Logical inferences from visual and auditory information in ruffed lemurs and sifakas

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1. Introduction

When navigating their physical or social world, both humans and non-human animals face problems where the information necessary for optimal action is incomplete or even missing. In such situations, being able to use the information available to reconstruct or infer what it is missing can be advantageous. Inferential reasoning therefore allows individuals to adaptively respond to situation when fragmentary information is available, by associating a perceivable and an inferred or imagined event (Premack, 1995). A dominant view in cognitive science is that inferential reasoning is dependent on language and requires a long developmental process in humans (Carruthers, 2002; Cesana-Arlotti, et al., 2018; Falmagne, 1990; Piaget, 1953). As such, both nonhuman animals and human infants might be limited in their abilities for reasoning, combining information flexibly, or in thinking abstractly (Premack, 2007; Penn et al., 2008; Spelke, 2002; Shettleworth, 2012). Thus, whether non-verbal creatures are able to make inferences is a crucial issue for understanding the evolution of intelligent behavior (e.g., Call, 2004; Sabbatini and Visalberghi, 2008; Schoegl et al., 2009; Schmitt and Fischer, 2009; Hill et al., 2011; see Völter and Call, 2017 for a review).

In fact, several lines of evidence indicate that preverbal human infants (Cesana-Arlotti et al., 2018) and some non-human animal species' (Völter and Call, 2017) are able to engage in at least simple forms of inferential reasoning. For example, inference by exclusion is the ability to select the correct alternative by excluding other potential alternatives. In the simplest version of a task assessing inference by exclusion in animals, individuals are presented with two opaque containers of which only one is baited with a food reward. Individuals are then provided with explicit information about the contents either the baited container, or the empty one. Then, they can choose between the two in order to get the food (Call, 2004). Thus, decision-makers can

potentially use the information that one container is empty to infer that the other container must have the reward. This paradigm has been used extensively to investigate inference by exclusion abilities across a wide range of species including primates, mammals and birds (see Völter and Call, 2017 for a review). In fact, many animal species can solve this problem, including great apes (chimpanzees - *Pan troglodytes,* bonobos - *Pan paniscus,* gorillas - *Gorilla gorilla,* orangutans - *Pongo pygmaeus* and *P. abeli*, Call, 2004), Old World monkeys (olive baboons - *Papio hamadryas anubis*, Schmitt and Fischer, 2009; Tonkean macaques - *Macaca tonkeana*, Petit et al., 2015), New World monkeys (capuchins - *Cebus apella*, Sabbatini and Visalberghi, 2008; spider monkeys - *Ateles geoffroyi*, Hill et al., 2011; cotton-top tamarins - *Saguinus oedipus*, Heimbauer et al., 2019), dwarf goats (*Capra aegagrus hircus*, Nawroth et al., 2014), dogs (*Canis familiaris*, Bräuer et al., 2006; Erdőhegyi et al., 2007), Asian elephants (*Elephas maximus*, Plotnik et al., 2014), and birds including ravens (*Corvux corax*, Schloegl et al., 2009), carrion crows (*Corvus corone corone,* Mikolasch et al., 2012), New Caledonian crows (*Corvus moneduloides*, Jelbert et al., 2015), keas (*Nestor notabilis,* Schloegl et al., 2009) and African grey parrots (*Psittacus erithacus*, Mikolasch et al., 2011; Pepperberg et al., 2013). While animals may solve this task using different kinds of strategies (Mikolasch et al., 2012; Schmitt and Fischer, 2009), this pattern suggests that a basic form of reasoning, or at least a precursor to that kind of inference, is both independent from language and widespread in the animal kingdom.

These results also show important variation in performance across species, with some species showing more successful performance than others. For example, while carrion crows and ravens can find food using inference by exclusion (Mikolasch et al., 2012), jackdaws (*Corvus monedula*) were unable to do so (Schloegl, 2011). Comparative work on non-human primates, so far comprising 14 species to date, also indicates that there is large variability in abilities (Call,

2004; Heimbauer et al., 2012; Maille and Roeder, 2012; Marsh et al., 2015; Schloegl et al., 2009). For example, while many primate species can use visual information to make inferences from exclusion about hidden rewards (e.g., visually showing animals that one location is empty), using auditory information (e.g. providing an audible cue, or lack of such a cue, that food is present by shaking a container) seems to be more challenging on the whole. While apes and capuchins monkeys seems to be able to use both visual and auditory information to locate food, orangutans, Tonkean macaques, baboons, rhesus monkeys (*Macaca mulatta*), and cotton-top tamarins were unable to use auditory information in similar contexts (Heimbauer et al., 2019; Hill et al., 2011; Petit et al., 2015; Schmitt and Fischer, 2009).

What is the origin of this kind of variation in cognition across species? Many views on the evolution of cognition have emphasized that socioecology may play an important role in shaping cognitive abilities. While social organization has long been thought to be the major selective pressure in primate cognitive evolution (Byrne and Whiten, 1988; Dunbar, 1998; Dunbar and Shultz, 2007; Humphrey, 1976; Jolly, 1966), other views argue that at least some cognitive abilities evolved in response to different cognitive challenge posed by various features of the diet. In particular, species foraging on more complex food—in terms of a heterogeneous spatiotemporal distribution, greater environmental uncertainty, or high degree of necessary processing—may have evolved more sophisticated cognitive skills and larger brains (Clutton-Brock and Harvey, 1980; Milton, 1981; Byrne 1997; Parker and Gibson 1997; Deaner et al. 2003; Rosati, 2017; MacLean et al. 2009; DeCasien et al., 2017; Parker and Gibson, 1997). Along these lines, empirical evidence highlights that ecological complexity may be especially important for understanding the evolution of memory, decision-making and executive functions—cognitive capacities that play a crucial role in supporting effective foraging behaviour (Addessi et al., 2011; De Petrillo et al., 2015;

Heilbronner et al., 2008; MacLean et al., 2012; Platt et al., 1996; Rosati et al., 2007; Rosati and Hare, 2012; Rosati and Hare, 2013; Rosati et al., 2014; Stevens et al., 2005; Stevens, 2014; see also De Petrillo and Rosati, 2019 and Rosati, 2017 for a review).

The ability to make these kinds of inferences may also be related to foraging behaviour and ecological complexity, as reasoning capacities can allow animals to select (and exclude) potential food patches based on whether they are plausibly resource-rich or depleted. For example, frugivorous species depend more on food sources that are patchily distributed in the environment, and more difficult to locate (Rosati, 2017; Milton, 1981). As such, they may need to make such inferences on a routine basis, whereas folivorous species feed on relatively homogenously distributed leaves where such inferences may be less important. A given species' natural history may further shape kinds of information that they preferentially attend to when making inferences. Given that only apes and capuchins show robust use of auditory information when making inferences by exclusion (Call, 2004; Sabbatini and Visalberghi, 2008), this suggests that some species may have evolved a propensity to also attend to auditory cues in foraging contexts in response their specific feeding ecology. For example, capuchin monkeys will tap nuts in order to assess their contents based on the sounds produced (Visalberghi and Néel, 2003), and also use stones to crack and open nuts (Visalberghi and Fragaszy, 2013). Similarly, apes may be able to flexibly use different kinds of causal cues, including auditory information (Bräuer et al., 2006), as they also forage on foods that are not directly visible like insects, and engage in extensive tool use behaviors including nut-cracking (Boesch and Boesch, 1990; Brewer and McGrew, 1990; McGrew, 2010; Sanz et al., 2009).

However, the evolutionary processes shaping abilities for logical reasoning in primates are currently unclear, as most work on inference by exclusion to date has focused on the proof of

existence of this skill in nonhuman animals, and often involve only single species (sometimes only a few individuals), or examine distantly related species that can be less useful for these kinds of evolutionary inferences due to phylogenetic signal in cognitive traits (MacLean et al., 2012; Nunn, 2011). In addition, in studies of primates there has been a heavy focus on anthropoid primates (monkeys and apes). Although understudied compared with anthropoids, strepsirrhine primates (lemurs and lorises) represent an important model of the ancestral primate mind (Fitchtel and Kappeler, 2010), and are a strong test for hypotheses about cognitive evolution because they exhibit high levels of diversity in evolutionarily-relevant characteristics such as social system, ecology, and activity patterns (Richard and Dewar, 1991; Fichtel and Kappeler, 2010; Rosati, 2017). Yet despite this diversity in evolutionarily-relevant characteristics, Malagasy primates are a monophyletic group with many overall similarities in lifestyle that accounts for other potential sources of variation in cognitive abilities, such as brain size (Horvath et al., 2008; Yoder et al., 1996; Karanth et al., 2005).

To date, however, little is known about logical inference abilities in lemurs with two main exceptions. First, one previous study examined transitive reasoning, a form of deductive reasoning according to which if A exceeds B, and B exceeds C, then A thereby exceeds C (MacLean et al., 2008). Yet only one study has investigated inference by exclusion abilities specifically in lemurs, testing a small sample of black and brown lemurs (n = 3 per species) on choices involving visual or auditory information (Maille and Roeder, 2012). This study showed limited evidence for inferential reasoning by exclusion in lemurs—but also more success at the auditory cue, which is surprising given data from anthropoids. Furthermore, while strepsirrhines generally have a less developed visual acuity than anthropoids (Kirk, 2004; Kirk and Kay, 2004), prior work shows that lemurs can in fact use visual cues to differentiate food items (Rushmore et al., 2012). Overall, this

study therefore suggests that lemurs may differ in their inference abilities compared to anthropoids, both in terms of their abilities to make inferences from exclusion and in the kinds of information they focus on to do so.

In the current study, we therefore investigated logical reasoning abilities in lemurs that differ in their wild ecology: red ruffed and black and white riffed lemurs (*Varecia* spp.) and Coquerel's sifaka (*Propithecus coquereli*). While both live in medium-sized family groups (mean group sizes for sifakas: 6.1; for ruffed lemurs: 5.4; MacLean et al., 2009, 2013), they exhibit major differences in their diet. Both black-and-white ruffed lemurs (*Varecia variegata*) and red ruffed lemurs (*V. rubra*, classed as *V. variegata* subspecies until recently; Mittermeier et al., 2008) are among the most highly frugivorous of lemurs, with diets that can exceed 90% fruit (Britt, 2000; Vasey, 2005; Schmidt et al., 2010). Sifakas, in contrast, are adapted for a leaf-based diet with specialized dentition and gut structure that allows the microbial fermentation of fibrous foods (Campbell et al., 2000; Richard, 1977). These robust ecological differences make these species a strong test case to examine how ecological complexity shapes cognitive abilities for inferential reasoning. We modified the task developed by Call (2004) for lemurs, and directly compared these species' abilities to make inferences from direct evidence versus by exclusion, using both visual and auditory information. In the first study we investigated lemurs' success in using direct visual and auditory information about the location of food. In the second study, we then examined lemurs' abilities to make direct inferences versus reason by exclusion to locate the food based on either complete or partial visual and auditory information. Since there is already evidence that both of these species can use visual cues to identify food (Rushmore et al., 2012), we predicted that both ruffed lemurs and sifakas could exploit direct visual information. However, frugivorous species might also benefit from attending to auditory cues, for example the sound of a fruit falling from a

tree, such that ruffed lemurs would be better able to use auditory information. Finally, we also predicted that the frugivorous ruffed lemurs would be generally better at making inference by exclusion compared to folivorous sifakas, due to differences in dietary complexity.

2. Study 1: Using direct evidence to find food

In Study 1, we examined whether lemurs can use complete visual versus auditory information to find food in one of two containers. Lemurs observed that one piece of food was hidden inside one of two possible containers but did not know which one. Then they were provided with either visual or auditory information about the content of both containers. We had two main goals with this study: (1) to test lemurs' ability to use visual versus auditory information; and (2) to identify lemurs who could use direct information in order to then subsequently test if they can make inferences by exclusion in Study 2.

2.1. Ethics Statement

All non-invasive behavioral tests had ethics approval from Duke University's Institution Animal Care and Use Committee (Protocol #A268-16-12).

2.2. Subjects

Our final sample comprised 19 lemurs at the Duke Lemur Center in Durham, North Carolina (see Table S1 for detailed subject information): ten ruffed lemurs (3 black-and-white ruffed lemurs and 7 red ruffed lemurs; 2 females and 7 males; ranging from 1 to 30 years old; mean age = 6.9 ± 0.7; analyses collapse across these groups given their overall similarity and recent classification as subspecies) and nine Coquerel's sifaka (4 females and 5 males; ranging from 2 to

29 years old; mean age = 12.4 ± 0.6, Table S1). Lemurs were housed in species-appropriate social groups, and all had access to indoor and outdoor rooms; many also could semi-free-range in forest enclosures for more than half the year temperature permitting. They had *ad libitum* access to water during the sessions, were not food-restricted for testing, and were fed a species- appropriate daily diet of fruit, vegetables, leaves, and chow. Subjects completed no more than one test session per day, and all tests were voluntary: if the lemur stopped participating, the session was stopped. To our knowledge, these lemurs were naïve to inference by exclusion tasks, and had little or no prior experience in relevant cognitive tasks that involved making choices between containers that contained hidden food (e.g., four individuals, 2 sifakas and 2 ruffed lemurs, had participated in MacLean et al., 2012 several years previously). All lemurs therefore completed several initial introductory sessions to familiarize them with the setup for these tasks (described below) before completing the main test session. An additional 9 subjects (8 sifakas and 1 ruffed lemur) were initially tested in those introductory sessions but were not tested in the main experiment because they either failed to reach criterion in the introductory sessions (N = 6) or stopped participating (N = 3).

2.3. Setup and general procedure

Lemurs were individually tested in one of their familiar indoor rooms. The primary experimenter (E1) sat outside the room, separated from the lemur by wire mesh, and presented the experiment on a plastic table (length 76.2 cm, width 45.72 cm, height 49.53 cm); a second identical table was placed inside the lemur's room so the lemur could sit on it (see Figure 1 for diagram of setup and Video S1 for example). A second experimenter (E2) filmed lemurs' choices and recorded choices live on paper (without directly interacting with the lemur or study materials). In the basic

procedure for the main test, E1 showed the lemur a reward and then baited one of two visually distinct boxes behind an occluder, out of the lemur's view. The experimenter then covered the boxes with a corresponding lid. Then E1 removed the occluder and presented either a visual cue (opening the lids) or auditory cue (shaking the boxes) for both boxes in succession (see Figure 1). Lemurs then could indicate their choice by either touching a box or approaching one of the boxes within 3 cm from their initial centered staring position (note that many lemurs habitually indicate choices by moving their heads directly near options, rather than touching with their hands; see Video S1). We used portions of Craisins as rewards for the ruffed lemurs, and portions of peanuts for the sifakas, as these species have different dietary needs; in order to produce a consistent auditory cue across the different food types, we hid a small rock in a secret compartment at the bottom of the boxes so that produced identical noise when shaken. To control for any olfactory cues, we rubbed both boxes with food before the session started.
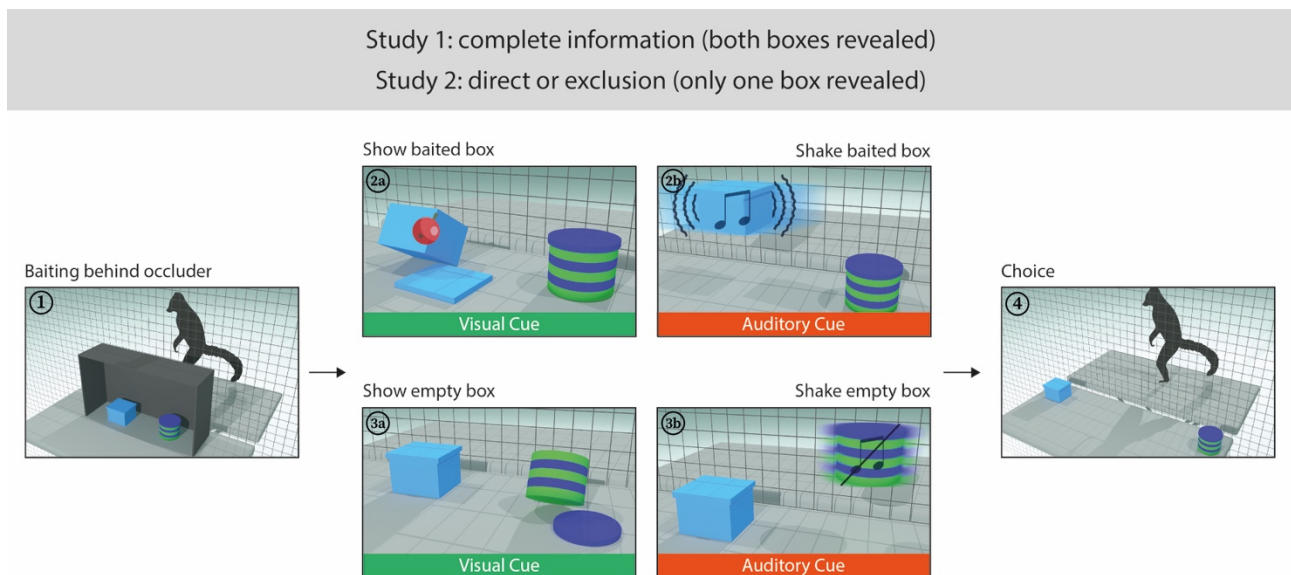
Figure 1: **Experimental setup for studies.** The experimenter (1) baited one of the two boxes with a food reward behind a black cardboard occluder. Once the occluder was removed, in study 1 the experimenter either revealed the contexts of both boxes, or in study 2 revealed just one (e.g., either the baited container or the empty one). In the visual information conditions, this involved opening the lids (panels 2a and 3a) and in the auditory information condition the experimenter shook both boxes (panels 2b and 3b). Finally, the lemur could make a choice (4).

2.4. Sessions and conditions

Lemurs completed three sessions: (1) a *familiarization session*, (2) an *introductory session* and (3) a *direct cue test session*. The familiarization and introductory sessions were implemented to introduce lemurs to this basic procedure and making binary choices between options, as most of these lemurs were fairly naïve to such situations as described previously**.** As such, in those sessions the baiting process occurred in full view of the subjects. Then, in the direct cue test the baiting occurred behind an occluder, out of the subject's view (see Figure 1).

2.5. Familiarization session

The familiarization session was designed to acclimate the lemurs to the basic procedure of making choices between two containers. Here, lemurs first experienced two trial types involving choices between two identical light-blue colored rectangular boxes (10.16 by 5 cm each) after observing food being placed in one of them. Then, they experienced two additional trial types where they were provided with either visual or auditory cue about the content of just one box in addition to observing it being baited. In both cases, lemurs indicated their choice by moving towards or touching a box on the side of the table from their initial center starting position. Within each familiarization session, the position of the reward (left or right box) was counterbalanced within a trial type and quasi-randomized with the restriction that it could not be on the same side more than twice in a row. Lemurs completed a minimum of 12 and a maximum of 16 total trials in the following order:

1. *Exposure: Visible food* (choice between two boxes; at least 2 trials). Here, the two boxes (with their lids on top) were placed in the center of the table, and the experimenter visibly placed a piece of food on the top of one of the box's lids. She then

moved the box apart to the sides of the table in view of the lemur, and let the subject choose. This allowed lemurs to learn to choose one of the boxes in response to clearly-visible food rewards. If the subject did not choose correctly chose on the first two trials, they could repeat up to two additional trials.

2. *Exposure*: *Hidden food* (choice between two boxes; at least 2 trials). Here, lemurs experienced that the food could be placed inside the boxes. The procedure was largely the same as in the visible trials, but the experimenter visibly placed a piece of food *inside* one of the boxes, and then tilted both boxes toward the subject at the same time. When the lemur had clearly seen the contents of the boxes, the experimenter moved the boxes apart, and the lemur could choose. If the subject did not choose correctly chose on the first two trials, they could repeat up to two additional trials.

3. *Visual cue experience trials* (one box; 4 trials). These trials were designed to introduce the lemurs to the visual cues used in the main test session, but note that lemurs did not need to use the cue to locate the food because there was only one box present. The experimenter placed a piece of food inside the box in full view of the subject, tilted the box and showed its content to the lemur for around 4 seconds, and then covered it with the lid. Finally, the experimenter has moved the box to one side of the table, and the subject could choose.

4. A*uditory experience trials* (one box; 4 trials). These trials introduced the auditory cues, again without need to use this cue to locate the food. Here, the experimenter placed a piece of food inside the single box in full view of the subject and then covered it with a lid. Then, she shook the box for 4 seconds. After the experimenter had moved the box to one side of the table, the subject chose.

To proceed to the next introductory session, lemurs had to choose correctly for two consecutive times in both of the initial exposure trials types. If they failed, they repeated the entire familiarization session the next day. In the visual and in the auditory experience trials, if the subject did not choose the box within 30s, the trial was aborted and repeated for a maximum of three consecutive times. If the subject did not choose, the session was halted and repeated on a different day. Lemurs completed a minimum of one session and a maximum of three sessions before reaching the criterion and proceeding to the introductory session (ruffed lemurs needed on average 1.2 sessions to reach the criterion, and sifakas needed on average 1.3 sessions to reach criterion in the familiarization session).

2.6. Introductory session

The *introductory session* provided lemurs with experience making binary choices about hidden food, a major component of the main test procedure. Here, lemurs were presented with choices between two visibly-different containers to help them differentiate the two locations: a light-blue colored rectangular box (10.16 by 5 cm) and a round box colored with dark blue and green stripes (10.16 cm; see Figure 1). Side assignment of the boxes was constant across subject and trials, with the rectangular box always on the left and the round box always on the right. The baiting location was counterbalanced and quasi-randomized as before. Lemurs completed a minimum of 14 and a maximum of 16 total trials in the following order:

1. *Exposure trials: Hidden food* (at least 2 trials). Lemurs completed additional trials that were identical to those of this trial type in the familiarization session. If the subject did not choose correctly chose on the first two trials, they could repeat up to two additional trials.

2. *Visual cue choice trials* (4 trials). The experimenter placed a piece of food inside one of the boxes in full view of the subject. Then, she tilted each box (left, then right) and showed their contents to the lemur for 4 seconds (Figure 1a) before covering them with the lids. After the experimenter had moved the boxes apart, the subject could choose a box. Note that lemurs observed the baiting, so they did not need to use the cue to locate the food in these trials unlike in the main test. To also ensure that lemurs understood that one box was always baited when two boxes were present, lemurs were allowed to self-correct and select the baited box within 30 seconds of their original choice if they initially approached the non-baited box.

3. *Auditory cue choice trials* (4 trials). The experimenter placed a piece of food inside one of the boxes in full view of the subject and then cover both boxes with lids. She then shook each box (left, then right) for 4 seconds each; shaking the baited box produced an audible sound, while shaking the box that was empty did not produced any noise. (Figure 1b). Lemurs again did not need to use the cue to locate the food in these trials as they observed the baiting, and were allowed to self-correct as in the visual cue trials.

4. *No cue control choice trials* (4 trials). These trials were designed to introduce the occluder and show the lemurs that they could not otherwise detect the presence of food without either auditory or visual cues. Here, the experimenter showed the lemur a piece of food and placed it inside one of the boxes, but here the baiting was blocked by the occluder. Then she removed the occluder and moved the boxes apart without giving any information about the content of either. Again, lemurs were allowed to self-correct.

Lemurs could self-correct in order to ensure they all experienced that one box was always baited, and across all sessions, lemurs self-corrected their choice in the 95% of the trials in which they

had previously selected the empty box. Importantly, in order to proceed to the main test, they had to demonstrate proficiency with correctly selecting the baited box first. In particular, lemurs had to select the baited box in 6 out of 8 total trials across the visual and auditory cue trials (note that there is no 'correct' response on the no-cue controls). This criterion was selected to ensure that lemurs showed a basic facility with the task without overtraining them on particular cues that they might not naturally use. Lemurs completed a minimum of one session and a maximum of six sessions before reaching the criterion (ruffed lemurs needed on average 2.5 sessions to reach the criterion and sifakas needed on average 2.2 sessions). Overall, lemurs chose the baited box significantly more when they watched the baiting than when no information about the content of the boxes was initially provided (paired samples t-test: *Cue trials*: Mean = 0.80 ± SE = 0.02; *No cued trials*: 0.37 ± 0.04; t_{18}= 10.751; $p < 0.0001$, see Table S1 for information about individuals performance).

2.7. Direct cue test session

In the main test, lemurs were then provided with information about the content of both boxes in two different sensory modalities. We used the same basic procedure as in the introductory session except for two main differences. First, the occluder was always used during the baiting process, so that the location of the food was not directly observed by the subject and could only be detected during the cue phase. In particular, here the experimenter either showed the contents of both boxes (visual trials) or shook both boxes (auditory trials) before the lemur made a choice. Second, subjects were not allowed to self-correct if they initially approached the non-baited box in these trials. Lemurs completed 8 *visual cue trials* and 8 *auditory cue trials* (see Figure 1 and Video S1). The trials were presented in blocks with the same modality with modality order (e.g.,

visual versus auditory trials first) counterbalanced across subjects. As in the introduction session, the boxes' locations were constant, and the side assignment of the baited location was counterbalanced and quasi-randomized. Finally, the cues (visually showing or auditory shaking) were always provided from left box to right box. Lemurs' first session (e.g. their initial performance) was analyzed for this study, but note that some individuals repeated the session before proceeding to Study 2, as detailed later (see Section 3.1).

2.8. Coding and data analysis

Choices were coded live by the experimenters, and a coder blind to the study's hypotheses coded 20% of all trials; the index of concordance was high (Cohen's kappa = 0.99). For analyses, we used Generalized Estimating Equations (GEE) to analyze test choices on a trial-by-trial basis while accounting for correlation of responses due to repeated measurements of the same subject (Liang and Zeger, 1986; Pekár and Brabec, 2018). We implemented models using the *geepack* software package in the statistics program R (R Development Core Team 2011) with exchangeable correlation structure to account for within-subject correlations across trials, and robust standard errors. Best fitting models were selected on the basis of the lowest QICu, i.e., quasi-likelihood ratio tests (Pan, 2001; Cui, 2007).

2.9. Data accessibility

All trial by-trial data from these studies will be made available in Dryad Digital Repository upon publication; see Table S1 for subject summary data.

2.10. Results and discussion

Our primary question in Study 1 concerned lemurs' abilities to use direct evidence from auditory versus visual modalities (see Figure 2). In fact, both species were successfully able to use visual information to locate the food, with overall performance significantly above chance in both species (*ruffed lemurs*: 0.76 ± 0.05; one sample t-test: $t_9 = 5.547$; $p = 0.0004$; *Coquerel's sifakas*: 0.76 ± 0.04; $t_8 = 6.825$; $p = 0.0001$, Figure 2a). However, we found a different pattern for auditory information. While ruffed lemurs were able to choose the baited location using sound (one sample: 0.64 ± 0.06; $t_9 = 2.400$; $p = 0.04$, see Figure 2a), sifakas did not (0.49 ± 0.05; $t_8 = -0.286$; $p = 0.78$, see Figure 2a). Comparisons between species showed a trend for ruffed lemurs to outperform sifakas for auditory information, but not visual cues (independent samples t-test comparing species; *visual cue*: $t_{16.67} = -0.227$; $p = 0.98$, n.s.; *auditory cue*: $t_{16.82} = 2.015$; $p = 0.06$, two-tailed). We found a similar pattern when we compared the first trial for each sensory modality, before lemurs got additional feedback and experience about correct responses. Overall, lemurs successfully used visual information from their first trial, but did not use auditory information successfully on their first trial (binomial test: *visual cue*: $p = 0.02$; *auditory cue*: $p = 0.65$; note that here we collapsed across species due to sample size, Figure 2b).
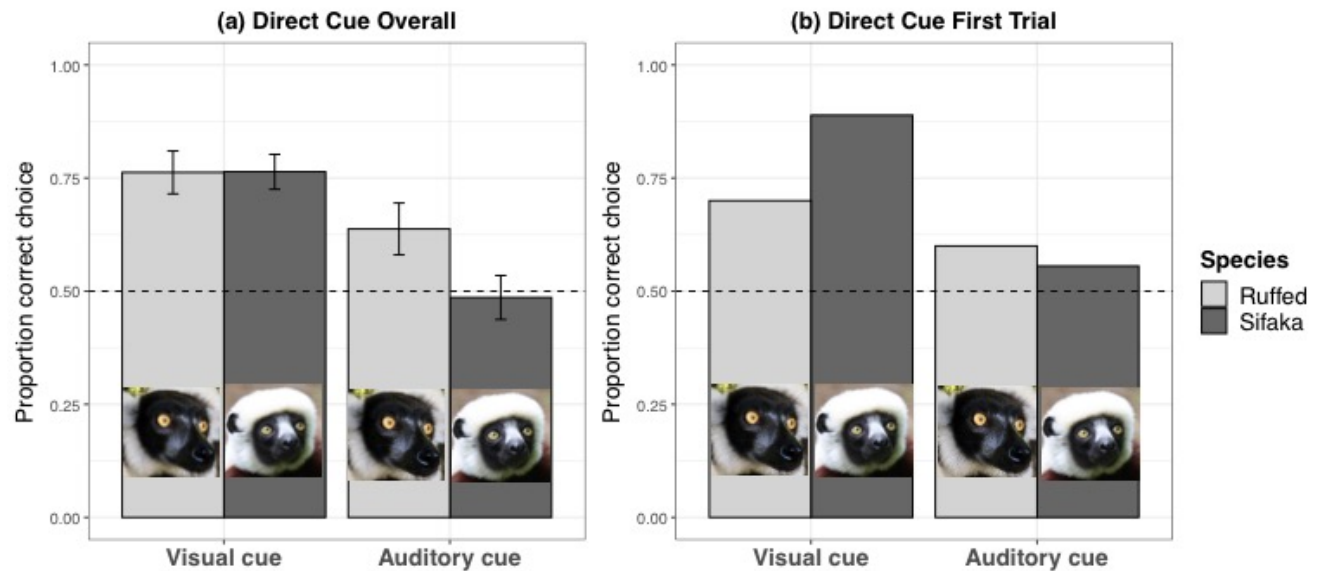
*Figure 2: **Mean proportion of choices of the baited box in Study 1**. a) Lemurs' mean proportion of correct choices for each sensory modality; error bars indicate standard error. b) Proportion of individuals who made the correct choice in their first trial of each sensory modality; note that there are no error bars here as each individual had only one trial. Dashed line indicates chance.*

We then used GEEs to directly compare species' performance across these different modalities of information, modeling test trial response as a binary outcome. Our base model included subject as a random factor to account for repeated trials, as well as *condition order* (visual cue first or auditory cue first), *trial number* (to account for any learning over trials), and the number of *introductory session to criterion* for that individual (to account for each individual's learning experiences prior to the main test). In a second model, we then added *trial type* (visual cue trials and auditory cue trials) to test whether lemurs showed different performance across modalities, which improved model fit [QICu = 383.40 in model 1 versus 394.90 in model 2, see Table 1 for parameters of this best-fitting model]. To examine whether there was a difference between the performance of the two species, we then added *species* as a factor. However, contrary

to our prediction, this predictor did not improve model fit compared with the second model [QICu = 383.54]. Finally, we tested the interaction between *species and trial type*, but this also did not improve fit [QICu = 384.00]. In the full model neither *species* nor the *species X trial type* interaction were significant predictors.

Predictor	Estimate	S.E.	Wald X^2	*p* value
Condition order (reference: auditory first)	0.135	0.239	0.32	0.57
Trial Number (1 to 16)	0.001	0.024	0.00	0.97
Introductory sessions to criterion	0.090	0.102	0.78	0.38
Trial Type (reference: visual cue)	-0.908	0.209	18.80	**< 0.001**

Table 1: Parameters from the best-fitting model predicting lemurs' choice in Study (Direct cue test). Additional models added *species* and the *species X trial type* interaction, which decreased model fit.

These results therefore indicate that both ruffed lemurs and sifakas could use visual information to locate food, even from their first trial. However, lemurs were also clearly more successful in using visual than auditory information to make their choices. This aligns with other diurnal primate species that also seem to find auditory cues more challenging to use in foraging contexts (Petit et al., 2015; Schmitt and Fischer, 2009; Heimbauer et al., 2019). While we did not find strong evidence that the species differed in their performance, ruffed lemurs seemed to exploit both auditory information and visual information, whereas sifakas did not, suggesting that such information might be more ecologically relevant for them.

3. Study 2: Inference by exclusion

In Study 2 we then directly compared lemur's abilities to use direct information versus indirect information (inference by exclusion) to locate food. As in Study 1, here lemurs saw a piece of food being hidden inside one of two boxes, behind an occluder. Then, they were provided with

either visual or auditory information about the content of only one box: either the baited box (direct cue) or the empty box (indirect cue).

3.1. Subjects

Eighteen of the nineteen subjects that participated in Study 1 were tested in study 2. Lemurs first had to successfully demonstrate proficiency with using direct information before they could proceed to this study, e.g. that they choose the baited box at least 6 of 8 trials in each sensory modality the Study 1 test session. Lemurs that did not initially pass this criterion in their first experience (the data analyzed in Study 1) could then repeat the same session up to three additional times. All lemurs from Study 1 passed this criterion except one ruffed lemur who was no longer available for testing due to a change in her social group. Ruffed lemurs needed on average 1.9 direct test sessions to reach the criterion, and sifakas needed on average 2.8 sessions.

3.2. General procedure

The general procedure of Study 2 was the same as that of Study 1. However, in the current experiment, lemurs received information about the content of only one box using either visual or auditory cues: either the content of the baited box (direct cue) or the empty box (inference by exclusion; see Figure 1 and Video S2). Note that in Study 1 lemurs had complete information about both boxes, whereas here lemurs only had information about one box (e.g., the baited box) in the direct cue condition. As in Study 1's test session, the occluder was always used during baiting. In the *direct visual cue*, E1 showed only the content of the baited box (e.g., the food), whereas in the *exclusion visual cue* she showed only the of the empty box. Likewise, in the *direct auditory cue*, E1 shook the baited box (which produced a noise) while in the *exclusion auditory cue*, she shook

only the empty box. Lemurs completed one session composed by 16 total trials divided into two blocks for each sensory modality. Within each sensory modality, the order of direct and inference by exclusion trials were quasi-randomized.

3.3. Coding and data analysis

Choices were coded in the same way as in Study 1. A coder unfamiliar with the aims of the study coded 100% of all trials with perfect inter-rater reliability. We used the same basic statistical analysis approach as in Study 1.

3.4. Results and discussion

Our primary question concerned lemurs' abilities to use either direct evidence or make inference by exclusion from auditory versus visual modalities (see Figure 3). We first examined lemurs' performance when presented with information about the content of the baited box (direct cue) and the content of the empty box (exclusion cues) in each sensory modality. In line with the findings from Study 1, both species were successfully able to use visual information to locate the food when direct information was presented (one-sample t-test: *ruffed lemurs*: 0.77 ± 0.06; $t_8 = 4.264$; $p = 0.003$; *Coquerel's sifakas*: 0.72 ± 0.07; $t_8 = 2.874$; $p = 0.02$; see Figure 3), whereas they did not use auditory information (*ruffed lemurs*: 0.64 ± 0.10; $t_8 = 1.348$; $p = 0.21$, n.s.; *Coquerel's sifakas*: 0.55 ± 0.06; $t_8 = 1.00$; $p = 0.35$, n.s.). When provided with information about the content of the empty box, neither species could locate the food above chance in either the visual cue condition (*ruffed lemurs*: 0.61 ± 0.10; $t_8 = 1.079$; $p = 0.31$, n.s.; *Coquerel's sifakas*: 0.53 ± 0.07; $t_8 = 0.359$; $p = 0.73$, n.s.) or the auditory cue condition (*ruffed lemurs*: 0.53 ± 0.06; $t_8 = 0.426$; $p = 0.68$, n.s.; *Coquerel's sifakas*: 0.53 ± 0.11; $t_8 = 0.262$; $p = 0.79$, n.s.).
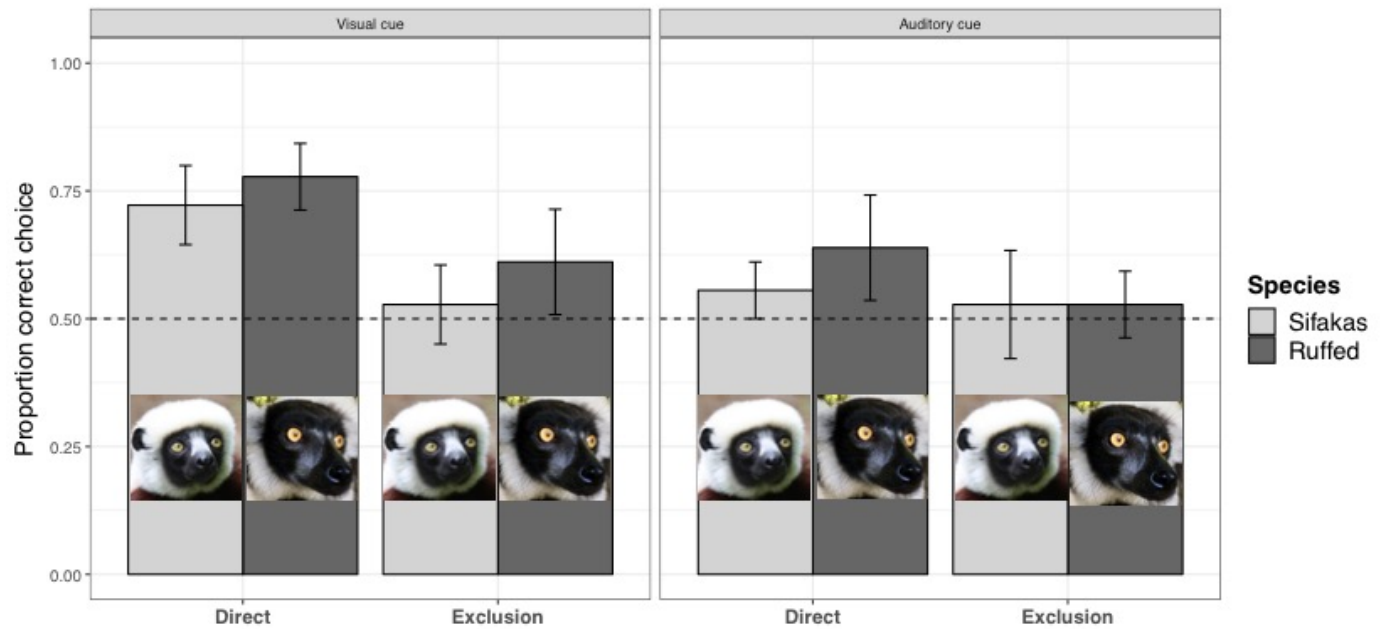
Figure 3: **Mean proportion of choices of the baited box in Study 2**. Proportion of choices of the baited box when either information about the content of the baited box (direct cue) or the content of the empty box (exclusion cue) was provided in the two sensory modalities. Error bars indicate standard error, and dashed line indicates chance.

As in Study 1, we then used GEEs to model each individual test trial response as a binary outcome. We fit a first model including subject as a random factor, and trial number, and number of Study 1 test sessions needed to meet criterion and proceed to this study. This model indicates that lemurs' overall performance was not affected by the number of trials or the number of the direct test sessions. To test lemurs' relative success with visual versus auditory information, we then added *trial type* (visual or auditory) which improved fit [QICu = 390.92 in model 1 versus 390.01 in model 2], confirming our results from study 1. We then tested whether lemurs were able to find the food with partial information by including the interaction between *trial type X cue type* (direct or exclusion) which also improve the model fit [QICu = 387.93]: lemurs were more successful in finding food using direct information, with no interaction with cue type (see Table 2 for the parameters from this best-fitting model). Finally, there was no significant improvement by

including *species* [QICu = 389.60] or the *species X cue type X trial type* interaction [QICu = 395.00], indicating no difference between the ruffed lemurs' and sifakas' performance across conditions.

Predictor	Estimate	S.E.	Wald X^2	*p* value
Condition order (reference: auditory first)	-0.330	0.267	1.52	0.22
Trial Number (1 to 16)	0.012	0.023	0.24	0.62
Study 1 sessions to criterion	-0.101	0.147	0.47	0.49
Trial Type (reference: visual cue)	-0.718	0.349	4.23	**0.04**
Cue Type (reference: direct cue)	-0.832	0.373	4.96	**0.03**
TrialType*CueType	0.551	0.544	1.02	0.31

Table 2: Parameters from the best-fitting model predicting lemurs' choice in Study 2 (Inference by exclusion test). Additional inclusion of species and species X trial type X Cue type did not improve model fit.

Overall, these results again confirm that lemurs are better at using direct visual information than direct auditory information to locate food, here in a slightly different setup where they only received information about the baited box (e.g., not the complete information about both boxes as provided in Study 1). However, we also found that they generally fail to reason by exclusion when they are provided with information about the content of the empty box.

4. General discussion

Our studies reveal three main findings. First, lemurs are able to locate food when they possess full information about the potential food locations, and are more adept at doing so when provided with visual compared to auditory information. In Study 1, both ruffed lemurs and sifakas successfully found the food when they could see the contents of both boxes. Even though all lemurs had to show additional proficiency at using both visual and auditory cues in the full information

context before proceeding to the second study, our results from Study 2 show that both species were again better at using visual information when they were provided with information only about the baited box. Second, only ruffed lemurs could use auditory information to some degree to locate food when both containers were shaken in Study 1. Finally, we found that both lemur species were unable to use inference by exclusion to find food. Along with prior work examining two *Eulemur* species (Maille and Roeder, 2012), this suggests that strepsirrhines are less adept at making inferences by exclusion compared to anthropoid primates. As shown in Figure 4, current data indicates that anthropoid primates tested in the two-location inference by exclusion paradigm (Call, 2004) show similar patterns of better performance with visual information than auditory information that we found with lemurs here. Indeed, only great apes and capuchins have demonstrated success in making inference by exclusion with auditory cues, while orangutans, Tonkean macaques, baboons, rhesus macaques, squirrel monkeys and cotton-top tamarins performed poorly when auditory cues were provided (Call, 2004; Petit et al., 2015; Sabbatini and Visalberghi, 2009; Schmitt and Fischer, 2009, see Figure 4).

		Direct Visual Cue	Exclusion Visual Cue	Direct Auditory Cue	Exclusion Auditory Cue
Apes	Chimpanzees[1,2,3]	✓	✓	✓	✓
	Bonobos[1,2,3]	✓	✓	✓	✓
	Gorillas[1]	✓	✓	✓	✓
	Orangutans[1]	✓	✓	X	X
	Siamangs[2]	✓	✓	X	X
Old World Monkeys	Tonkean macaques[4]	✓	✓	✓	X
	Rhesus macaques[4]	✓	X	X	
	Olive baboons[4,5]	✓	✓	X	X
New World Monkeys	Capuchin monkeys[6,7,8,9]	✓	✓	✓	✓
	Squirrel monkeys[9]	✓	X	✓	X
	Spider monkeys[2]	✓	✓		
	Cotton-top tamarins[10]	✓	✓	X	X
Strepsirrhine	Black lemurs[11]	✓	X	✓	X
	Brown lemurs[11]	✓	X	✓	✓
	Ruffed lemurs	✓	X	✓	X
	Coquerel's sifakas	✓	X	X	X

Figure 4: **Distribution of inference by exclusion abilities across primates.** Patterns of performance across different primate species tested on inference by exclusion tasks to date, including results from the present study. [1]Call, 2004: [2]Hill et al., 2011, [3]Bräuer et al., 2006; [4]Petit et al., 2015; [5]Schmitt and Fischer, 2009; [6]Sabbatini and Visalberghi, 2008; [7]Paukner et al., 2009; [8]Heimbauer et al., 2012; [9]Marsh et al. 2015; [10]Heimbauer and Johns, 2019; [11]Maille and Roeder, 2012

What can account for the variation in logical reasoning abilities across species, as well as the different proficiency that animals seem to have for visual versus auditory information? Current evidence aligns with the hypothesis that dietary ecology can at least partially explain these results. For example, many anthropoid primates tested to date rely primarily on foraging that target fruits or leaves that can be easily found by using visual cues alone (Schmitt and Fischer, 2009; Petit et al., 2015; Heimbauer et al., 2012). As a result, these species may have evolved a propensity to favor visual information over auditory information in foraging contexts. In fact, only a few species

tested thus far, in particular capuchins and chimpanzees, succeed at using auditory cues to solve inference by exclusion tasks; these species more heavily rely on extractive foraging and consequently may need to use sound as cue to locate food in their wild environments (Sabbatini and Visalberghi, 2008; Schmitt and Fischer, 2009). Our results extend this ecological hypothesis to variation in strepsirrhine primates' cognition. Both ruffed lemurs and sifakas are diurnal species who likely preferentially exploit visual over auditory information in their environment. Yet we also found that more frugivorous ruffed lemurs, but not folivorous sifakas, were able to use both direct visual and direct auditory cues to find food. Similarly, previous studies have shown that both ruffed lemurs and ring-tailed lemurs can flexibly rely on different sensory cues when they search for food using either visual or olfactory cues in isolation, whereas sifakas required both kinds of sensory information in tandem to best detect food, a difference also interpreted in terms of their differing dietary complexity (Rushmore et al., 2012). In contrast, the only previous work examining inference by exclusion in lemurs suggested that black and brown lemurs performed better with auditory information than with visual information (Maille and Roeder, 2012). While that study had a small sample size, it is notable that *Eulemur* species tend to be cathemeral, showing a mixture of daytime and night-time activity (Curtis and Rasmussen, 2006; Donati et al., 2009), and auditory cues may be especially useful for locating food in low-light conditions. Thus, an important question for future work concerns cognitive abilities in nocturnal strepsirrhines in general, and species that use extractive foraging techniques like the aye-aye (*Daubentonia madagascariensis*) in particular. Uniquely amongst strepsirrhine primate, aye-ayes regularly use tap-scanning behaviour to extract hidden invertebrates (Erickson, 1991, 1994) more similar to the extractive foraging of capuchins and chimpanzees. Thus, this ecological view predicts that they

would be especially sensitive to or even prioritize auditory information, unlike many other anthropoids and the sifaka and ruffed lemurs tested here.

Our findings show that both ruffed lemurs and sifakas failed to make inferences by exclusion across sensory modalities, unlike many anthropoid primates tested to date (see Figure 4). One possibility is that differential experience with cognitive testing may play a role. For example, more capuchin monkeys could use auditory information to solve an inference by exclusion task when they could first directly experience the properties of the full and empty containers (Sabbatini and Visalberghi, 2008). More generally, as discussed earlier, the lemurs tested here had fairly limited experience with cognitive experiments involving binary choices, unlike many other primate populations assessed so far. While these lemurs did demonstrate motivation to participate (as all tasks were voluntary) and succeeded at initial familiarization and introductory sessions, this study involved only one experimental session for the exclusion task. Another possibility is that this represents a true phylogenetic gap between anthropoid primates and strepsirrhines. Indeed, the only prior study of lemurs did not find strong evidence for inference by exclusion abilities (Maille and Roeder, 2012), whereas most studies of anthropoids find that they can succeed at least when visual information is provided (Call 2004; Hill et al., 2011; Petit et al., 2015; Schmitt and Fischer, 2009; Sabbatini and Visalberghi, 2008; Paukner et al., 2009; Heimbauer et al., 2012; Marsh et al., 2015; Heimbauer et al., 2019). Notably, anthropoids and strepsirrhines differ in many aspects of their typical social organization, diet, and activity patterns, and there was a major adaptive shift in morphology and behavior at the base of the anthropoid clade (Kay et al., 2004; van Schaik and Kappeler, 1996; Williams et al., 2010; Wright, 1999). This includes major reorganization of sensory systems and the brain as a whole (Gilad et al., 2004; Jacobs, 2008; Kirk and Kay, 2004; Kirk, 2004; Isler et al., 2008), which is relevant for

understanding cognitive and behavioral evolution across primates. As such, more studies of cognition across diverse strepsirrhine species are crucial to reconstruct the evolutionary history of logical inferential abilities, as well as the evolutionary roots of the primate mind more generally.

A final important question concerns whether current evidence for inference by exclusion abilities from multiple nonhuman species that have been assessed using the two-option task (e.g., Call, 2004) represents true instances of logical reasoning. Indeed, animals may solve this task also by using simpler alternative strategies, for instance through the learning of a simple rule to avoid the container that does not provide the food (Mikolasch et al., 2012; Schmitt and Fischer, 2009), although other work controls for this possibility (Call, 2004). In addition, recent work from developmental psychology argues that animals and young children tested in this basic setup may in fact represent both A and B as the two possible locations for the reward, but without considering dependent relationship between them (the 'maybe A, maybe B' interpretation; Mody and Carey, 2016). In this view, when individuals see that location A is empty, they eliminate A from their possible options and therefore avoid choosing it. However, since A and B are considered independent from each other, instead of updating their information about location B and consequently following the logic that food must be in B if it is not in A, individuals simply search on location B based on their initial premise that the food might have been in B. Thus, to demonstrate true logical inference by disjunctive syllogism, it may be necessary to use a new variant of the task with more than two options that can discriminate between the 'A not B' and the 'maybe A, maybe B' interpretations (Mody and Carey, 2016). Otherwise, animal evidence from the two-location task might rather represent a simpler precursor to human-like logical inference, and representation of these logical concepts might indeed require human-like language. Yet the current work, taken in tandem with prior studies, also demonstrates the power of a comparative approach—it is precisely because many different

nonhumans have been tested on the two-container task that it is possible to tease apart what skills are present across many diverse species and how they are used. A crucial next question is then how or to what extent animals' logical inferences resemble those found in humans, as well as what selective pressures led to the emergence of more complex reasoning abilities like those seen in our species.

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