

No Experimental Evidence For Yawn Contagion In Galahs (*Eolophus Roseicapilla*)

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Abstract – Yawning is a ubiquitous behavior among vertebrates, yet evidence for yawn contagion is sparce. Nevertheless, over the past decade yawn contagion has been documented in an increasing number of species. Still, quite some studies fail to show yawn contagion in other species. The lack of contagious yawning in some species, but not in others, raises questions about the evolutionary origin and adaptive function of this response. Yet, the restricted research focus on mostly social mammals limits its explanatory value on an evolutionary scale. Yawn contagion is relatively understudied outside mammalian species, and so far, yawn contagion has only been documented in one bird species: budgerigars (Melopsittacus undulatus). To allow a more comparative approach, also among birds, we studied the presence of contagious yawning in another, highly social, bird species, the galah (Eolophus roseicapilla). We presented video stimuli composed of yawn footage and non-yawn control footage to fifteen captive galahs in two different studies differing in the size and number of repetitions of the on-screen stimuli, while also taking into account approximations of visual attention and the affiliation strength with the on-screen individual. We found no evidence for yawn contagion in galahs in either study, which contrasts with findings in budgerigars. Budgerigars and galahs do, however, have a highly similar socio-ecology and the methods used to test for yawn contagion were highly similar too. Although more work is needed, these combined results therefore underline earlier findings of convergent evolution of contagious yawning in mammals and birds, yet suggest that it happened in very restrictive lineages only. The specific selection pressures that have contributed to the evolution of this trait in this select group of animals remain obscure.

Keywords - Contagious yawning, Parrots, Avian cognition, Behavioral experiments, Synchronization

Yawning is defined as a wide opening of the jaw accompanied by an inhalation, followed by contraction of muscles, and slower closing of the jaw while exhaling (Barbizet, 1958). Yawning is ubiquitous across vertebrates (fish: Baenninger, 1987; reptiles: Luttenberger, 1975; Wilkinson et al., 2011; birds and mammals: Massen et al., 2021; Provine, 2005) and already occurs in the embryonic stage in humans (de Vries et al., 1982). There have been plenty of propositions about the function of yawning, but the hypothesis that seems to have received the most empirical support is that yawning serves to cool the brain, thereby potentially increasing vigilance (Gallup et al., 2009; Gallup & Gallup, 2007; Gallup &

Meyers, 2021; Gallup & Wozny, 2025; Kotake et al., 2024; Maraffa et al., 2017; Thompson, 2017; Zenker & Kubik, 1996).

The act of yawning after witnessing someone else yawn is referred to as contagious yawning, and this can be triggered by seeing or hearing someone yawn (Massen et al., 2015; Pedruzzi et al., 2024), or even just by reading or thinking about yawning (Provine, 2005). On an ultimate level, there are two nonmutually exclusive hypotheses that explain the function of contagious yawning. One is the behavioral synchronization hypothesis, which states that a function of yawn contagion may be the synchronization of activities between group members (reviewed in Gallup, 2022). Evidence for this hypothesis was found in wild lions (*Panthera leo*), who showed more activity synchrony after contagious yawns were observed (Casetta et al., 2021). The other explanation is the group vigilance hypothesis, which is derived from the brain-cooling hypothesis (Gallup & Gallup, 2007). After a yawn is copied by other group members, vigilance may spread in a social group, and so far three experimental studies showed an increase in vigilance in humans after witnessing another individual yawn (Gallup & Meyers, 2021; Gallup & Wozny, 2024; 2025). Whereas spontaneous yawning is widespread, contagious yawning seems to be mostly restricted to highly social mammals (for a review see Massen & Gallup, 2017).

From a phylogenetic perspective, the presence of contagious yawning across a wide range of highly social mammalian species (Massen & Gallup, 2017) may suggest a common ancestor that was capable of contagious yawning. Especially in the hominid lineage, contagious yawning seems widespread (Provine, 1986; Anderson et al., 2004; Campbell et al., 2009; Demuru & Palagi, 2012; Massen et al., 2012; van Berlo et al., 2020). However, common ancestry is contested by the lack of evidence for contagious yawning in gorillas (Gorilla gorilla gorilla, Amici et al., 2014; Palagi et al., 2019). This can be explained by either a loss of the trait in an ancestor of gorillas, or the emergence of contagious yawning through convergent evolution. Furthermore, earlier records on contagious yawning in apes (Anderson et al., 2004) and the lack thereof in other primates; e.g., mandrills (Mandrillus sphinx: Baenninger, 1987), grey-cheeked mangabeys (Lophocebus albigena) and long-tailed macaques (Macaca fascicularis) (Deputte, 1978), suggested a clear dichotomy in contagious yawning between hominids and other primates, and indeed, also more recent studies failed to show yawn contagion in non-ape primates; e.g., black-and-white ruffed lemurs (Varecia variegata, Reddy et al., 2016), ring-tailed lemurs, (Lemur catta, Reddy et al., 2016), and common marmosets (Callithrix jacchus, Massen et al., 2016). Yet, others have since shown evidence for yawn contagion in several other, sometimes closely related, non-ape primates; e.g., stump-tailed macaques (Macaca arctoides: Paukner & Anderson, 2006), geladas (Theropithecus gelada: Palagi et al., 2009), redcapped mangabeys (Cercocebus torquatus: Pedruzzi et al., 2022), indri (Indri indri: Valente et al., 2022), spider monkeys (Ateles geoffroyi: Valdivieso-Cortadella et al., 2023), and drills (Mandrillus leucophaeus, Galotti et al., 2024a). Similarly, across non-primate mammals results are mixed with some reports failing to show yawn contagion; e.g. lions (Pantera leo: Baenninger, 1987), and horses (Equus caballus, Malavasi, 2014), whereas others find some evidence for yawn contagion in for example dogs (Canis familiaris; e.g., Joly-Mascheroni et al., 2008; Neilands et al., 2020), wolves (Canis lupus: Romero et al., 2014) highyawning Sprague-Dawley rats (Rattus norvegicus, Moyaho et al., 2015), sheep (Yonezawa et al., 2016), pigs (Sus scrofa: Norscia et al., 2021), lions (Casetta et al., 2021), spotted hyenas (Crocuta crocuta: Casetta et al., 2022), and horses (Galotti et al., 2024b) again making conclusions about evolutionary homology or analogy difficult.

Although the debate on the evolution of contagious yawning in mammals is thus not yet settled, an even larger knowledge gap exists in non-mammalian research. Thus far, contagious yawning has only been thoroughly studied in three non-mammalian species. In the red-footed tortoise (*Chelonoidis carbonarius*), no evidence for yawn contagion was found (Wilkinson et al., 2011). Likewise, observational research in juvenile ravens (*Corvus corax*) did not find evidence for contagious yawning (Gallup et al., 2022). However, robust evidence for contagious yawning was found in budgerigars (*Melopsittacus undulatus*; Gallup et al., 2015; unpublished data; Miller et al., 2012); Miller and colleagues (2012) using an observational study, whereas Gallup et al. (2015) found experimental evidence of yawn contagion using both live and video triggers, the latter of which was later replicated (Gallup et al., unpublished data). To date, the budgerigar remains the only non-mammalian species with evidence for yawn contagion. However,

there is little to infer from the results in two phylogenetically distant bird species, so a knowledge gap on evolution of yawn contagion in birds remains.

To shed more light on the function and evolutionary history of yawn contagion in birds, we studied contagious yawning in galahs (*Eolophus roseicapilla*), a cockatoo species. Like other species that show contagious yawning, galahs are highly social. Wild galahs live in large flocks, sometimes exceeding a thousand birds (Rowley, 1990), which suggests the need for some degree of behavioral (state) synchronization, which has been proposed as a function of yawn contagion, and for which there is now some empirical evidence too (Casetta et al., 2021; 2022). Further, predation by native avian raptors (Rowley, 1990) might have served as an evolutionary pressure to spread vigilance in a social group, which may also incite yawn contagion as is theorized by the group vigilance hypothesis (Gallup & Gallup, 2007), and for which there now also is some empirical evidence (Gallup & Meyers, 2021; Gallup & Wozny, 2024; 2025).

There are roughly three methods to study yawn contagion: observational research, experimental research using live trigger yawns, and experimental research using video trigger yawns. Using observational methods, contagious yawning can be studied in a naturalistic context. In this method, yawns that occur within a certain timeframe (usually 3-5 min) after a conspecific's spontaneous yawn are classified as contagious (e.g., Ake & Kutsukake, 2023). However, using a (long) timeframe poses high risks of type I errors (Kapitány & Nielsen, 2017). Alternatively, the temporal clustering of yawns can be analyzed (Miller et al., 2012) or deviations from a baseline yawn frequency can be recorded (Campbell & Cox, 2019). Another alternative is to study yawn contagion experimentally, either with live triggers or video triggers. When two individuals are housed together, the clustering of yawns can be investigated. Then, this can be compared with yawn clustering in a condition where the individuals have no visual access to each other (Gallup et al., 2015). Alternatively, researchers can train animals to display a yawn-like behavior on command (Wilkinson et al., 2011). As another option, video stimuli of yawns can be used. These stimuli can be displayed to animals as a group (e.g., Massen et al., 2012) or individually during temporary separation from their group (e.g., Campbell et al., 2009). Typically, video stimuli in yawn contagion studies are minutes-long sequences of yawns (e.g., Campbell et al., 2009; Gallup et al., 2015), quite dissimilar to natural circumstances. Therefore, Anderson (2010) argued that stimuli like these constitute a supernormal stimulus, that may show an exaggerated reaction. Nevertheless, as a proof of concept such stimuli can be very useful.

In this study, we therefore presented video stimuli of yawns to individual galahs to test for yawn contagion. Previous research showed that a range of bird species are capable of recognizing individuals of their own species on video images (Ophir & Galef, 2003; Partan et al., 2005; Rieucau & Giraldeau, 2009; Ryan & Lea, 1994; Shimizu, 1998; Watanabe et al., 1993). Additionally, research has shown that budgerigars react similarly to on-screen and real conspecifics, both when interaction with the on-screen bird was possible (Ikkatai et al., 2016), and when interaction was not possible (Moravec et al., 2010; Mottley & Heyes, 2003). Moreover, video stimuli has proven effective in inducing yawn contagion in budgerigars (Gallup et al., 2015).

This study aimed to test whether galahs yawn contagiously in response to yawns of conspecifics. As previous research has shown that the strength of the contagion response may differ based on the familiarity or social closeness with the stimulus subject (e.g., Palagi et al. 2009; Demuru & Palagi, 2012; Campbell et al. 2011), we also aimed to test to what extent social affiliation strength may modulate the potential yawn response of the galahs. Note, however, that other studies did not find a familiarity bias (e.g., Massen et al., 2012; 2015; Neilands et al., 2020; van Berlo et al., 2020) and have for example found biases related to dominance (Massen et al., 2012). Consequently, there is quite some discussion (e.g., Yoon & Tennie, 2010; Massen & Gallup 2017; Neilands et al., 2020; Palagi et al., 2022) about whether this response bias is due to empathy biases, with empathy as a potential underlying mechanism for yawn contagion, or whether this simply reflects attention biases. Therefore, we paid extensive attention to the design of our study and took additional measures to control for attention to the stimulus.

We hypothesized that the galahs would yawn contagiously since other species with high sociality also show contagious yawning (Massen & Gallup, 2017), in particular the similarly flock-living budgerigar

(Gallup et al., 2015; Wyndham, 1980a). We also expected a positive relationship between affiliation strength and yawn contagion, in line with previous results showing an increase in yawn contagion with higher affiliation (either due to an attentional bias or not; Massen & Gallup, 2017). To test these hypotheses we conducted two, relatively similar, studies. In both studies, we presented the galahs with moving video stimuli, which contained yawns and non-yawn control footage of their strongest and weakest affiliated group member. The two studies differed in the size of the screen on which the stimuli were presented and in the number of repetitions of said stimuli. We predicted that galahs would show a higher yawn frequency when presented with yawn footage compared to presentation of a non-yawn control stimulus. In addition, we expected a higher likelihood of yawn contagion when the bird on the screen was strongly affiliated compared to footage of a weakly affiliated individual.

General Methods

As studies 1 and 2 were highly similar, we first discuss the general methods, before shortly stating the specifics of the respective studies.

Ethics Statement

The procedures of this study were communicated with- and approved by- Avifauna bird park. Avifauna bird park is a member of the European Association of Zoo and Aquaria (EAZA) and thus fulfils the legal and ethical regulations on captive animal welfare. Due to the non-invasive nature of this study further ethical review and approval were waived.

Sample and Study Site

This research was conducted on a group of nineteen galahs (*Eolophus roseicapilla*) housed in Avifauna Bird Zoo, Alphen aan den Rijn, The Netherlands. Fifteen galahs chose to voluntarily participate in the experiment: six adult females, six adult males, and three juveniles of unknown sex. The mean age of the galahs at first participation in the experiment was 6.8 years (sd = 4.5; min = 0.2 years; max = 15.0 years; see Supplementary Table 1 for individual demographics). The galahs were housed in a mixed species enclosure together with 5 eclectus parrots (*Eclectus roratus*). The enclosure (see Figure 1) consisted of an outside aviary (8.5 m long, 15.5 m wide, 4.1 m high) and eight identical interconnected inside enclosures (each 1.3 m long, 1.8 m wide, 2. 3m high). In the outside aviary, there were nine nesting boxes, several perches, two small trees, along with some vegetation and a small pond. In each inside enclosure, there were two perches and a water bowl. Apart from being visible to zoo visitors in their aviary, the galahs, along with several other species, participated in daily flight demonstrations between April 1st and October 31st. During these demonstrations, the birds are released out of their enclosures to fly towards a stand where visitors can observe the birds' natural behavior.

This group of galahs had been trained, using positive reinforcement, to approach animal caretakers upon their request. When requested, the birds would also allow themselves to be transported on the caretakers' hand. This is useful for husbandry procedures, such as bird weighing or separation from the group to administer medication. The galahs are weighed every other day to be able to monitor their weight after and before participation in the flight demonstrations. Because of their training, most birds could easily and voluntarily be separated from the group for our experiment by a caretaker's request, although a bird could always choose to not honour the caretaker's request to approach and in these cases would not participate in our experiments on that day. From March until the end of October, the birds were fed a mixture parakeet seeds and a variety of fresh vegetables and fruits after the flight demonstration (around 2:00 PM). During the off-season, the birds had ad libitum access to food, which was provided between 8:00 and 10:00 AM. Water was available *ad libitum* all year round.

Figure 1

Schematic Plan of The Enclosure



Note. A schematic plan of the enclosure, consisting of an $8.5 \times 15.5 \times 4.1$ m outside aviary and eight interconnected indoor enclosures (1.3 x 1.8 x 2.3 m each). In the outside aviary, there were several perches, some vegetation, and a small pond in the center. Figure adapted from de Vries (2023).

Stimuli

To create the stimuli, we recorded, opportunistically, two yawns per galah in the group with a Canon Legria HF R606 video camera. Yawns were defined as a wide opening of the jaw accompanied by an inhalation, followed by contraction of muscles, and slower closing of the jaw while exhaling (cf. Barbizet, 1958), and further operationalized as: wide opening of the beak, sometimes with stretching of the neck, followed by a brief pause and then a passive closure (cf. Gallup et al. 2015). The yawns were filmed from the front or side. Using the video editing software Kdenlive version 22.12.3, the recorded yawns were then cut from the raw video files and edited into silent stimuli. The isolated yawn clips started 3 frames before the first frame on which the beak could be observed to open and ended 3 frames after the beak could be observed to be closed. For two of the thirty-four yawns used, the start or end of the yawn was not completely visible due to visual obstructions (e.g., the yawning bird turning its head or another bird was sitting in the line of sight of the camera). However, no yawns that were clearly incomplete were used as stimuli. To standardize the stimuli, all yawn clips were slowed down or sped up to match the average clip duration (2.4s). For this, the playback speeds were altered to between 60% and 233% of the original speed. Note that only three out of the thirty-four clips had to be sped up to more than 150% of the original playback speed. For every yawn clip, a respective clip featuring non-yawn control footage was also created. Control clips were taken from the same raw video file as the yawn clips, within 10 seconds of the yawn. The control clips matched the yawn clips in duration, visual similarity of the footage, and were slowed down or sped up to the same degree as the respective yawn clips.

Before the stimulus started, a 5.7 s attractor was shown (a video of a caretaker placing down food in the inside enclosures; in accordance with Massen et al., 2012; van Berlo et al., 2020). After the attractor, depending on the condition, the stimulus started with either a yawn or control clip (2.4 s), featuring a specific 'stimulus' individual that varied per test individual (depending on the treatment). This was followed by a 1 s bright yellow screen, followed by the second, other, 2.4 s clip of that same stimulus individual, followed by another 1s bright yellow screen. In the remainder of the stimulus, the two different yawn or two different control clips of that stimulus individual alternated, each time with a 1 s yellow screen in between. The purpose of the yellow screens was to provide alternating visuals to try to keep the birds' attention to the screen. After the first stimulus ended (the number of repetitions of the specific stimuli differed per experiment), the screen turned black so that the bird could be observed post-stimulus before the second stimulus began.

The individual that was presented on the screen was either the strongest affiliate or the weakest affiliate of the galah in the trial. Affiliation strength was based on the proportion of social proximity (i.e., within one wing's length) from 213 scan samples collected between February 16th and August 23rd 2023 (minimum time between scans was 45 minutes). This data was supplemented with all occurrences observations made by the experimenter, who noted it down when birds that were not seen together in scans were in social proximity. All birds had multiple weakest affiliates (i.e., zero times observed in proximity). In these cases, the experimenter chose which of these weakest affiliates would be used in the experiment based on their interpretation of the group dynamics. In the resulting matching schedule, each bird's footage was shown about an equal number of times, so pseudo-replication was avoided (see Supplementary Table 1 for the matching schedule). In two cases, the strongest affiliate of a bird was a juvenile bird of which no yawns were filmed, as they hatched during the course of this study. In these cases, the second strongest affiliate was used as a stimulus in the strong affiliation treatment.

Experimental Setup

Experimental trials took place between 9:00 AM and 1:30 PM (but mostly before noon). A caretaker brought the bird into one of the inside enclosures, where it waited before being picked up by the experimenter. Before the start of the trial, the experimenter requested the bird on their hand. If a bird did not want to cooperate or seemed too stressed, the protocol was terminated, and the bird was brought back to the outside aviary. If the bird cooperated, the experimenter carried the bird to the experimental enclosure. Note that all the birds had extensive experience with being moved from the outside aviary to any of the indoor enclosures, as well as with being moved, voluntarily, from one inside enclosure to the other.

We conducted experiments in one of the eight identical inside enclosures. In the enclosure (schematically depicted in Figure 2), one low perch at 1.2 m height spanned the width of the enclosure, while a shorter high perch (at 2.0 m height) was perpendicular to the low perch. Three doors led to two neighboring inside enclosures and the outside aviary, respectively. On the door to the outside aviary, there was a little perch at a height of 1.7 m. In one corner of the enclosure, a water bowl was present. The screen that was used to present the stimuli was set up facing the low perch (see Figure 2). Two cameras were used to record the experiment. A stationary camera recorded the part of the low perch that was directly in front of the screen (Figure 2). The other camera was held by the experimenter to record the bird if it went out of frame of the stationary camera. The experimenter filmed as covertly as possible from a neighboring enclosure through the ajar door, to avoid distracting the bird. The other two doors were closed during the experiment, but the bird was free to move anywhere in the experimental enclosure. We made sure that each bird was sufficiently habituated to the experimental set-up before the bird participated in the experiment. As the specific habituation procedures differed in both studies, these procedures are outlined in their respective methods sections below.

Procedure

A trial started with the experimenter starting the recording on both cameras and leading the bird to sit in front of the screen. Then, the playback was started. The bird was carefully recorded until the end of the trial, 5 min 35 s after the first on-screen depiction of a galah. Experimental trials were always conducted in sessions of two trials. In between trials, the experimenter put the bird back in front of the screen, if necessary, and started the second trial by initiating the second stimulus playback. The time in between trials typically was two to three minutes. After the second trial ended, the bird was allowed back into the outside aviary. If, during a trial, a bird showed undesirable behavior (e.g., manipulating the stationary camera), the experimenter intervened and put the bird back on the perch in front of the screen. If intervention happened

more than two times in a trial, the session was terminated and repeated on another day. A session termination occurred three times, all with the same individual.

In each trial, either yawning or control clips were presented to the bird. If we presented yawn clips in the first trial, we presented control footage in the second and vice versa. The yawn and control clips within a session were always of the same individual (either the strongest or weakest affiliate). All birds were subjected to two sessions: one with a yawn and control trial of the strongest affiliated individual, and one with a yawn and control trial of the weakest affiliated individual. Thus, within one study, the galahs participated in two sessions of two trials each. As we conducted two studies, the overall total number of trials doubled to eight. Across individuals, the order of presentation was counterbalanced for yawn/control clips and strongest/weakest affiliates. Additionally, we counterbalanced the order of the yawn/control clips and affiliation between the two studies (see Supplementary Table 2). We tried to plan the birds' two sessions per experiment within one week. During the course of the experiments, however, we noticed that birds seemed less attentive when there were only a few days in between testing sessions, so from then, we made sure that there were at least six days and at most around two weeks in between testing sessions.

Figure 2

Dutside aviary Closed door 1.3m
Closed door
Closed d

A Schematic Depiction of The General Experimental Set-Up in an Inside Enclosure

Note. In study 1, the screen was an Apple iPad Air 2 that was positioned at eye level for the galahs using a microphone stand. The screen was at 40 cm distance from the perch. In study 2, the screen was a large monitor (Samsung T240HD; screen size of 33×52 cm; 61 cm diagonal) positioned at 90 cm distance from the perch on a table. The center of the screen was 25 cm below the height of the low perch.

Behavior Coding of Videos

During behavior coding, we scored yawns, self-directed behaviors, two levels of approximations of attention, and out of sight. We started scoring these behaviors from the first moment that a galah was depicted on-screen and stopped scoring when 5 min 35 s had passed. Yawns (point behaviors) were defined as a wide opening of the beak (without vocalizations), sometimes accompanied by extending the neck, followed by a passive, slower closure of the beak (based on Barbizet, 1958; Gallup et al., 2015). As yawning might be a sign of anxiety (a proxy of stress) in birds (Miller et al., 2010), we scored other measures of stress as well to avoid classifying stress-induced yawns as contagious yawns. There are indications that self-preening may be indicative of anxiety in birds (Henson et al., 2012). Similarly, in primates, self-grooming and scratching elevate in stressful conditions (Maestripieri et al., 1992; Troisi, 2002). Although there is no conclusive evidence of a causal link between self-directed behaviors and anxiety, we still chose

to measure self-directed behaviors (i.e., the duration behavior self-preening and the point behaviors scratching and stretching) to be able to classify the context of yawns during the experiment.

We considered it highly relevant to score a measure of attention to the screen. As true attention might be impossible to measure, we decided to use two approximations of attention: visual access to the screen (VA) and sitting in front of the screen (SI), both of which were duration behaviors. We only scored these two behaviors during the stimulus presentations. A bird had visual access to the screen when it had its beak pointed perpendicularly towards the plane of the screen or at most 90 degrees to the either side. As a stricter approximation of attention, we also scored sitting in front of the screen when a bird was sitting still in front of the screen for at least one second. As the screen had different properties in both studies, sitting in front of the screen is defined slightly differently in each study (see the respective methods sections below). Naturally, sitting in front of the screen could only be scored when a bird also had visual access.

Analysis

All statistical analyses were done using RStudio (version 2023.09.1; RStudio Team, 2020). We assessed inter-observer reliability by calculating the intra-class coefficient (ICC; two-way mixed effects model). We considered an ICC > .9 to be a sufficient level of agreement.

We used Bayesian regression models to analyze our data. For this, we used the *brms* package (v2.20.4; Bürkner, 2017, 2021) in RStudio, which created the models in the Stan computational framework. We ran all models with 4 chains and 11,000 iterations, 1,000 of which were warmup iterations. In all of the models, we allowed intercepts to vary by individual ID. Furthermore, for all models we checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation between iterations (Depaoli & van der Schoot, 2017). We found no divergences or excessive autocorrelation in any model. To identify potential model misspecification, we used the *DHARMa* package (Hartig, 2022) to inspect the distribution of scaled residuals and we performed posterior predictive checks to make sure that our models did not generate predictions that departed excessively from our original data (Gabry et al., 2019).

First, in both experiments we investigated VA and SI as a function of stimulus type (factor: yawn/control) interacting with relationship quality (factor: high/low) in separate models. The dependent variable in these models was proportional, i.e., the proportion of time having either visual access (VA model) or sitting in front of the screen (SI model). Therefore, we used a beta error distribution. Because the beta distribution cannot handle 0s or 1s, we recoded 0s to 0.001 and 1s to 0.999 (Smithson & Verkuilen, 2006).

Second, we aimed to study what variables may influence the occurrence of observing a yawn of our test animals. However, in our first experiment, we witnessed no yawns as a response to either yawn or control stimuli, making any such analyses obsolete. For Experiment 2, however, we did explore the variables that influenced the occurrence of yawning within a trial in a model with Bernoulli error distribution. In this analysis, we only included trials in which the subject had 3 or more seconds of visual access to the screen. Due to the length of a yawn/control clip being 2.4 s, we did not want to consider cases in which a bird might have not even seen one clip of yawn/control footage. As predictors we included occurrence of self-directed behavior (factor: yes/no) and the interaction between stimulus type (factor: yawn/control) and relationship quality (factor: high/low). While we originally also wanted to control for VA and SI during the trial, again the low number of trials with yawns (4 out of 54) made us decide to not add measures of VA and SI to the model to avoid overfitting.

Because both the beta models and the Bernoulli model had a similar link function (logit), we used identical prior specifications for all models. For the Intercept and the variance parameters, we used brms's default weakly informative prior specification (Student's t prior with mean = 0, sd = 2.5 and df = 3 and half-Student's t prior with same scale parameters, respectively). For the fixed effect priors, we specified three different prior specifications in order to test the prior sensitivity of our model, especially for the Bayes factor calculations (see later). We ran each model with a very conservative Gaussian(0, 0.5) prior, a slightly

less conservative Gaussian(0, 1) prior, and a less conservative, but still regularizing Gaussian(0, 2) prior. We have included the results for all three models.

For all models, we reported the Odds Ratio (OR) and its 95% credible interval (95% CI) to indicate effect size. As an indicator of effect existence, we reported the probability of direction (pd) of the posterior distribution (Makowski et al., 2019). Lastly, we reported Bayes factor, a measure of how well the data are explained by either the null model (no effect) or the alternative model. We report the BF01, which reflects to what extent the null model should be favored over the alternative model (BF01). In line with recent best practices, we explicitly state here that we assumed prior odds of 1 for the null and alternative model, which means that the Bayes factor equals the posterior odds (Tendeiro et al., 2024). We considered a BF01 > 3 to be moderate support for the null hypothesis, and a BF01 > 10 to be strong support in favor of the null hypothesis, respectively (Lee & Wagenmakers, 2013). Because Bayes factors are known to be very sensitive to prior specification, we ran each model with three different prior specifications to investigate how sensitive the BF01 values were to prior specification (Tendeiro et al., 2024).

In the text, we report the OR, 95% CI and pd based on the model with intermediately conservative priors, and report the BF01 for all three prior specifications. Full information about the estimates of each model is available in the supplements. The datasets and materials generated and/or analyzed during the current study are available via DataverseNL: <u>https://doi.org/10.34894/3X2ZPQ</u>

Study 1

Methods

Study 1 was conducted between May 19th and September 20th 2023. In study 1, the stimuli consisted of a total of 10 yawn or control clips over a stimulus length of 35s. To present the stimuli, we mounted an Apple iPad Air 2 (9.7 inch) on a K&M 19790 Tablet Stand Holder attached to a regular metal microphone stand. The iPad screen was at 40cm distance from the perch. The bottom of the iPad was positioned 10cm above the height of the low perch, so that the middle of the iPad was at about eye level of a perched galah. The stationary camera was a Canon Legria HF G25 mounted atop a tripod behind the iPad. The experimenter further recorded the experiment using a hand-held Canon Legria HF R606 camera. Before participation in the experiment, all birds were habituated to the experimental set-up. A bird was considered habituated when it calmly watched emotionally neutral galah footage while in the experimental environment for 20-30 s. Habituation was typically done a few days to up to about two weeks before the first experimental trial. All birds that participated in the experiment were habituated within two or three habituation sessions.

In the actual experiment, all birds participated in all four trials, except for one bird in one session, who did not want to cooperate anymore after the first trial, leaving that particular session unfinished. On two occasions, the between-session interval exceeded two weeks: for one bird there were thirty-two days in between the two successful testing sessions, because this bird's trials had to be terminated three times. For another bird, there was exactly three months in between the two testing sessions of round one because she did not want to cooperate in the period in between (see Supplementary Table 2).

In study 1, sitting in front of the screen was coded when a bird's body was 'sticking out' above the iPad as seen from behind the iPad (the stationary camera angle). In four trials, sitting in front of the screen could not be scored due to a mistake in the camera set-up. Interobserver reliability was calculated between JvO, who coded all trials, and LV, who coded a random selection of 18.6% of the trials. The two observers reached an overall ICC of .99. Every behavior had a separate ICC of at least .96.

Results Study 1

59 trials from 15 participating galahs were included in the analysis of study 1. 49% of the included trials had a yawn stimulus, and 49% of trials showed a strongest affiliate. The most notable result from

study 1 was the complete absence of any yawns by the galahs during the trials. The trial average of visual access to the screen was 30.3 s (median = 34.5; sd = 76.3). During one trial, a bird had less than three seconds of visual access. Every trial the galahs sat in front of the screen for an average of 16.4 s (median = 15.0; sd = 13.4). In 59.3% of trials, galahs performed self-directed behavior. The trial average of out of sight was 6.6 s (median = 1.0; sd = 12.9).

Because of the absence of any yawns during study 1, we could not investigate yawning as a dependent variable in our analyses. However, we did analyze the VA and SI as a function of condition and affiliation strength (Supplementary Table 3). Regarding visual access (results summarized in Figure 3a), we found evidence for absence of an interaction effect between condition and affiliation strength (OR = 0.9, 95% CI [0.68; 1.18], pd = 0.78, BF01 = 10.48; 5.29; 2.81), although the BF01 in the model with most conservative priors should be considered as weak evidence. In addition, we found moderate-to-strong evidence for absence of an effect of condition on visual access (OR = 1.02, 95% CI [0.78; 1.34], pd = 0.55, BF01 = 13.94; 7.14; 3.91) and of affiliation strength on visual access (OR = 1.01, 95% CI [0.76; 1.33], pd = 0.52, BF01 = 13.85; 7.34; 3.60). Altogether, the results suggest that condition and affiliation strength did not influence visual access.

Figure 3



Effect of Stimulus Condition and Affiliation Strength on (A) Visual Access and (B) Sitting in Front of The Screen in Study 1

Note. The density plots depict the posterior distributions for each category with their associated 95% credible interval (black line). The colored lines represent the individual means per category. Please note that the lines are horizontally jittered to avoid complete overlap, resulting in some estimates in the plot appearing to be slightly below 0 or above 1.

Roughly the same pattern was seen in the model for sitting in front of the screen (see Figure 3b; Supplementary Table 4). Again, we found evidence of absence for the interaction between condition and affiliation strength (OR = 0.91, 95% CI [0.64; 1.31], pd = 0.70, BF01 = 9.36; 4.72; 2.58) and the main effects of condition (OR = 1.03, 95% CI [0.72; 1.46], pd = 0.56, BF01 = 10.85; 5.51; 2.91) and affiliation strength (OR = 1.06, 95% CI [0.75; 1.53], pd = 0.63, BF01 = 10.44; 5.23; 2.78). Note, however, that the models with the most conservative prior specification yielded only weak evidence for the null hypothesis. Altogether, the results suggest that condition and affiliation strength did not influence the amount of time sitting in front of the screen.

Discussion Study 1

We studied contagious yawning in galahs by presenting video stimuli of yawns to 15 birds. Although we expected to find yawn contagion, we did not observe a single yawn during the experimental trials. Because of the absence of yawns, running a model with yawning as an outcome variable was uninformative. Our results contrast with research in budgerigars, who consistently show yawn contagion in a similar set-up (Gallup et al., 2015; unpublished data). Considering the fact that the socio-ecologies of, and thus the selection pressures acting upon galahs and budgerigars, are highly similar (Rowley, 1990; Wyndham, 1980a), our findings were even more surprising. The only clear methodological difference between our study and the studies in budgerigars (Gallup et al., 2015), was the stimulus duration. We presented 35 s of video stimulus in every trial, while the budgerigars were presented 10-15 min of footage (Gallup et al., 2015). Additionally, we figured that the iPad screen might be too small for the galahs, as on screen, the galahs depicted are smaller than real-life galahs. Thus, galahs might not be stimulated enough to evoke potential contagious yawns. Because of this, we decided to conduct a second study, with a larger screen and a longer stimulus duration.

Study 2

Methods

In study 2, we aimed to find out whether galahs yawned contagiously in an adapted experimental set-up. Using a larger screen and more repetitions of the clips, we aimed to uncover whether the lack of yawns in study 1 was attributable to the experimental design, or whether it could be an indication of an absence of contagious yawning in galahs.

We conducted study 2 between June 30th and October 2nd, 2023. In this study, the stimuli consisted of 68 repetitions of the yawn or control clips, spanning 4 min 01 s. In the experimental enclosure, we placed a small folding table with a large monitor (Samsung T240HD; screen size of 33 x 52 cm; 61 cm diagonal) on top of it. The monitor's screen was at a distance of 90cm from the low perch and the center of the screen was 25cm below the low perch's height. A stationary GoPro Hero 3 recorded from the base of the monitor and the experimenter recorded using a handheld Canon Legria HF G25 camera. One of the juvenile galahs was tested in a different enclosure, albeit with the exact same size and set-up, because this animal was moved to another enclosure within the zoo between study 1 and 2. We tested this bird in an adjacent empty inside aviary in which we put one table for the bird to perch on and one table for the monitor, with 90 cm between the edge of the table and the monitor. As the galahs were already familiar with study 1's set-up, habituation took less time. Habituating only took one short session, which was done a few days to a few minutes before the first trial.

Despite the difference in stimulus duration across studies, the observation time was kept equal in both studies, to allow for comparisons. In both studies, observing stopped at 5 min 35 s after the start of the first galah depiction (see Figure 4). This meant that the post-stimulus time in study 2 trials was 1 min 34 s, compared to 5 min 00 s in study 1.

For one bird, the experimenter accidentally showed the stimuli in the wrong order (i.e., an order that was assigned to another bird, see Supplementary Table 2). For two birds, the between-session interval exceeded two weeks (28 and 32 days respectively, see Supplementary Table 2) because they did not want to cooperate within the intended timeframe. One bird only cooperated in one session due to motivation issues (see Supplementary Table 2). In study 2, there were no instances where a trial had to be terminated by the experimenter.

The inter-observer reliability was based on the intra-class coefficient between observations by JvO, who coded all trials, and LV, who coded a pseudo-random selection of 22.2% of the trials. To ascertain good agreement on our most important outcome variable, yawning, an initial random sample of the trials was supplemented with more trials in which possible yawns were present. The overall intra-class coefficient between JvO and LV was near perfect (.998). For all individual behaviors, the ICC value exceeded .99,

except for out of sight (ICC = .53). However, as the incongruence in assessment of this behavior did not affect any results, the labor investment of recoding was deemed disproportional.

Figure 4

A Schematic Depiction of The Differences Between Studies 1 and 2 in The Timelines in Trials (Not To Scale)



Note. Behavior scoring started when the stimulus presentation started. Attention to the screen was only scored during stimulus presentation. All other behaviors were scored during and after the stimulus. The post-stimulus observation time was different between studies 1 and 2, to match both studies' trial durations. Hence, easy comparisons could be made between the two set-ups.

Results Study 2

In study 2, 15 galahs participated in 58 included experimental trials (50% yawn condition; 48.3% with strongest affiliate footage). One bird only completed the first session due to a lack of motivation. Over the course of study 2, we observed six yawns by four unique individuals. For all trials in studies 1 and 2 combined, this translated to a rate of 0.56 yawns/hour. Four trials yielded <3 s of VA. One of these four trials featured a yawn, so this left five yawns from three unique individuals in the dataset. Four of these yawns were exhibited in a trial with a strongest affiliate (two in control trials, two in yawn trials), and the remaining yawn was observed in a yawn trial in which a weakest affiliate was depicted. Figure 5 depicts the circumstances in which yawns occurred. On average, the galahs had visual access to the screen for 123.7 s (median = 122.5; sd = 81.8) and sat in front of the screen for an average of 75.8 seconds (median = 55.0; sd = 77.5). In 50% of trials, a galah performed self-directed behavior. On average, birds were out of sight for 6.7 s per trial (median = 2.5; sd = 14.0).

For the yawn model (Supplementary Table 5), we investigated how occurrence of self-directed behaviors and the interaction between condition and affiliation strength affected the occurrence of yawning. As might be expected because of the low number of yawns, we did not find convincing evidence either for or against the null hypothesis for any of the predictors: interaction condition and affiliation strength (OR = 1.64, 95% CI [0.54; 5.29], pd = 0.81, BF01 = 1.57; 1.23; 1.25), occurrence of self-directed behavior (OR = 0.48, 95% CI [0.11; 1.74], pd = 0.87, BF01 = 0.95; 0.86; 0.87), affiliation strength (OR = 1.64, 95% CI [0.53; 5.34], pd = 0.81, BF01 = 1.61; 1.23; 1.25), and condition (OR = 0.95, 95% CI [0.30-2.93], pd = 0.53, BF01 = 2.51; 1.76; 1.79).

Figure 5

Descriptive Plot Showing the Association Between (A) Visual Access to The Screen and (B) Sitting in Front of Screen, Respectively, and Occurrence of Yawning (Binomial) Per Stimulus Condition in Study 2



Note. We did not statistically test this association, because of the low number of yawns that occurred.

The visual access model (Figure 6a, Supplementary Table 6) showed moderate-to-weak evidence against an interaction between condition and affiliation strength on the proportion of VA (OR = 1.19, 95% CI [.88; 1.60], pd = 0.87, BF01 = 6.95; 3.56; 1.91). We found, however, a moderate robust effect of affiliation strength, as a main effect on VA, i.e., there was slightly more visual access to the screen when strongly affiliated individuals were presented in the stimuli (OR = 1.57, 95% CI [1.14; 2.14], pd = 1.00, BF01 = 0.25; 0.15; 0.10). Lastly, the VA model showed moderate-to-weak evidence against an effect of condition on VA (OR = 0.89, 95% CI [.66; 1.19], pd = 0.79, BF01 = 9.54; 4.93; 2.54).

The sitting in front of screen-model (Figure 6b, Supplementary Table 7) showed moderate-to-weak evidence against an interaction between condition and affiliation strength on the proportion of SI (OR = 1.23, 95% CI [.92; 1.65], pd = 0.92, BF01 = 4.95; 2.61; 1.50). We found no clear effect of affiliation strength on sitting in front of screen, with very low BF01 values (OR = 1.28, 95% CI [.94; 1.73], pd = 0.94, BF01 = 3.64; 1.89; 1.07). Lastly, the model showed moderate-to-weak evidence against an effect of condition on SI (OR = 0.88, 95% CI [.65; 1.19], pd = 0.79, BF01 = 9.42; 4.77; 2.55).

Figure 6



Effect Of Affiliation and Stimulus Condition On (A) Visual Access and (B) Sitting in Front Of The Screen in Study 2

Note. The density plots depict the posterior distributions for each category with their associated 95% credible interval (black line). The colored lines represent the individual means per category. Please note that the lines are horizontally jittered to avoid complete overlap, resulting in some estimates in the plot appearing to be slightly below 0 or above 1.

General Discussion

In two similar experiments, we did not find evidence for or against yawn contagion, nor an affiliation effect on yawn contagion in galahs. However, when putting our results into context, we conclude that it is highly unlikely that contagious yawning is present in galahs (see below). From study 1, we could not conclude whether contagious yawning was present. The data did not allow for analyses, because we observed zero yawns in our experimental trials. In study 2, we observed five yawns (three in the yawn condition) but found no evidence for or against a difference between the yawn and control conditions, thus no evidence for or against contagious yawning. Further, we found no evidence for or against an effect of affiliation strength on the relationship between condition and yawning. This means that we cannot conclude whether yawns from strongly affiliated individuals elicited more yawns than yawns from weakly affiliated individuals. Additionally, we found evidence against an effect of (approximated) attention to the screen on the relationship between condition. We discuss the implications of the results on yawn contagion in further detail below.

Galahs paid equal attention to yawn and control stimuli. We ran four similar analyses on factors influencing attention towards the screen (analyses for two approximations of attention in two studies). Three out of four analyses showed that galahs paid equal attention to yawn and control stimuli, and one analysis showed no clear direction of an effect This means that the lack of evidence in favour of yawn contagion cannot be explained by a difference in attention between the yawn and control stimuli. One of the four models showed a significant effect of an attention bias towards strongest affiliated individuals, suggesting at the very least that there is some form of individual recognition of the birds on the screen. However, two models showed evidence against such an effect, although these where the models in study 1 where the exposure, and consequently the amount of attention to the stimuli, were short. This created less variation and thus made finding an effect more difficult. The other model on study 2, with the longer exposure, did

not show evidence for or against an attention bias. Thus, overall, we showed that galahs pay equal attention to yawn and control clips, but results on the existence of an attention bias based on affiliation in galahs are relatively inconclusive.

Contagious Yawning

Although our results showed no statistical evidence for the absence of contagious yawning in galahs, we consider it likely that contagious yawning is absent in galahs. Firstly, and most importantly, the yawning rate that we found does not seem to differ from the baseline yawning rate in this group of galahs. From previously collected focal samples on this group, 14 yawns were observed in almost 36 hours of focal observations (Malone & de Vries, unpublished data). This translates to a rate of 0.39 yawns/hr. This does not seem to differ too much from the 0.56 yawns/hr that we observed in our experimental trials. Consequently, although the observed number of yawns is small, the yawn rate in our studies did not exceed the baseline yawn rate. Therefore, we deem the presence of yawn contagion in galahs highly unlikely.

Secondly, if contagious yawning were present in galahs, we argue that our method would have shown it, since this method was validated in another parrot species, the budgerigar (Gallup et al., 2015). Galahs and budgerigars are evolutionarily relatively closely related; i.e., the last common ancestor lived about 35MYA (Kumar et al., 2017), and are mostly similar in biology and socio-ecology. Both species form lasting bonds with breeding pairs and interact within coordinated flocks throughout the year (Rowley, 1990; Wyndham, 1980a). Both species are highly social, and mates engage in allopreening (Rowley, 1990; Zocchi & Brauth, 1990). Whereas galahs are usually sedentary, flocks of juveniles can be nomadic (Rowley, 1990). Budgerigars are nomadic and flock size constantly changes in size and composition, depending largely on food availability. Budgerigars remain in smaller groups during drought, and congregate in much larger flocks of over 1,000 during breeding seasons (Wyndham, 1980a). Similarly, galah flock sizes have also been observed to exceed 1,000 (Rowley, 1990). A comparison of the visual systems of galahs and budgerigars would be interesting to consider, but we are not aware of any literature on the visual system of galahs. Lastly, both species feed primarily on seeds and ground vegetation (Rowley, 1990; Wyndham, 1980b). Because of the proven success of our experimental method in a highly similar species, we think that the absence of yawn contagion in galahs is not attributable to our experimental method. Similar to the budgerigars, the galahs were shown yawn and control stimuli on a similarly sized, regular screen (Gallup et al., 2015). In our study 2, the on-screen galahs appeared around 1.5 - 2 times larger than real life, similar to the ratio in the budgerigar study (Gallup et al., 2015). The only differences were the shorter duration of our stimuli (up to four minutes, compared to ten to fifteen minutes) and the addition of yellow screens in between yawns (with the goal of increasing attention). However, brightly colored screens were used in previous yawn contagion studies without any problems (e.g., Massen et al., 2012; van Berlo et al. 2020), and we argue that the galahs showed enough attention towards our presented stimuli. On average, the galahs sat in front of the screen during, on average, 23.0 yawns per yawn trial in study 2, and even had visual access to, on average, 34.9 yawns per vawn trial in that second experiment. It is unknown how much time the budgerigars attended to the screen, but this was likely not the case for the whole stimulus either. We suppose exposing galahs to this number of yawns would be sufficient to evoke contagious yawns, if yawn contagion were present, as has been shown in different studies using a similar set-up and procedure (e.g., Massen et al., 2012; van Berlo et al., 2020).

It could be argued that the lack of contagious yawns could be explained because it would not be ecologically relevant to yawn contagiously in an experimental environment, or that the galahs may not recognize the footage as being conspecifics that are yawning. However, then we would also expect these same issues in budgerigars, but this was not the case (Gallup et al., 2015). In contrast to our study, however, the budgerigars were in their test compartment 45 minutes prior to the experiment to secure maximum habituation to the setting, as previous studies have shown that stress may inhibit yawn (contagion) in the short-term (Eldakar et al., 2017; Gallup, 2022; Miller et al., 2010). Nevertheless, we deem it unlikely that a lack of habituation could explain the lack of yawns in this experiment. The galahs were only allowed to participate in the experiment after they watched the screen calmly for around thirty seconds in a prior

session, we paid particular attention to stress as an ethical consideration, and terminated any session when we saw even the slightest indication of stress. Finally, these birds had ample experience with being transported between enclosures by animal trainers and experimenters on a voluntary basis. This is in contrast to the budgerigars, who were in fact caught for the experiment. All this taken together, we conclude that that galahs likely do not yawn contagiously.

Implications for the Phylogenetic History of Contagious Yawning

The apparent absence of contagious yawning in galahs suggests convergent evolution of the trait in restrictive avian lineages. However, we are careful in drawing strong conclusions because of the small sample size (N = 2). Budgerigars and galahs are phylogenetically relatively close: their last common ancestor lived 35 million years ago (Kumar et al., 2017) Therefore, contagious yawning might have evolved separately in the ancestors of budgerigars, and not in the galah's ancestors. Alternatively, contagious yawning was present in a shared ancestor of budgerigars and galahs, but galahs lost the trait over evolutionary history. Notably, the hourly yawn rate of spontaneous yawning in budgerigars is 2.1 - 2.9(Miller et al., 2010; 2012), which is substantially higher than the rate in galahs (0.39), which suggests that the behavior in general may be diminished in the latter species, although this should be confirmed by studies in the wild. Nevertheless, diminished spontaneous yawning does not exclude the trait to be contagious, yet we find no evidence for yawn contagion in the galah in our study.

Interestingly, contagious yawning possibly evolved independently on multiple occasions, since yawn contagion is present in restricted taxa that are phylogenetically distant (e.g., birds and mammals; Massen & Gallup, 2017). Yet, as discussed above, studies on mammals suggest both homologous and analogous evolutionary pathways. Either way, more research is needed on the evolution of contagious yawning in birds and other animals.

Limitations, Strengths, and Future Directions

This study's main limitation was the small number of yawns exhibited by the galahs. Because of this, our models could not gauge the effect of our experimental manipulations on the yawning frequency. A much larger number of trials would allow to draw more robust conclusions, but we deem this unfeasible. Another alternative would be to extend the period of habituation prior to the display of the video stimuli to for example 45min prior to the start of the video stimuli (cf. Gallup et al., 2015). Although it remains an empirical question, it has been proposed that contagious yawning should be enhanced among individuals that are experiencing low levels of arousal or a down regulation of vigilance (Gallup, 2022). Longer habituation may lower arousal levels in the galah, although longer separation of their conspecifics may also increase their arousal. Although there thus is no clear directionality with regard to the expectation regarding contagious yawning, this could be tested empirically.

Sometimes we observed a behavior that seemed to resemble yawning, but was a slightly different behavior on closer inspection. This was a yawn-like behavior accompanied by crop movements. It can be described as an opening of the beak in a yawn-like fashion, followed by extension of the neck and tilting of the neck backwards. Sometimes the crop can be seen moving during the neck extensions. The extension of the neck and head-tilting is sometimes repeated several times, during which the bird's beak does not close. We are not aware of any scientific literature on this behavior, but in online forums this behavior is classified as crop adjustment (e.g., ParrotForums, 2014). We are interested in scientifically exploring the function of this yawn-like behavior and therefore propose further research into this.

We argue that we approximated attention to the screen as closely as possible by scoring visual access to and sitting in front of the screen. For even more accurate measurements, future research could use eye tracking for a more accurate indication of the birds' gaze (Kano et al., 2022; Tyrrell et al., 2014). Additionally, the question arises whether the galahs understood what was being depicted on the screen, i.e., did they see that yawns were being depicted and did they see this in the same way as a 'real life' yawn? We are unaware of any research that looked into the responses of galahs to on-screen depictions compared to

the real-life entities. However, we expect that galahs would do so, since budgerigars have shown to react similarly to behavior of real conspecifics and their on-screen representations (Gallup et al., 2015; Ikkatai et al., 2016; Moravec et al., 2010; Mottley & Heyes, 2003, but see D'Eath & Dawkins, 1996). However, to test this expectation, and further validate our study's conclusions, we suggest future research into the similarity of responses of galahs to on-screen depictions compared to real life.

A downside of using video stimuli consisting of repeated yawns, is the risk of producing a supernormal stimulus (Anderson, 2010). We agree that a compilation of yawns on a video screen is not the same as a single yawn of a real conspecific. However, as a proof of concept, we think using this method is justified. There are other limitations of using video stimuli in animal research. Video screens are designed for the human eye, which differs from other animal's eyes in color vision, flicker-fusion frequency, perception of depth and visual acuity (D'Eath, 1998). For example, parrot eyes can detect ultraviolet light (Graham et al., 2006) which may not be displayed by a screen designed for humans (D'Eath, 1998). Furthermore, in birds, video presentation might degrade some information, such as information used for individual recognition (Lea & Dittrich, 1999), although the exact mechanism of this information degradation remains unknown. Because there is a lack of literature on the visual system of galahs, we recommend future research on this to validate our findings. Despite the limitations of video presentations, video footage has successfully elicited similar behaviors compared to real-life depictions of those behaviors (D'Eath, 1998), including contagious yawns (reviewed in Massen & Gallup, 2017).

There are several alternative methods to study yawn contagion, one of which is observational research (e.g., Ake & Kutsukake, 2023; Campbell & Cox, 2019; Miller et al., 2012). Observational research studies yawns in a more naturalistic context compared to our experimental design, but it can be more difficult to distinguish between spontaneous and contagious yawns due to difficulties in keeping track of gaze. Other alternative methods include an experimental design using live triggers (cf. study 1 in Gallup et al., 2015) or training a 'trigger' animal to perform a yawn-like behavior (Wilkinson et al., 2011), but these methods may be very labour and time intensive, and may not be easily implemented in a zoo environment. If, somehow, our experimental set-up inhibited yawning in the galahs, we therefore, propose that future research should try and replicate our findings using observational methods (e.g., Ake & Kutsukake, 2023; Campbell & Cox, 2019; Miller et al., 2012; Gallup et al. 2022).

In the sample of fifteen galahs, three juvenile galahs were included, whose ages at the start of the experiment ranged from 0.2 to 0.4 months. In humans, chimpanzees, and dogs (Helt et al., 2010; Madsen et al., 2013; Madsen & Persson, 2013; Millen & Anderson, 2010), contagious yawning seems absent in early life. We are not sure whether it would be logical to assume whether (if yawn contagion would be present) juvenile galahs would also have developed the trait yet. Galahs do develop more quickly than humans, chimpanzees, and dogs (the included juvenile galahs already fledged and ate independently), so we suspect that traits like these should have had the chance to develop already. Still, we are careful in using the data on the juvenile birds as evidence for or against yawn contagion. However, we do not think that leaving the juveniles out of the data would have impacted the results, since the adult birds still showed similar results (adults: four total yawns, two of which in the yawn condition).

We argue that the most important future direction is to research yawn contagion in more avian species. By establishing which bird species yawn contagiously and which do not, we can gain information about the evolutionary origins of yawn contagion. If we know when yawn contagion evolved and under which selection pressures, this may provide information about the function of yawn contagion as well.

Conclusion

In short, we found that galahs do not yawn contagiously in response to video stimuli of yawns. The absence of yawn contagion could not be explained by a lack of approximated attention to the stimuli. Because the relatively closely related budgerigar does yawn contagiously, this suggests that contagious yawning might have evolved independently in restrictive avian lineages. We suggest that this finding could be confirmed with more research into the understanding of video presentations by galahs and research into the contagious yawning in a naturalistic setting via observations. Also, we call for more research into the

presence of contagious yawning in other bird species, to gain better understanding of the evolution and function of yawn contagion.

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Data Availability: The datasets and materials generated and/or analyzed during the current study are available via DataverseNL: <u>https://doi.org/10.34894/3X2ZPQ</u>

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Supplementary Material

Table S1

Individual	Age At First Participation	Sex	Completed Trials		Strongost Affiliato	Waalaast Affiliata
			Study 1	Study 2	Subligest Affiliate	weakest Ammate
AN	6y0m	М	4	4	TE	BO
BO	15y0m	М	4	4	PI	TE
BR	5y9m	F	3	2	GR	AN
BU	7y0m	Μ	4	4	RA	TJ
GA	0y4m	?	4	4	GW ^a	GR
GR	7y0m	М	4	4	BR	LI
GW	0y4m	?	4	4	GA ^a	BO
LI	5y9m	F	4	4	TJ	GU
MI	6y3m	F	4	4	DA	TE
RA	7y0m	F	4	4	BU	GU
TE	9y2m	F	4	4	AN	BU
TJ	5y9m	М	4	4	LI	GU
YU	0y2m	?	4	4	GA	ZM
ZM	13y0m	М	4	4	ZP	BR
ZP	13y1m	F	4	4	ZM	PI

An Overview Of The Galahs That Participated In The Experiment

Note. For every individual, we show its age at first participation in the experiment, sex (M/F/unknown), the amount of trials it participated in (further details in supplementary table B) and their respective strongest and weakest affiliates. ^aFor these birds, their strongest affiliate was a juvenile individual of whom no yawns were recorded, so the individual displayed in the table is their second strongest affiliate.