

## Research



**Cite this article:** Neilands P, Claessens S, Ren I, Hassall R, Bastos APM, Taylor AH. 2020 Contagious yawning is not a signal of empathy: no evidence of familiarity, gender or prosociality biases in dogs. *Proc. R. Soc. B* **287**: 20192236.  
<http://dx.doi.org/10.1098/rspb.2019.2236>

Received: 24 September 2019

Accepted: 21 January 2020

**Subject Category:**

Behaviour

**Subject Areas:**

behaviour, cognition, evolution

**Keywords:**

contagious yawning, empathy, comparative cognition, dogs

**Author for correspondence:**

Patrick Neilands

e-mail: [pnei460@aucklanduni.ac.nz](mailto:pnei460@aucklanduni.ac.nz)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4831671>.

# Contagious yawning is not a signal of empathy: no evidence of familiarity, gender or prosociality biases in dogs

Patrick Neilands, Scott Claessens, Ivy Ren, Rebecca Hassall, Amalia P. M. Bastos and Alex H. Taylor

School of Psychology, University of Auckland, Auckland, 1010, New Zealand

PN, 0000-0002-8880-8674; SC, 0000-0002-3562-6981

Contagious yawning has been suggested to be a potential signal of empathy in non-human animals. However, few studies have been able to robustly test this claim. Here, we ran a Bayesian multilevel reanalysis of six studies of contagious yawning in dogs. This provided robust support for claims that contagious yawning is present in dogs, but found no evidence that dogs display either a familiarity or gender bias in contagious yawning, two predictions made by the contagious yawning–empathy hypothesis. Furthermore, in an experiment testing the prosociality bias, a novel prediction of the contagious yawning–empathy hypothesis, dogs did not yawn more in response to a prosocial demonstrator than to an antisocial demonstrator. As such, these strands of evidence suggest that contagious yawning, although present in dogs, is not mediated by empathetic mechanisms. This calls into question claims that contagious yawning is a signal of empathy in mammals.

## 1. Introduction

Empathy, broadly defined as emotional and mental sensitivity to another's state [1], appears to play a key role in humans' prosocial and cooperative behaviour [2–4]. While there are many aspects of empathy, all empathetic responses are ultimately predicated upon an observer having some form of access to another individual's emotional state [1]. Perception–action mechanism accounts argue that this access is granted by state-matching: when an observer perceives a particular state in another individual, neural representations of that state are activated in the observer, resulting in the experience of a similar state [1,5,6]. It has been suggested that this perception–action mechanism evolved early in mammals [1,5,6] and underpins the helping behaviour seen in many non-human mammals [7–14]. However, it is difficult to rule out simpler explanations for helping behaviour that do not require empathy, such as associative learning [12,15] or alternative motivations such as a desire to seek social contact [16–18] or explore novel objects [19].

Contagious yawning has emerged as a potentially powerful tool to help resolve this impasse. Contagious yawning occurs when observing another individual yawn induces yawning in the observer [20]. The contagious yawning–empathy hypothesis posits that both contagious yawning and empathy are mediated by the same perception–action mechanism [1,6,21–23]. This hypothesis makes several testable predictions about the propensity of individuals to engage in contagious yawning. First, individuals who report lower levels of empathy should be less likely to engage in contagious yawning. Second, as people show greater empathy for kin and friends, they should be more likely to yawn when exposed to yawning from familiar yawners compared to unfamiliar yawners [21,24]. Finally, it has been hypothesized that, due to more direct involvement in offspring care, female mammals may experience a greater level of empathy than males [25–28] and thus it has been predicted that female mammals should be more likely to engage in contagious yawning [29].

Evidence of each of these predictions has been found in humans. Firstly, subpopulations reporting lower levels of empathy, such as children with autism spectrum disorder (ASD) [30] or adults who score highly in psychopathic traits [31], are less likely to engage in contagious yawning. Secondly, both empathy and contagious yawning appear to share a familiarity bias: people experience more empathy for friends and family than strangers and are more likely to contagiously yawn when familiar people yawn [21,24] (but see [32]). Finally, although both men and women are equally likely to engage in contagious yawning, women who do engage in contagious yawning yawn more frequently than men who engage in contagious yawning [29]. While this provides some evidence of a gender bias in human contagious yawning, there is currently much debate surrounding this finding [33,34].

Based on this evidence from humans, it has been suggested that the widespread presence of contagious yawning across mammals demonstrates that the perception–action mechanism underpinning empathy is phylogenetically ancient and thus that the helping behaviours seen in mammals are driven by at least a rudimentary form of empathy [1,35,36]. This conclusion rests on two key premises. First, it assumes that contagious yawning is indeed widespread across mammals. Second, it assumes that contagious yawning in animals is underpinned by the same perception–action mechanism mediating empathy. However, there is currently a lack of robust evidence for either of these assumptions [37].

Firstly, there is a lack of conclusive evidence that contagious yawning is widespread across mammals. A comprehensive review of the contagious yawning literature by Massen & Gallup [37] demonstrates that the majority of studies on contagious yawning are focused on non-human primates, particularly chimpanzees, with few studies looking at contagious yawning in non-primates. Furthermore, research into contagious yawning in other species has mostly been restricted to a single study. Chimpanzees are the only non-human species of mammal to have consistently shown contagious yawning across multiple studies [38–45]. There is no evidence of contagious yawning in gorillas [44,46] and for both bonobos [24,36,44,47,48] and dogs [35,49–54], the evidence is mixed: some studies have shown evidence for contagious yawning while other studies have found no effect. As well as making it difficult to draw conclusions regarding the presence of contagious yawning in these species, this lack of consistency in replication brings into question claims for contagious yawning in other species that are based on a single study [24,35,36,44,47,49–64]. Given the small sample sizes used in many of these studies [65], their findings may simply reflect either false positives or negatives rather than the true presence or absence of contagious yawning. Such issues are particularly compounded by the variation in study design across different species [66]. In particular, relying on observational rather than experimental methodologies can be problematic due to the influence of synchronized circadian rhythms making it more likely that animals in a group may spontaneously yawn at the same time [37]. As such, it is difficult to say with certainty that there is evidence for contagious yawning in non-human mammals outside of chimpanzees, let alone discern the phylogenetic pattern of contagious yawning across all mammals.

Secondly, contagious yawning in non-human animals may not be mediated by empathetic mechanisms. Contagious yawning in animals may be the result of stress [54,57], an affiliation strategy [67], a means of communication [61], or a

mechanism to improve collective vigilance within groups [37,68,69] rather than being related to empathy via a perception–action mechanism. A powerful way to test between these hypotheses is to examine if the patterns of behaviours predicted by the contagious yawning–empathy hypothesis, such as the familiarity bias and the gender bias, are also seen in animals. Such biases can be thought of as cognitive signatures; a particular suite of behaviours that should be seen if contagious yawning is mediated by a perception–action mechanism but not if it is mediated by another cognitive mechanism [70]. Evidence for the familiarity bias has been found in studies on chimpanzees [40,41], dogs [50,64], bonobos [36], gelada baboons [58], and wolves [64], but other studies on chimpanzees [42,43] and dogs [51,53] have not found evidence for this bias, and one study on rats has even found the opposite pattern [61]. In terms of the gender bias, there is currently no consistent support for the prediction that females are more likely to contagiously yawn than males across mammals [37]. Instead of females being more likely to engage in contagious yawning, there appears to be some evidence of an interaction between the gender of the observed yawner and the subject, but this pattern is not consistent. Bonobos yawn more when an individual of the opposite gender yawns and yawn more in general when the observed yawner is female [36]. Female geladas are also more likely to engage in contagious yawning than males but only when the observed yawner is female [58]. By contrast, in chimpanzees, male yawning is more contagious for other males than female yawning is for other females [42], while there is no evidence of any gender bias in dogs [35]. As such, there is currently no conclusive evidence for either signature across mammals, which brings into question whether contagious yawning is mediated by a perception–action mechanism shared with empathetic processes.

Here, we tested the contagious yawning–empathy hypothesis in dogs by reanalysing past data and also employing a novel experimental paradigm. First, we established that there is robust evidence for contagious yawning outside of chimpanzees and humans by conducting a Bayesian multilevel reanalysis of a combined dataset from six studies of contagious yawning in dogs. We then examined our combined dataset for evidence of the familiarity bias and the gender bias. Finally, we ran a study to search for a novel signature predicted by the contagious yawning–empathy hypothesis: the prosociality bias. In humans, empathy is modulated by social experience: people experience greater empathy for people who interact with them in a fair or prosocial manner [71,72]. Similarly, dogs show a preference for those who interact with them in a positive manner rather than a negative manner [73]. Therefore, we carried out an experiment to test whether dogs show a prosociality bias (i.e. yawn more contagiously when in the presence of a human who has been nice to them rather than one who has ignored them). We predicted that, if contagious yawning is mediated by empathetic processes in dogs, we would find evidence for the familiarity, gender, and prosociality biases in our study.

## 2. Methodology

### (a) Reanalysis

The aim of this reanalysis was to answer three questions relating to the contagious yawning–empathy hypothesis. First, do dogs show contagious yawning? Second, if dogs do contagiously

yawn, do they demonstrate a familiarity bias or gender bias as predicted by the contagious yawning–empathy hypothesis? Third, do any aspects of study design affect how likely dogs are to show contagious yawning? As the only non-primate species of mammal where contagious yawning has been studied multiple times, dogs are an ideal species to determine whether there is robust evidence for contagious yawning outside of chimpanzees and humans. Unfortunately, the methodological and analytical differences between these studies [35,66] limits the use of traditional meta-analytic techniques to assess the totality of the evidence [74]. Therefore, to explore these three questions, we constructed a database (for details on how the database was constructed, see supplementary methods in the electronic supplementary material) containing all the trials from six studies [35,49–51, 53,54] of contagious yawning in dogs and conducted a Bayesian multilevel analysis on the resulting dataset. Unfortunately, the original dataset of the seventh study was not available for reanalysis [52]. Despite this, the available dataset of 257 dogs is the largest database constructed for investigating contagious yawning.

In this analysis, the dependent variable of interest was the probability that yawning would occur at all and the number of recorded yawns. To model these dependent variables, we conducted multilevel hurdle models with random effects for subjects nested within studies. Model construction and comparison occurred in two phases. Firstly, we constructed a null (intercept-only) model, a Treatment-only model, a Familiarity-only model, a Treatment + Familiarity model, a Treatment  $\times$  Familiarity model, a Gender-only model, a Treatment + Gender model, and a Treatment  $\times$  Gender model. The Treatment factor had two levels: a yawning level where participants were exposed to a demonstrator yawning and a control level where the participants were exposed to a demonstrator either gaping or making a non-yawning sound. The Familiarity factor also had two levels: a familiar level where the dog's owner was the demonstrator and an unfamiliar level where an unknown experimenter was the demonstrator. Finally, the Gender factor had two levels: whether the dog was male or female. Treatment was included as a random slope grouped by subjects nested within studies, as each study followed a within-subjects design, gender was included as a random slope grouped by study and familiarity was included as a fixed effect. All factors were used to predict both the probability and rate of yawning simultaneously. These models were used to test whether dogs exhibited contagious yawning and, if so, whether this contagious yawning was affected by the familiarity of the demonstrator or the gender of the dogs.

Secondly, after determining that the Treatment-only model was the most parsimonious model, we compared the Treatment-only model to models including one of four study design aspects as fixed effects as well as a full model including all these factors. The four study design aspects were presentation type (whether the dogs were presented with visual and auditory demonstrations or just auditory demonstrations), demonstrator type (whether dogs saw a live or recorded demonstration), demonstrator species (whether the demonstrator was a human or dog), and observer type (whether the subject was a pet or shelter dog). These models were used to determine whether the effect of Treatment persisted after controlling for various aspects of study design. This allowed us to assess whether the study design had an effect on the dogs' propensity to contagiously yawn.

Rather than engage in null-hypothesis testing, we focused on model estimation in order to assess the evidence for the contagious yawning–empathy hypothesis in dogs [75]. Model estimation allows for better accounting of uncertainty in our results and a greater focus on the size of the effect of interest and is, therefore, the more informative approach [75,76]. We used two main methods for model estimation. Firstly, we used the expected log pointwise predictive density approximated by leave-one-out cross-validation (ELPD-LOO) to compare models

[77]. The higher a model's ELPD-LOO score, the better that model's out-of-sample prediction. This allows us to determine which model makes the best predictions. Secondly, for individual models, we directly compared different model-estimated yawning probabilities and rates by calculating posterior differences [78]. Directly comparing yawning probabilities and rates allowed us to estimate the size and uncertainty of the effect.

All statistical analyses were conducted in R v. 3.5.1 [79] using the brms package [80]. Hamiltonian Monte Carlo estimation was run with Stan [81]. Figures were produced with the ggplot2 package [82]. Data, code, full model fits, details about prior distributions, and Markov Chain Monte Carlo (MCMC) chain diagnostics are accessible at <https://osf.io/c2f3k/>.

## (b) Experiment methodology

### (i) Participants

A total of 32 dogs (17 females) were recruited for this study. All dogs were pet dogs (aged 2–10 years old) which were accompanied to the laboratory by their owners (see electronic supplementary material, table S1 for details of dogs included in the study).

### (ii) Protocol

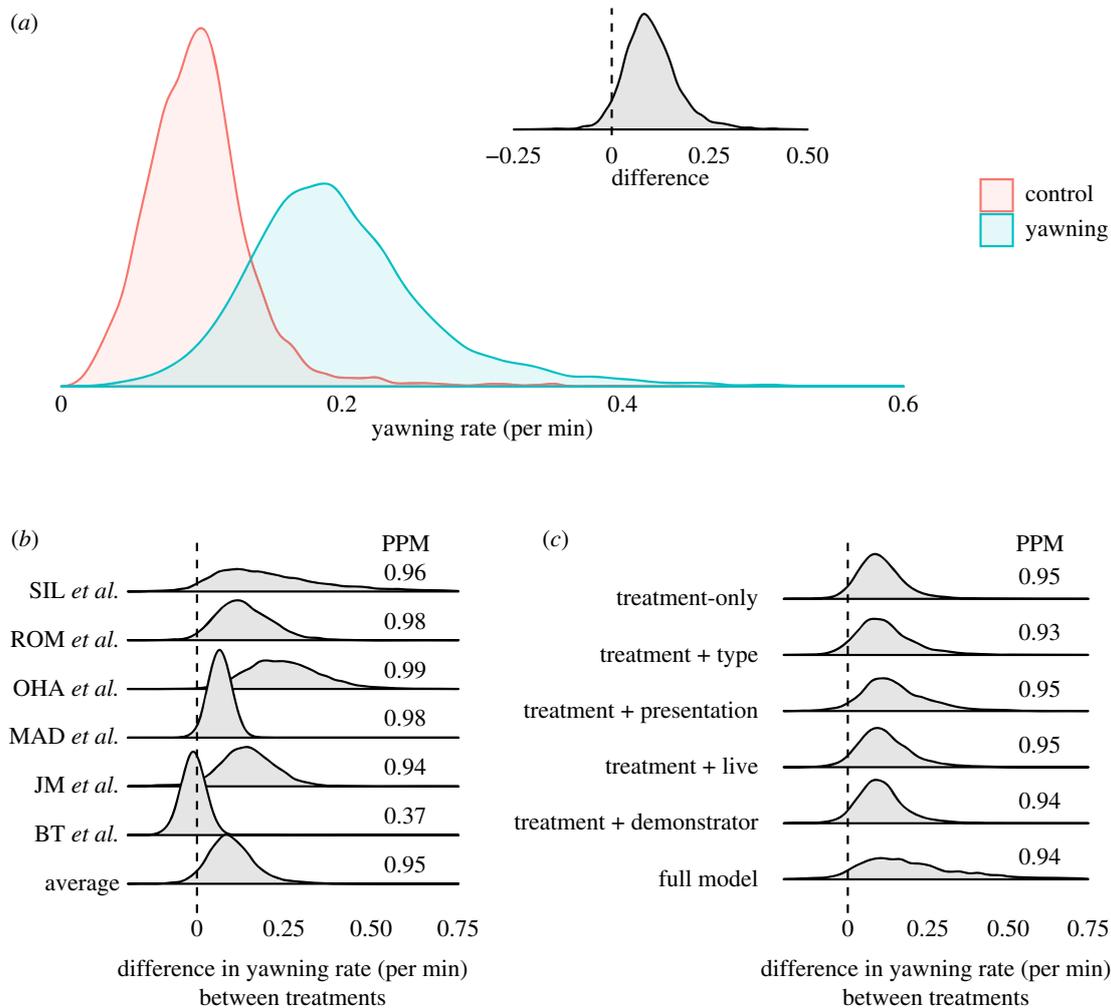
Dogs took part in two treatments: a prosocial treatment and an antisocial treatment. Each treatment consisted of an interaction phase and a yawning phase. The interaction phase was adapted from an earlier study [73] where dogs showed a preference for a prosocial over an antisocial experimenter. In the prosocial interaction phase, the dog and experimenter entered the testing room (3.6 m  $\times$  3.4 m) and the experimenter interacted with the dog in a positive way for 2 min. Depending on the preferences of the dog, this interaction involved either playing with the dog or simply petting and stroking it. In the antisocial interaction phase, the experimenter and dog entered the same testing room and the experimenter walked around the room, ignoring the dog and avoiding eye contact for 2 min. The only interaction that the experimenter had with the dog was to take out a piece of food and ask the dog to sit. After the dog obeyed, the experimenter ate the treat. This occurred a total of three times. To control for the presence of food, in the prosocial phase, the experimenter also stood up three times and took out a piece of food. After holding the food for 5 s, the experimenter ate it and resumed their positive interactions with the dog (see electronic supplementary material, videos S1 and S2).

The yawning phase was the same in both treatments. After the interaction phase, the owner entered the room and settled the dog on a dog bed and the experimenter sat opposite the dog, leaving a 1.5 m gap between them. After the dog settled, the experimenter began to yawn. Each yawn consisted of the experimenter calling the dog's name and then yawning by stretching their hands above their heads and making an audible yawn (see electronic supplementary material, figure S1 for a photo of a yawn). Yawns were repeated every 30 s for 5 min. A tone was played through headphones to the experimenter to ensure that experimenters were consistent in the number of yawns they produced.

The dog took part in both treatments in the same session with an approximately 10-min break between each treatment. The order in which the prosocial and antisocial treatments were presented, as well as which experimenter was prosocial or antisocial, was counterbalanced across dogs.

### (iii) Data analysis

The number of times that the dogs yawned was coded by an experimenter blind to treatment. A yawn was coded when a dog opened their mouth and inhaled, followed by a brief period of apnoea where the mouth remained open before the dog exhaled [20]. Using the same multilevel hurdle models as in the previous



**Figure 1.** Dogs yawn more often in the yawning treatment than in the control treatment. (a) Density plots of posterior predicted yawning rates in the control and yawning treatments in the Treatment-only model. The median estimated yawning rate of dogs is higher in the yawning treatment than in the control treatment. Similarly, dogs yawn more frequently in the yawning treatment than the control treatment in the large majority of MCMC samples (positive posterior mass (PPM) = 0.95). (b) Density plots showing posterior differences between control and yawning treatments, split by study. Five of six studies show similar differences in contagious yawning rates (PPM: 0.94–0.99), with only one study not showing this pattern (PPM = 0.37). (c) Density plots showing posterior differences between control and yawning treatments across models controlling for various aspects of study design. Across all models, differences in contagious yawning rates stay consistent (PPM: 0.93–0.95). Code to reproduce this plot can be found at <https://osf.io/c2f3k/>. (Online version in colour.)

analyses, we constructed a null (intercept-only) model, a Sociality-only model (prosocial demonstrator versus antisocial demonstrator), a Trial-only model (first versus second trial), a Sociality + Trial model, and a Sociality  $\times$  Trial model. Similarly to the previous analysis, we used ELPD-LOO comparison to determine which models would best predict out-of-sample data. For individual models, we looked at the posterior differences between treatments.

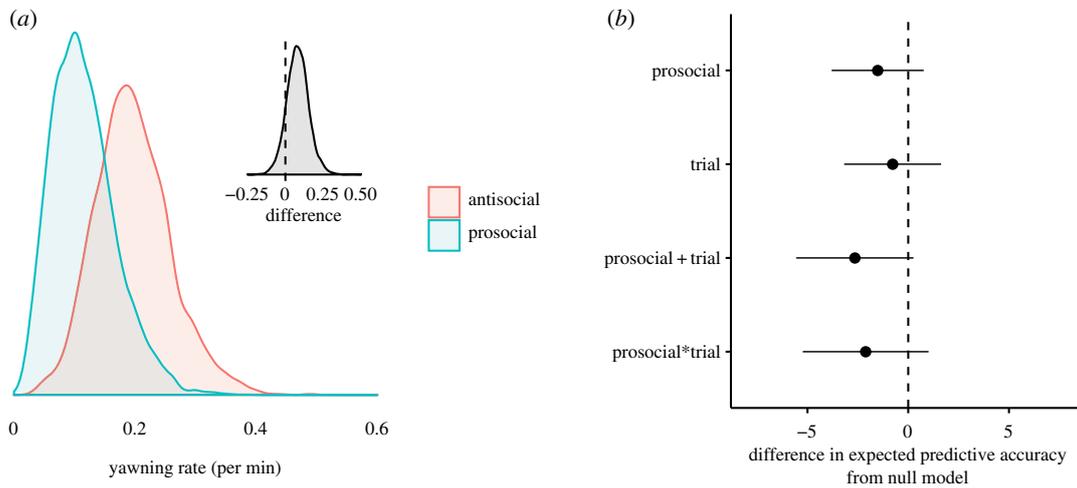
### 3. Results

#### (a) Dogs contagiously yawn and this effect is robust to variation in study design

The model comparison suggests that the Treatment-only model outperforms the null model (ELPD-LOO difference  $\pm$  95% credible interval =  $32.5 \pm 13.1$ ). The Treatment-only model provides additional support for the effect of treatment on yawning rate (results are qualitatively similar regardless of the model chosen). The model-estimated median probability of yawning is 0.39 in the yawning treatment and 0.19 in the control treatment (electronic supplementary material, figure S2a). Similarly, the model-estimated median yawning rate in the yawning

treatment (0.19 yawns per minute) is roughly double the model-estimated median yawning rate in the control treatment (0.10 yawns per minute; figure 1a). To formally compare these treatments, we calculated the proportion of the posterior difference mass above zero, which is the proportion of MCMC samples in our posterior distribution where the yawning probability or rate is higher in the yawning treatment than the control treatment (positive posterior mass; PPM; figure 1a inset). As predicted, for the large majority of MCMC samples, both the probability of yawning (PPM = 0.97) and the yawning rate (PPM = 0.95) are greater in the yawning treatment than in the control treatment. The random intercept and slope in this model also allowed us to repeat this comparison for each individual study (figure 1b; electronic supplementary material, figure S2b). For five of the six studies, the PPM is high for both yawning probability and rate, with only one study failing to cluster with the other studies. This suggests that our conclusions are not being unduly driven by any single study in our sample. Taken together, model comparison and estimation suggest that contagious yawning is present in dogs.

This finding is robust to variation in study design. Model comparisons suggest that controlling for the species of the



**Figure 2.** Dogs do not yawn more for prosocial yawners than antisocial yawners. (a) Density plots of posterior predicted yawning rates in the prosocial and antisocial Treatments in the Sociality-only model. Dogs yawn marginally more in the antisocial treatment than in the prosocial treatment. However, this difference probably does not reflect a true effect because while dogs are more likely to yawn more for the antisocial demonstrator than the prosocial demonstrator in a majority of MCMC samples, this is not consistent as in 12% of samples, dogs yawned more for the prosocial demonstrator (Antisocial PPM: 0.88). (b) Expected predictive accuracy was quantified by looking at the ELPD-LOO. Black dots represent the difference between models compared to the null model and the lines represent 95% credible intervals. Positive values imply stronger model performance and models where the 95% CIs do not cross zero differ substantially in performance from the null model. Including either Sociality or Trial as factors into the model does not substantially improve performance in comparison to the null model. Code to reproduce this plot can be found at <https://osf.io/c2f3k/>. (Online version in colour.)

demonstrator (Treatment + Demonstrator), whether the demonstration is live or recorded (Treatment + Live), visual or auditory presentation (Treatment + Presentation), and whether the dog was a pet or shelter dog (Treatment + Type) does little to affect out-of-sample prediction (electronic supplementary material, figure S3). Regardless of which factors were being controlled for, the effect of Treatment remains stable across all the models, including a full model controlling for all these factors (figure 1c; electronic supplementary material, figure S2c). This suggests that differences in study design between studies do not have a large impact on dogs' contagious yawning.

### (b) Dogs do not show the familiarity bias when contagiously yawning

Including familiarity as a factor has very little impact on the model's out-of-sample prediction. While both the Treatment + Familiarity and Treatment  $\times$  Familiarity models outperform the null model (electronic supplementary material, figure S4b), including familiarity does not improve model performance compared to the Treatment-only model (electronic supplementary material, figure S4c). If dogs display the familiarity bias, they should be more likely to yawn and yawn more frequently in the yawning treatment than in the control treatment for familiar demonstrators only. In contrast to this prediction, looking at the Treatment  $\times$  Familiarity model, we found no evidence of this. The differences between treatments for probability of yawning were similar regardless of familiarity, (Familiar PPM = 0.99, Unfamiliar PPM = 0.95; electronic supplementary material, figure S5) and differences between treatments for the rate of yawning were higher in the unfamiliar trials than familiar trials (Familiar PPM = 0.83; Unfamiliar PPM = 0.94; electronic supplementary material, figure S4a). Crucially, the difference between these differences (i.e. the interaction effect) is not consistent with the familiarity bias hypothesis, for either probability (PPM = 0.88) or rate of yawning (PPM = 0.49).

### (c) Dogs do not show a gender bias when contagiously yawning

Including the subject's gender as a factor does not affect the model's out-of-sample prediction (electronic supplementary material, figure S6b,c). If dogs displayed the gender bias predicted by the contagious yawning–empathy hypothesis, female dogs should be more likely to contagiously yawn than males in the yawning treatment. However, looking at the Treatment  $\times$  Gender model, there is no evidence of this. The differences between treatments are similar regardless of gender, for both the probability of yawning (Male PPM = 0.96; Female = 0.98; electronic supplementary material, figure S7) and the rate of yawning (Male PPM = 0.92; Female PPM = 0.90; electronic supplementary material, figure S6a). Furthermore, the difference between these differences is not consistent with the gender bias hypothesis, for either the probability (PPM = 0.55) or rate (PPM = 0.50) of yawning.

### (d) Dogs do not show a prosociality bias when contagiously yawning

Looking at our experimental data, including additional factors to the null model does not substantially improve model fit (figure 2b). As including additional factors does not result in increased explanatory power, the null model was the most parsimonious model. This suggests that whether the demonstrator behaved prosocially or antisocially towards the dogs had little effect on their propensity to yawn. The Sociality-only model tells a similar story. The model-estimated median probability of yawning of 0.55 in the prosocial treatment was lower than the probability of 0.59 in the antisocial treatment (electronic supplementary material, figure S8). Similarly, the model-estimated median yawning rate in the prosocial treatment (0.11 yawns per minute) was also slightly lower than in the antisocial treatment (0.19 yawns per minute; figure 2a), the opposite direction to our predictions. This lack of effect

can be further quantified by considering the PPM, which reveals no difference between treatments for both the probability (PPM=0.65) and the rate of yawning (PPM=0.88). Taken together, both model comparison and estimation suggests that there is no evidence that dogs yawn more in the prosocial treatment than in the antisocial treatment, as would be predicted by the contagious yawning–empathy hypothesis.

#### 4. Discussion

By combining the data from six different studies, the resulting dataset is the largest used to date to examine the presence of contagious yawning in a non-human mammal. This allowed us to draw conclusions about the presence and absence of contagious yawning and the signatures predicted by the contagious yawning–empathy hypothesis with a greater level of certainty than by relying on individual studies alone. Our reanalysis shows that dogs do exhibit contagious yawning, showing higher probabilities and rates of yawning for yawning demonstrators compared to control demonstrators. This provides robust support for the claims that contagious yawning is present in dogs [35,49–51]. In order to test whether this contagious yawning is related to mechanisms underpinning empathy, we examined this dataset for evidence of the familiarity bias and gender bias. However, dogs in our reanalysis showed no evidence of either of these biases. Similarly, when we ran a novel experiment to look for a prosociality bias, we found that the dogs in our experiment were no more likely to yawn for prosocial demonstrators than antisocial demonstrators. Dogs, therefore, show no evidence for any of the familiarity, gender, or prosociality biases predicted by the contagious yawning–empathy hypothesis. This suggests that contagious yawning in dogs is not mediated by an empathy-related perception–action mechanism [52–54]. The presence of contagious yawning in non-human animals, therefore, cannot be assumed to be evidence for a perception–action mechanism shared between humans and other mammals, as has been previously proposed [1,35,41,58]. That is not to say that some non-human animals do not necessarily experience some form of empathy but that contagious yawning cannot be taken as a diagnostic signal for the presence of these empathetic processes. Furthermore, these results, alongside the arguments put forward by Massen & Gallup in their recent review [37], bring into question the validity of the contagious yawning–empathy hypothesis more broadly.

It is important to acknowledge several caveats to our conclusions. Firstly, in both our reanalysis and experiment, the subjects were primarily responding to interspecific yawns from human demonstrators. While it is possible that dogs would respond differently to conspecific and interspecific yawning, there are several reasons to believe that this is not the case. Research in other species such as chimpanzees suggests that they respond similarly to conspecific and interspecific yawns [41], and, in our reanalysis, controlling for demonstrator type did not improve model fit. Nevertheless, more rigorous comparisons between how dogs respond to conspecific and interspecific yawning would be a useful future line of research. Secondly, it is important to note that the familiarity, gender, and prosociality biases are indirect measures of empathy [37]. As such, care needs to be taken in interpreting these biases and there remains substantial debate over how to do so. For example, it has been argued that both the tendency

for children with ASD to be less prone to contagious yawning [83] and the familiarity bias [37,84,85] can be explained in terms of differences in attending to yawners rather than differences in empathetic response. Similarly, the gender bias reported in humans [29] is not straightforward to interpret and there is debate over whether it simply reflects a false positive in the literature [33,34]. By contrast, proponents of the contagious yawning–empathy hypothesis argue that the familiarity bias continues to be found even when controlling for differences in subjects' attention [40,41] and that the negative results for the gender bias in previous studies reflects methodological issues with prior experiments [34]. Furthermore, although alternative hypotheses such as the attentional hypothesis could explain the presence of a single bias such as the familiarity bias, only the contagious yawning–empathy hypothesis predicts the presence of all three biases. As such, testing for all three biases represents a powerful test of the contagious yawning–empathy hypothesis. Finally, searching for a novel signature, the prosociality bias, required a novel experimental methodology where dogs were exposed to a prosocial experimenter that interacted with them and an antisocial experimenter that ignored them. Previous work which used a similar methodology demonstrated that dogs do show a preference for the prosocial demonstrator [73], and so if the contagious yawning–empathy hypothesis is correct, dogs should have reacted with increased yawning to the prosocial demonstrator. However, further work would be useful in confirming the presence or absence of the prosociality bias in dogs and other species such as humans.

Research into contagious yawning has been dominated by the contagious yawning–empathy debate [37]. However, contagious yawning is an interesting phenomenon in its own right as its evolutionary roots and ultimate function remain a mystery [20]. Contagious yawning in animals may be the result of stress [54,57], an affiliation strategy [67], a means of communication [61], or a mechanism to improve collective vigilance within groups [37,68,69] rather than being related to empathy via a perception–action mechanism. Future research into contagious yawning should include a greater focus on testing between these and other hypotheses. For example, the affiliation hypothesis might predict that contagious yawning should be seen more frequently during reconciliation periods after conflict while the collective vigilance hypothesis posits that contagious yawning should increase in response to external disturbances [37,86]. However, it is important to note that these theories are not necessarily mutually exclusive [87] and that factors such as stress appear to influence yawning propensity in complex ways [88,89]. Additionally, an important next step is to consider evidence of contagious yawning outside of mammals. While there has been some work looking at contagious yawning in budgerigars [86,90] and tortoises [91], research has otherwise been sparse outside of the mammalian class.

Future research would benefit from systematically testing contagious yawning across multiple species. One barrier to such projects is that studying a range of different species often requires different experimental set-ups to make such testing feasible. There is a concern that such a range of methodological approaches may make cross-species and cross-study comparisons difficult, if not impossible [35,66]. However, our finding that the effect of treatment on yawning probabilities and rates remains stable when controlling for various aspects of study design suggests that the presence of

contagious yawning is relatively robust to differences in experimental design. As such, while it is important to use broadly similar designs (for instance, comparing animals' yawning rates when exposed to either a yawning demonstrator or control demonstrator), there could be considerable flexibility in other aspects of study design. For example, our results suggest that animals' yawning probabilities and rates to either live demonstrators or recorded demonstrators are comparable. Therefore, our findings suggest that more ambitious cross-species work can be carried out with confidence in the validity of the subsequent comparisons.

To conclude, our results provide robust support for the hypothesis that contagious yawning is found in dogs, the first non-human species of mammal where it has been clearly shown outside of chimpanzees. However, we found no evidence that dogs yawn more in response to either familiar human yawners compared to unfamiliar human yawners, or to prosocial human yawners compared to antisocial human yawners. Additionally, we found no evidence that female dogs were more likely to yawn in response to a yawning demonstrator than male dogs. As such, these findings cast doubt on the widespread assertion that contagious yawning is mediated by the same perception–action mechanism as empathy [1,6,35,41,58]. Instead, they support recent claims that there is no link between contagious yawning and empathetic processes [37,67] and underline the importance of developing more direct measures of empathy in non-human animals [37,92]. However, while our results suggest that researchers cannot rely on contagious yawning as a diagnostic signal of empathy, our additional findings that the effect of

contagious yawning appears to be robust to variations in experimental methods suggest that cross-species comparisons may be a powerful way to disentangle the evolutionary roots of this behaviour.

**Ethics.** The present study was conducted in accordance with the Animal Welfare Act 1999 and approved by the University of Auckland Animal Ethics Committee R001826 and the University of Auckland Human Ethics Committee R018410. Dogs were recruited through owners' responses to online applications. Written informed consent for participating in this study was obtained from the owners.

**Data accessibility.** All supporting data and code for this study can be found at <https://osf.io/c2f3k/>. The datasets for the reanalysis and our prosociality bias experiment are also available in the electronic supplementary material.

**Authors' contributions.** P.N. and A.H.T. conceived the study. P.N., A.H.T., I.R., R.H., and A.P.M.B. designed the experiment. P.N., I.R., R.H., and A.P.M.B. collected the data. P.N. and S.C. conceived and carried out the statistical analysis. All authors were involved in writing the manuscript.

**Competing interests.** We declare we have no competing interests.

**Funding.** A.H.T. was supported in this work by a Rutherford Discovery Fellowship and a Prime Minister's McDiarmid Emerging Scientist Prize from the Royal Society of New Zealand.

**Acknowledgements.** We thank Romana Gruber for help with data collection and owners and their dogs for giving up their time to help us with this project. We are grateful for the authors of Joly-Mascheroni *et al.* [48], Silva *et al.* [50], O'Hara *et al.* [53], and Madsen & Persson [51] for providing their full datasets online, and for the authors of Romero *et al.* [35] and Buttner & Strasser [54] for providing full datasets upon request. We thank three anonymous reviewers and Jorg Massen for helpful comments on this manuscript.

## References

- de Waal FBM, Preston SD. 2017 Mammalian empathy: behavioural manifestations and neural basis. *Nat. Rev. Neurosci.* **18**, 498–509. (doi:10.1038/nrn.2017.72)
- Batson CD, Duncan BD, Ackerman P, Buckley T, Birch K. 1981 Is empathetic concern a source of altruistic motivation? *J. Pers. Soc. Psychol.* **40**, 290–302. (doi:10.1037/0022-3514.40.2.290)
- Eisenberg N, Miller PA. 1987 The relation of empathy to prosocial and related behaviors. *Psychol. Bull.* **101**, 91–119. (doi:10.1037/0033-2909.101.1.91)
- Morelli SA, Rameson LT, Lieberman MD. 2014 The neural components of empathy: predicting daily prosocial behavior. *Soc. Cogn. Affect. Neurosci.* **9**, 39–47. (doi:10.1093/scan/nss088)
- Preston S, de Waal FBM. 2002 Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* **25**, 1–72. (doi:10.1017/s0140525x02280012)
- de Waal FBM. 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. (doi:10.1007/BF00302695)
- Langford DJ, Crager SE, Shehzad Z, Smith SB, Sotocinal SG, Levenstadt JS, Chanda ML, Levitin DJ, Mogil JS. 2006 Social modulation of pain as evidence for empathy in mice. *Science* **312**, 1967–1970. (doi:10.1126/science.1128322)
- Church RM. 1959 Emotional reactions of rats to the pain of others. *J. Comp. Physiol. Psychol.* **52**, 132–134. (doi:10.1037/h0043531)
- Masserman JH, Wechkin S, Terris W. 1964 'Altruistic' behaviour in rhesus monkeys. *Am. J. Psychiatry* **121**, 584–585. (doi:10.1176/ajp.121.6.584)
- Wechkin S, Masserman JH, Terris W. 1964 Shock to a conspecific as an aversive stimulus. *Psychon. Sci.* **1**, 47–48. (doi:10.3758/bf03342783)
- Custance D, Mayer J. 2012 Empathic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: an exploratory study. *Anim. Cogn.* **15**, 851–859. (doi:10.1007/s10071-012-0510-1)
- Quervel-Chaumette M, Faerber V, Faragó T, Marshall-Pescini S, Range F. 2016 Investigating empathy-like responding to conspecifics' distress in pet dogs. *PLoS ONE* **11**, 1–15. (doi:10.1371/journal.pone.0152920)
- Sanford EM, Burt ER, Meyers-Manor JE. 2018 Timmy's in the well: empathy and prosocial helping in dogs. *Learn. Behav.* **46**, 374–386. (doi:10.3758/s13420-018-0332-3)
- Vasconcelos M, Hollis K, Nowbahari E, Kacelnik A. 2012 Pro-sociality without empathy. *Biol. Lett.* **8**, 910–912. (doi:10.1098/rsbl.2012.0554)
- Silberberg A, Allouch C, Sandfort S, Kearns D, Karpel H, Slotnick B. 2014 Desire for social contact, not empathy, may explain 'rescue' behavior in rats. *Anim. Cogn.* **17**, 609–618. (doi:10.1007/s10071-013-0692-1)
- Schwartz LP, Silberberg A, Casey AH, Kearns DN, Slotnick B. 2017 Does a rat release a soaked conspecific due to empathy? *Anim. Cogn.* **20**, 299–308. (doi:10.1007/s10071-016-1052-8)
- Hachiga Y, Schwartz LP, Silberberg A, Kearns DN, Gomez M, Slotnick B. 2018 Does a rat free a trapped rat due to empathy or for sociality? *J. Exp. Anal. Behav.* **110**, 267–274. (doi:10.1002/jeab.464)
- Ueno H, Suemitsu S, Murakami S, Kitamura N, Wani K, Takahashi Y, Matsumoto Y, Okamoto M, Ishihara T. 2019 Rescue-like behaviour in mice is mediated by their interest in the restraint tool. *Sci. Rep.* **9**, 10648. (doi:10.1038/s41598-019-46128-5)
- Guggisberg AG, Mathis J, Schneider A, Hess CW. 2010 Why do we yawn? *Neurosci. Biobehav. Rev.* **34**, 1267–1276. (doi:10.1016/j.neubiorev.2010.03.008)
- Norscia I, Palagi E. 2011 Yawn contagion and empathy in *Homo sapiens*. *PLoS ONE* **6**, 1–5. (doi:10.1371/journal.pone.0028472)
- Platek SM, Mohamed FB, Gallup GG. 2005 Contagious yawning and the brain. *Cogn. Brain Res.* **23**, 448–452. (doi:10.1016/j.cogbrainres.2004.11.011)

23. Platek SM, Critton SR, Myers TE, Gallup GG. 2003 Contagious yawning: the role of self-awareness and mental state attribution. *Cogn. Brain Res.* **17**, 223–227. (doi:10.1016/S0926-6410(03)00109-5)
24. 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)
25. Christov-Moore L, Simpson EA, Coudé G, Grigaityte K, Iacoboni M, Ferrari PF. 2014 Empathy: gender effects in brain and behavior. *Neurosci. Biobehav. Rev.* **46**, 604–627. (doi:10.1016/j.neubiorev.2014.09.001)
26. Langford DJ *et al.* 2010 Social approach to pain in laboratory mice. *Soc. Neurosci.* **5**, 163–170. (doi:10.1080/17470910903216609)
27. Romero T, Castellanos MA, De Waal FBM. 2010 Consolation as possible expression of sympathetic concern among chimpanzees. *Proc. Natl Acad. Sci. USA* **107**, 12 110–12 115. (doi:10.1073/pnas.1006991107)
28. Taylor S, Klein LC, Lewis BP, Gruenewald TL, Gurung RA, Updegraff JA. 2000 Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. *Psychol. Rev.* **107**, 411–429. (doi:10.1037//0033-295X.107.3.411)
29. Norscia I, Demuru E, Palagi E. 2016 She more than he: gender bias supports the empathic nature of yawn contagion in *Homo sapiens*. *R. Soc. Open Sci.* **3**, 150459. (doi:10.1098/rsos.150459)
30. Senju A, Maeda M, Kichui 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)
31. Rundle BK, Vaughn VR, Stanford MS. 2015 Contagious yawning and psychopathy. *Pers. Individ. Dif.* **86**, 33–37. (doi:10.1016/j.paid.2015.05.025)
32. Massen JJM, Church AM, Gallup AC. 2015 Auditory contagious yawning in humans: an investigation into affiliation and status effects. *Front. Psychol.* **6**, 1735. (doi:10.3389/fpsyg.2015.01735)
33. Gallup AC, Massen JJM. 2016 There is no difference in contagious yawning between men and women. *R. Soc. Open Sci.* **3**, 160174. (doi:10.1098/rsos.160174)
34. Norscia I, Demuru E, Palagi E. 2016 Difference in contagious yawning between susceptible men and women: why not? *R. Soc. Open Sci.* **3**, 160477. (doi:10.1098/rsos.160477)
35. 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)
36. 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)
37. Massen JJM, Gallup AC. 2017 Why contagious yawning does not (yet) equate to empathy. *Neurosci. Biobehav. Rev.* **80**, 573–585. (doi:10.1016/j.neubiorev.2017.07.006)
38. Anderson JR, Myowa-Yamakoshi M, Matsuzawa T. 2004 Contagious yawning in chimpanzees. *Proc. R. Soc. Lond. B* **271**, 468–470. (doi:10.1098/rsbl.2004.0224)
39. Campbell MW, Carter JD, Proctor D, Eisenberg ML, De Waal FBM. 2009 Computer animations stimulate contagious yawning in chimpanzees. *Proc. R. Soc. B* **276**, 4255–4259. (doi:10.1098/rspb.2009.1087)
40. Campbell MW, de Waal FBM. 2011 Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS ONE* **6**, 19–22. (doi:10.1371/journal.pone.0018283)
41. Campbell MW, de Waal FBM. 2014 Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees. *Proc. R. Soc. B* **281**, 20140013. (doi:10.1098/rspb.2014.0013)
42. Massen JJM, Vermunt DA, Sterck EHM. 2012 Male yawning is more contagious than female yawning among chimpanzees (*Pan troglodytes*). *PLoS ONE* **7**, 1–5. (doi:10.1371/journal.pone.0040697)
43. Madsen EA, Persson T, Sayehli S, Lenninger S, Sonesson G. 2013 Chimpanzees show a developmental increase in susceptibility to contagious yawning: a test of the effect of ontogeny and emotional closeness on yawn contagion. *PLoS ONE* **8**, e76266. (doi:10.1371/journal.pone.0076266)
44. 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)
45. Campbell MW, Cox CR. 2019 Observational data reveal evidence and parameters of contagious yawning in the behavioral repertoire of captive-reared chimpanzees (*Pan troglodytes*). *Sci. Rep.* **9**, 13271. (doi:10.1038/s41598-019-49698-6)
46. Palagi E, Norscia I, Cordon G. 2019 Lowland gorillas (*Gorilla gorilla gorilla*) failed to respond to others' yawn: experimental and naturalistic evidence. *J. Comp. Psychol.* **133**, 406–416. (doi:10.1037/com0001175)
47. Stevens JM, Daem H, Verspeek J. 2017 Bonobos do not yawn along with video models of yawning conspecifics. Conference Paper. In *15th Conference of the German Primate Society 2017, Zurich, Switzerland, 15–17 February*.
48. Tan J, Arieli D, Hare B. 2017 Bonobos respond prosocially toward members of other groups. *Sci. Rep.* **7**, 1–11. (doi:10.1038/s41598-017-15320-w)
49. Joly-Mascheroni RM, Senju A, Shepherd AJ. 2008 Dogs catch human yawns. *Biol. Lett.* **4**, 446–448. (doi:10.1098/rsbl.2008.0333)
50. Silva K, Bessa J, de Sousa L. 2012 Auditory contagious yawning in domestic dogs (*Canis familiaris*): first evidence for social modulation. *Anim. Cogn.* **15**, 721–724. (doi:10.1007/s10071-012-0473-2)
51. Madsen EA, Persson T. 2013 Contagious yawning in domestic dog puppies (*Canis lupus familiaris*): the effect of ontogeny and emotional closeness on low-level imitation in dogs. *Anim. Cogn.* **16**, 233–240. (doi:10.1007/s10071-012-0568-9)
52. 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)
53. O'Hara SJ, Reeve AV. 2011 A test of the yawning contagion and emotional connectedness hypothesis in dogs, *Canis familiaris*. *Anim. Behav.* **81**, 335–340. (doi:10.1016/j.anbehav.2010.11.005)
54. Buttner AP, Strasser R. 2014 Contagious yawning, social cognition, and arousal: an investigation of the processes underlying shelter dogs' responses to human yawns. *Anim. Cogn.* **17**, 95–104. (doi:10.1007/s10071-013-0641-z)
55. Deputte BL. 1994 Ethological study of yawning in primates I. Quantitative analysis and study of causation in two species of old world. *Ethology* **98**, 221–245. (doi:10.1111/j.1439-0310.1994.tb01073.x)
56. Baenninger R. 1987 Some comparative aspects of yawning in *Betta splendens*, *Homo sapiens*, *Panthera leo*, and *Papio sphinx*. *J. Comp. Psychol.* **101**, 349–354. (doi:10.1037/0735-7036.101.4.349)
57. Paukner A, Anderson JR. 2006 Video-induced yawning in stump-tail macaques (*Macaca arctoides*). *Biol. Lett.* **2**, 36–38. (doi:10.1098/rsbl.2005.0411)
58. Palagi E, Leone A, Mancini G, Ferrari PF. 2009 Contagious yawning in gelada baboons as a possible expression of empathy. *Proc. Natl Acad. Sci. USA* **106**, 19 262–19 267. (doi:10.1073/pnas.0910891106)
59. Massen JJM, Šlipogor V, Gallup AC. 2016 An observational investigation of behavioral contagion in common marmosets (*Callithrix jacchus*): indications for contagious scent-marking. *Front. Psychol.* **7**, 1–11. (doi:10.3389/fpsyg.2016.01190)
60. Reddy RB, Krupenye C, Maclean EL, Hare B. 2016 No evidence of contagious yawning in lemurs. *Anim. Cogn.* **19**, 889–898. (doi:10.1007/s10071-016-0986-1)
61. Moyaho A, Rivas-Zamudio X, Ugarte A, Eguibar JR, Valencia J. 2015 Smell facilitates auditory contagious yawning in stranger rats. *Anim. Cogn.* **18**, 279–290. (doi:10.1007/s10071-014-0798-0)
62. Yonezawa T, Sato K, Uchida M, Matsuki N, Yamazaki A. 2017 Presence of contagious yawning in sheep. *Anim. Sci. J.* **88**, 195–200. (doi:10.1111/asj.12681)
63. Rossman ZT, Hart BL, Greco BJ, Young D, Padfield C, Weidner L, Gates J, Hart LA. 2017 When yawning occurs in elephants. *Front. Vet. Sci.* **4**, 1–7. (doi:10.3389/fvets.2017.00022)
64. Romero T, Ito M, Saito A, Hasegawa T. 2014 Social modulation of contagious yawning in wolves. *PLoS ONE* **9**, e105963. (doi:10.1371/journal.pone.0105963)
65. Stevens JR. 2017 Replicability and reproducibility in comparative psychology. *Front. Psychol.* **8**, 1–6. (doi:10.3389/fpsyg.2017.00862)
66. Campbell MW, de Waal FBM. 2010 Methodological problems in the study of contagious yawning. In *The mystery of yawning in physiology and disease* (ed. O Walusinski), pp. 120–127. Basel, Switzerland: Karger Publishers.
67. Yoon JMD, Tennie C. 2010 Contagious yawning: a reflection of empathy, mimicry, or contagion? *Anim. Behav.* **79**, 2007–2009. (doi:10.1016/j.anbehav.2010.02.011)

68. Miller ML, Gallup AC, Vogel AR, Clark AB. 2012 Auditory disturbances promote temporal clustering of yawning and stretching in small groups of budgerigars (*Melopsittacus undulatus*). *J. Comp. Psychol.* **126**, 324–328. (doi:10.1037/a0026520)
69. Gallup AC, Gallup GG. 2007 Yawning as a brain cooling mechanism: nasal breathing and forehead cooling diminish the incidence of contagious yawning. *Evol. Psychol.* **5**, 147470490700500. (doi:10.1177/147470490700500109)
70. Taylor AH. 2014 Corvid cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* **5**, 361–372. (doi:10.1002/wcs.1286)
71. Bernhardt BC, Singer T. 2012 The neural basis of empathy. *Annu. Rev. Neurosci.* **35**, 1–23. (doi:10.1146/annurev-neuro-062111-150536)
72. Singer T, Seymour B, O’Doherty JP, Stephan KE, Dolan RJ, Frith CD. 2006 Empathic neural responses are modulated by the perceived fairness of others. *Nature* **439**, 466–469. (doi:10.1038/nature04271)
73. Nitzschner M, Melis AP, Kaminski J, Tomasello M. 2012 Dogs (*Canis familiaris*) evaluate humans on the basis of direct experiences only. *PLoS ONE* **7**, e46880. (doi:10.1371/journal.pone.0046880)
74. Borenstein M, Hedges LV, Higgins JPT, Rothstein HR. 2009 When does it make sense to perform a meta-analysis? In *Introduction to meta-analysis*, pp. 357–364. Chichester, UK: John Wiley & Sons.
75. Kruschke JK, Liddell TM. 2018 The Bayesian new statistics: hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. *Psychon. Bull. Rev.* **25**, 178–206. (doi:10.3758/s13423-016-1221-4)
76. Cumming G. 2014 The new statistics: why and how. *Psychol. Sci.* **25**, 7–29. (doi:10.1177/0956797613504966)
77. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432. (doi:10.1007/s11222-016-9696-4)
78. McElreath R. 2018 *Statistical rethinking: a Bayesian course with examples in R and Stan*, 2nd edn. Boca Raton, FL: CRC Press.
79. R Core Team. 2018 R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
80. Bürkner P-C. 2017 brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28. (doi:10.18637/jss.v080.i01)
81. Stan Development Team. 2018 RStan: the R interface to Stan. R package version 2.19.2, <http://mc-stan.org/>.
82. Wickham H. 2009 *Ggplot2: elegant graphics for data analysis*, 1st edn. New York, NY: Springer.
83. Usui S, Senju A, Kikuchi Y, Akechi H, Tojo Y, Osanai H, Hasegawa T. 2013 Presence of contagious yawning in children with autism spectrum disorder. *Autism Res. Treat.* **2013**, 971686. (doi:10.1155/2013/971686)
84. Méary D, Li Z, Li W, Guo K, Pascalis O. 2014 Seeing two faces together: preference formation in humans and rhesus macaques. *Anim. Cogn.* **17**, 1107–1119. (doi:10.1007/s10071-014-0742-3)
85. Schino G, Sciarretta M. 2016 Patterns of social attention in mandrills, *Mandrillus sphinx*. *Int. J. Primatol.* **37**, 752–761. (doi:10.1007/s10764-016-9936-7)
86. 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)
87. Gallup AC. 2011 Why do we yawn? Primitive versus derived features. *Neurosci. Biobehav. Rev.* **35**, 765–769. (doi:10.1016/j.neubiorev.2010.09.009)
88. Eldakar OT, Tartar JL, Garcia D, Ramirez V, Dauzonne M, Armani Y, Gallup AC. 2017 Acute physical stress modulates the temporal expression of self-reported contagious yawning in humans. *Adapt. Hum. Behav. Physiol.* **3**, 156–170. (doi:10.1007/s40750-017-0060-5)
89. Miller ML, Gallup AC, Vogel AR, Clark AB. 2010 Handling stress initially inhibits, but then potentiates yawning in budgerigars (*Melopsittacus undulatus*). *Anim. Behav.* **80**, 615–619. (doi:10.1016/j.anbehav.2010.05.018)
90. Gallup AC, Swartwood L, Militello J, Sackett S. 2015 Experimental evidence of contagious yawning in budgerigars (*Melopsittacus undulatus*). *Anim. Cogn.* **18**, 1051–1058. (doi:10.1007/s10071-015-0873-1)
91. Wilkinson A, Sebanz N, Mandl I, Huber L. 2011 No evidence of contagious yawning in the red-footed tortoise *Geochelone carbonaria*. *Curr. Zool.* **57**, 477–484. (doi:10.1093/czoolo/57.4.477)
92. Gallup AC, Church AM. 2015 The effects of intranasal oxytocin on contagious yawning. *Neurosci. Lett.* **607**, 13–16. (doi:10.1016/j.neulet.2015.09.007)