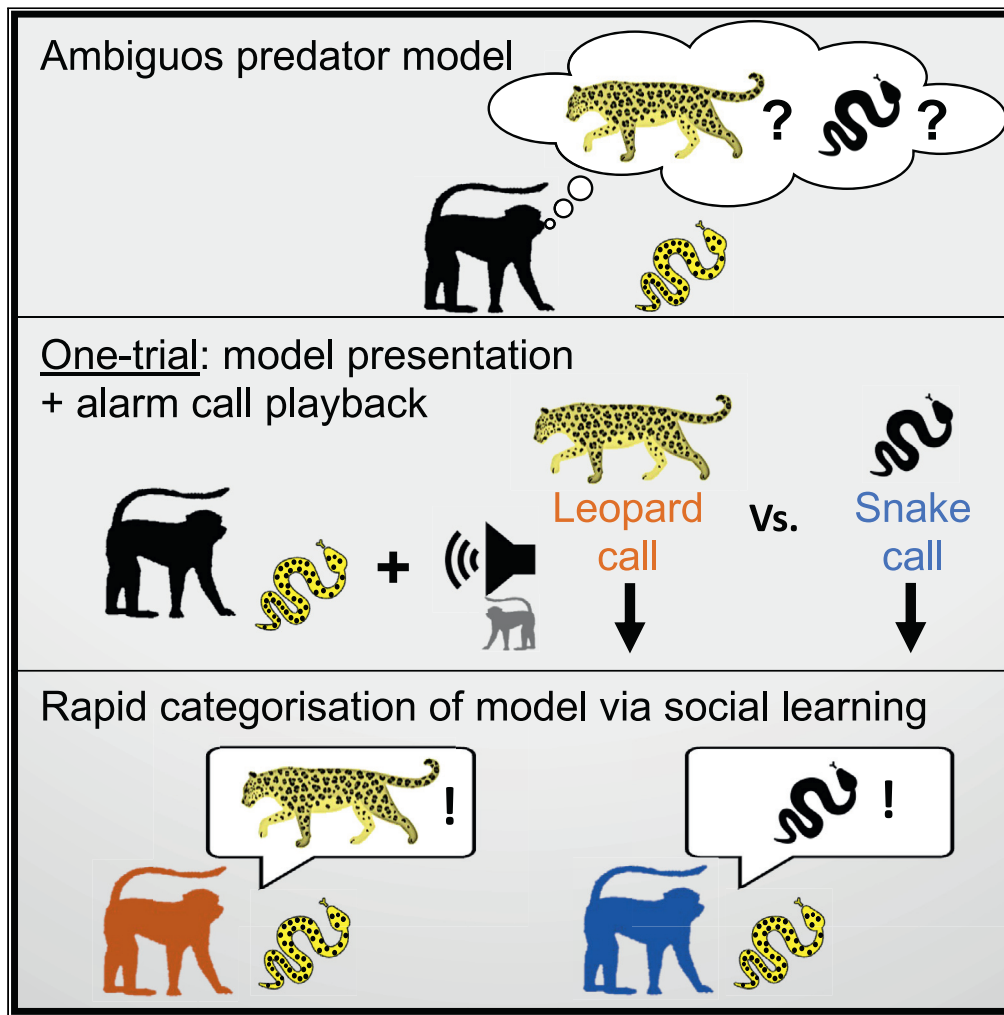


## Article

## Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys



Julián León,  
Constance Thiriau,  
Clémentine Bodin,  
Catherine  
Crockford, Klaus  
Zuberbühler

julian.leon@unine.ch

**Highlights**

We exposed mangabeys to chimeric predator models with both snake and leopard features

Juveniles categorised the ambiguous predator by attending to others' alarm calls

Subjects formed model-call associations after one single call exposure

This knowledge was potentially retained and communicated subsequently to others

León et al., iScience 25,  
104853  
September 16, 2022 © 2022  
The Author(s).  
[https://doi.org/10.1016/  
j.isci.2022.104853](https://doi.org/10.1016/j.isci.2022.104853)

## Article

## Acquisition of predator knowledge from alarm calls via one-trial social learning in monkeys

Julián León,<sup>1,2,6,\*</sup> Constance Thiria,<sup>2</sup> Clémentine Bodin,<sup>2</sup> Catherine Crockford,<sup>3,4</sup> and Klaus Zuberbühler<sup>1,2,5</sup>

## SUMMARY

**How do animals learn to classify the world and what is the role of social learning during this process? Here, we show that young sooty mangabeys, *Cercocebus atys*, of Taï Forest, Côte d'Ivoire, learn to rapidly classify an unfamiliar predator by attending to others' alarm calls and that such knowledge is retained over long periods. We experimentally exposed subjects to chimeric predator models with both snake- and leopard-like features, combined with playbacks of conspecific snake (N = 12) or leopard alarms (N = 13). Adults classified the chimeras as non-threatening but for juveniles, we found that one single alarm call exposure was sufficient to allocate the chimera to the snake or leopard category, suggesting plausibility judgments in experienced adults. We then retested N = 10 juveniles with the same models more than a year after their first experience and found that they continued to show their original response, indicating long-term retention of socially learned predator categorisation.**

## INTRODUCTION

How do non-human primates learn to classify predators? Early research on the vervet monkey alarm call system have shown that infants are, to some extent, predisposed from birth to discriminate between the basic predator classes (aerial vs terrestrial), but with experience become increasingly more competent in recognising the few predatory species that pose an actual threat (e.g., martial eagles, leopards). Social learning is a likely driver during this process, with behavioral effects on alarm call production and antipredator responses (Hauser, 1989; Seyfarth and Cheney, 1980, 1986). More recent fieldwork has shown that predator category formation can be astonishingly rapid. West African green monkeys produced aerial alarm calls when exposed to a drone for a first time (Wegdell et al., 2019), while in subsequent encounters the mere sound of the drone was already sufficient to elicit scanning the sky and running for cover. In another field experiment, Wheeler et al (2019) showed that, after a small number of trials, capuchin monkeys learned to associate novel sounds with the presence of predators and that they could retain such knowledge for many months.

Rapid and efficient learning is clearly adaptive in the predation context, a powerful selection force with considerable fitness consequences, but often very limited learning opportunities (Curio, 1976). Moreover, many species are faced with a range of regionally varying predator species that require different antipredator responses (Bidner, 2014; Stephan and Zuberbühler, 2008, 2014). Rapid learning has been also demonstrated in the foraging context, such as taste aversion in laboratory rats (Garcia et al., 1955) or fast-mapping in a dog trained to fetch toys (Kaminski et al., 2004). While rapid learning is well documented, it still remains unclear how exactly animals acquire such knowledge. Group-living animals grow up surrounded by more experienced group members, suggesting that social learning is important to obtain information from interacting or observing more experienced ones (Galef and Laland, 2005; Heyes and Galef, 1996). A classic example is Curio et al' (1978) study on blackbird mobbing behavior, which could be conditioned to novel raptor models and even random objects (plastic bottles), as long as the social input was adequate. Similar experiments with rhesus monkeys showed that individuals that were naive and initially fearless of snakes came to avoid them, after observing the aversive response of a more experienced individual toward a snake (Mineka and Cook, 1993).

In this study, we investigated the role of social learning in predator category formation in a terrestrial forest primate, the sooty mangabeys (*Cercocebus atys*). In Taï Forest, Côte d'Ivoire, mangabeys are hunted by leopards (*Panthera pardus*) (Zuberbühler and Jenny, 2002), crowned eagles (*Stephanoaetus coronatus*)

<sup>1</sup>Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland

<sup>2</sup>Taï Monkey Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire

<sup>3</sup>Institute of Cognitive Sciences Marc Jeannerod, CNRS, 69330 Lyon, France

<sup>4</sup>Tai Chimpanzee Project, Centre Suisse de Recherches Scientifiques, 01 BP1303 Abidjan 01, Cote d'Ivoire

<sup>5</sup>School of Psychology and Neuroscience, University of St. Andrews, Saint Andrews, Scotland KY16 9JP, UK

<sup>6</sup>Lead contact

\*Correspondence: julian.leon@unine.ch

<https://doi.org/10.1016/j.isci.2022.104853>





**Figure 1. Chimeric models**

Illustrations of two custom-made, snake-leopard chimeric animal models with visual features of two predators; leopard colour pattern and viper body shape. The two models differed in the surface structure, one being a painted wooden item (left) and the other being covered with commercially printed fabric (right).

(Shultz and Thomsett, 2007) but they are also vulnerable to accidental snakebites, notably by highly venomous Gaboon and rhinoceros vipers (*Bitis gabonica*; *B. nasicornis*) (Penner et al., 2008). Sooty mangabeys frequently encounter leopards (1.04 per observation week), crowned eagles (8.94 per observation week), and large vipers (2.83 per observation week; Methods S1). Leopards attack primates on the ground or in the lower canopy but monkeys can protect themselves by rapid climbing. Vipers do not pursue and are no longer dangerous once discovered and monitored (Crockford et al., 2015). Mangabeys produce acoustically distinct alarm calls to both predators (Range and Fischer, 2004). Predator detection is probably strongly visually guided, with evidence from other primates that the spotted leopard coat and distinct body shape of vipers are sufficient to trigger alarm calling (Coss et al., 2005; Coss and Ramakrishnan, 2000; Crockford et al., 2015; Pessoa et al., 2014; Schel and Zuberbühler, 2009).

Here, we experimentally tested whether free-ranging sooty mangabeys could socially learn to categorise a visually ambiguous animal model with features of both leopards and vipers (Figure 1). We first examined how subjects from different age groups reacted spontaneously to these chimeric animal models, deliberately designed to create ambiguity for classification and thus preventing individuals from making predictions about dangerousness, hunting technique or appropriate alarm call behaviour. We were interested in whether subjects would rely on other group members' apparent assessments of the chimera, if given the opportunity. We operationalised this in a second experiment with juveniles, by first letting a subject encounter the chimera, immediately followed by playbacks of snake or leopard alarm calls by a familiar (but invisible) group member. Later that same day, we presented the chimeric model for a second time to the same subjects and registered their responses. If subjects attended to others' alarm calls (i.e., their categorisations), we predicted that they should use this information in the future encounters with the chimera (see Table 1 for definitions of antipredator behaviours).

## RESULTS & DISCUSSION

### Baseline responses

We tested two immobile chimeric predator models with both snake-like and leopard-like features, which we positioned on a subject's anticipated travel path (Methods S2). We collected data from subjects belonging to two different groups (TMP group: adults: N = 6 adults, old juveniles (OJ): N = 4, young juveniles (YJ): N = 5; TCP group: OJ: N = 3, YJ: N = 1); see methods section for group sizes and composition). Adults consistently ignored the model (Bayes factor  $BF_{10} = 18.14$ , see methods section for interpretation of Bayes factors and Table S1 for equivalent frequentist statistics; Table S2), suggesting that they perceived the chimeras as irrelevant or at least non-threatening. In contrast, 9 of 13 juveniles treated the model as a potential predator. However, we did not find that juveniles had any clear bias to classify

**Table 1. Definitions and predictions of behavioural responses**

Behavioural response	Definition	Prediction
Snake antipredator behaviours	Subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls	Snake > Leopard
Number of pauses	Subject stops walking by halting all limb movement at the same time. Individuals pause more when caution is required to ascertain the nature and location of a nearby stationary threat.	Snake > Leopard
Leopard antipredator behaviours	Subject escapes climbing into a tree, flees and/or emits leopard alarm calls	Leopard > Snake
Move >10 m	Subject displaces more than 10 m away from the model after detecting it. Individuals increase their distance from a nearby chaser threat.	Leopard > Snake

the chimera as a threat (Bayes factor  $BF_{10} = 1.49$ ; Table S1). Specifically, 5 of 7 old juveniles and 4 of 6 young juveniles showed strong antipredator behaviour (Table S2). Although, at first sight, the models looked more similar to a snake-like animal than to a leopard-like one, there was no evidence for subjects having an overall bias to one or the other predator (snake response: OJ:  $N = 2$ ; YJ:  $N = 3$ ; leopard response: OJ:  $N = 3$ ; YJ:  $N = 1$ ; Bayes factor  $BF_{10} = 0.3$ ; Table S1). These results suggest that juveniles categorised the chimeric models either as non-threatening animal or that, if they considered it a threat, either as snake or a leopard.

### Experiment 1: Categorisation of chimeras

We then carried out the first experiment on individuals other than those used in the baseline condition ( $N = 25$ ; OJ:  $N = 13$ , YJ:  $N = 12$ ; Table 2 and Table S3). Experimental trials consisted of two conditions: 1) presentation of a model, this time in conjunction with a playback of either snake or leopard alarms and 2) a subsequent assessment (Methods S2). As in the baseline condition adults consistently ignored the models, we decided to conduct the experiment with juveniles only. In each presentation trial, the chimera was shown to a subject and, as soon it had detected it, we played back either snake or leopard alarm calls of a familiar group member from a nearby concealed speaker (Figure S1). In subsequent assessment trials a few hours later (mean = 2.75 h; range: 1.2–20.0 h), we investigated whether subjects retained the relevant knowledge by presenting the model for a second time, this time without accompanying alarm calls.

In the assessment trials, we found that 5 of 25 juveniles (20.0%) produced alarm calls ( $N = 4$  snake condition,  $N = 1$  leopard condition; Table S3) that matched the ones experienced during playback. This suggests that subjects had learned to categorise the chimeric models from attending to others and that they were able to transmit this new knowledge with their own alarm calls (Bayes factor  $BF_{10} = 10.5$ ; Table S1). These response rates may not seem particularly high, but they are comparable to what is usually observed in juveniles during natural encounters. During 177 and 133 h of focal animal data on adults and immatures, respectively, we registered  $N = 14$  viper and  $N = 4$  leopard encounters events. In only  $N = 3$  viper and  $N = 1$  leopard encounters, a juvenile was the first individual to alarm call (22.2% of all observed snake and leopard natural encounters), suggesting that alarm calling was mainly initiated by more experienced adults and subadults, an effect also found in other primate studies (Dezecache et al., 2019; Hollén et al., 2008; Mielke et al., 2019). We found no evidence that juvenile age, the presence of audiences within 10 m or model type (paint or fabric) explained differences in alarm responses (Bayes factor, Age:  $BF_{10} = 0.7$ ; Audience:  $BF_{10} = 0.7$ ; Model Type:  $BF_{10} = 1.9$ ; Table S1). Finally, the call providers during the presentation trials were always different and did not follow any evident categorisation pattern (two adult females and one adult, subadult and juvenile male each).

Regarding non-vocal responses, 13 of 25 subjects (52.0%) showed evidence that they treated the chimera as belonging to either the snake or the leopard category. These learned associations were more easily established with snake (snake GLM, estimate =  $-3.29$ , SE = 1.16,  $z = -2.82$ ,  $p = 0.004$ ; Figure 2A; Table 1 and Table S4A; Video 1) than leopard alarms (leopard GLM, estimate = 2.99, SE = 1.57,  $z = 1.9$ ,  $p = 0.05$ ; Figure 3A, Table 1 and Table S4C; Video 2), suggesting that the chimera was perceived as more snake-like than

**Table 2. Juveniles' behavioural responses in assessment trials (N = 26; one trial was aborted)**

Play back alarm call	Responses				
	Snake	$\bar{x}$ N pauses (sd)	Leopard	Move >10 m	Ignore
Snake (N = 13)	9	2.38 (1.85)	0	1	3
Leopard (N = 12)	1	1 (1.04)	4	7	4

Snake and leopard refers to antipredator behaviours. Leopard and move >10 m responses are not mutually exclusive.

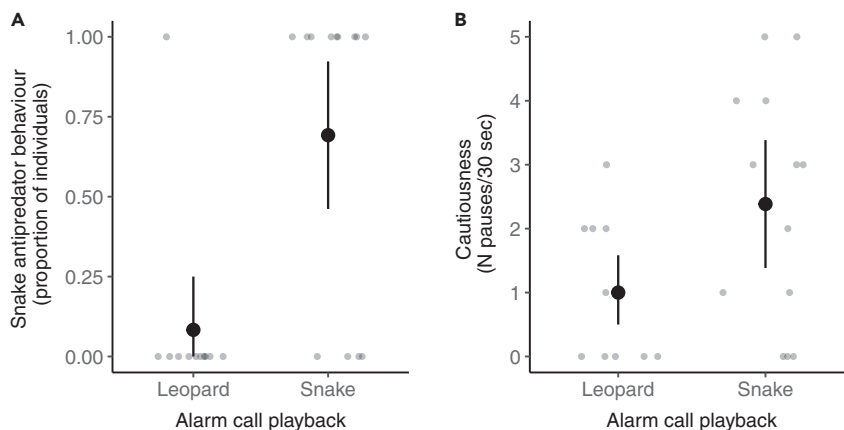
leopard-like (9 of 13 (69.2%) juveniles responded with snake antipredator behavior; while only 4 of 12 (33.3%) responded with leopard antipredator behavior). The fact that subjects exposed to snake alarm calls moved more cautiously when encountering the chimeric model again supports this idea (number of pauses GLM, estimate =  $-0.86$ , SE =  $0.34$ ,  $z = -2.51$ ,  $p = 0.011$ ; [Figure 2B](#); [Table 1](#) and [Table S4B](#); [Video 1](#)). Nevertheless, 7 of 12 subjects (58.3%) that heard leopard alarms increased their distance to the model (move >10 m GLM, estimate =  $2.8$ , SE =  $1.1$ ,  $z = 2.53$ ,  $p = 0.011$ ; [Figure 3B](#); [Table 1](#) and [Table S4D](#); [Video 3](#)). Although we did not record many strong leopard-type escape responses to the chimera when hearing leopard alarms during the model presentations, the observed behaviours were in line with what occurs during natural encounters with smaller cat-like species, particularly genets (*Genetta* spp.) and civets (*Civettictis civetta*; J León, unpublished data), suggesting that juveniles classified the chimera as a cat-like carnivore. Finally, seven more individuals ignored the model and two subjects that heard each type of alarm responded with mismatched behaviours: the one that heard snake alarms increased her distance to the model, while the subject that heard leopard alarms showed snake-type antipredator behaviour ([Table 2](#) and [Table S3](#)).

We also tested if the time interval between presentation and assessment trials had an effect on the responses of subjects. Although both trials were usually conducted on the same day, the number of hours since the presentation trials did not have a significant effect on the response to the chimeric model during the assessment trials, suggesting that learning was stable in the short-term (corresponding response in function of time interval between trials GLMM: estimate =  $0.01$ , SE =  $0.01$ ,  $z = 1.04$ ,  $p = 0.29$ ).

In contrast to subjects in the baseline condition, who equally—and spontaneously—treated the chimera as a predator animal belonging equally to the snake and leopard category, subjects in experiment 1 categorised more easily the chimera as a snake-like threat. This is not very surprising since the chimeric model looked more similar to a snake-like animal than a leopard-like one. Thus, the learned associations were probably more readily established with snake alarm calls. Similarly, only a slight majority of subjects showed strong antipredator responses after categorising the chimeras as either a snake or a leopard, which was in line with natural observations. In fact, during natural predator encounters juveniles showed low response rates, while most antipredator behaviours, including alarm calls, were initiated by adults. This suggests that primate antipredator behaviours develop through a combination of simple maturation, personal experience and social inputs from other group members.

In sum, our study demonstrated that sooty mangabeys can socially learn to classify novel objects from one single social learning experience, by attending to the referential properties of others' alarm calls. This finding aligns with the hypothesis that non-human primates become communicatively competent by learning to understand of how natural events usually unfold, specially by observing how others behave in unfamiliar situations ([Zuberbühler et al., 2022](#)).

Although predation is a major force of natural selection, actual predation attempts on particular individuals are often rare, while inconsequential encounters with predators are quite common. Hence, young individuals probably have opportunities to see predators, but it may be much more difficult to learn how to categorise them. To overcome this challenge, the ability to socially learn from how experienced group members react during predator sightings is clearly adaptive ([Curio et al., 1978](#); [Keen et al., 2020](#); [Magrath et al., 2015](#); [Potvin et al., 2018](#)). Our field experiment adds to this line of research by showing how categorisation of novel objects can occur by attending to the referential information of others' vocalizations.



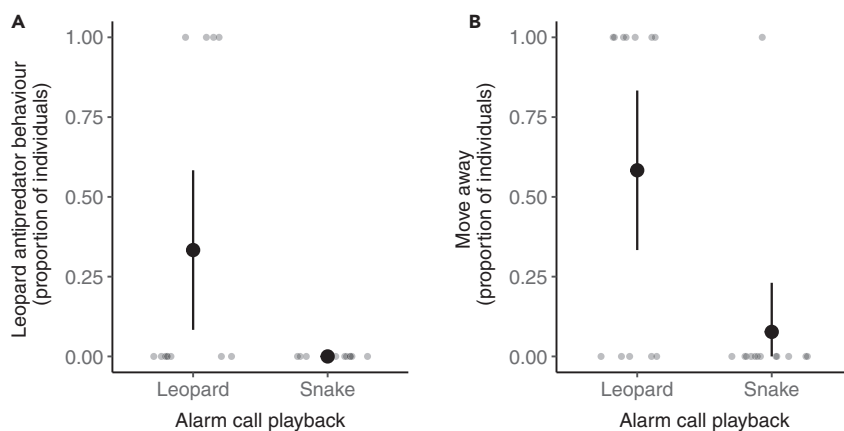
**Figure 2. Sooty mangabey behavioural responses after detecting the chimeric model during the assessment trials**

(A) Proportion of individuals showing snake antipredator behaviour.

(B) Number of pauses. Black dots indicate medians, vertical lines indicate a 95% percentage interval, and grey dots indicate individual values for each subjects' response. Leopard condition N = 12, snake condition N = 13.

### Experiment 2: Long-term retention

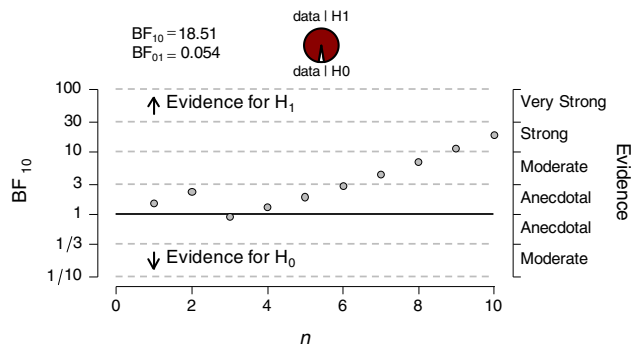
To assess whether the socially learned categorisation of the chimeric models was retained, we conducted retest trials almost 2 years after the first encounters. We were able to expose 10 of the original subjects to the same chimeric model for a third time after an average interval of 603 days (range 534–718 days). Remarkably, 9 of 10 subjects (90.0%) still exhibited the same reaction as in the assessment trials, indicating that associations formed during the initial exposure were retained permanently (Bayes factor  $BF_{10} = 18.51$ ; Tables S1 and S5). It should be noted, though, that 3 of 10 subjects ignored the models in the initial exposure, so it is unknown if they have retained a previously learned association or relied on other cues to categorise the chimeras. Moreover, we found no evidence of any memory decay, when taking into account intervals between assessment and retest trials (Figure 4). We could retest only one of the five subjects who had a vocal response during the first experiment. One of ten subjects (10.0%) produced an alarm call (snake) during the retests; however, he was the same subject who gave a vocal response before and we were able to retest. This caller heard snake alarms when first presented to the chimera, suggesting that alarm calling could be part of socially learned antipredator behaviour to some extent. However, the variation in the responses and the small sample size in the retest trials suggests that the role of social learning in the retention of knowledge partially acquired through vocal signals should be interpreted with some caution.



**Figure 3. Sooty mangabey behavioural responses after detecting the chimeric model during the assessment trials**

(A) Proportion of individuals showing leopard antipredator behaviour.

(B) Proportion of individuals moving >10 m away from the model. Black dots indicate medians, vertical lines indicate a 95% percentage interval, and grey dots indicate individual values for each subjects' response. Leopard condition N = 12, snake condition N = 13.



**Figure 4. Bayes factor sequential sampling plot for retest trials**

Accumulation of evidence after each of the  $N = 10$  retest trial data points is added as a function of its time interval between its corresponding assessment trials. The probability wheel at the top illustrates the ratio of the evidence in favour of the two hypotheses. Estimated Bayes factors for null ( $BF_{01}$ ) and alternative ( $BF_{10}$ ) hypotheses suggested that the data were 0.054:1 in favour of the absence of effect, or rather, 18.51 times more likely to occur under the presence of a long-term association effect than without it.

### Limitations of the study

We have shown that mangabeys can rapidly acquire predator knowledge from others' alarm calls by one-trial social learning, a conclusion based on the following limitations. First, a general problem in animal cognition research, especially in the wild, is low sample size, and our study is no exception. Habituation of wild primates to human observers is extremely time-consuming and a major financial commitment so it is difficult to see how address the problem at our study site. The main alternative is by replication in other species or with novel experimental designs. Specific to this study, it was impossible to find the 'perfect' chimera, i.e., a creature with equal amounts of 'leopard-ness' and 'snake-ness'. Although we found no evidence for a bias towards one of the two predator classes in naïve subjects, a wider range of chimera models would have been preferable, varying both in shape and colour patterns. Related to this, it would be interesting to see how far into the 'unnatural' models could have been made (e.g., random objects) before subjects no longer accepted them as a potential predator (see Curio et al., 1978). Future research may want to explore these avenues.

### Conclusions

Rapid learning and long-term retention is highly adaptive in the predation context (Griffin, 2004; Wegdell et al., 2019; Wheeler et al., 2019). Despite the limitations of the study, here, we showed that alarm calls can serve as vehicles for rapid and highly efficient one-trial social learning, provided the subject has not yet reached adulthood. Remarkably, one such experience is sufficient to permanently stamp such knowledge into the monkey's mind, with no clear evidence for memory decay. Our study thus demonstrates that non-human primates can learn to identify and classify a novel danger by attending to referential signals and potentially retain such knowledge and communicate it subsequently to others. The effect was not seen in adults who ignored the models, suggesting they were better capable of distinguishing plausible from implausible events, and likely classified the model as irrelevant and non-threatening. Among the juvenile cohort, however, there were no performance differences in the categorisation of the chimeric model, with individuals up to 4 years attending to others' alarm calls as a basis for social learning. Whilst alarm call production is relatively inflexible at the species level, local variation in predators might drive selection for social learning of appropriate local alarm call usage. Whether such a selection pressure drives social learning of call usage more broadly, for example also in social contexts, remains to be tested.

### STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability

- Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Experimental design
  - Baseline condition
  - Experiment 1: Categorisation of chimeras
  - Experiment 2: Long-term retention
  - Behavioral response variables
- QUANTIFICATION AND STATISTICAL ANALYSIS

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.104853>.

## ACKNOWLEDGMENTS

We thank the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire for support and permission to conduct research in the Taï National Park. Fieldwork was made possible thanks to Paterson Kalo, Landri Bele and the rest of the Taï Monkey Project (TMP) assistants, to whom we express our gratitude. We thank the Taï Chimpanzee Project (TCP) and its staff for support in the field. We also thank Mélissa Berthet and Alison Ashbury for helpful discussions and comments on the early drafts of this manuscript. This work was funded by the Swiss National Science Foundation Agreement project grants 31003A\_166458 (KZ) and 310030\_185324 (KZ), and the Swiss National Centre of Competence in Research (NCCR) Evolving Language, Swiss National Science Foundation Agreement #51NF40\_180888 (KZ).

## AUTHOR CONTRIBUTIONS

J.L. and K.Z. conceived the study; J.L., C.T. and C.B. conducted the experiments; J.L. analysed data; C.C. provided access to the TCP study group; J.L. and K.Z. wrote the manuscript.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: March 16, 2022

Revised: June 16, 2022

Accepted: July 25, 2022

Published: September 16, 2022

## REFERENCES

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.
- Audacity Team (2020). Audacity: Free Audio Editor and Recorder.
- Bidner, L.R. (2014). Primates on the menu: direct and indirect effects of predation on primate communities. *Int. J. Primatol.* 35, 1164–1177. <https://doi.org/10.1007/s10764-014-9797-x>.
- Center for Conservation Bioacoustics (2014). Raven Pro: Interactive Sound Analysis Software (Cornell Lab Ornithol).
- Ramakrishnan, U., and Coss, R. (2000). Perceptual aspects of leopard recognition by wild bonnet macaques (*Macaca radiata*). *Beyond Behav.* 137, 315–335.
- Coss, R.G., Ramakrishnan, U., and Schank, J. (2005). Recognition of partially concealed leopards by wild bonnet macaques (*Macaca radiata*): the role of the spotted coat. *Behav. Process.* 68, 145–163. <https://doi.org/10.1016/j.beproc.2004.12.004>.
- Crockford, C., Wittig, R.M., and Zuberbühler, K. (2015). An intentional vocalization draws others' attention: a playback experiment with wild chimpanzees. *Anim. Cognit.* 18, 581–591. <https://doi.org/10.1007/s10071-014-0827-z>.
- Curio, E. (1976). *The Ethology of Predation* (Springer Science & Business Media).
- Curio, E., Ernst, U., and Vieth, W. (1978). Cultural transmission of enemy recognition: one function of mobbing. *Science* 202, 899–901. <https://doi.org/10.1126/science.202.4370.899>.
- Dezecache, G., Crockford, C., and Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behav. Ecol. Sociobiol.* 73, 104. <https://doi.org/10.1007/s00265-019-2716-6>.
- Galef, B.G., and Laland, K.N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience* 55, 489–499.
- Garcia-Rivera, J., Morris, M.P., and Koelling, R.A. (1955). Conditioned aversion to saccharin resulting from exposure to gamma radiation. *Science* 122, 1089–1090. <https://doi.org/10.1126/science.122.3179.1089>.
- Gelman, A., and Su, Y.-S. (2020). Arm: Data Analysis Using Regression and Multilevel/hierarchical Models.
- Griffin, A.S. (2004). Social learning about predators: a review and prospectus. *Learn. Behav.* 32, 131–140. <https://doi.org/10.3758/BF03196014>.



- Hauser, M.D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (*Cercopithecus aethiops*) vocalizations. *J. Comp. Psychol.* 103, 149–158. <https://doi.org/10.1037/0735-7036.103.2.149>.
- Heyes, C., and Galef, B., Jr. (1996). *Social Learning in Animals: The Roots of Culture* (Elsevier).
- Hollén, L.I., Clutton-Brock, T., and Manser, M.B. (2008). Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints? *Behav. Ecol. Sociobiol.* 62, 821–829.
- Jeffreys, H. (1939). *The Theory of Probability*, 1st ed. (Oxford University Press).
- Kaminski, J., Call, J., and Fischer, J. (2004). Word learning in a domestic dog: evidence for “fast mapping”. *Science* 304, 1682–1683. <https://doi.org/10.1126/science.1097859>.
- Keen, S.C., Cole, E.F., Sheehan, M.J., and Sheldon, B.C. (2020). Social learning of acoustic anti-predator cues occurs between wild bird species. *Proc. Biol. Sci.* 287, 20192513. <https://doi.org/10.1098/rspb.2019.2513>.
- Magrath, R.D., Haff, T.M., Fallow, P.M., and Radford, A.N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol. Rev. Camb. Phil. Soc.* 90, 560–586. <https://doi.org/10.1111/brv.12122>.
- McCullagh, P., and Nelder, J.A. (1989). *Generalized Linear Models*, Second. (Chapman & Hall/CRC).
- McGraw, W.S., and Zuberbühler, K. (2007). The monkeys of the Tai forest: an introduction. In *Monkeys of the Tai Forest: An African Primate Community*, Cambridge Studies in Biological and Evolutionary Anthropology, K. Zuberbühler, R. Noë, and W.S. McGraw, eds. (Cambridge University Press), pp. 1–48. <https://doi.org/10.1017/CBO9780511542121.002>.
- Mielke, A., Crockford, C., and Wittig, R.M. (2019). Snake alarm calls as a public good in sooty mangabeys. *Anim. Behav.* 158, 201–209. <https://doi.org/10.1016/j.anbehav.2019.10.001>.
- Mineka, S., and Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. *J. Exp. Psychol. Gen.* 122, 23–38. <https://doi.org/10.1037/0096-3445.122.1.23>.
- Penner, J., Fruteau, C., Range, F., and Rodel, M. (2008). Finding a needle in a haystack: new methods of locating and working with rhinoceros vipers (*Bitis rhinoceros*). *Herpetol. Rev.* 39, 310.
- Pessoa, D.M.A., Maia, R., de Albuquerque Ajuz, R.C., De Moraes, P.Z.P.M.R., Spyrides, M.H.C., and Pessoa, V.F. (2014). The adaptive value of primate color vision for predator detection. *Am. J. Primatol.* 76, 721–729. <https://doi.org/10.1002/ajp.22264>.
- Potvin, D.A., Ratnayake, C.P., Radford, A.N., and Magrath, R.D. (2018). Birds learn socially to recognize heterospecific alarm calls by acoustic association. *Curr. Biol.* 28, 2632–2637.e4. <https://doi.org/10.1016/j.cub.2018.06.013>.
- R Core Team (2020). *R: A Language and Environment for Statistical Computing*.
- Range, F., and Fischer, J. (2004). Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Tai National Park. *Ethology* 110, 301–321. <https://doi.org/10.1111/j.1439-0310.2004.00973.x>.
- Schel, A.M., and Zuberbühler, K. (2009). Responses to leopards are independent of experience in Guereza colobus monkeys. *Beyond Behav.* 146, 1709–1737. <https://doi.org/10.1163/000579509X12483520922007>.
- Seyfarth, R.M., and Cheney, D.L. (1986). Vocal development in vervet monkeys. *Anim. Behav.* 34, 1640–1658. [https://doi.org/10.1016/S0003-3472\(86\)80252-4](https://doi.org/10.1016/S0003-3472(86)80252-4).
- Seyfarth, R.M., and Cheney, D.L. (1980). The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Z. Tierpsychol.* 54, 37–56. <https://doi.org/10.1111/j.1439-0310.1980.tb01062.x>.
- Shultz, S., and Thomsen, S. (2007). Interactions between African crowned eagles and their prey community. In *Monkeys of the Tai Forest: An African Primate Community*, Cambridge Studies in Biological and Evolutionary Anthropology, K. Zuberbühler, R. Noë, and W.S. McGraw, eds. (Cambridge: Cambridge University Press), pp. 171–193. <https://doi.org/10.1017/CBO9780511542121.008>.
- Simmons, J.P., Nelson, L.D., and Simonsohn, U. (2011). False-positive psychology: undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychol. Sci.* 22, 1359–1366. <https://doi.org/10.1177/0956797611417632>.
- Smid, S.C., McNeish, D., Miočević, M., and van de Schoot, R. (2020). Bayesian versus frequentist estimation for structural equation models in small sample contexts: a systematic review. *Struct. Equ. Model.: A Multidiscip. J.* 27, 131–161. <https://doi.org/10.1080/10705511.2019.1577140>.
- Stephan, C., and Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (*Cercopithecus diana diana*). *Behav. Ecol. Sociobiol.* 68, 321–331. <https://doi.org/10.1007/s00265-013-1647-x>.
- Stephan, C., and Zuberbühler, K. (2008). Predation increases acoustic complexity in primate alarm calls. *Biol. Lett.* 4, 641–644. <https://doi.org/10.1098/rsbl.2008.0488>.
- Team, J. (2020). *JASP (Version 0.14.1)*.
- van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Eitz, A., Evans, N.J., Gronau, Q.F., Haaf, J.M., et al. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychon. Bull. Rev.* 28, 813–826. <https://doi.org/10.3758/s13423-020-01798-5>.
- Wegdell, F., Hammerschmidt, K., and Fischer, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nat. Ecol. Evol.* 3, 1039–1042. <https://doi.org/10.1038/s41559-019-0903-5>.
- Wheeler, B.C., Fahy, M., and Tiddi, B. (2019). Experimental evidence for heterospecific alarm signal recognition via associative learning in wild capuchin monkeys. *Anim. Cognit.* 22, 687–695. <https://doi.org/10.1007/s10071-019-01264-3>.
- Zuberbühler, K., and Jenny, D. (2002). Leopard predation and primate evolution. *J. Hum. Evol.* 43, 873–886. <https://doi.org/10.1006/jhev.2002.0605>.
- Zuberbühler, K., León, J., Deshpande, A., and Quintero, F. (2022). Socially scripted vocal learning in primates. *Curr. Opin. Behav. Sci.* 46, 101153. <https://doi.org/10.1016/j.cobeha.2022.101153>.

## STAR★METHODS

## KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Repository data	This paper	<a href="https://osf.io/t93xa/">https://osf.io/t93xa/</a>
Experimental models: Organisms/strains		
Sooty mangabeys ( <i>Cercocebus atys</i> )	Taï forest, Côte d'Ivoire	N/A
Software and algorithms		
Audacity	N/A	<a href="https://www.audacityteam.org/">https://www.audacityteam.org/</a> ; v.2.2.2
Raven Pro	N/A	<a href="https://ravensoundsoftware.com/">https://ravensoundsoftware.com/</a> ; v.1.4
Solomon coder	N/A	<a href="https://solomon.andraspeter.com/">https://solomon.andraspeter.com/</a> ; v.19.08.02
R	N/A	<a href="https://cran.r-project.org/">https://cran.r-project.org/</a> ; v.4.0.3
JASP	N/A	<a href="https://jasp-stats.org/">https://jasp-stats.org/</a> ; v.0.14.1
Other		
Speaker amplifier	AER	Alpha

## RESOURCE AVAILABILITY

## Lead contact

Further information and requests for resources and methods can be directed to the lead contact, Julián León ([jj.leon34@gmail.com](mailto:jj.leon34@gmail.com)).

## Materials availability

Physical materials were not used within this study.

## Data and code availability

- All data reported in this paper are included in the Supplemental Information file.
- All original code has been deposited at OSF and is publicly available as of the date of publication. DOI is listed in the [key resources table](#).
- Any additional information required to reanalyse the data reported in this paper is available from the [lead contact](#) upon request.

## EXPERIMENTAL MODEL AND SUBJECT DETAILS

The study was conducted from August 2019 to March 2020 and March to August 2021 with two groups of free-ranging sooty mangabeys in Taï National Park, Ivory Coast. Both groups were fully habituated to human observers ([McGraw and Zuberbühler, 2007](#)). We first collected baseline data to the chimera model from 15 subjects (6 adults, 3 old and 5 young juveniles) from the main study group and 4 juveniles (3 old and 1 young juveniles) from one group whose home range was about 4 km Northwest of the main study group ([Mielke et al., 2019](#)). All experiments were conducted on the main study group, whose size was around 81 individuals during the study period, including 30 adults (23 females, 7 males; >5 years old), 12 subadults (6 females, 6 males; 4–5 years old), 17 old juveniles (9 females, 8 males; 3–4 years old) and 22 young juveniles (10 females, 12 males; 1–2 years old).

Data collection was approved by the Centre Suisse de Recherches Scientifiques (CSRS), the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the Office Ivoirien des Parcs et Réserves (OIPR) of Côte d'Ivoire.

## METHOD DETAILS

### Experimental design

We fabricated two chimeric animal models with mixed visual features of leopards and vipers, using wood, acrylic paint and fabric as materials (Figure 1). Natural encounters with leopards, Gaboon and rhinoceros vipers are common occurrences in the study area. To avoid habituation and minimize stress, we presented chimeric animal models once per week, which was within the monkeys' natural range of experience with the mentioned ground predators (Methods S1, Figure 1 and Table S6).

We followed sooty mangabeys and collected behavioural data from dawn to dusk for a second study. We used 20-min focal animal samples (Altmann, 1974) to record detailed behavioural data for all members of the main study group. We chose the first focal subject opportunistically and then sampled all individuals of the same age-sex class before making repeated samples of the same individual. During 930 focal samples (531 samples on adult and 399 on immatures subjects), we were able to document natural encounters with leopards (N = 4) and Gaboon and rhinoceros vipers (N = 14). Additionally, we recorded the vocal responses produced in N = 5 leopard model, a realistic-looking plush toy, presentations. We recorded all alarm calls with a Marantz PMD 661 MKII digital recorder and an MKH 416-P48U3 Sennheiser directional microphone. Sound files were stored and processed as .wav files with 44.1 kHz sampling rate, 16 bits amplitude resolution using Audacity 2.2.2 (Audacity Team, 2020) and Raven 1.4 software (Center for Conservation Bioacoustics, 2014). Recordings were screened for exemplars with low signal-to-noise ratio, absence of signal overlap and recording distances of less than 10 m. We extracted 31 alarm calls (leopard alarm: N = 15; snake alarm: N = 16, see Figure S2) from 29 individuals (N = 26 adults, N = 2 old and N = 1 young juveniles) that were used as playback stimuli.

### Baseline condition

The study consisted of a baseline and two assessment conditions (Methods S2). In the baseline condition, we presented a chimeric model to N = 6 adults, N = 7 old and N = 6 young juveniles, to describe the non-primed, spontaneous reactions to the models. All focal subjects were in the periphery of the group. As subjects had no prior experience with the model, they were prevented from making predictions about its dangerousness, hunting technique, mode of attack or appropriate alarm call. We decided to exclude adults from further experimental trials, as they consistently ignored the chimeric models in the baseline condition (N = 6) (Table S2).

### Experiment 1: Categorisation of chimeras

We conducted a total of N = 26 experimental trials (N = 13 old; N = 13 young juveniles), each consisting of a model presentation in conjunction with an alarm playback (presentation trial), followed by a subsequent assessment (assessment trial), consisting of a second model presentation sometime after the first one (Table S3). One trial with a young female juvenile was aborted because of a technical problem with the playback speaker during the presentation of the chimeric model, resulting in a final dataset of N = 25 trials.

During the presentation trial, the chimeric model was shown to a subject and, as soon as it detected the model, we played back either leopard alarms (N = 13) or snake alarms (N = 13). By simultaneously broadcasting another individual's alarm calls when model detection occurred, subjects were offered pivotal information on how to interpret the unfamiliar animal model. To avoid pseudo-replication, we used a different playback stimulus (N = 26 alarm calls from 24 call providers) for each trial and ensured that we never broadcast a call from a call provider that was in the audience. 12 adult and 1 juvenile female and 8 adult, 2 subadult and 1 juvenile male were used as call providers (Table S7). We could not ascertain if some call providers were more effective in instilling knowledge in juveniles than others (e.g., hierarchy, kin or social bond effects), but by always broadcasting a different call stimulus and trying to avoid using call providers twice, we are confident that the identity of the caller did not have a major effect on our results. All stimuli were broadcasted using an Apple iPod touch digital player connected to an AER alpha speaker amplifier. The two types of chimeric models and the playback stimuli were presented in a randomized but counterbalanced way.

We then presented the chimeric model for a second time to the same subject and registered his or her response. Assessment trials were usually conducted on the same day (mean = 2.75 h; range: 1.2–20.0 h), but only after the subject had left the area of the first encounter and had engaged in other activities.

Assessment trials were conducted only if no other predator-related event had occurred during the previous hour and when subjects were in the periphery of the group, usually isolated with no other individual within 5–10 m.

### Experiment 2: Long-term retention

After a break of nearly two years (mean = 603 days; range: 534–718 days), an experimenter (CB) naive to the original study revisited the group and managed to retest  $N = 11$  subjects ( $N = 7$  old,  $N = 4$  young juveniles).  $N = 4$  subjects were originally primed with leopard alarm calls and  $N = 7$  originally with snake alarm calls.  $N = 1$  trial (old juvenile primed with snake alarms) was aborted because the subject became interrupted by a social interaction during the model presentation, resulting in a final dataset of  $N = 10$ . Experimental conditions were identical to experiment 1.

### Behavioral response variables

For each trial, we noted the identity and behavioural responses of the subject, type of model (paint or fabric), play backed alarm call (snake or leopard), time of model detection and audience composition within a 10–15 m radius of the subject. We distinguished four behavioural responses: snake antipredator behaviour (scored as 1 when subject stays and scans the forest floor, approaches and inspects, jumps aside, stands bipedally and/or emits snake alarm calls; binary), number of locomotor pauses 30 s before and after a model was detected (numeric), leopard antipredator behaviour (scored as 1 when subject escapes climbing into a tree, flees and/or emits leopard alarm calls; binary), and whether or not the subject moved >10 m from the model (scored as 1 when subject displaces more than 10 m away from the model after detecting it; binary) (Table 1). To estimate observer reliability, a second observer (Auriane Le Floch) blind-coded (21/43) 48.8% of trials, resulting in an excellent interrater reliability (Cohen's kappa for Snake antipredator behaviours:  $K = 1$ ; Leopard antipredator behaviours:  $K = 1$ ; Move >10 m:  $K = 0.84$  and intraclass correlation coefficient for the number of pauses:  $ICC = 0.91$ ). We used a Panasonic HC-V500 camera for video recordings and a Solomon coder ([solomon.andraspeter.com](http://solomon.andraspeter.com)) to analyse video recordings on a frame-by-frame basis (25 frames  $s^{-1}$ ).

### QUANTIFICATION AND STATISTICAL ANALYSIS

Contrary to frequentist methods, Bayesian analyses do not rely on asymptotic theory, a property that can be a drawback when analysing small sample size datasets (Smid et al., 2020). Hence, we used a mix of GLMs and Bayesian analyses as a way to overcome any potential small sample size issue, an inherent problem in primate cognition research, both in captivity and in the wild.

We used a series of Generalized Linear Models (McCullagh and Nelder, 1989) using R version 4.0.3 (R Core Team, 2020) and the functions 'bayesglm' (for binary variables; family = Binomial) and 'glm' (for numeric variable; family = Poisson) of the packages arm (Gelman and Su, 2020) and stats (R Core Team, 2020), respectively.

Each model tested a different behavioural response variable, coded from the assessment trials videos, against the same set of four fixed effects predictor variables. The predictor variables were as follows: (1) Playback Stimulus (snake or leopard alarm calls), (2) Juvenile Age (young or old), (3) Audience (alone or in company) and (4) Model Type (paint or fabric). Playback stimulus was our main variable of interest and was considered the test predictor, with the other three variables considered to be control predictors. None of the control predictors had a significant effect on the behavioural responses (Table S4). To check whether the control factor Model Type (paint or fabric) drove the results (Simmons et al., 2011), we re-ran all the analyses without it. The results were robust. Additionally, we included the interaction Playback Stimulus and Juvenile Age, to detect if younger individuals had any association preference for the chimeric model to a particular predator type. In all models, this interaction was not significant; thus, we removed it, and then reran the models (Table S4). A test of over-dispersion showed no cause for concern with dispersion parameters <1. To count for multiple testing, of the same behavioural response,  $p$  values were subjected to Bonferroni corrections, such that values below  $p = 0.0125$  were considered significant.

Finally, we conducted one-sided Bayesian binomial tests, on JASP (Team, 2020) to analyse subjects' behavioural responses during control condition and retest trials and their vocal response during assessment trials. We specified a test value of 0.5, and  $a = b = 1$  for the prior distribution of  $\theta$  under  $\mathcal{H}_1$ . To interpret Bayes

factors, we followed the classification of strength of evidence proposed by van Doorn et al. ([van Doorn et al., 2021](#)) in line with [Jeffreys \(1939\)](#): a Bayes factor smaller than 3 was interpreted as weak evidence, a Bayes factor between 3 and 10 was interpreted as moderate evidence, and a Bayes factor greater than 10 was interpreted as strong evidence for the alternative  $H_1$  relative to the null hypothesis  $H_0$ . We also conducted frequentist statistics (binomial test) on the same behavioural and vocal responses to help interpretability of the results. We found no change in our results and conclusions ([Table S1](#)).