up study with two male Tonkean macaques (one was the escapee at the origin of the project) confirmed the conditionability of yawning. After establishing increased yawning rates with continuous reinforcement as before, we introduced a fixed ratio 3 schedule in which a reward was given only after three yawns were produced; these fixed ratio 3 schedule sessions produced peak yawn rates in both males (Anderson and Wunderlich 1988). Finally, the Tonkean macaque males also showed clear examples of spontaneous recovery: short-lived resurgences of yawning at the start of each new extinction session.

Together, these experiments indicated that adult male macaques have some degree of voluntary control of their yawning, which can be affected by reinforcement schedules similar to many other behaviors. These findings nicely complemented other descriptions in the literature that suggested purposeful expression and withholding of

yawning in some primates; for example, in wild baboons: “males with the best canines displayed them most often to other males” (Packer 1979, p. 42). Similar to another phylogenetically old behaviour that originally evolved for a different function, namely self-scratching (Diezinger and Anderson 1986), in some primate species the physiological reflex of yawning appears to have been co-opted into the communicatory repertoire, with a role for learning as well as physiological triggers. Because they have some degree of control over the production of yawns, adult males can conceivably use their yawning facultatively, depending on their social status, physical condition, and the context.

Contagious yawning in human children

At around the same time as we were trying to condition natural behaviors (facial expressions, scratching, yawning) in various primate species [see references above, Anderson et al. (1990) and Mitchell and Anderson (1993)], Robert Provine’s (1986, 1989) experimental-ethological approach to yawning in humans brought another perspective and fresh ideas. His use of videos of yawns to investigate releasing stimuli and mechanisms of contagious yawning stimulated new questions:

1. Why had contagious yawning never been reported in any nonhuman primates? (Does it exist in them or, as was widely held, is it a uniquely human phenomenon?)
2. Why not try to use video stimuli to investigate contagious yawning in nonhuman primates, and possibly other species?

As I scoured the human and animal literature in search of relevant information, another issue became apparent: the absence of any quantitative information or controlled studies about contagious yawning in human infants and young children. Based on observations of his own children, Piaget (1951) had suggested that infants in their second year of life might yawn if they saw somebody else yawn, but I could find no systematic studies or normative data on the development of contagious yawning. So, inspired by Provine (1986, 1989), to investigate the development of this behaviour we ran the following study. We showed 87 children aged between 2 and 11 years a video of an adult chatting and looking toward the camera, and stopping to yawn approximately every 10 s. As a control we used an identical video except that smiles replaced the yawns. An observer unobtrusively recorded any yawns by the children as they watched the videos and for 5 min after they returned to their playgroup or classroom.

What we found was an unexpected yawning gap in development (Anderson and Meno 2003). No child below

the age of 5 years yawned during the yawn video or afterwards, whereas children in each age group from 5 to 11 years yawned at least once, with 50% or more of children aged 9, 10, and 11 years doing so. In another phase of the study, children either listened to (preschoolers and young school-children) or read (older children) a story during which “Mr. Lazy” yawned 10 times, and another story in which “Mr. Happy” smiled 10 times. The yawning story elicited no yawns in preschoolers or 5 year olds, and in only a few 6 year olds, whereas most children aged 7 years or more yawned at least once while reading the story or shortly afterwards. In summary, this study showed the effectiveness of yawn videos for eliciting contagious yawning in older children, along with reading or thinking about yawning (Provine 1986, 1989; Baenninger and Greco 1991). It also established that children reached adult-like susceptibility to contagious yawning by 9–11 years of age. Most striking, however, was the discovery that children younger than 5 years appeared largely immune to the contagious effects of yawning, despite the occurrence of spontaneous yawns in toddlers, infants, newborns, and even fetuses (Giganti and Salzarulo 2010; Walusinski 2010b).

In a second study in young children (Millen and Anderson 2011), we focused on the identity of the yawning model. Our reasoning was that the unfamiliarity of the model in the videos used by Anderson and Meno (2003) might have somehow inhibited yawning in younger children, and that perhaps yawns by mothers—who are highly familiar to and socially bonded with their infants—would be more effective yawn-releasing stimuli. First, we asked a small group of mothers to keep a log of the occurrence, time and context every time they saw their infant yawn (the infants’ ages ranged from 6 to 34 months), for a 1-week period. Although we made no specific request, we expected the mothers to report any occurrences of contagious yawning. But none of them did; their data indicated infant yawning peaks in the morning and during daytime nap periods, especially after waking up and around mealtimes, but zero instances of contagious yawning, either from mother to infant or vice versa.

The second part of the study by Millen and Anderson (2011) consisted of a video presentation experiment. Each infant ($n = 22$; mean age, 23.7 months) sat on their mother’s lap and watched as still images of babies and animals yawning were projected onto a flat-screen color monitor. At random intervals during the presentation a silent, color video clip of the mother yawning appeared; this happened five times during each presentation. A control stimulus set consisting of baby smile and animal “smile” pictures interspersed with videos of the mother smiling was also presented. Each child was observed for 5 min before, during, and 5 min after each presentation. We found that no children yawned during the smile presentation, and only two did so afterwards. More importantly, although 77% of adults who

watched one of the yawn presentations yawned during or within 5 min of watching it, only three of the 23 children did so: two during the presentation (each to an animal picture), and one post-presentation. These data reinforced our earlier conclusion that, compared to older children and adults, infants and preschool children are markedly less susceptible to contagious yawning; they do not even catch yawns from their mothers.

Contagious yawning has recently become quite a popular research topic in developmental psychology. The literature features studies that compare susceptibility in typically developing children and children with autistic spectrum disorder (e.g., Senju et al. 2007; Mariscal et al. 2019), and attempts to facilitate contagious yawning in younger children, for example, by using live models instead of video (Helt et al. 2010) or by ensuring that children pay sufficient attention to the model's eyes (Senju et al. 2009; Hoogenhout et al. 2013; Usui et al. 2013). A recent study using preferential looking and functional near-infrared spectroscopy found that infants as young as 3 months—who do not show contagious yawning—clearly distinguished between yawn and non-yawn videos (Tsurumi et al. 2019). This suggests that, in human infants, the neural requisites for detecting yawns are already in place, ahead of the emergence of contagious yawning. Why this should be, and other unknowns about the development of this behaviour, may become less puzzling as research continues in what is currently a vibrant field.

Experimental studies of contagious yawning in chimpanzees and other primates

Returning to those earlier questions about why nobody had ever described contagious yawning in any nonhuman species and whether video stimuli could be used to investigate this phenomenon in primates, Kyoto University's Primate Research Institute was an ideal place to try to answer at least the second one. There, chimpanzees living in a large and complex, semi-naturalistic environment could be invited to temporarily leave their group and come into a familiar laboratory where they could be tested in a relaxed atmosphere (Matsuzawa 2020). For our study (Anderson et al. 2004), "being tested" simply meant being given the opportunity to watch video clips of chimpanzees. On offer were four videos showing several examples of either familiar or unfamiliar chimpanzees yawning, or moving their mouths but not yawning. Six adult females of the group participated (three with their 3-year-old infants), and they watched each video four times (each lasted 3 min) interspersed with 5-min distraction periods between each video. Our question was simple: would yawn videos elicit yawns in the chimpanzee observers? (Fig. 2).

Fig. 2 Jeje, an adult male chimpanzee (22 years old), yawning Photo: Tetsuro Matsuzawa

Counts of the adult chimpanzees' rates of yawning during the test sessions showed an average of 4.7 yawns during and after the control videos, compared to 10 during and after the yawn videos, with no effect of familiarity of the models. Although the difference was not significant at the group level, it was highly significant for two of the females. We also noted that, despite exposure to yawns by their mothers and the videos, none of the three infants yawned during any of the sessions. This study thus revealed that our nearest evolutionary neighbors are susceptible to contagious yawning, and that video is an effective tool for comparative studies of the phenomenon. Furthermore, young chimpanzees appeared to resemble young humans in their apparent immunity to the contagion effect. Linking our findings to the literature, we speculated that individual and species differences in contagious yawning might be related to other socio-cognitive and socio-emotional capacities, including self-recognition and empathy [see Anderson and Matsuzawa (2006) for additional analyses and discussion of this study].

Studies of contagious yawning in chimpanzees and other primates have flourished since Anderson et al. (2004). Several authors have reported induced yawning in chimpanzees and bonobos in response to videos of yawning, with manipulations of video content used to investigate possible sex differences and psychological factors, including affiliation and empathy (Amici et al. 2014; Campbell and de Waal 2011, 2014; Massen et al. 2012; Tan et al. 2017); chimpanzees were even shown to catch yawns from computer-animated chimpanzees (Campbell et al. 2009). Two studies have reported no contagious yawning in response to conspecific yawn videos in gorillas (Amici et al. 2014; Palagi et al. 2019), which is interesting in view of the more limited evidence for mirror self-recognition in gorillas compared to chimpanzees (Anderson and Gallup 2015). One study that

focused on young chimpanzees corroborated our original observation that 3-year-old chimpanzees did not yawn when exposed to yawns. Madsen et al. (2013) presented orphaned, sanctuary-housed chimpanzees with a live human model yawning; the chimpanzees were divided into infants (mean age 2.8 years) and juveniles (mean age 7.0 years). Only the older group showed increased yawning after seeing the human yawn, and they did not imitate simple opening and closing of the mouth. The authors concluded that the infant chimpanzees [like those in Anderson et al. (2004)] appeared immune to the contagiousness of yawning.

To my knowledge, there is only one study of video-influenced yawning in monkeys. Paukner and Anderson (2006) reported that a group of stump-tailed macaques yawned more frequently during and after presentation of a video of conspecific yawns than a video of non-yawn mouth movements (e.g., chewing). Unfortunately, however, six of the 10 yawns on video were by an adult male. As the monkeys also showed increased self-scratching in response to the yawn video, it seems likely that their anxiety levels were raised by the sight of an adult male yawning; yawning itself can also be elicited by nervousness or anxiety. Although some authors cite Paukner and Anderson (2006) as evidence of contagious yawning in stump-tailed macaques, we in fact cautioned against drawing such a conclusion; the question should be revisited.

One video study has been done with lemurs. After confirming that both ring-tailed and ruffed lemurs responded differently to videos showing a positive scene (a familiar caretaker presenting food) and a negative scene (a potential predator walking), Reddy et al. (2016) presented videos of conspecifics yawning and control videos to individual lemurs, and later to four groups of lemurs. Most of the lemurs did not yawn at all during the video sessions, regardless of whether the lemur in the video was familiar to them or a stranger. The authors discussed possible scenarios for the emergence of contagious yawning in primate evolution, but also pointed out that visual stimulation on its own (as in their videos) might not be salient enough to trigger any effect in the prosimians. By contrast, a reliable trigger for one captive 3-year-old male ring-tailed lemur was a human opening his mouth wide and slowly tilting his head back (as if yawning), whereas the same head movement by the human but without him opening his mouth did not elicit a response from the lemur (Roeder et al. 1994). The authors emphasized that the lemur never received rewards for yawning and in fact appeared to have little control over his elicited yawns; the human's simulated yawns acted like a supernormal stimulus. The same authors also described more yawning by female ring-tailed lemurs than males during presentations of an unfamiliar adult female to a small group, and related this observation to female dominance in these prosimians.

Contagious yawning in other species?

A report of no evidence of contagious yawning in red-footed tortoises (Wilkinson et al. 2011) led to the award of an Ig Nobel prize. Two types of yawn stimuli were presented to observer tortoises: from live demonstrators that had been trained to yawn, and from video clips of demonstrators yawning spontaneously; both types gave negative results. As well as showing that tortoises appear to lack mechanisms that underly contagious yawning in other species, Wilkinson et al. (2011) succeeded in using successive approximation and positive reinforcement to shape yawns or yawn-like responses in a reptile.

The first evidence for contagious yawning in an avian species came from observations of a captive flock of budgerigars (Miller et al. 2011). The overall frequency of yawning was low (1–3 yawns/bird per observation hour), but a yawn by one bird was likely to be followed within 40 s by another bird yawning, sometimes leading to “a cascade of yawns among the others” (Miller et al. 2011, p. 269). This phenomenon was confirmed experimentally by Gallup et al. (2015). Individual birds were removed from their group and placed in a cage adjacent to another cage containing a familiar or an unfamiliar bird, sometimes with an opaque visual barrier separating the two cages. Significantly more yawns occurred within 5 min of yawns by the adjacent bird when it was visible than in the control condition, with no effect of familiarity. In a second experiment, a video of a single conspecific yawning elicited yawning by observer budgerigars without also eliciting signs of anxiety [remember that this was a confounding factor in the study of stump-tailed macaques by Paukner and Anderson (2006) discussed above]. For Gallup et al. (2015), the large size of natural flocks of budgerigars might be a reason for the lack of any effect of familiarity on contagious yawning, in contrast to the ingroup effect reported in chimpanzees, for example (Campbell and de Waal 2011). Further observational and experimental studies on avian species should be worth waiting for.

A line of laboratory rats has been bred for high spontaneous yawning rates, and they have been shown to respond with contagious yawning especially to auditory cues of yawning associated with olfactory cues from strangers (Moyaho et al. 2015). Auditory cues are known to sometimes trigger contagious yawning in humans (Massen et al. 2015), but unlike in the rats studied by Moyaho et al. (2015), in primates (including humans, see below), social closeness is often reported to facilitate contagious yawning. This study in rodents highlights the likelihood of different underlying mechanisms and functions of yawning and contagious yawning across species.

In view of their multiple synchronized activities within herds and their facial recognition abilities, sheep were tested

for contagious yawning by Yonezawa et al. (2017). Twelve castrated sheep were individually separated from their herd and observed with a familiar herd-mate in an adjacent stall, with and without an opaque divider between them. Eight of 72 yawns recorded for the subjects when the adjacent sheep's face was visible occurred within 1 min of the latter yawning, compared to none of 42 yawns when the latter was shielded from the subjects' view. However, six sheep exposed to a video of a sheep yawning showed no contagious yawning. The authors suggested that research along these lines might be valuable for animal welfare practices. Recent studies of other mammals have presented data on social correlates of yawning, but with no mention of contagion [horses (Górecka-Bruzda et al. 2016); sea lions (Palagi et al. 2019)].

Several studies have been published on yawning and contagious yawning in dogs. Joly-Mascheroni et al. (2008) reported that 21 of 29 domestic dogs yawned when an unfamiliar human sitting in front of them repeatedly yawned (or more accurately, simulated yawns), but not when the human made non-yawn mouth movements. Subsequent studies affirming contagious yawning in dogs have examined the effectiveness of auditory cues only and familiarity [yawns sounds were effective, especially if the yawner was the dog's owner (Silva et al. 2012)], ontogeny [puppies younger than 7 months did not show the behaviour (Madsen and Pearson 2013)], and have used physiological measures to try to clarify links between contagious yawning, empathy, and arousal (Romero et al. 2013; Buttner and Strasser 2014). However, both Harr et al. (2009) and O'Hara and Reeve (2011) reported no convincing evidence of contagious yawning in dogs, and a recent study that set out to investigate whether oxytocin might affect contagious yawning in dogs also found no convincing evidence for the phenomenon (Kis et al. 2020). A reanalysis of results from some of the earlier dog studies led to the conclusion that contagious yawning is indeed present but that no link with empathy has been established (Nielands et al. 2020). This latter conclusion was supported by an experiment in which dogs were no more likely to catch yawns from a human who had just behaved prosocially towards them than from an antisocial human. Clearly, more research is required to resolve various issues surrounding contagious yawning in dogs. Finally, in another canid—wolves—an observational study of a captive pack revealed evidence of contagious yawning (i.e., yawns occurring within 3 min of a first wolf yawning), especially between close social partners (Romero et al. 2014). This finding was taken as further support of a relationship between contagious yawning and empathy. [See Massen and Gallup (2017) for a critical discussion of empathy-related accounts of contagious yawning.]

The final example of research with nonprimate mammals comes from two reports on elephants. Rossman et al. (2017)

described a small percentage of yawns in a group of nine semi-tame African elephants as possible contagious yawns. Five of the six instances were by elephants arousing from recumbent postures at nighttime and seeing another arousing elephant yawning. A more recent study on the same group (with some different members) yielded similar data, along with data suggesting that some elephants yawned contagiously after seeing simulated yawns by their human handler (Rossman et al. 2020). The authors called for more observations of yawning in free-ranging elephants.

Natural yawning and contagious yawning in primates

Back to primates, and the question of why contagious yawning has never been reported in many thousands of hours of observations on captive and free-ranging groups. Two possible reasons for this are that it does not exist, or that it does exist but has been consistently missed by observers. One observational study of a captive group of chimpanzees focused on different yawn types (identified through video microanalysis) but did not report any contagious yawning (Vick and Paukner 2010). The authors suggested that the phenomenon might depend on the kind of yawns involved. They also found no sex difference in overall frequency of yawning. Comparative studies of macaque species have revealed commonalities and divergences in aspects of yawning. For example, in captive Japanese macaques males yawned more than females from a young age, whereas in longtailed macaques this difference emerged only after puberty (Troisi et al. 1990). Furthermore, yawning frequency correlated with dominance in adult male longtailed but not Japanese macaques. The authors pointed out that different motivational states (e.g., aggression and anxiety or tension) could result in males of different social rank yawning at similar rates. No examples of possible contagious yawning were reported. As a “despotic” species, Japanese macaques in a zoo were compared with a zoo group of a “tolerant” species, namely Tonkean macaques (Zanella et al. 2017). Both species displayed two types of yawns—“covered teeth” and “uncovered gums”—with the latter being more frequent in males of both species. However, uncovered gums yawns were generally more frequent in Tonkean macaques, and were expressed especially in tense situations such as feeding competition. Again, contagious yawning did not feature in the results. In a rare example of a study of yawning in wild prosimians, Zannella et al. (2015) reported no sex differences in frequency of yawning in ring-tailed lemurs or Verreaux's sifakas. This finding supported the sexual dimorphism hypothesis, which states that a sex difference is less likely in low-dimorphic species. Links between yawning and behavioral transitions, and between yawning and

second yawner was potentially able to see or hear the first yawn; to ensure that no one else would become aware of the study, which was important because simply knowing that yawning is being observed can influence its occurrence, and often inhibits it (Baenninger and Greco 1991; Gallup et al. 2019). The effectiveness of this delay was confirmed: when I asked colleagues and family members shortly after the study ended, they replied that they sometimes noticed me writing in the notebook, but all were oblivious to any link with yawning. For all my yawns, and as many of other people's yawns as possible, I noted the time, place, and general activity and posture for everyone present. "Present" was defined as within normal speaking distance; if nobody was present, I was "alone." At night I kept the diary, pen and a small flashlight under my pillow. If I yawned while my partner was asleep, it was recorded as an "alone" yawn.

To the findings: over the 71 days of record keeping I yawned on average 14 times per day (median, 13; range, 1–31) (Fig. 4). Yawning clearly peaked in the morning (shortly after I awoke), with a 2-h lag at weekends (when later bedtimes were usually followed by waking up later the following morning) (Fig. 5). Another, less pronounced increase occurred at around 2200 hours, before I went to bed, and another small peak at around 0200 hours at weekends, which probably reflected tiredness due to being up late. During weekdays yawning also increased slightly between 1500 hours and 1600 hours, the time of a coffee break at work when colleagues gathered in a common room to sit and chat. Fifty-seven percent of my yawns occurred while I was sitting down, 23.2% while lying down (mostly in bed in the morning) and 19.8% while I was standing up and stationary; only 0.7% (3.5% of yawns while upright) happened while I was walking.

Almost half of (48%) of my yawns occurred when I was alone. I caught yawns from others infrequently: only 60 (6%) of all my yawns occurred within 2 min of seeing someone else yawn (Fig. 6); of 427 yawns by other people that might have caused me to yawn, 14% did so. Eighty of my 1,000 yawns (8%) were contagious for somebody else: 17% of

467 occasions when such an effect was possible. To look for an association between social closeness and contagious yawning, I categorized my relationships with other people as "close" (partner, immediate kin), "familiar" (colleague, friend), or "unfamiliar" (stranger). Table 1 shows that 90% of yawns that I caught were from someone with whom I had a socially close relationship (i.e., 54 of my 60 socially induced yawns). By contrast, I yawned only five times after seeing a familiar person yawn, and only once after a stranger yawned ($\chi^2 = 13.7$, $df = 2$, $p = 0.001$). Table 1 also shows how often other people caught my yawns. Again, when my yawns were contagious it was especially for people with whom I shared a strong relationship ($\chi^2 = 25.23$, $df = 2$, $p < 0.001$). The percentage of yawns by strangers that caused me to yawn (2%) was notably lower than the percentage of my yawns that caused strangers to yawn (25%).

How do my yawn data relate to the literature on yawning in humans? First, my average daily yawn frequency fell within the (rather wide) normal range of between five and 30. At 14 yawns/day it was close to the 13.5/day reported by students who logged their yawns between 0800 and 2400 hours each day for 1 week (Giganti and Zilli 2011),

Fig. 5 Mean frequency of the author's yawns by hour on weekdays and on weekends

Fig. 4 Frequency count of the author's yawns per day

Fig. 6 Percentages of 1000 of the author's yawns in different social contexts. *Contagious* The author's yawn was contagious for someone else, *Induced* the author caught someone else's yawn

Table 1 Incidence of caught and contagious yawns by the author when in the presence of different categories of people

	Category of the other individual		
	Close	Familiar	Unfamiliar
I did not catch another individual's yawn	245	75	47
I caught another individual's yawn	54	5	1
Total	299	80	48
Another individual did not catch my yawn	202	169	16
Another individual caught my yawn	63	11	6
Total	265	180	22

Close Partner, immediate kin; *Familiar* colleague, friend; *Unfamiliar* stranger

but higher than the 7–8 yawns/day reported by volunteers in another short-duration, self-monitoring study (Baenninger et al. 1996). However, for reasons already mentioned, in these studies some yawns might have gone unreported. Also, in Baenninger et al. (1996) three of the six volunteers

were over 45 years old, and research has shown that yawning decreases with ageing (Zilli et al. 2008). Second, my overall yawn profile suggests that I was a “morning type,” preferring to get up early and struggling to stay awake beyond normal bedtime; by contrast “evening types” prefer to go to bed later and report difficulty in wakening in the morning [mean daily yawn frequencies for these groups are 11 and 23, respectively (Zilli et al. 2007)]. Third, over 80% of my yawns occurred when I was sitting or lying down, as predicted by the association between yawning and boredom, sleepiness, and attempts to increase vigilance or arousal (Provine et al. 1987a, b; Dacquin et al. 2001). Most yawns reported by a group of students who kept records of their yawns for 1 week were also associated with sedentary activities such as driving, studying or reading, and watching television (Greco et al. 1993).

The fact that almost half of my 1000 yawns occurred in the absence of anyone else challenges ideas that a major function of yawning is communication. Although yawning can explicitly signal that one is tired, bored, nervous, or perhaps even sexually aroused (see Barbizet 1958; Guggisberg et al. 2010; Seuntjens 2010), the communicatory

aspect of yawning in humans appears likely to be secondary to more fundamental functions. Finally, although my contagious yawning data predate the emergence of the modern social closeness hypothesis, they accord with reports that contagious yawns are especially likely between people with strong emotional ties to each other, such as kin and close friends (Norscia and Palagi 2011; Palagi et al. 2014); this even appears to be the case for yawns that are heard but not seen (Norscia et al. 2020). Kapitány and Nielsen (2017) discuss methodological issues in the study of contagious yawning in humans.

Concluding comments

The list of hypotheses that have been proposed about the functions of yawning and contagious yawning is too long to be presented here (see, e.g., Smith 1999; Walusinski 2010a; Gallup 2011; Krestel et al. 2018). These behaviors continue to attract research attention in a wide range of disciplines including neurological, neuropharmacological, physiological and medical sciences, and in perceptual, social, developmental and comparative psychology. I hope that this editorial might stimulate further interest in the ethology and psychology of yawning. Although it may never become a major, stand-alone research issue, as I have tried to show, yawning can be relevant to several “bigger” topics, and useful data can often be obtained with little more than careful observation, patience, and if possible, a video camera. Researchable questions about yawning and its functions touch on development, learning, communication, arousal and stress, social affiliation, and more. When does yawning occur in a given species, and in what specific contexts? How do age and sex affect frequency and form of yawning? How does yawning vary with species’ sexual dimorphism and social organization? What other factors might contribute to individual variability in yawning? How general is the ability to learn to control aspects of yawning, which has been studied so far only in adult male macaques? We still have much to learn about this ubiquitous, quite banal, yet mysterious behaviour in our own and in other species.

References

- Altmann SA (1967) The structure of primate social communication. In: Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 325–362
- Amici F, Aureli F, Call J (2014) Response facilitation in the four great apes: is there a role for empathy? *Primates* 55:113–118
- Anderson JR (2010) Non-human primates: a comparative developmental perspective on yawning. In: Walusinski O (ed) The mystery of yawning in physiology and disease. Karger, Basel, pp 63–76
- Anderson JR, Gallup GG Jr (2015) Mirror self-recognition: a review and critique of attempts to promote and engineer self-recognition in primates. *Primates* 56:317–326
- Anderson JR, Matsuzawa T (2006) Yawning: an opening into empathy? In: Matsuzawa T, Tomonaga M, Tanaka M (eds) Cognitive development in chimpanzees. Springer, Tokyo, pp 233–245
- Anderson JR, Meno P (2003) Psychological influences on yawning in children. *Curr Psychol Lett* 11: 2. <https://cpl.revues.org/document390.html>
- Anderson JR, Wunderlich D (1988) Food-reinforced yawning in *Macaca tonkeana*. *Am J Primatol* 16:165–169
- Anderson JR, Fritsch C, Favre B (1990) Operant conditioning of scratching in lemurs. *Primates* 31:611–615
- Anderson JR, Myowa-Yamakoshi M, Matsuzawa T (2004) Contagious yawning in chimpanzees. *Proc R Soc B* 271:S468–S470
- Baenninger R (1987) Some comparative aspects of yawning in *Betta splendens*, *Homo sapiens*, *Panthera leo*, and *Papio sphinx*. *J Comp Psychol* 101:349–354
- Baenninger R (1997) On yawning and its functions. *Psychon Bull Rev* 4:198–207
- Baenninger R, Greco M (1991) Some antecedents and consequences of yawning. *Psychol Rec* 41:453–460
- Baenninger R, Binkley S, Baenninger M (1996) Field observations of yawning and activity in humans. *Physiol Behav* 59:421–425
- Barbizet J (1958) Yawning. *J Neurol Neurosurg Psychiatry* 21:203–209
- Bertrand M (1969) The behavioral repertoire of the stump-tail macaque. Karger, Basel
- Buttner AP, Strasser R (2014) Contagious yawning, social cognition, and arousal: an investigation of the processes underlying shelter dogs’ responses to human yawns. *Anim Cogn* 17:95–104
- Campbell MW, Cox CR (2019) Observational data reveal evidence and parameters of contagious yawning in the behavioral repertoire of captive-reared chimpanzees (*Pan troglodytes*). *Sci Rep* 9:13271. <https://doi.org/10.1038/s41598-019-49698-6>
- Campbell MW, de Waal FBM (2011) Ingroup-outgroup bias in contagious yawning by chimpanzees supports links to empathy. *PLOS ONE* 6(4):e18213. <https://doi.org/10.1371/journal.pone.0018283>
- Campbell MN, de Waal FBM (2014) Chimpanzees empathize with group mates and humans, but not with baboon or unfamiliar chimpanzees. *Proc R Soc B* 281:20140013. <https://doi.org/10.1098/rspb.2014.0013>
- Campbell MW, Carter JD, Proctor D, Eisenberg ML, de Waal FBM (2009) Computer animations stimulate contagious yawning in chimpanzees. *Proc R Soc B* 276:4255–4259. <https://doi.org/10.1098/rspb.2009.1087>
- Corey TP, Shoup-Knox ML, Gordis EB, Gallup GG Jr (2012) Changes in physiology before, during, and after yawning. *Front Evol Neurosci* 3:7. <https://doi.org/10.3389/fnevo.2011.00007>
- Dacquin G, Micallef J, Blin O (2001) Yawning. *Sleep Med Rev* 5:299–312
- Deputte B (1994) Ethological study of yawning in primates. 1. Quantitative analysis and study of causation in two species of Old World monkeys (*Cercocebus albigena* and *Macaca fascicularis*). *Ethology* 98:221–245
- Diezinger F, Anderson JR (1986) Starting from scratch: a first look at a “displacement activity” in group-living rhesus monkeys. *Am J Primatol* 11:117–124
- Eguibar JR, Uribe CA, Cortes C, Bautista A, Gallup AC (2017) Yawning reduces facial temperature in the high-yawning sub-line of Sprague-Dawley rats. *BMC Neurosci* 18(1):3. <https://doi.org/10.1186/s12868-016-0330-3>
- Gallup AC (2011) Why do we yawn? Primitive versus defined features. *Neurosci Biobehav Rev* 35:765–769

- Gallup AC, Eldakar OT (2013) The thermoregulatory theory of yawning: what we know from over 5 years of research. *Front Neurosci* 6:188. <https://doi.org/10.3389/fnins.2012.00188>
- Gallup AC, Gallup GG Jr (2007) Yawning as a brain cooling mechanism: nasal breathing and forehead cooling diminish the incidence of contagious yawning. *Evol Psychol* 5:92–101
- Gallup AC, Swartwood L, Militello J, Sackett S (2015) Experimental evidence of contagious yawning in budgerigars (*Melopsittacus undulatus*). *Anim Cogn* 18:1051–1058
- Gallup AC, Church AM, Miller H, Risko EF, Kingstone A (2019) Social presence diminishes contagious yawning in the laboratory. *Sci Rep* 1:25405. <https://doi.org/10.1038/s41598-018-36570-2>
- Giganti F, Salzarulo P (2010) Yawning throughout life. In: Walusinski O (ed) The mystery of yawning in physiology and disease. Karger, Basel, pp 26–31
- Giganti F, Zilli I (2011) The daily time course of contagious and spontaneous yawning among humans. *J Ethol* 29:215–219
- Górecka-Bruzda A, Fureix C, Ouvrard A, Bourjade M, Hausberger M (2016) Investigating determinants of yawning in the domestic (*Equus caballus*) and Przewalski (*Equus ferus przewalskii*) horses. *Sci Nat*. <https://doi.org/10.1007/s00114-016-1395-7>
- Gothard KM, Erickson CA, Amaral DG (2004) How do rhesus monkeys (*Macaca mulatta*) scan faces in a visual paired comparison task? *Anim Cogn* 7:25–36
- Greco M, Baenninger R, Govern J (1993) On the context of yawning: when, where, and why? *Psycho Rec* 43:175–183
- Guggisberg AG, Mathis J, Schnider A, Hess CW (2010) Why do we yawn? *Neurosci Biobehav Rev* 34:1267–1276
- Hadidian J (1980) Yawning in an Old World monkey, *Macaca nigra* (Primates: Cercopithecidae). *Behaviour* 75:133–147
- Harr AL, Gilbert VR, Phillips KA (2009) Do dogs (*Canis familiaris*) show contagious yawning? *Anim Cogn* 12:833–837
- Helt MS, Eigsti I-M, Snyder PJ, Fein DA (2010) Contagious yawning in autistic and typical development. *Child Dev* 81:1620–1631
- Hoogenhout M, van der Straaten K, Pileggi MA, Malcolm-Smith S (2013) Young children display contagious yawning when looking at the eyes. *J Child Adolesc Behav* 1:101. <https://doi.org/10.4172/jcalb.1000101>
- Joly-Mascheroni RM, Senju A, Shepherd AJ (2008) Dogs catch human yawns. *Biol Lett* 4:5. <https://doi.org/10.1098/rsbl.2008.0333>
- Kapitány R, Nielsen M (2017) Are yawns really contagious? A critique and quantification of yawn contagion. *Adapt Hum Behav Physiol* 3:134–155
- Kis A, Tóth K, Kanizsár O, Topál J (2020) The effect of oxytocin on yawning by dogs (*Canis familiaris*) exposed to human yawns. *Appl Anim Behav Sci* 223:104916. <https://doi.org/10.1016/j.applanim.2019.104916>
- Krestel H, Bassetti CL, Walusinski O (2018) Yawning—its anatomy, chemistry, role, and pathological considerations. *Prog Neurobiol* 161:61–78
- Leone A, Ferrari PF, Palagi E (2014) Different yawns, different functions? Testing social hypotheses on spontaneous yawning in *Theropithecus gelada*. *Sci Rep* 4:4010. <https://doi.org/10.1038/srep04010>
- Louboungou M, Anderson JR (1987) Yawning, scratching, and protruded lips: differential conditionability of natural acts in pigtail monkeys (*Macaca nemestrina*). *Primates* 28:367–375
- Madsen EA, Persson T (2013) Contagious yawning in domestic dog puppies (*Canis lupus familiaris*): the effect of ontogeny and emotional closeness on low-level imitation in dogs. *Anim Cogn* 6:233–240
- Madsen EA, 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(19):e76266. <https://doi.org/10.1371/journal.pone.0076266>
- Mariscal MG, Oztan O, Rose SM, Libove RA, Jackson LP, Sumiyoshi RD, Trujillo TH, Carson DS, Phillips JM, Garner JP, Hardan AY, Parker KJ (2019) Blood oxytocin concentration positively predicts contagious yawning behavior in children with autism spectrum disorder. *Autism Res* 12:1156–1161
- Massen JJM, Gallup AC (2017) Why contagious yawning does not (yet) equate to empathy. *Neurosci Biobehav Rev* 80:573–585
- Massen JJM, Vermunt DA, Sterck EHM (2012) Male yawning is more contagious than female yawning among chimpanzees. *PLOS ONE* 7(7):e40697. <https://doi.org/10.1371/journal.pone.0040697>
- Massen JJM, Duvsh K, Eldakar OT, Gallup AC (2014) A thermal window for yawning in humans: yawning as a brain cooling mechanism. *Physiol Behav* 130:145–148
- Massen JJM, Gallup AC CAM (2015) Auditory contagious yawning in humans: an investigation into affiliation and status effects. *Front Psychol* 6:1735. <https://doi.org/10.3389/fpsyg.2015.01735>
- Matsuzawa T (2020) WISH cages: constructing multiple habitats for captive chimpanzees. *Primates* 61:139–148
- Millen A, Anderson JR (2011) Neither infants nor toddlers catch yawns from their mothers. *Biol Lett* 7:440–442
- Miller ML, Gallup AC, Vogel AR, Vicario SM, Clark AB (2011) Evidence for contagious yawning in budgerigars (*Melopsittacus undulatus*): an observational study of yawning and stretching. *Behav Process* 89:264–270
- Mitchell RW, Anderson JR (1993) Discrimination learning of scratching, but failure to obtain imitation and self-recognition in a long-tailed macaque. *Primates* 34:301–309
- Moyaho A, Rivas-Zamudio X, Ugarte A, Eguibar JR, Valencia J (2015) Smell facilitates auditory contagious yawning in stranger rats. *Anim Cogn* 18:279–290
- Nielands P, Claessens S, Ren I, Hassall R, Bastos APM, Taylor AH (2020) Contagious yawning is not a signal of empathy: no evidence of familiarity, gender or prosociality biases in dogs. *Proc R Soc B* 287:20192236. <https://doi.org/10.1098/rspb.2019.2236>
- Norscia I, Palagi E (2011) Yawn contagion and empathy in *Homo sapiens*. *PLOS ONE* 6(12):28472. <https://doi.org/10.1371/journal.pone.0028472>
- Norscia I, Zanolli A, Gamba M, Palagi E (2020) Auditory contagious yawning is highest between friends and family members: support to the emotional bias hypothesis. *Front Psychol* 11:442. <https://doi.org/10.3389/fpsyg.2020.00042>
- O'Hara SJ, Reeve AV (2011) A test of the yawning contagion and emotional connectedness hypothesis in dogs, *Canis familiaris*. *Anim Behav* 81:335–340
- Packer C (1979) Male dominance and reproductive activity in *Papio anubis*. *Anim Behav* 27:37–45
- Palagi E, Guillén-Salazar L-M (2019) Spontaneous yawning and its potential functions in South American sea lions (*Otaria flavescens*). *Sci Rep* 9:17226. <https://doi.org/10.1038/s42598-019-53613-4>
- Palagi E, Leone A, Mancini G, Ferrari PF (2009) Contagious yawning in gelada baboons as a possible expression of empathy. *Proc Natl Acad Sci USA* 106:19262–19267
- 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, Norscia I, Cordoni G (2019) Lowland gorillas (*Gorilla gorilla gorilla*) failed to respond to others' yawn: experimental and naturalistic evidence. *J Comp Psychol* 133:3
- Paukner A, Anderson JR (2006) Video-induced yawning in stump-tail macaques (*Macaca arctoides*). *Biol Lett* 2:36–38
- Piaget J (1951) Play, dreams and imitation in childhood. Norton, New York

- Pierce JD (1985) A review of attempts to operantly condition alloprimate vocalization. *Primates* 26:202–213
- Povine RR (1986) Yawning as a stereotyped action pattern and releasing stimulus. *Ethology* 72:448–455
- Provine RR (1989) Faces as releasers of contagious yawning: an approach to face detection using normal human subjects. *Bull Psychon Soc* 27:211–214
- Provine RR, Hamernik HB, Curchak BC (1987) Yawning: relation to sleeping and stretching in humans. *Ethology* 76:152–160
- Provine RR, Tate BC, Geldmacher LL (1987) Yawning: no effect of 3–5% CO₂, 100% O₂, and exercise. *Behav Neural Biol* 48:382–393
- Reddy RB, Krupeyne C, MacLean E, Hare B (2016) No evidence for contagious yawning in lemurs. *Anim Cogn* 19:5. <https://doi.org/10.1007/s10071-016-0986-1>
- Redican WK (1975) Facial expressions in nonhuman primates. In: Rosenblum LA (ed) *Primate behavior: developments in field and laboratory research*, vol 4. Academic Press, New York, pp 103–194
- Roeder JJ, Fornasieri I, Anderson JR (1994) Yawning in ringtailed lemurs. In: Roeder JJ, Thierry B, Anderson JR, Herrenschildt N (eds) *Current primatology*, vol II. Social development, learning and behaviour. Université Louis Pasteur, Strasbourg, pp 77–80
- 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(8):e105963. <https://doi.org/10.1371/journal.pone.0105963>
- Rossman ZT, Hart BL, Greco BJ, Young D, Padfield C, Weidner L, Gates J, Hart LA (2017) When yawning occurs in elephants. *Front Vet Sci* 4:22. <https://doi.org/10.3389/fvets.2017.00022>
- Rossman ZT, Padfield C, Young D, Hart BL, Hart LA (2020) Contagious yawning in African elephants (*Loxodonta africana*): responses to other elephants and familiar humans. *Front Vet Sci* 7:252. <https://doi.org/10.3389/fvets.2020.00252>
- Senju A, Maeda M, Kikuchi Y, Hasegawa T, Tojo Y, Osanai H (2007) Absence of contagious yawning in children with autism spectrum disorder. *Biol Lett* 3:706–708
- Senju A, Kikuchi Y, Akechi H, Hasegawa T, Tojo Y, Osanai H (2009) Brief report: does eye contact induce contagious yawning in children with autism spectrum disorder? *J Autism Dev Disord* 39:1598–1602
- Seuntjens W (2010) The hidden sexuality of the yawn and the future of chasmology. In: Walusinski O (ed) *The mystery of yawning in physiology and disease*. Karger, Basel, pp 55–62
- Silva K, Bessa J, de Sousa L (2012) Auditory contagious yawning in domestic dogs (*Canis familiaris*): first evidence for social modulation. *Anim Cogn* 15:721–724
- Smith EO (1999) Yawning: an evolutionary perspective. *Hum Evol* 14:191–198
- Tan J, Ariely D, Hare B (2017) Bonobos respond prosocially toward members of other groups. *Sci Rep* 7:14733. <https://doi.org/10.1038/s41598-017-15320-w>
- Troisi A, Aureli F, Schino G, Rinaldi F, de Angelis N (1990) The influence of age, sex and rank on yawning behavior in two species of macaques (*Macaca fascicularis* and *M. fuscata*). *Ethology* 86:303–310
- Tsurumi S, Kanazawa S, Yamaguchi MK (2019) Infant brain activity in response to yawning using functional near-infrared spectroscopy. *Sci Rep* 9:10631. <https://doi.org/10.1038/s41598-019-47129-0>
- Usui S, Senju A, Kikuchi Y, Akechi H, Tojo Y, Osanai H, Hasegawa T (2013) Presence of contagious yawning in children with autism spectrum disorder. *Autism Res Treat*. <https://doi.org/10.1155/2013/971686>
- Vick S-J, Paukner A (2010) Variation and context of yawns in captive chimpanzees (*Pan troglodytes*). *Am J Primatol* 72:262–269
- Walusinski O (2010a) *The mystery of yawning in physiology and disease*. Karger, Basel
- Walusinski O (2010b) Fetal yawning. In: Walusinski O (ed) *The mystery of yawning in physiology and disease*. Karger, Basel, pp 33–41
- Wilkinson A, Sebanz N, Mandl I, Huber L (2011) No evidence of contagious yawning in the red-footed tortoise *Geochelone carbonaria*. *Curr Zool* 57:477–484
- Yonezawa T, Sato K, Uchida M, Matsuki N, Yamazaki A (2017) Contagious yawning in sheep. *Anim Sci J* 88:195–200
- Zannella A, Norsia I, Stanyon R, Palagi E (2015) Testing yawning hypotheses in wild populations of two strepsirrhine species: *Propithecus verreauxi* and *Lemur catta*. *Am J Primatol* 77:1207–1215
- Zannella A, Stanyon R, Palagi E (2017) Yawning and social styles: different functions in tolerant and despotic macaques (*Macaca tonkeana* and *Macaca fuscata*). *J Comp Psychol* 131:179–188
- Zilli I, Giganti Uga F (2008) Yawning and subjective sleepiness in the elderly. *J Sleep Res* 17:3030–3308
- Zilli I, Giganti F, Salzarulo P (2007) Yawning in morning and evening types. *Physiol Behav* 91:218–227

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.