No Evidence for Contagious Yawning in Lemurs

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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 & Aureli 1997) or by a pet dog who is anxious when separated from his owner (Lund & Jorgensen 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 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 et al. 2008). The connection to empathy is supported by evidence in humans: subjects who yawn in response to videos of others yawning have fewer schizotypical 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 & 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; Demuru & Palagi 2012; Palagi et al. 2014).

Contagious yawning can also be induced experimentally. Both chimpanzees and stumptail macaques yawn when shown videos of yawning conspecifics (Anderson et al. 2004; Paulkner and Anderson 2006; Amici et al. 2014). Importantly, authors noted that these stumptail 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 (Paulkner 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 & deWaal 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 & DeWaal 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. 2009; O'Hara & 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 & 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. 2012; MacLean et al. 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 strepsirrhines 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 (Zanella et al. 2015). These recent findings corroborate previous reports that ring-tailed lemurs occasionally yawn during intergroup encounters (Pereira & Kappeler 1997; Nunn & 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 (Sauther 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 strespirhine 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. 2013; 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; Paulkner & 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; 2012; 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 & Scordato 2007) 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 to 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 x 2.1 meters 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).

Apparatus & Procedure

We showed lemurs two silent video clips, both 30 seconds 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-meter 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, two days to three 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-second 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 minutes 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-minute 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 & 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 Ranks Tests and adopting a directional hypothesis testing framework following the conventions ($\delta = 0.01$, $Y = 0.04$) recommended by Rice and Gaines (1994). Accordingly, the null hypothesis was rejected when the 1-tailed p value was $\leq .04$ in the predicted direction, or $\geq .99$ 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 & deWaal 2011), each subject watched footage of a groupmate and footage of a stranger.

Subjects:

We tested 20 lemurs (ring-tailed lemurs, 3 Male, 7 Female, age range: 1-21 years; ruffed lemurs: 4 Male, 6 Female, age range: 2-22 years) living in four social groups that were housed separately from one another (Table 1).

Apparatus & 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-second yawning or control clip that was repeated in a looped sequence for a total duration of five minutes. Example frames from these videos are shown in Figure 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 two 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 one-minute habituation period during which a solid blue "blank" screen was projected. After this time, we played either the yawning or control video for five minutes. Immediately following the first video, we projected the blank screen for one minute, and then played the second video for five minutes.

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., Paulkner 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 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) (Figure 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.

Ring-tailed lemurs spent more time alarm grunting in the fox condition than in the caretaker condition, grunting, on average, for 58 ± 48.8 seconds in the fox condition compared to 17 ± 18.4 seconds 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) (Figure 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 (Figure 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 strepsirhine species. However, lemurs did demonstrate that they respond meaningfully to video footage in general; they moved upward and made alarm calls while viewing 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 haplorine 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 lemurs 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 & 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 (less than 5 percent of the time, Nakamichi & Koyama 1997). Consequently, ring-tailed lemur daughters, unlike Old World monkey daughters, do not always rank immediately below their mothers (Nakamichi & 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 & DeWaal 1992).

In addition to a lack of alliances, lemurs show minimal post-conflict affiliation with other individuals (Fichtell & 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 & Whiten 1998), long-tailed macaques (Aureli & van Schaik 1991), chimpanzees (DeWaal & van Roosmalen 1979), dolphins (Tamaki et al. 2006), rooks (Seed et al. 2007), domestic horses (Cozzi et al. 2010), goats (Schino 1998), hyenas (Hofer & East 2000), dogs (Cools et al. 2008), and wolves (Cordoni & Palagi 2008). This affiliation is thought to reduce anxiety and future aggression (e.g. Castles & 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 minutes 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 minutes post-conflict and found that more affiliation occurred in post-conflict periods compared to control periods (Rolland & 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 2009).

Given these peculiarities of lemur social 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; budgeriars form cohesive flocks and wolves are obligate carnivores that acquire food by hunting cooperatively with groupmates (Wyndham 1980; Peterson & 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 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 elicitied 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 and colleagues (2008) found that 72 percent of dogs tested yawned contagiously in response to a live human who yawned, but in a later study Harr and colleagues (2009) 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 (Pongracz 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 and colleagues (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 stumptail macaques (e.g. Anderson et al. 2004; Paulkner & 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. Scordato & Drea 2007). 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. 2012).

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).

References

Altmann SA (1967) The structure of primate social communication. Social communication among primates:325-362

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

Anderson JR, Myowa–Yamakoshi M, Matsuzawa T (2004) Contagious yawning in chimpanzees Proceedings of the Royal Society of London B: Biological Sciences 271:S468-S470

Aureli F, van Schaik CP (1991) Post-conflcit behaviour in long tailed macaques (*Macaca fascicularis*): II. coping with the uncertainty. Ethology 89: 101–114

Baenninger R (1997) On yawning and its functions Psychonomic bulletin & review 4:198-207

Baker KC, Aureli F (1997) Behavioural indicators of anxiety: an empirical test in chimpanzees Behaviour 134:1031-1050

Bray J, Krupenye C, Hare B (2014) Ring-tailed lemurs (*Lemur catta*) exploit information about what others can see but not what they can hear Animal cognition 17:735-744

Campbell MW, De Waal FB (2011) Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy PloS one 6:e18283

Campbell MW, de Waal FB (2014) Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees Proc Biol Sci 281:20140013 doi:10.1098/rspb.2014.0013

Castles DL, Whiten A (1998) Post-conflict behaviour of wild olive baboons: Stress and self-directed behaviour. Ethology 104: 148–160

Cools AK, Van Hout AJM, Nelissen MH (2008). Canine Reconciliation and Third-Party-Initiated Postconflict Affiliation: Do Peacemaking Social Mechanisms in Dogs Rival

Those of Higher Primates? Ethology114: 53-63

Cozzi A, Sighieri C, Gazzano A, Nicol CJ, Baragli P (2010) Post-conflict friendly reunion in a permanent group of horses (*Equus caballus*).Behavioural processes 85: 185-190

de Waal FB (2008) Putting the altruism back into altruism: the evolution of empathy Annu Rev Psychol 59:279-300 doi:10.1146/annurev.psych.59.103006.093625

De Waal FBM, van Roosmalen A (1979) Reconciliation and consolation among chimpanzees. Behav. Ecol. Sociobiol 5: 55–66

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

Drea CM, Scordato ES (2008) Olfactory communication in the ringtailed lemur (*Lemur catta*): form and function of multimodal signals. In: Chemical Signals in Vertebrates 11. Springer, pp 91-102

Fichtel C, Kappeler PM (2010) Human universals and primate symplesiomorphies: establishing the lemur baseline. In *Mind the Gap* (pp. 395-426). Springer Berlin Heidelberg

Gallup AC (2011) Why do we yawn? Primitive versus derived features Neuroscience & Biobehavioral Reviews 35:765-769

Harcourt AH, DeWaal FB (1992). *Coalitions and alliances in humans and other animals*. Oxford University Press.

Harr AL, Gilbert VR, Phillips KA (2009) Do dogs (*Canis familiaris*) show contagious yawning? Anim Cogn 12:833-837 doi:10.1007/s10071-009-0233-0

Harr AL, Gilbert VR, Phillips KA (2009) Do dogs (*Canis familiaris*) show contagious yawning? Animal cognition 12:833-837

Hofer H, East ML (2000). Conflict management in female-dominated spotted hyenas. In *Natural Conflict Resolution*, F Aureli and F de Waal, eds. Berkeley: University of California Press: pp. 232–234.

Joly-Mascheroni RM, Senju A, Shepherd AJ (2008) Dogs catch human yawns Biology Letters 4:446-448

Kappeler PM (1993) Reconciliation and post-conflict behaviour in ringtailed lemurs, *Lemur catta* and redfronted lemurs, *Eulemur fulvus rufus*. Animal Behaviour 45: 901-915

Kendal RL, Custance DM, Kendal JR, Vale G, Stoinski TS, Rakotomalala NL, Rasamimanana H (2010) Evidence for social learning in wild lemurs (*Lemur catta*) Learning & Behavior 38:220-234

Kutsukake N, Clutton-Brock TH (2008) Do meerkats engage in conflict management following aggression? Reconciliation, submission and avoidance. Animal Behaviour 75::1441-53

Leone A, Ferrari PF, Palagi E (2014). Different yawns, different functions? Testing social hypotheses on spontaneous yawning in *Theropithecus gelada*. Scientific reports 4.

Lund JD, Jørgensen MC (1999) Behaviour patterns and time course of activity in dogs with separation problems Applied Animal Behaviour Science 63:219-236

Macedonia JM, Taylor LL (1985) Subspecific divergence in a loud call of the ruffed lemur (*Varecia variegata*) American Journal of Primatology 9:295-304

MacLean EL et al. (2012) How does cognition evolve? Phylogenetic comparative psychology Animal cognition 15:223-238

MacLean EL et al. (2014) The evolution of self-control Proceedings of the National Academy of Sciences 111:E2140-E2148

MacLean EL, Mandalaywala TM, Brannon EM (2012) Variance-sensitive choice in lemurs: constancy trumps quantity Animal cognition 15:15-25

MacLean EL, Merritt DJ, Brannon EM (2008) Social complexity predicts transitive reasoning in prosimian primates Animal behaviour 76:479-486

Marechal L, Genty E, Roeder JJ (2010) Recognition of faces of known individuals in two lemur species (*Eulemur fulvus* and *E. macaco*) Animal Behaviour 79:1157-1163

Merritt D, Maclean EL, Jaffe S, Brannon EM (2007) A comparative analysis of serial ordering in ring-tailed lemurs (*Lemur catta*) J Comp Psychol 121:363-371 doi:10.1037/0735-7036.121.4.363

Merritt DJ, Maclean EL, Crawford JC, Brannon EM (2011) Numerical rule-learning in ring-tailed lemurs (*Lemur catta*) Front Psychol 2:23 doi:10.3389/fpsyg.2011.00023

Miller ML, Gallup AC, Vogel AR, Vicario SM, Clark AB (2012) Evidence for contagious behaviors in budgerigars (*Melopsittacus undulatus*): an observational study of yawning and stretching Behav Processes 89:264-270 doi:10.1016/j.beproc.2011.12.012

Moyaho A, Rivas-Zamudio X, Ugarte A, Eguibar JR, Valencia J (2015) Smell facilitates auditory contagious yawning in stranger rats Animal cognition 18:279-290

Nakamichi M, Koyama N (1997) Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *International Journal of Primatology* 18(1): 73-93

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

Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*) Behavioral Ecology and Sociobiology 57:50-61 doi:10.1007/s00265-004-0830-5

O'Hara SJ, Reeve AV (2011) A test of the yawning contagion and emotional connectedness hypothesis in dogs, Canis familiaris Animal Behaviour 81:335-340

Palagi E, Antonacci D, Norscia I (2008) Peacemaking on treetops: first evidence of reconciliation from a wild prosimian (*Propithecus verreauxi*) Animal Behaviour 76: 737–747

Palagi E, Leone A, Mancini G, Ferrari P (2009) Contagious yawning in gelada baboons as a possible expression of empathy Proceedings of the National Academy of Sciences 106:19262-19267

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

Palagi E, Paoli T, Tarli SB (2005) Aggression and reconciliation in two captive groups of *Lemur catta*. *International Journal of Primatology* 26: 279-294

Paukner A, Anderson JR (2006) Video-induced yawning in stumptail macaques (Macaca arctoides) Biol Lett 2:36-38 doi:10.1098/rsbl.2005.0411

Pereira ME, Kappeler PM (1997) Divergent systems of agonistic behaviour in lemurid primates Behaviour 134:225-274

Peterson RO, Ciucci P (2003) The wolf as a carnivore Wolves: behavior, ecology, and conservation:104-130

Platek SM, Critton SR, Myers TE, Gallup GG (2003) Contagious yawning: the role of self-awareness and mental state attribution Cognitive Brain Research 17:223-227 doi:10.1016/s0926-6410(03)00109-5

Pongrácz P, Miklósi Á, Dóka A, Csányi V (2003) Successful Application of Video-Projected Human Images for Signalling to Dogs Ethology 109:809-821

Provine RR (1986) Yawning as a stereotyped action pattern and releasing stimulus Ethology 72:109-122

Rice WR, Gaines SD (1994) Heads I win, tails you lose': testing directional alternative hypotheses in ecological and evolutionary research Trends in Ecology and Evolution 9:235-236

Rolland N, Roeder JJ (2000) Do ringtailed lemurs (*Lemur catta*) reconcile in the hour post-conflict?: a pilot study. Primates 41: 223-227

Romero T, Ito M, Saito A, Hasegawa T (2014) Social modulation of contagious yawning in wolves

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

Sandel AA, MacLean EL, Hare B (2011) Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates Animal Behaviour 81:925-931

Sauther ML (1989) Antipredator behavior in troops of free-rangingLemur catta at Beza Mahafaly Special Reserve, Madagascar International Journal of Primatology 10:595-606

Sauther ML, Sussman RW, Gould L (1999) The socioecology of the ringtailed lemur: thirty-five years of research Evolutionary Anthropology Issues News and Reviews 8:120-132

Seed AM, Clayton NS, Emery NJ (2007) Postconflict third-party affiliation in rooks, *Corvus frugilegus*. Current Biology 17: 152-158

Senju A, Maeda M, Kikuchi Y, Hasegawa T, Tojo Y, Osanai H (2007) Absence of contagious yawning in children with autism spectrum disorder Biol Lett 3:706-708 doi:10.1098/rsbl.2007.0337

Seyfarth RM, Cheney DL (2013) Affiliation, empathy, and the origins of theory of mind Proceedings of the National Academy of Sciences 110:10349-10356

Silva K, Bessa J, de Sousa L (2012) Auditory contagious yawning in domestic dogs (Canis familiaris): first evidence for social modulation Animal cognition 15:721-724

Smith E (1999) Yawning: an evolutionary perspective Human evolution 14:191-198

Stoinski T, Drayton L, Price E (2011) Evidence of social learning in black-and-white ruffed lemurs (Varecia variegata) Biology letters 7:376-379

Tamaki N, Morisaka T, Taki M (2006). Does body contact contribute towards repairing relationships?: The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. Behavioural processes, 73: 209-215

Vasey N (2007) Impact of seasonality and reproduction on social structure, ranging patterns, and fission–fusion social organization in red ruffed lemurs. In: Lemurs. Springer, pp 275-304

Wyndham E (1980) Diurnal cycle, behaviour and social organization of the Budgerigar Melopsittacus undulatus Emu 80:25-33

Zannella A, Norscia I, Stanyon R, Palagi E (2015) Testing yawning hypotheses in wild populations of two strepsirrhine species: Propithecus verreauxi and Lemur catta Am J Primatol 77:1207-1215 doi:10.1002/ajp.22459

Figure Captions

Table 1. Lemur subjects in all experiments.

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

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

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

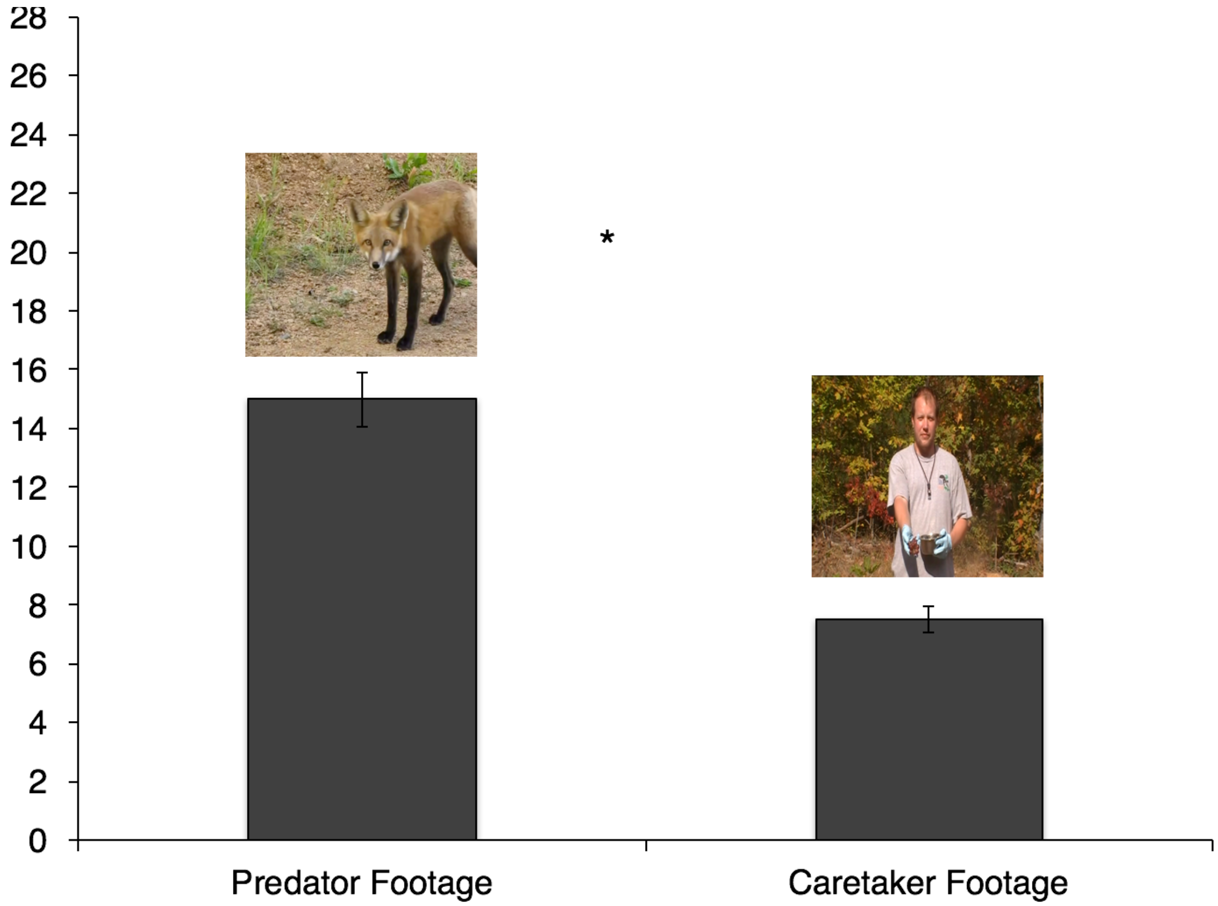
Figure 4. Number of individuals who yawned in individual and group contexts in experiment 2.

Group	**Subject**	**Species**	**Sex**	**Age (years)**	**S 1**	**S 2**	**E 2**
1	Pyxis	*V v. rubra*	F	17	X	X	X
1	Hunter	*V v. rubra*	M	16	X	X	X
1	Scorpius	*V v. rubra*	M	5	X	X	X
1	Aries	*V v. rubra*	M	5	X	X	X
1	Esther	*V v. rubra*	F	3	X	X	X
1	Orion	*V v. rubra*	M	3			X
1	Phoebe	*V v. rubra*	F	3	X	X	X
2	Carina	*V v. rubra*	F	8	X	X	X
2	Alphard	*V. v. rubra*	M	23	X		
2	Avior	*V v. rubra*	M	4			X
2	Hydra	*V. v. rubra*	F	4	X		
2	Lyra	*V v. rubra*	F	4	X	X	X
2	Pandora	*V v. rubra*	F	<1		X	X
2	Cordelia	*V v. rubra*	F	<1		X	X
3	Schroeder	*L. catta*	F	20	X	X	X
3	Edelweiss	*L. catta*	F	2	X		
3	Liesl	*L. catta*	F	4	X	X	X
3	Aracus	*L. catta*	M	21	X	X	X
3	Johan	*L. catta*	M	2			X
3	Rolfe	*L. catta*	M	1	X	X	X
3	Brigitta	*L. catta*	F	1		X	X
3	Gretl	*L. catta*	F	<1		X	X
4	Sprite	*L. catta*	F	11		X	X
4	Ginger	*L. catta*	F	6	X	X	X
4	Randy	*L. catta*	M	6	X	X	X
4	Schweppes	*L. catta*	M	2			X

4	Sobe	*L. catta*	F	1		X	X
4	Sarsparilla	*L. catta*	F	1		X	X
4	Crystal Light	*L. catta*	F	2	X		
4	Canada Dry	*L. catta*	F	1	X	X	X
4	Izze	*L. catta*	F	<1		X	X
4	Jones	*L. catta*	M	<1		X	X
4	Stewart	*L. catta*	M	<1		X	X

Figure 1.

Figure 2.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Predator Footage
Caretaker Footage

Figure 3.

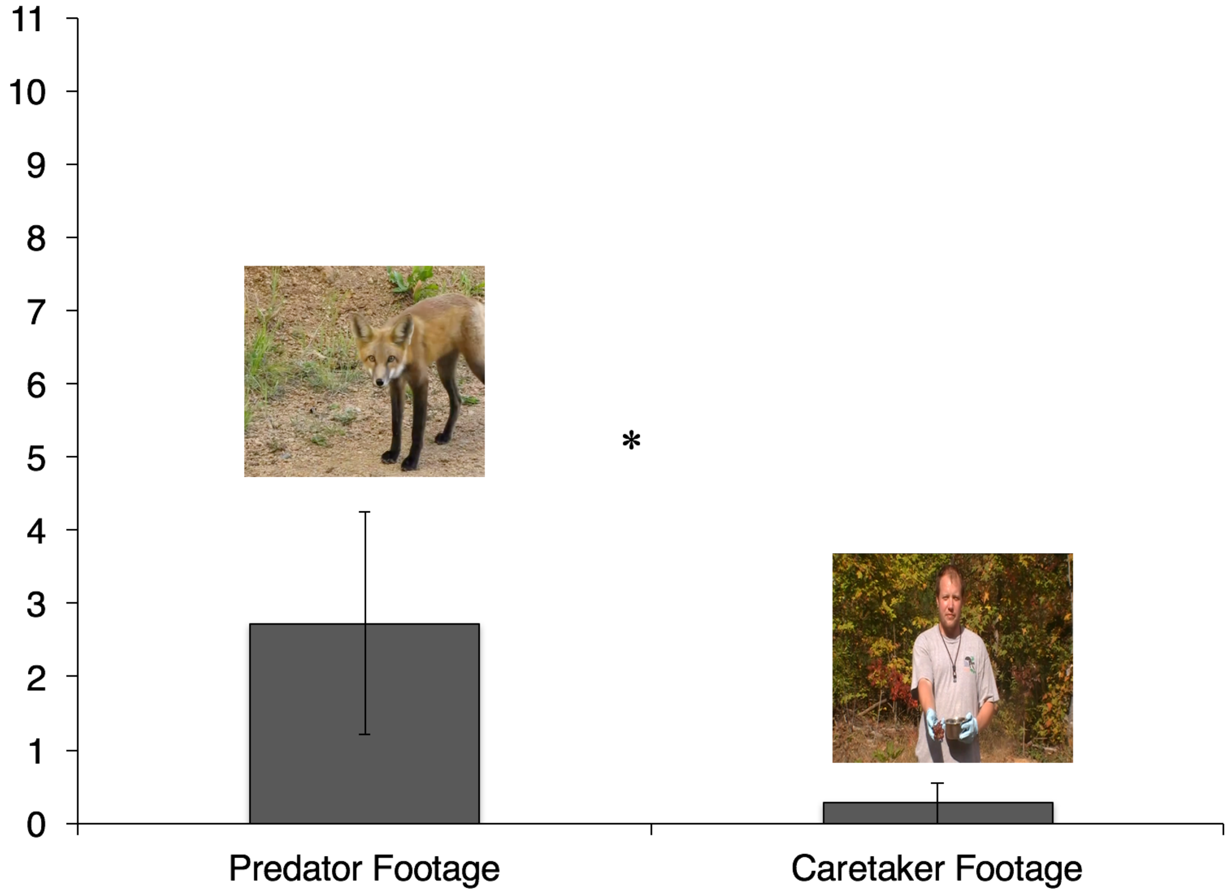
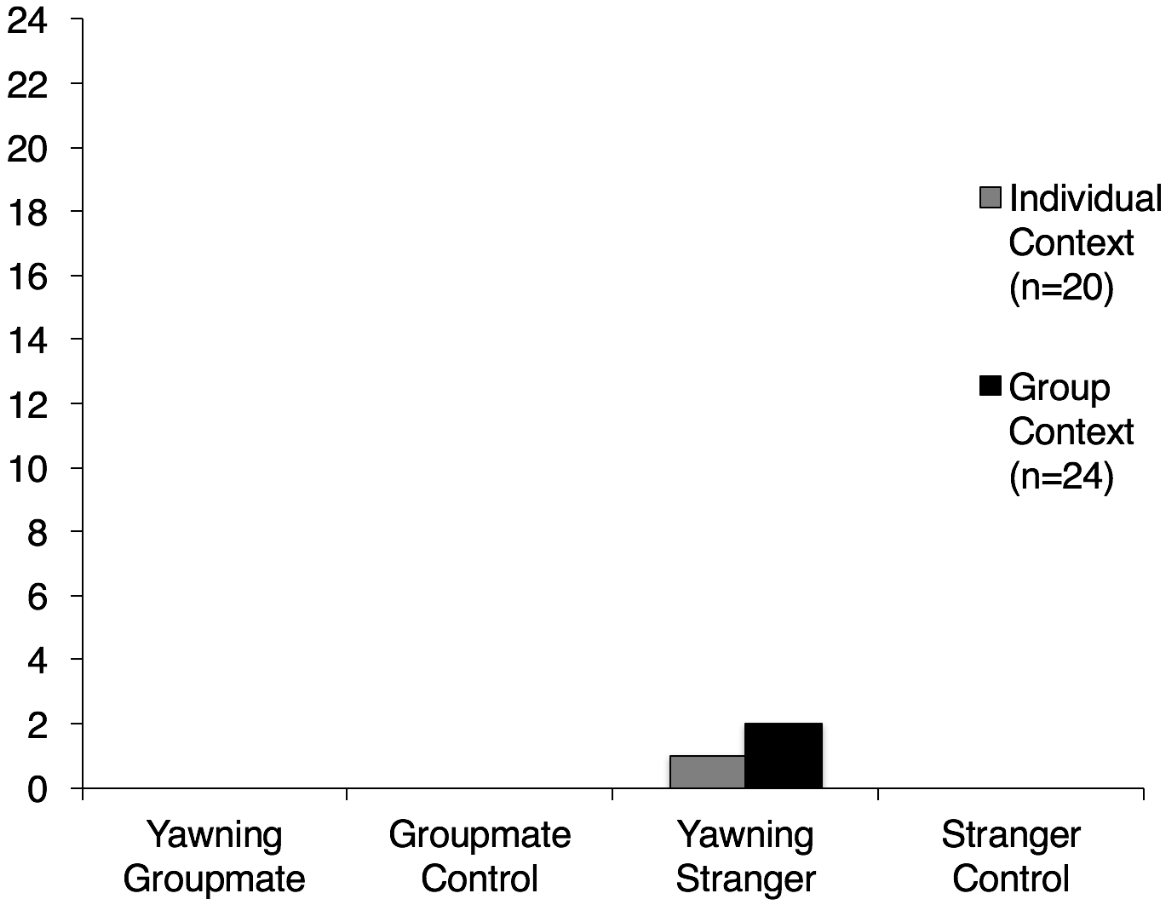


Figure 4.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Individual Context (n=20)
Group Context (n=24)
Yawning Groupmate
Groupmate Control
Yawning Stranger
Stranger Control