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ORIGINAL PAPER

Experimental evidence of contagious yawning in budgerigars (*Melopsittacus undulatus*)

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Abstract Experimental evidence of contagious yawning has only been documented in four mammalian species. Here, we report the results from two separate experimental studies designed to investigate the presence of contagious yawning in a social parrot, the budgerigar (*Melopsittacus undulatus*). In Study 1, birds were paired in adjacent cages with and without visual barriers, and the temporal association of yawning was assessed between visual conditions. In Study 2, the same birds were exposed to video stimuli of both conspecific yawns and control behavior, and yawning frequency was compared between conditions. Results from both studies demonstrate that yawning is contagious. To date, this is the first experimental evidence of contagious yawning in a non-mammalian species. We propose that future research could use budgerigars to explore questions related to basic forms of empathic processing.

Keywords Yawning · Contagious yawning · Empathy · Avian cognition

Introduction

Yawning is characterized by a powerful gaping of the jaw with inspiration, a brief period of peak muscle contraction, and a passive closure of the jaw with shorter expiration (Barbizet 1958). Nonsocial yawning, also known as spontaneous yawning, is believed to be relatively widespread among vertebrates (Baenninger 1987) and may function in promoting cortical arousal (Baenninger 1997) and/or state change (Provine 1986, 1996, 2005) by decreasing brain temperature (Eldakar et al. in press; Gallup and Gallup 2007, 2008; Gallup and Eldakar 2012; Massen et al. 2014; Shoup-Knox et al. 2010). Contagious yawning, which can be elicited by sensing or thinking about the action in others (Provine 2005), appears to be a more recently derived behavior that may function in group coordination and vigilance in social species (Gallup and Gallup 2007; Gallup 2011; Miller et al. 2012a).

To date, experimental evidence of contagious yawning is restricted to humans (*Homo sapiens*; e.g., Provine 1986; Platek et al. 2003), chimpanzees (*Pan troglodytes*) in response to conspecifics (Amici et al. 2014; Anderson et al. 2004; Campbell et al. 2009; Campbell and de Waal 2011; Massen et al. 2012) and human yawns (Campbell and de Waal 2014; Madsen et al. 2013; but see Amici et al. 2014), domesticated dogs (*Canis familiaris*) in response to human yawns (Joly-Mascheroni et al. 2008; Madsen and Persson 2013; Romero et al. 2013; Silva et al. 2012; but see Harr et al. 2009; O'Hara and Reeve 2011; Buttner and Strasser 2014), and, most recently, a subline of high-frequency yawning Sprague–Dawley rats (*Rattus norvegicus*; Moyaho et al. 2014). Video-induced yawning has also been reported in stumptail macaques (*Macaca arctoides*; Paukner and Anderson 2006), but this response also co-occurred with heightened self-directed behaviors and thus appears to be due to social tension or stress rather than contagion. Species that have thus far failed to show contagious yawning in an experimental design include bonobos (*Pan paniscus*), orangutans (*Pongo abelii*), and gorillas (*Gorilla gorilla*) in response to both conspecific and human yawns (Amici et al. 2014), and domesticated dogs and red-footed tortoises (*Geochelone carbonaria*) in response to conspecifics (Harr et al. 2009; Wilkinson et al. 2011).

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Observational evidence for contagious yawning to conspecifics has been reported in bonobos (Demuru and Palagi 2012; Palagi et al. 2014), gelada baboons (*Theropithecus gelada*; Palagi et al. 2009), budgerigars (*Melopsittacus undulatus*; Miller et al. 2012b), and wolves (*Canis lupus lupus*; Romero et al. 2014).

Research suggests that contagious yawning is triggered by mechanisms that differ from those involved in other involuntary actions (Amici et al. 2014). In particular, contagious yawning is thought to represent a basic form of empathy rooted in a perception–action mechanism known as state matching or emotional contagion (Preston and de Waal 2002). Consistent with this view, previous research has documented a strong association between contagious yawning and empathy (for a discussion, see Campbell and de Waal 2014). For example, in humans, contagious yawning is more common among participants who score high on empathy measures (Platek et al. 2003; but see Bartholomew and Cirulli 2014), and thinking about yawning has been shown to activate brain areas implicated in empathic processing (e.g., Platek et al. 2005; Nahab et al. 2009). Comparative studies investigating the developmental onset and decline of contagious yawning also generally support this view (Anderson and Meno 2003; Bartholomew and Cirulli 2014; Giganti et al. 2012; Madsen et al. 2013; Madsen and Persson 2013; Massen et al. 2014), since empathy-related capacities in humans emerge in early childhood and decline in old age (Bailey and Henry 2008; Perner and Lang 1999). Growing comparative research also demonstrates a positive relationship between contagious yawning and group affiliation or social closeness/bonding (Campbell and de Waal 2011; Demuru and Palagi 2012; Norscia and Palagi 2011; Palagi et al. 2009; Romero et al. 2013, 2014; Silva et al. 2012), which supports a connection with empathic processing. For example, an initial study on chimpanzees provided evidence for an ingroup bias for contagious yawning (Campbell and de Waal 2011). In particular, captive chimpanzees shown video stimuli of other chimpanzees yawning demonstrate contagion to ingroup members but not to unfamiliar conspecifics. Subsequent studies, however, have failed to demonstrate a familiarity bias for chimpanzees viewing human yawns (Campbell and de Waal 2014; Madsen et al. 2013), and at least one study provided evidence that relationship quality among chimpanzees did not predict yawn contagion (Massen et al. 2012). There has also been mixed support for domesticated dogs to yawn more in response to yawns from familiar humans (Madsen and Persson 2013; O'Hara and Reeve 2011).

Since contagious yawning may represent a primitive form of empathy, unequivocally demonstrating the presence of this behavior in a laboratory animal, with the ability to manipulate it experimentally, could be important for exploring basic questions related to this cognitive capacity. For example, budgerigars (*M. undulatus*), a species of social parrot indigenous to Australia, represent a good candidate species because these birds form lasting bonds with breeding pairs and interact within coordinated flocks throughout the year (Wyndham 1980). Furthermore, previous research has demonstrated that these birds show automatic imitation to video stimuli (Mui et al. 2008), whereby the sight of another's action tends to elicit the same action in the observer (Sturmer et al. 2000). Using a naturalistic approach, Miller et al. (2012b) initially examined this species and revealed that yawns were temporally clustered in an undisturbed, established flock of captive budgerigars. These findings suggest yawning is contagious, similar to the other aforementioned observational studies; however, such methods cannot completely account for circadian physiological synchrony and/or collectively sensed environmental stimuli (both of which influence the expression of yawning, see Baenninger 1997).

Here, we describe two separate experimental studies designed to investigate the presence of contagious yawning in budgerigars in a controlled laboratory setting. Study 1 paired birds in adjacent cages with and without visual barriers, and the frequency of potentially contagious yawns (i.e., those occurring within a restricted temporal proximity) was compared based on the opportunity for visual information transfer. Given that in the wild, the group size and composition of budgerigars can fluctuate depending upon the season (Wyndham 1983) and that both sexes within this species show vocal call convergence to ingroup members when housed in captivity (Farabaugh et al. 1994; Hile et al. 2000), pairs of familiar and unfamiliar birds were tested together in this experiment to assess the potential for a familiarity bias in this response. Unlike chimpanzees or wolves, however, in which observing unfamiliar conspecifics may elicit hostility and familiarity biases for contagious yawning have been reported (Campbell and de Waal 2011; Romero et al. 2014), budgerigars show more fluid flocking and thus we did not expect a strong bias for contagious yawning. Since previous research has demonstrated that budgerigars respond to video displays of real and virtual conspecifics (Mui et al. 2008; Moravec et al. 2010; Mottley and Heyes 2003), Study 2 compared the yawn frequency of the same birds from Study 1 during exposure to video presentations of yawns versus control behaviors.

Methods and results

Subjects

The budgerigars in these studies were from a population maintained within the vivarium at the State University of

New York at Oneonta, Oneonta, NY, USA. The temperature of this indoor facility is maintained at 21 °C, the light/dark cycle is set to 12:12 hours (0700; 1900 hours), and food, water, and supplements are provided ad libitum. With the intention of testing for ingroup/outgroup effects, two isolated populations of budgerigars (11-bird group, 13-bird group) were purchased as juveniles from commercial vendors in March 2014. From the onset, these groups have been kept in the same room, but within separate aviaries (1.626 m × 0.533 m × 1.575 m) with a visual barrier between them to prevent the birds from seeing one another. To enhance potential ingroup/outgroup effects, the birds in each group were initially selected for different coloration. One group is comprised of all dark and light green birds, whereas the other group consists of a combination of varied colored birds (e.g., Greywing blue, Skyblue Cinnamon, Albino, Lutino). The two experiments reported below tested the same 16 birds (15 males, three females), which included eight from each aviary (seven males, one female; six males, two females). Both experiments were approved by the local Institutional Animal Care and Use Committee (# 2014–02; 2014–05).

Procedure and analysis: Study 1

The first experiment was conducted across a period of 3 weeks during July 2014. Each testing day, two birds were caught from their main aviaries at 1115 hours, taken to a separate testing room within the vivarium, and placed in individual housed cages (0.305 m × 0.254 m × 0.279 m) connected to one another (see Fig. 1). The cage was designed to accommodate a plastic opaque barrier that could be positioned between the two individual cages, which allowed for conditions with and without visual contact/information transfer. The cage was positioned toward a tripod with a digital camcorder, and to ensure the birds faced in this direction, all other external surfaces of the cage were covered with cardboard. The perches in each individual cage were positioned at an angle to promote visual contact between the pair while still providing a view of yawning behavior (Fig. 1). No food or water was provided during testing in order to maximize visual attention between the birds and the rate of behavioral responses.

After the birds were caught and transferred to the testing room, an experimenter started a digital camcorder and then exited the facility. The birds were given an acclimation period of 1 h and 45 min, and during this time, the opaque barrier was positioned between the cages to keep the birds visually occluded from one another. A researcher would then reenter the room at designated times to remove the barrier while remaining occluded from the birds. Depending upon the condition sequence for the given pair (see below), the visual barrier could be removed at 1300 hours after the

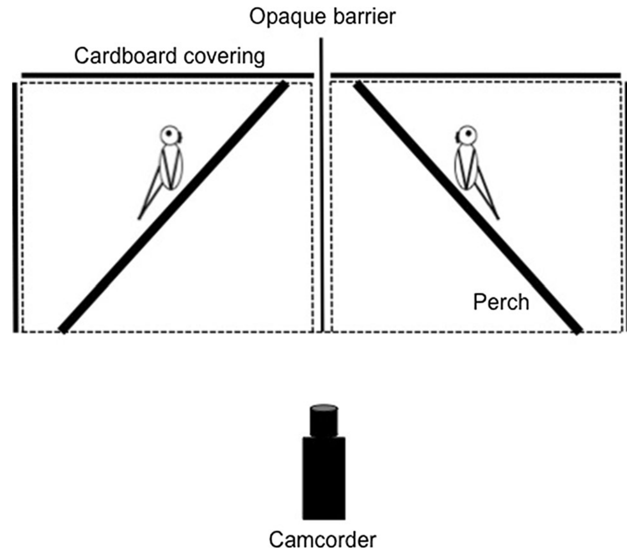

Fig. 1 Experimental setup. In Study 1, two birds were placed in individually housed cages connected to one another. A slight separation between the adjacent cages allowed for an opaque barrier to be positioned within, providing conditions with and without visual contact to the neighboring bird. The perches were positioned at an angle to promote visual contact between the pair while still providing a view of yawning behavior from the camcorder. This cage was also used in Study 2, but a total of four birds (two in each side) were tested at a time. The opaque barrier was removed to allow visual contact between the group, and a laptop computer display was positioned just in front of the camcorder

acclimation. Another 15-min acclimation period was provided before the first behavioral recording session began from 1315 to 1415 hours. At the end of this session, the visual barrier was then either replaced or removed (given the sequence), and another 15-min acclimation period was provided. The second and final recording session then began at 1430 hours and concluded at 1530 hours. Therefore, a total of 2 h of behavioral recordings were taken each day.

Each bird was tested twice in this fashion, once paired with a bird from the same main aviary (ingroup member) and once paired with an unfamiliar bird from the visually occluded aviary (outgroup member). The unfamiliar/outgroup pairings represented the first visual contact between these birds. The sequence and order of conditions were counterbalanced to account for documented circadian effects of yawning in this species (Miller et al. 2012b). The trial orders of testing were as follows: (1) an ingroup pairing starting with the visible condition and followed by the occluded condition, then an outgroup pairing starting with the occluded condition followed by the visible condition, (2) an ingroup pairing starting with the occluded condition and followed by the visible condition, then an outgroup pairing starting with the visible condition and followed by the occluded condition, (3) an outgroup pairing starting with the visible condition and followed by the occluded condition, then an ingroup pairing starting with the occluded condition followed by the visible condition, and (4) an outgroup pairing starting with the occluded condition followed by the visible condition, then an ingroup pairing starting with the visible condition and followed by the occluded condition. Four birds were tested in each trial order.

Trained researchers scored the 32 h of recordings for time spent with visual access toward the matched pair during the visible condition and all yawns across conditions. Visual attention toward the matched pair was considered present except in cases when the bird was directly facing in the opposite direction. Yawning is characterized as a wide opening of the beak with stretching of the neck, followed by a brief pause and then a passive closure (see Fig. 2). There was moderate agreement between the three raters for both attention and yawning behavior (12.5 % overlap: attention, k = 0.530; yawns, k = 0.584). Following the same criteria of a previous study on gelada baboons (Palagi et al. 2009), yawns that occurred within 5 min of a previous yawn from the adjacent bird were considered contagious. Those that occurred outside of this window were classified as spontaneous. Statistical analyses consisted of a Mann–Whitney test to assess potential differences in yawning rate between the two groups, and Wilcoxon signed-rank tests to assess differences in total attention, and contagious and spontaneous yawns between conditions. Since previous research has already shown significant observational support for contagious yawning in this species (Miller et al. 2012b), a one-tailed test was applied when comparing contagious yawns between the visual and occluded conditions. All means and SEM reported are per bird. Analyses were performed with IBM SPSS Statistics version 21 for Mac OS, with α set to 0.05.

Results: Study 1

A total of 131 yawns were recorded ($M = 8.188$, SEM = 1.137) during the 32 h of behavioral observation. There was no difference in the total yawn frequency between the green and multicolored birds ($M \pm$ SEM 8.000 ± 2.087 vs. 8.375 ± 1.085; $Z = -0.427$, $p = 0.669$), and visual attention (s) toward the adjacent bird did not vary as a function of ingroup and outgroup parings ($M \pm$ SEM 3382.87 ± 95.372 vs. 2851.81 ± 295.209; $Z = -0.785$, $p = 0.433$).

A total of 37 yawns occurred within 5 min of a previous yawn from the adjacent bird ($M = 2.31$, SEM = 0.590). As predicted, these temporally clustered yawns were more frequent when the birds could see one another (i.e., cued visually) compared to when visual access was occluded ($M \pm$ SEM 1.750 ± 0.544 vs. 0.561 ± 0.241; $Z = -1.740$, $p = 0.041$; see Fig. 3). These findings provide further evidence that this behavior is socially contagious in this species. There was, however, no difference in the number of contagious yawns between ingroup and outgroup pairings ($M \pm$ SEM 0.690 ± 0.218 vs. 1.060 ± 0.243; $Z = -0.849$, $p = 0.396$).

There was no difference between visible and occluded conditions for yawns occurring outside a 5-min window (i.e., spontaneous yawns) of a previous yawn from the matched pair ($M \pm$ SEM 3.250 ± 0.536 vs. 2.625 ± 0.591; $Z = -0.885$, $p = 0.376$). That is, in general, yawning was not more frequent when the birds could see one another. Similar to the results pertaining to contagious yawning, there was no difference in the number of spontaneous yawns between ingroup and outgroup pairings ($M \pm$ SEM 2.938 ± 0.661 vs. 2.938 ± 0.544; $Z = -0.396$, $p = 0.692$).

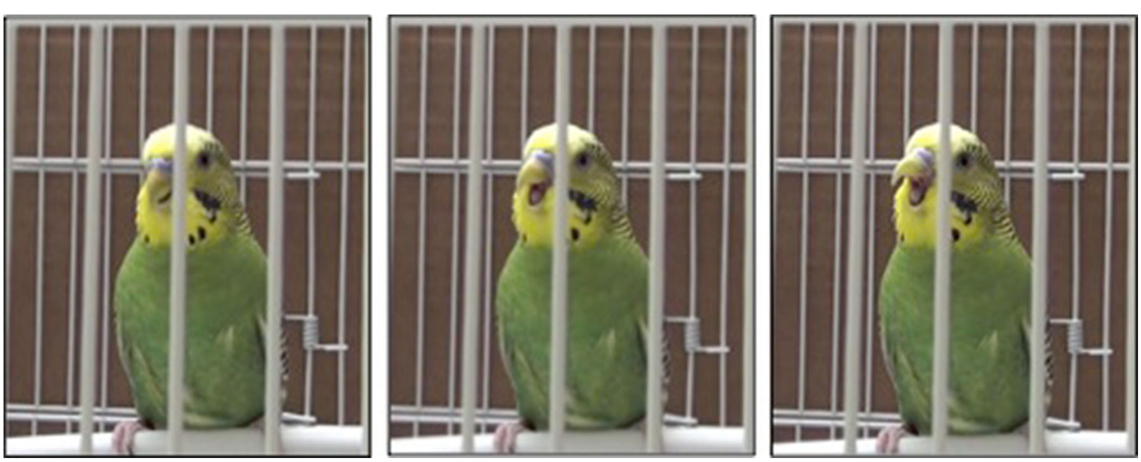

Fig. 2 Images of a budgerigar yawning (beginning to peak)

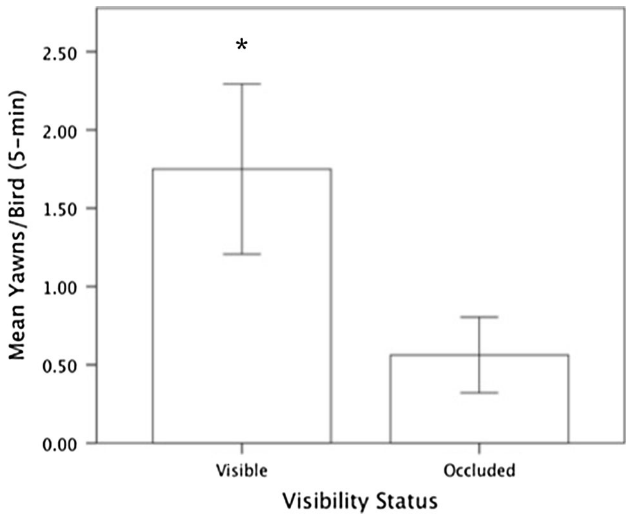

Fig. 3 Study 1. The frequency of yawning within 5 min of a previous yawn from the adjacent bird was significantly higher in the visible condition, suggesting that this behavior is contagious (M ± SEM; $*p < 0.05$)

Procedure and analysis: Study 2

Having confirmed the existence of contagious yawning using an ecologically valid approach in Study 1, the second experiment was designed to test whether video stimuli could be used to induce this response. This experiment was conducted across two successive days in December 2014. Each testing day, two independent trials were performed consecutively, in which four birds were caught from a single aviary, moved to a testing room within the vivarium, and placed as pairs in two individually housed cages connected to one another (same testing cage as Study 1; Fig. 1). A laptop computer (0.376 × 0.259 m) used to present the video stimuli was placed 0.230 m from the testing cage, and a tripod with a digital camcorder was positioned just above the display screen. As in Study 1, all other external surfaces of the cage were covered with cardboard to ensure the birds faced toward the laptop and camera. No food or water was provided during testing in order to maximize the rate of behavioral responses.

The video stimuli were created from an HD video recording of a single budgerigar perched in an isolated cage in which we identified a total of seven yawns. Because Study 1 showed no ingroup bias for contagious yawning, we did not take recordings of birds from both aviaries. Using iMovie, all yawns were extracted as individual clips ranging from 2.5 to 4.5 s. These clips were then multiplied, randomized, and coupled together to form a contagious yawning stimulus (4 min, 26 s). Using the same HD video, seven matched non-yawning clips were extracted, multiplied, and coupled together to form a comparison control stimulus (4 min, 32 s). During the experiment, each stimulus was set to repeat using Microsoft Windows Media Player during the respective conditions. Testing within groups was not a methodological concern given that even if the birds responded contagiously to the yawns from cage mates, it would be expected that the frequency of these behaviors would be lower in the control condition.

After being caught and transferred to the testing room, the birds were provided a 45-min acclimation period. The first 15 min of this period included a muted display of a national geographic video of penguins accessed from www.youtube.com. This video was presented to habituate the birds to a video presentation. Following this, the birds were presented with consecutive 15-min displays of the experimental and control stimuli (order counterbalanced). The first 5 min of each stimulus was treated as an additional acclimation period, since this represented the first video footage of a conspecific presented to these birds. This also allowed us to account for a brief interruption with the manual transition from the first to the second stimulus display on the laptop. Unlike Study 1, a trained researcher remained in the testing room to coordinate the display of video stimuli. In total, this provided 10 min of behavioral recording for each condition.

Each day, the first group of birds was caught at 1345 hours (Time 1) and released at 1500 hours. Immediately following this, the second group was caught and positioned in the testing cage at 1515 hours (Time 2). The second group followed the same procedures as the first before being released at 1630 hours. On the first testing day, two groups of four green birds were tested, and the next day, the eight remaining multicolored birds were tested in two additional independent trials. The trial and condition order were counterbalanced to control for documented circadian effects of yawning in this species (Miller et al. 2012b). The order of testing was as follows: (1) Time 1, control–experimental, (2) Time 2, experimental–control, (3) Time 1, experimental–control, and (4) Time 2, control–experimental. Four birds were tested in each trial order.

A trained researcher, blind to the condition, scored the subsequent recordings for time spent attending toward the video display (s) and all yawns. Self-directed behaviors (scratching and preening) were also recorded as a measure of anxiety or stress between conditions, yet these were very infrequent (see below). A second independent rater showed moderate to perfect agreement when scoring these videos (25 % overlap: attention, k = 0.583; yawning, k = 0.882 and self-directed behaviors, k = 1.000). Statistical analyses consisted of a Mann–Whitney test to compare the yawning frequency between the two groups of birds and Wilcoxon signed-rank tests to assess differences in total attention and yawns between conditions. Similar to Study 1, a one-tailed test was applied when comparing yawns between experimental and control conditions. All means and SEM reported are per bird. Analyses were performed with IBM SPSS Statistics version 21 for Mac OS, with α set to 0.05.

Results: Study 2

A total of 26 yawns were recorded across the 80 min of behavioral observation ($M = 1.625$, SEM = 0.531). There was no difference in yawn frequency between the green and multicolored groups ($M \pm$ SEM 1.000 ± 0.732 vs. 2.250 ± 0.750; $Z = -1.494, p = 0.135$), and the time spent attending to the video stimulus (s) did not vary between the control and experimental conditions ($M \pm$ SEM 536.25 ± 32.926 vs. 567.25 ± 13.203; $Z = -0.628$, $p = 0.530$). As predicted, yawning frequency was significantly higher during the presentation of the experimental (yawning) stimulus ($M \pm$ SEM 1.188 ± 0.430 vs. 0.438 ± 0.157; $Z = -1.897$, $p = 0.029$; see Fig. 4). Only five self-directed behaviors were recorded across the entire observation period (three occurring in the control condition and two in the experimental), suggesting that stress/anxiety was not contributing to this effect. Thus, these findings demonstrate that contagious yawning can be manipulated experimentally in this species through the use of visual stimuli.

Discussion

Yawning in response to sensing or thinking about the action in others may represent a primitive form of empathy. Despite the potential importance of identifying various non-human species showing this capacity, comparative investigations of contagious yawning have been limited. These two experimental studies reveal the presence of contagious yawning in budgerigars in a controlled laboratory setting, corroborating a previous observational report assessing the temporal distribution of yawns in an undisturbed flock (Miller et al. 2012b). The experiment in Study 1 provides an ecologically valid measure of social contagion utilizing the signaling of a live demonstrator producing real yawns (improving upon Wilkinson et al. 2011). Temporally classified contagious yawns during these trials (i.e., those occurring within 5 min of a yawn from the matched pair) occurred more than three times as often when the birds could see one another, whereas there was no difference in the frequency of spontaneous yawning across visibility conditions. The experiment in Study 2 used a more traditional laboratory-based methodology for testing contagious yawning (e.g., Anderson et al. 2004), by presenting small groups of birds with repeated video clips of conspecific yawns and control behavior. In comparison with matched control stimuli, budgerigars in this experimental condition yawned more than twice as often and this response was not linked with indicators of stress or anxiety (i.e., self-directed behaviors). It is important to note, however, that this represents a modest effect given the magnitude of the video stimulus (over 150 yawns were displayed during the 10-min experimental session).

We found no evidence of an ingroup bias for contagious yawning in budgerigars. That is, yawns appeared similarly contagious between birds housed within the same aviary and across outgroup pairs. Previous experiments on chimpanzees and domesticated dogs have demonstrated mixed support for a familiarity bias in contagious yawning (Campbell and de Waal 2011; Romero et al. 2013; Silva et al. 2012; but see Madsen et al. 2013; Madsen and Persson 2013), while observational studies on primates (human and non-human) and wolves have shown a positive association with social closeness and affiliation (Demuru and Palagi 2012; Norscia and Palagi 2011; Palagi et al. 2009, 2014; Romero et al. 2014). There may be reasons to suspect that budgerigars would be less sensitive to familiarity or social closeness for various forms of state matching since they naturally live in much larger, more fluid groups of unrelated individuals than the abovementioned species and can form flocks of over 1000 coordinated members in the wild (Wyndham 1980). Conversely, we have recently discovered evidence of an ingroup bias for stretching in this species (unpublished data), a more overt behavior directly relevant to flocking. It remains possible that limitations in the current study do not permit a true comparison to the documented ingroup/outgroup effects of contagious yawning in other species. For example, since all of the budgerigars were housed in the same room, this permitted vocal communication between the two

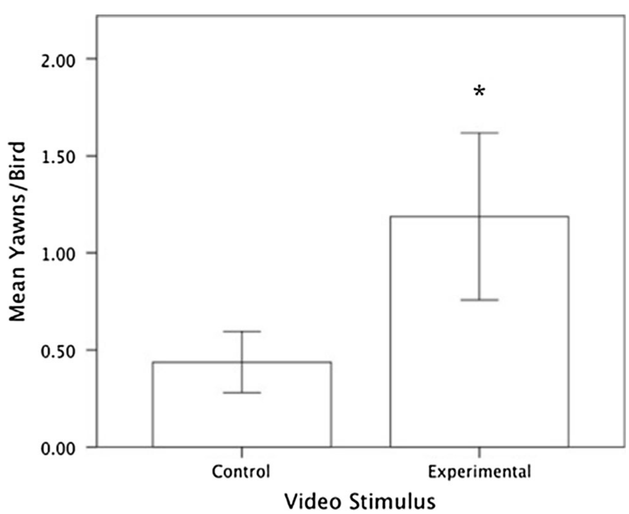

Fig. 4 Study 2. The frequency of yawning was significantly higher during the presentation of the experimental (yawn) stimulus, demonstrating that contagious yawning can be experimentally manipulated (M ± SEM; *$p < 0.05$)

groups and perhaps created some degree of familiarity or social affiliation prior to testing. Previous research has demonstrated that vocal call convergence occurs among budgerigars housed in captivity (Farabaugh et al. 1994; Hile et al. 2000), though in our study, vocalizations between the pairs were uncommon to nonexistent. Another limitation to the current study was that the degree of social closeness between cage mates was not recorded prior to the experiment, so this effect could not be assessed along a continuum.

In summary, budgerigars represent the first non-mammalian species, and only the fifth species to date (including humans, chimpanzees, domesticated dogs, and a subline of high-yawning Sprague–Dawley rats), to show contagious yawning in an experimentally controlled setting. These findings provide an example of convergent evolution. Given the association between contagious yawning and empathy, we suggest additional comparative research be conducted to assess the prevalence of contagious yawning in other social vertebrates. Furthermore, since empathic responses have already been demonstrated in avian species (e.g., Edgar et al. 2011; Wascher et al. 2008), and the current findings show that contagious yawns can be experimentally manipulated, we propose that budgerigars represent a good model for exploring primitive forms of empathic processing.

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