

No evidence for contagious yawning in lemurs

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Abstract Among some haplorhine primates, including humans, relaxed yawns spread contagiously. Such contagious yawning has been linked to social bonds and empathy in some species. However, no studies have investigated contagious yawning in strepsirhines. We conducted an experimental study of contagious yawning in strepsirhines, testing ring-tailed and ruffed lemurs ($n = 24$) in a paradigm similar to one that has induced contagious yawning in haplorhines. First, in a control experiment, we investigated whether lemurs responded to projected video content in general (experiment 1). We showed them two videos to which we expected differential responses: one featured a terrestrial predator and the other a caretaker holding food. Next, to test for yawn contagion, we showed individual lemurs life-size video projections of groupmates and conspecific strangers yawning, and control footage of the same individuals at rest (experiment 2). Then, to examine whether a group context might enhance or allow for contagion, we exposed subjects to the same videos in a group setting (experiment 3). Lemurs produced alarm vocalizations and moved upward while viewing the predator, but not the caretaker, demonstrating that they do perceive video

content meaningfully. However, lemurs did not yawn in response to yawning stimuli when tested alone, or with their groupmates. This study provides preliminary evidence that lemurs do not respond to yawning stimuli similarly to haplorhines, and suggests that this behavior may have evolved or become more exaggerated in haplorhines after the two major primate lineages split.

Keywords Contagious yawning · Lemurs · Strepsirhine · Emotional contagion

Introduction

Yawning is an activity common to most vertebrates (Baenninger 1997; Smith 1999; Gallup 2011) yet its physiological and social functions are still debated. For instance, yawning is purported to prevent respiratory infections and to increase oxygen levels in the blood and brain (Baenninger 1997; Smith 1999; Gallup 2011). In some species, yawns also convey important social or emotional information. A yawn might be given, for example, by a male baboon (*Papio cynocephalus*) during a threatening dominance display (Altmann 1967), by a captive chimpanzee who has just heard social commotion among her neighbors (Baker and Aureli 1997) or by a pet dog who is anxious when separated from his owner (Lund and Jørgensen 1999). Animals may also produce different types of yawns in different contexts. For example, after social conflicts, gelada monkey males often vocalize and then yawn, showing their canines, while female geladas yawn when affiliatively lip-smacking and grooming others (Leone et al. 2014).

Sometimes, however, yawns appear to serve no clear physiological or social function. In these cases, for many

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species, including those described above, yawns that occur in a relaxed context spread contagiously from individual to individual (Palagi et al. 2009). In humans, yawn contagion is so powerful that people yawn when watching videos of others yawning, when reading about yawning, or when being instructed to think about yawning (Provine 1986). Such non-conscious contagion has been linked to a basic level of empathy (de Waal 2008). The connection to empathy is supported by evidence in humans: subjects who yawn in response to videos of others yawning have fewer schizotypal personality traits and exhibit better perspective-taking skills (Platek et al. 2003). In addition, contagious effects are more powerful among individuals who share social bonds. For instance, humans are more likely to yawn in response to the yawns of friends and family than acquaintances (Norscia and Palagi 2011). Given its connection to empathy and sociality, comparative data on contagious yawning may yield insights into social and cognitive evolution.

It is important to note that while species from birds, to fish, to snakes produce long, gaping mouth movements that we identify as yawns, it is unclear whether those movements represent the same physiological processes across taxa (Baenninger 1997; Smith 1999). For instance, among mammals, carnivores seem to yawn more frequently than herbivores (Baenninger 1997). Although yawning may serve different functions across species, contagious yawning is nevertheless found in a wide range of species.

Observational studies have found contagious yawning in taxa as diverse as birds and bonobos. In captivity, budgerigars, which form cohesive flocks in the wild, are observed to yawn and stretch after conspecifics have yawned and stretched (Miller et al. 2012). Wolves also contagiously yawn, doing so more often if they share a close social bond with the initial yawner (Romero et al. 2014). Among primates, captive bonobos and geladas are more likely to yawn after conspecifics do, particularly if those conspecifics are kin or preferred social partners (Palagi et al. 2009, 2014; Demuru and Palagi 2012).

Contagious yawning can also be induced experimentally. Both chimpanzees and stump-tail macaques yawn when shown videos of yawning conspecifics (Anderson et al. 2004; Paukner and Anderson 2006; Amici et al. 2014). Importantly, authors noted that these stump-tail macaques also displayed nervous behaviors while yawning, suggesting that yawns produced could have been motivated by social stress, so it is unclear whether these yawns were induced by empathy-like capacities (Paukner and Anderson 2006). In a similar video playback experiment, chimpanzees were more likely to yawn after watching footage of a yawning groupmate than a yawning stranger (Campbell and de Waal 2011).

Contagious yawning is not only induced by conspecifics. Captive chimpanzees with human caretakers are more likely to yawn in response to a familiar chimpanzee or human than to an unfamiliar chimpanzee (Campbell and de Waal 2014). Dogs may yawn when watching a human experimenter yawn in person (Joly-Mascheroni et al. 2008) and do so more often when the human is familiar (Romero et al. 2013; although see Harr et al. 2009a, b; O'Hara and Reeve 2011). These interspecific results further emphasize the possibility that emotional bonds influence contagious behavior since dogs may be closely bonded to their human owners and captive apes to their human caretakers.

Understanding how and when such rudimentary empathetic capabilities evolved is key to understanding the evolution of complex social cognition, as both empathy and cognition are entwined with the evolution of sociality (Seyfarth and Cheney 2013). The comparative method affords a powerful approach for answering questions about how, when, and why particular cognitive capabilities have evolved (MacLean et al. 2012a, b, 2014). This approach requires data from broad phylogenetic samples in order to estimate the evolutionary origins of particular traits. Among our closest relatives, nonhuman primates, only haplorhines have been the focus of research on contagious yawning. No study has examined whether contagious yawning occurs in strepsirhines—the other major primate lineage including lemurs, lorises, galagos, and pottos. Therefore, comparative data from strepsirhines will bear importantly on whether contagious yawning is common to all primates or unique to the haplorhine lineage.

Compared to haplorhines, little is known about yawning behavior in general in strepsirhine primates. However, a recent study closely examined the context of yawns that occurred among wild ring-tailed lemurs (*Lemur catta*) and Verreaux's sifakas (*Propithecus verreauxi*) (Zannella et al. 2015). Like many animals described above, lemurs of both species yawned after events expected to produce anxiety, such as within-group aggressive incidents, encounters with unfamiliar stimuli, or attacks by predators (Zannella et al. 2015). These recent findings corroborate previous reports that ring-tailed lemurs occasionally yawn during intergroup encounters (Pereira and Kappeler 1997; Nunn and Deaner 2004). In addition to yawning when anxious, both ring-tailed lemurs and sifakas, like other animal species, yawned when they changed behavioral state in relaxed contexts, such as rising from rest to walk to a nearby place (Zannella et al. 2015).

Here, we used a video playback experiment comparable to those used in haplorhines to determine whether contagious yawning occurs in free-ranging, captive ring-tailed lemurs and ruffed lemurs (*Varecia variegata*) in relaxed settings. Ring-tailed lemurs form large, hierarchical, cohesive social groups (Sauter et al. 1999), while ruffed

lemurs live in fission fusion communities (Vasey 2007). Given their complex social systems, these two species are ideal candidates to test whether contagious yawning occurs in strepsirhines.

The evidence for contagious yawning in haplorhines as well as several diverse non-primate species suggests that the phenomenon is evolutionarily ancient and would thus appear in strepsirhine as well as haplorhine primates. Furthermore, lemurs show evidence of social learning (Stoinski et al. 2011; Kendal et al. 2010) and other forms of complex social cognition (Sandel et al. 2011; MacLean et al. 2012a, b; Bray et al. 2014), suggesting that they likely possess basic empathetic processes. Thus, we expected that both ring-tailed lemurs and ruffed lemurs would demonstrate contagious yawning.

Methods

Experiment 1: Video stimulus validation

We modeled our approach after experimental paradigms used in monkeys and apes that rely on video stimuli to test contagious yawning (Anderson et al. 2004; Paukner and Anderson 2006; Amici et al. 2014). Many species respond to behaviors presented in videos, and, as lemurs have been shown to make appropriate choices between still onscreen images (MacLean et al. 2008, 2012a, b; Merritt et al. 2007, 2011), and to discern a conspecific's identity from photographs (Marechal et al. 2010), it is likely that lemurs are capable of perceiving individuals on a screen. However, lemurs also heavily rely on olfactory cues to gather social information (e.g., Drea and Scordato 2008) and no previous study that we are aware of has used video playbacks to induce behavioral responses in lemurs. Thus, we performed experiment 1 to test whether lemurs could meaningfully perceive moving images on a screen.

We exposed lemur subjects to video playbacks for which we expected them to produce differential responses: footage of a predator and footage of their primary human caretaker. These lemurs occasionally encounter several potential predator species in their free-ranging enclosures, including wild gray foxes (*Urocyon cinereoargenteus*). Upon seeing these foxes, ruffed lemurs become attentive and emit vocalizations (RBR, pers. obs.). When lemurs see their caretakers, they tend to approach them or do not change their behavior (RBR, pers. obs.).

Study site and subjects

For this and the subsequent experiments, we tested lemurs housed at the Duke Lemur Center in Durham, North Carolina, USA. Most social groups consisted of 5–10

individuals living in semi free-ranging enclosures with seasonal access to fenced portions of forest as well as indoor and outdoor rooms. Testing took place in indoor rooms, which were connected by doors that experimenters could open and close. Individual room dimensions were 2.2 × 2.1 m and groups typically had one outdoor and one indoor enclosure per adult individual. Subjects were fed a daily diet of fruit and monkey chow and had access to water ad libitum.

In experiment 1, we tested 28 subjects (ring-tailed lemurs: 7 M, 10 F, 0.7–21 years; ruffed lemurs: 4 M, 7 F, 0.8–16 years) (Table 1).

Table 1 Lemur subjects in all experiments

Group	Subject	Species	Sex	Age (years)	S1	S2	E2
1	Pyxis	<i>V v. rubra</i>	F	17	X	X	X
1	Hunter	<i>V v. rubra</i>	M	16	X	X	X
1	Scorpius	<i>V v. rubra</i>	M	5	X	X	X
1	Aries	<i>V v. rubra</i>	M	5	X	X	X
1	Esther	<i>V v. rubra</i>	F	3	X	X	X
1	Orion	<i>V v. rubra</i>	M	3			X
1	Phoebe	<i>V v. rubra</i>	F	3	X	X	X
2	Carina	<i>V v. rubra</i>	F	8	X	X	X
2	Alphard	<i>V v. rubra</i>	M	23	X		
2	Avior	<i>V v. rubra</i>	M	4			X
2	Hydra	<i>V v. rubra</i>	F	4	X		
2	Lyra	<i>V v. rubra</i>	F	4	X	X	X
2	Pandora	<i>V v. rubra</i>	F	<1		X	X
2	Cordelia	<i>V v. rubra</i>	F	<1		X	X
3	Schroeder	<i>L. catta</i>	F	20	X	X	X
3	Edelweiss	<i>L. catta</i>	F	2	X		
3	Liesl	<i>L. catta</i>	F	4	X	X	X
3	Aracus	<i>L. catta</i>	M	21	X	X	X
3	Johan	<i>L. catta</i>	M	2			X
3	Rolfe	<i>L. catta</i>	M	1	X	X	X
3	Brigitta	<i>L. catta</i>	F	1		X	X
3	Gretl	<i>L. catta</i>	F	<1		X	X
4	Sprite	<i>L. catta</i>	F	11		X	X
4	Ginger	<i>L. catta</i>	F	6	X	X	X
4	Randy	<i>L. catta</i>	M	6	X	X	X
4	Schweppes	<i>L. catta</i>	M	2			X
4	Sobe	<i>L. catta</i>	F	1		X	X
4	Sarsaparilla	<i>L. catta</i>	F	1		X	X
4	Crystal light	<i>L. catta</i>	F	2	X		
4	Canada dry	<i>L. catta</i>	F	1	X	X	X
4	Izze	<i>L. catta</i>	F	<1		X	X
4	Jones	<i>L. catta</i>	M	<1		X	X
4	Stewart	<i>L. catta</i>	M	<1		X	X

Apparatus and procedure

We showed lemurs two silent video clips, both 30 s in length. One clip showed footage of a red fox (*Vulpes vulpes*) walking, and the other, footage of subjects' caretaker presenting a bowl of grapes. Using a Vivitek d510 DLP projector, we projected videos to life-size dimensions onto a 2.2-m screen placed outside the mesh of an indoor room. We allowed group members to remain together in the brick-walled room during the video playback. We chose not to isolate individuals because predator response could be mediated by the presence of groupmates and because viewing a predator might be a stressful experience for lemurs.

Groups had four total test sessions conducted on separate days, 2 days–3 weeks apart. In each session, the group watched a single video that featured either a fox or their caretaker. Each group spent two sessions watching the fox video and two watching the caretaker video. The order in which subjects watched the videos was counterbalanced between groups. Before starting each video, we scattered dried fruit on the ground at the front of the enclosure to encourage individuals to be on the ground when the video began. We began the playback when all lemurs had finished swallowing and no fruit remained on the ground. As a result of group dominance relationships, certain individuals would not co-feed, and some lemurs remained resting on ledges or supports above the ground when the video started.

During test sessions, one experimenter recorded subjects' activities with a handheld camera, while a second experimenter coded behavioral responses. A second camera captured most of the enclosure at a wide angle. We filmed for the duration of the 30-s video playback and for two subsequent minutes.

An experimenter then coded behavioral responses from video. From these videos, we recorded (1) whether subjects moved upward, defined as moving vertically into a new level of the testing room when the room was divided into three levels: lower, middle, and upper, during the 30-second video, and (2) the alarm vocalizations they made during the video playback and for 1.5 min following its conclusion. For ring-tailed lemurs, who may produce alarm "click" or grunt-like vocalizations in response to terrestrial predators (Sauther 1989) we recorded the amount of time in the 2-min period that grunts were audible from the group. As ring-tailed lemurs do not open their mouths when they produce these grunts, it was impossible to score the vocalizations at the individual level. For ruffed lemurs, we recorded the number of alarm vocalizations made by specific individuals. Vocalizations could be attributed to specific individuals in ruffed lemurs due to the open-mouth postures that accompany vocalizations in this species

(Macedonia and Taylor 1985). These vocalizations included rumbling sounds, often made by one individual, and roars, in which multiple group members typically participated.

A second coder who was blind to the condition and hypothesis coded 20 % of the videos for reliability. Inter-observer reliability was excellent, both for subjects' movement during the trial (Cohen's Kappa = 0.92), the duration of alarm vocalizations in ring-tailed lemurs ($R = 0.73$, $p < 0.05$), and the number of alarm vocalizations in ruffed lemurs, for which agreement was perfect.

Analyses

We tested the prediction that more upward movement and alarm vocalizations would occur in the fox condition compared to the caretaker condition using related samples Wilcoxon signed-rank tests and adopting a directional hypothesis testing framework following the conventions ($\delta = 0.01$, $\Upsilon = 0.04$) recommended by Rice and Gaines (1994). Accordingly, the null hypothesis was rejected when the one-tailed p value was ≤ 0.04 in the predicted direction, or ≥ 0.99 in the unanticipated direction.

Experiment 2: Contagious yawning

Session 1: Individual condition

Here we explored whether ring-tailed lemurs and ruffed lemurs yawned contagiously by exposing individuals to video projections of yawning conspecifics. To understand whether social bonds and familiarity might affect contagious behaviors (e.g., Campbell and de Waal 2011), each subject watched footage of a groupmate and footage of a stranger.

Subjects

We tested 20 lemurs (ring-tailed lemurs, three males, seven females, age range 1–21 years; ruffed lemurs: four males, six females, age range 2–22 years) living in four social groups that were housed separately from one another (Table 1).

Apparatus and procedure

In experiment 2, we showed lemurs experimental and control videos. The projection methods were identical to those in experiment 1. Experimental videos contained footage of a lemur yawning, while control videos showed the same individual at rest. We filmed both yawning and control footage when animals were relaxed. All videos contained a 5-s yawning or control clip that was repeated in

a looped sequence for a total duration of 5 min. Example frames from these videos are shown in Fig. 1. The lemurs featured in these videos were the same sex and of similar age. They were current groupmates of some subjects but strangers to others so that footage shown to one lemur group as a groupmate could be shown to the other lemur group as a stranger, and all subjects of a given species experienced identical stimuli.

Each subject partook in two testing sessions up to 2 weeks apart. In each session, subjects watched an experimental (conspecific yawning) and control (conspecific resting) video; in one session, the featured individual was a groupmate, and in the other, a stranger. The order in which subjects watched groupmates and strangers was counterbalanced between subjects, as was the order in which they watched yawning and control stimuli within each of these sessions.

Yawning and control sessions were identical in format. We tested subjects in brick-walled rooms so that they could not view their groupmates, though they could potentially hear them if they vocalized. To attract subjects' attention at the start of each playback, an experimenter tapped lightly on the back of the projector screen. We began each session with a 1-min habituation period during which a solid blue "blank" screen was projected. After this time, we played either the yawning or control video for 5 min. Immediately following the first video, we projected the blank screen for 1 min and then played the second video for 5 min.

One experimenter live-coded the number of yawns that occurred in each video condition, while a second experimenter recorded the subject with a handheld video camera that was focused on the subject's face as the subject moved freely within the test room. Another camera captured the enclosure and subject in its entirety. A second coder who

was blind to the test condition and to the hypothesis of the experiment watched 20 % of the videos and coded them for reliability. Inter-observer reliability was perfect.

Session 2: Group context

In a second experimental session, lemurs watched videos in a group. It may be that social context is an important component of behavioral contagion, and a solitary context is insufficient to stimulate contagious yawning, as some studies that identified contagious yawning in haplorhine primates tested subjects simultaneously in a group setting (e.g., Paukner and Anderson 2006). To understand whether a group context might enhance, or allow for behavioral contagion in lemurs, we exposed subjects to the yawning and control videos they had watched in experiment 1, but this time, we presented the videos to the entire group.

Subjects

We tested 24 lemurs (ring-tailed lemurs: 7 M, 10 F, 0.7–21 years; ruffed lemurs: 4 M, 7 F, 1–16 years) in experiment 2, most of whom had participated in session 1 (Table 1). Certain individuals from session 1, who had been moved from the DLC, or integrated into new social groups within the DLC, were not able to participate in session 2. In addition, some lemurs who had been too young to be isolated in session 1 could participate in session 2.

Eight months elapsed between the end of session 1 and start of session 2. The stimuli and presentation methods for session 2 were identical to those of session 1, except that in session 2, subjects of the four study groups watched the

Fig. 1 Frames from yawning stimuli video (*left*) and control stimuli video (*right*) of ruffed lemurs (*top*) and ring-tailed lemurs (*bottom*)



videos with all of their group members present, including individuals who were featured in stimuli videos.

Each group had two test sessions: one in which they watched yawning and control footage of a groupmate and one in which they watched yawning and control footage of a stranger. The order in which we showed yawning and control footage was counterbalanced between groups within species. The order in which groups watched groupmate and stranger videos was also counterbalanced between groups.

Experimenters live-coded the number of yawns that occurred during all test sessions and the identities of the yawners. A second coder who was blind to the test condition and to the hypothesis of the experiment coded 20 % of session videos for reliability. Inter-observer reliability was perfect.

Results

Experiment 1: Video stimulus validation

Across species, individuals moved to a higher location in the enclosure more often in the fox condition than in the caretaker condition ($n = 28$, $Z = -2.89$, $p < 0.01$) (Fig. 2). The same analysis within each species revealed that ring-tailed lemurs, but not ruffed lemurs showed a pattern to move upwards more often during the fox than the caretaker video (ring-tailed lemurs: $n = 17$, $Z = -3.00$, $p < 0.01$; ruffed lemurs: $n = 11$, $Z = -0.58$, $p = 0.28$). This is possibly because more ring-tailed lemur than ruffed lemur individuals began watching the video from the ground.

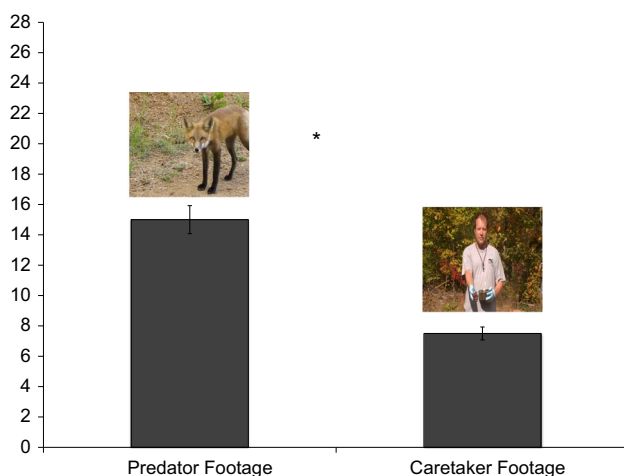


Fig. 2 Average number of individuals to move up while watching predator video footage and caretaker video footage in experiment 2 ($n = 28$)

Ring-tailed lemurs spent more time alarm grunting in the fox condition than in the caretaker condition, grunting, on average, for 58 ± 48.8 s in the fox condition compared to 17 ± 18.4 s in the caretaker condition. Ruffed lemurs also made significantly more alarm vocalizations in the fox condition than in the caretaker condition ($n = 11$, $Z = -2.39$, $p = 0.01$) (Fig. 3). Only one individual vocalized in the caretaker condition. There were a total of 30 alarm vocalizations in the fox condition, with an average of 2.73 ± 5.0 calls per individual, and a total of three alarm vocalizations in the caretaker condition, with an average of 0.27 ± 0.91 calls per individual.

Experiment 2: Contagious yawning

In the individual yawning sessions, only one yawn occurred across all 20 individuals in all four conditions. An adult female ruffed lemur yawned once in the stranger yawning condition. In group yawning sessions, only two yawns occurred across all 24 individuals in all four conditions. Two ruffed lemurs each yawned once during the stranger yawning condition (Fig. 4).

Discussion

Lemurs did not yawn contagiously in response to videos of yawning groupmates or strangers. Our findings are consistent across individual and group contexts, with large samples, and between two of the most socially complex strepsirrhine species. However, lemurs did demonstrate that they respond meaningfully to video footage in general; they moved upward and made alarm calls while viewing

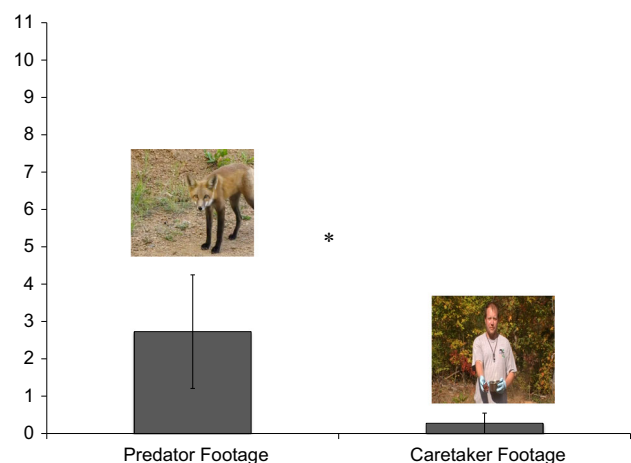


Fig. 3 Average number of alarm calls per individual ruffed lemurs ($n = 11$) while watching predator and caretaker video footage in experiment 2

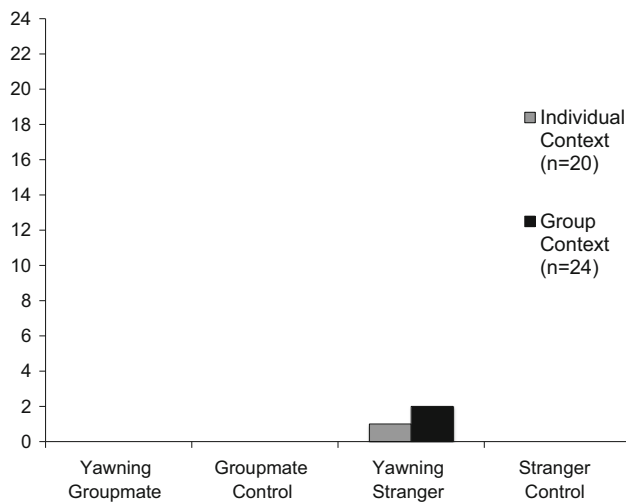


Fig. 4 Number of individuals who yawned in individual and group contexts in experiment 2

footage of a predator but not a caretaker. This study provides the first evidence that lemurs do not respond to yawning video stimuli in the same way as haplorhine primates, and suggests the possibility that strepsirhines do not yawn contagiously.

Given that many social animals, including wolves and budgerigars in addition to haplorhine primates, yawn contagiously with conspecifics, it seems surprising that lemurs did not do so. However, several aspects of interindividual social relationships in lemurs differ in relevant ways from those of haplorhines and other social mammals. First, even lemur species that live in large social groups appear to engage in fewer cooperative activities than haplorhines and are characterized by more within-group competition (for review, see: Fichtel and Kappeler 2010). For example, ring-tailed lemurs form matrilineal groups where females, like female Old World monkeys, affiliate most often with kin, grooming with them and maintaining close spatial proximity to them frequently. Despite the similarities of these affiliative kin behaviors, ring-tailed lemurs, unlike Old World monkeys, rarely recruit or assist others in coalitionary aggression. Ring-tailed lemur mothers rarely support even their daughters in fights (<5 % of the time, Nakamichi and Koyama 1997). Consequently, ring-tailed lemur daughters, unlike Old World monkey daughters, do not always rank immediately below their mothers (Nakamichi and Koyama 1997). The absence of such alliances in lemurs contrasts not only to certain Old World monkeys, but to many social mammals who form coalitions against others, including chimpanzees and wolves discussed above (for review, see: Harcourt and De Waal 1992).

In addition to a lack of alliances, lemurs show minimal post-conflict affiliation with other individuals (Fichtel and

Kappeler 2010). After aggressive conflicts, individuals of a wide range of species show increased affiliation with their former opponents or with other groupmates, including baboons (Castles and Whiten 1998), long-tailed macaques (Aureli and van Schaik 1991), chimpanzees (De Waal and van Roosmalen 1979), dolphins (Tamaki et al. 2006), rooks (Seed et al. 2007), domestic horses (Cozzi et al. 2010), goats (Schino 1998), hyenas (Hofer and East 2000), dogs (Cools et al. 2008), and wolves (Cordoni and Palagi 2008). This affiliation is thought to reduce anxiety and future aggression (e.g., Castles and Whiten 1998) and has implications for group cohesion.

Several captive studies have examined post-conflict affiliation in ring-tailed lemurs specifically. One study found no evidence for affiliation in the 10 min following a conflict, a typical time length examined in species above (Kappeler 1993), but a follow-up study on the same group observed opponents for 70 min post-conflict and found that more affiliation occurred in post-conflict periods compared to control periods (Rolland and Roeder 2000). A later study reexamined post-conflict association in ring-tailed lemurs at the dyadic level with a larger sample size and found that breeding seasonality may influence the behavior: pairs of ring-tailed lemurs showed increased affiliation after a conflict in the social group with breeding females but not in the social group with lactating females who are less likely to be tolerant of males (Palagi et al. 2005). Other lemur species, including redfronted brown lemurs and Verreaux's sifakas, do show some post-conflict affiliation (Kappeler 1993; Palagi et al. 2008). Post-conflict association has not to our knowledge been studied in ruffed lemurs, but like ring-tailed lemurs, this species also experiences seasonal shifts in social behavior (Vasey 2007).

Given these peculiarities of lemur social relationships, one interpretation of our main result is that contagious yawning capabilities evolved in haplorhine primates after the lineage split from strepsirhines and that the phenomenon seen in other distantly related vertebrates like budgies and wolves is the result of convergent evolution linked to the social relationships between individuals in these species; budgerigars form cohesive flocks and wolves are obligate carnivores that acquire food by hunting cooperatively with groupmates (Wyndham 1980; Peterson and Ciucci 2003). Another possibility is that contagious yawning occurred at very low levels in a primate ancestor and became exaggerated as the result of selection in some social species and not others. In our study, yawns occurred infrequently, but importantly, they occurred exclusively in conditions where lemurs watched yawning stimuli. Although this evidence certainly does not suggest that contagious yawning is a strong phenomenon in lemurs, it is consistent with the possibility that contagious yawning is evolutionarily ancient but has evolved to be more prevalent

and easily elicited in haplorhines and other social species, but not in ring-tailed or ruffed lemurs.

An alternative explanation for our results is that lemurs *do* yawn contagiously but that visual stimuli alone are not sufficient to induce such behavior. Some research suggests that this is the case for pet dogs. Joly-Mascheroni et al. (2008) found that 72 % of dogs tested yawned contagiously in response to a live human who yawned, but in a later study Harr et al. (2009a, b) showed 15 dogs video footage of unfamiliar dogs and humans yawning and only one subject yawned contagiously. Video was insufficient to produce contagious yawning in dogs. Yet, dogs, like lemurs in this study, do produce responses to video in other contexts. For instance, dogs pay attention to a familiar human's communicative cues that occur onscreen (Pongrácz et al. 2003). This suggests that dogs can perceive and respond to the content of videos, but that a contagious yawning response requires additional cues. For instance, Silva et al. (2012) found that auditory cues were integral to the contagious yawning response in dogs; auditory playbacks of humans yawning alone caused dogs to contagiously yawn.

Like pet dogs, lemurs may produce some but not all natural behaviors in response to video alone, but require other cues, not conveyed in video, to yawn contagiously. Our videos did not include sounds and it is possible that auditory cues are important for contagious yawning in lemurs. However, unlike dog yawns, lemur yawns are silent to human observers and solely visual playbacks did induce yawning in apes and in stump-tail macaques (e.g., Anderson et al. 2004; Paukner and Anderson 2006), though visual stimuli are perhaps relatively more salient to haplorhine compared to strepsirhine primates who use olfaction to communicate important social information (e.g., Drea and Scordato 2008). Olfactory cues can induce yawning in rodents (Moyaho et al. 2015) and lemurs sometimes yawn when presented with sticks scent-marked by other lemurs (Sandel, pers. comm.), though, importantly, these yawn responses do not occur in response to the yawns of groupmates and likely represent phenomena different than empathy-related contagious yawning investigated here. Issues of the importance of auditory, olfactory, and other cues in potentially inducing contagious yawning in lemurs could be informed through an observational study of yawning in lemur social groups.

We hope this study will be the first of many that explore across a range of species the distribution of contagious yawning in order to understand its phylogenetic origin and ultimate function (MacLean et al. 2012a, b).

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the Institutional Animal Care and Use Committee at Duke University (Protocol # A199-11-08).

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