

Metacognition in Canids: A Comparison of Dogs (*Canis familiaris*) and Dingoes (*Canis dingo*)

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Metacognition refers to the ability to monitor one's own mental states. In the current study, we investigate whether domesticated dogs (*Canis familiaris*) and nondomesticated dingoes (*Canis dingo*) demonstrate metacognition by seeking information to remedy their own ignorance. In 2 studies, we used a naturalistic information-seeking paradigm in which subjects observed a human experimenter hiding a food reward behind an apparatus. Subjects could seek information by looking through a central window-like section of the apparatus to see where the reward was hidden. In Study 1, we tested whether dogs and dingoes were willing to seek information when interacting with the apparatus, finding that both species readily sought information when it was available to them. Study 2 provided a direct test of whether dogs and dingoes would seek information to rectify their own ignorance. We found evidence that both dogs and dingoes sought out information and were more likely to do so when they did not already know where the treat was hidden. These results provide additional evidence suggesting that domesticated dogs seek information in the face of ignorance, as well as the first evidence of similar behavior in a nondomesticated canid.

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The capacity to think about one's own mental states—known as *metacognition* (Flavell, 1979)—informs much of human experience. Many of our daily tasks require the ability to reflect on our current state of knowledge and to realize that it is deficient. Additionally, metacognition is thought to underlie a wide array of other cognitive processes, such as independent learning (Vrugt & Oort, 2008), cooperative action (Frith, 2012), and theory of mind (Goldman, 2006). Indeed, some have argued that deficits in metacognition may also play an important role in some mental illnesses,

like anxiety (Wells, 1995) and depression (Papageorgiou & Wells, 2003). Because of its connection to so many different mental abilities, metacognition represents a foundational human cognitive capacity.

But are humans alone in their capacity to think about their own knowledge states or do nonhuman animals share this capacity? Recent work suggests that some nonhuman primates—such as great apes and rhesus macaques (*Macaca mulatta*)—share the ability to represent their knowledge states and selectively take

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action to remedy their ignorance (Beran, Smith, & Perdue, 2013; Call, 2010; Call & Carpenter, 2001; Hampton, Zivin, & Murray, 2004; Marsh & MacDonald, 2012a; Rosati & Santos, 2016). However, metacognition does not appear to be restricted to the primate lineage. Despite being phylogenetically distant from primates, scrub jays (*Aphelocoma californica*) selectively seek out information when they are ignorant of the location of a hidden food reward (Watanabe & Clayton, 2016), suggesting that some bird species may also have the ability to represent their own knowledge states. This unexpected pattern of metacognitive information-seeking across species opens new questions about the phylogenetic spread of this representational capacity.

Given that the capacity for metacognition may be shared across scrub jays and diverse primate species, it is possible that metacognition represents a basic cognitive ability that evolved before the last common ancestor of birds and primates. If this is the case, then we should expect all species that share that last common ancestor of birds and primates to show similar metacognitive capacities. However, it is also possible that metacognitive abilities evolved independently in scrub jays and primates, potentially due to similar ecological pressures. To distinguish between these two possibilities, we need to further map out both the presence *and* absence of metacognitive abilities across diverse taxonomic groups. In particular, it will be informative to identify which species do *not* show metacognitive abilities to examine the possibility that metacognition is a cognitive capacity that evolved before our last common ancestor with birds. Besides some initial evidence suggesting that rats (*Rattus norvegicus*) and capuchin monkeys (*Sapajus apella*) fail to selectively seek out information that they lack (Paukner, Anderson, & Fujita, 2006; Roberts, McMillan, Musolino, & Cole, 2012), there is a notable dearth of reported failures of metacognitive information-seeking in nonhuman animals.

Until recently, the domesticated dog held the distinction of being one of the few tested species not to engage in information-seeking behaviors when ignorant about the location of a reward. The first study to test canine metacognition investigated whether dogs would seek out information about which of two boxes held a hidden food reward (Bräuer, Call, & Tomasello, 2004). Dogs could choose a box by pressing a lever to receive the food if the reward was inside. However, before making a choice, dogs were allowed to seek out information about the contents of each box by looking through a window on the opposite side of the box or by using ambient olfactory cues. This study found that dogs almost never looked through the windows to check which box contained the reward. Only one dog consistently looked through the windows, and it did so even on trials when it had seen which box was baited. Additionally, when subjects did not witness the hiding of the treat, they chose the correct box at chance levels, suggesting that dogs also failed to use olfactory cues to find the hidden treat. This pattern of performance thus suggested little evidence of metacognition in dogs.

In another investigation of canine metacognitive information-seeking, McMahan, Macpherson, and Roberts (2010) gave dogs the opportunity to gain information by reorienting themselves. Before beginning the study, experimenters trained dogs to knock over boxes to get food rewards inside. Eventually, dogs were trained that a reward was always hidden under a particular box that was marked by a single white side. During training, four boxes (three fully black boxes and one black box with a single white

side) were oriented forward, such that the informative sides of the boxes were completely visible. Then, during each testing session, the four boxes were rotated 0, 45, 90, and 135 degrees such that the informative sides of the boxes were progressively less visible from the starting position of the dog. Thus, to succeed in later trials, dogs had to walk around the boxes to see which box had the white side. Dogs chose the correct box above chance when the informative sides of the boxes were still visible from the dogs' starting position. However, once the boxes were rotated such that the dogs had to walk around the boxes to seek out information, dogs' performance dropped to chance, suggesting that dogs did not seek out information about the location of the treat.

Although these studies failed to find evidence of metacognitive information-seeking, dogs' performance may not have reflected their underlying cognitive competence. These earlier studies relied on learned associations and required dogs to engage in costly behaviors to gain information. Specifically, dogs had to walk *beyond* the location of the treat and inhibit a previously trained behavior (i.e., knocking over boxes in McMahan et al., 2010, and pushing levers in Bräuer et al., 2004) to gain visual access to the location of the treat. A more recent study suggests that these features of past experimental designs may have taxed dogs' inhibitory control, and thus led to performance issues that impeded their ability to seek information (Belger & Bräuer, 2018). In this study, dogs were presented with a task in which a reward (i.e., a food or a toy) was hidden on either the right side or the left side of an apparatus. Dogs only had one opportunity to make one choice on each trial; thus, if dogs chose the unbaited side, they would fail to get the reward. Before selecting a side, dogs could see where the reward was hidden by simply walking up to gaps in the apparatus that afforded them visual access to the reward. When presented with this low-cost option for seeking information, dogs approached the gaps that allowed them to see the reward's location if they did not know where the reward was hidden. However, when dogs already knew the location of the reward (i.e., because they witnessed the baiting process), dogs tended to forgo seeking information and went straight to the side where they witnessed the reward being hidden. Belger and Bräuer's (2018) findings provide initial evidence that dogs may exhibit metacognition, as seeking out new information, but not redundant information, is considered to be one of the hallmarks of metacognition.

However, despite this new evidence, it appears that metacognition in dogs may be somewhat limited. Although dogs sought information before searching behind the apparatus when they were ignorant of the hiding location of the reward, they failed to show metacognition in other contexts (Belger & Bräuer, 2018). Specifically, in a follow-up investigation, dogs failed to seek information more often when the time delay between seeing the reward hidden and being released to retrieve the reward was increased. Crucially, this was the case even though longer delays negatively impacted dogs' ability to locate the reward accurately (Belger & Bräuer, 2018). Thus, dogs failed to use the low-cost information-seeking option in a context where they no longer had a clear memory of where the reward was hidden. This finding may suggest that although dogs are capable of metacognition, their ability to seek information when ignorant may be fragile and interestingly untethered to memory strength.

Given the inconclusive evidence to date on dogs' information-seeking abilities, one of the goals of the current article was to build

on the existing studies to provide additional insight into this still open question. Using a naturalistic information-seeking paradigm based on a procedure previously used with rhesus macaques (Rosati & Santos, 2016) and inspired by Call and Carpenter's (2001) work with apes, we developed an information-seeking setup that allowed dogs to gather visual information at a relatively low cost. As with dogs tested in Belger and Bräuer's (2018) study, subjects in the current study were presented with a low-cost information-seeking option that only required them to walk forward. Specifically, dogs had the opportunity to gain visual access to the location of a hidden treat by looking through an unoccluded section on the front of a barrier before approaching one of two possible locations where a treat was hidden. Given that the unoccluded section of the barrier was at the front, nearest to their starting position, dogs only needed to make a minor deviation from their natural route of travel toward the possible locations of the hidden treat, therefore reducing the inhibitory control required to successfully gain information about the treat's location.

In addition to providing further evidence to strengthen the metacognitive status of domesticated dogs, we also examined how domestication may have affected metacognition in canines. Across domestication, dogs faced selection pressures for traits favorable for working cooperatively with humans (Hare & Tomasello, 2005; Johnston, McAuliffe, & Santos, 2015; Miklósi & Topál, 2013; Topál, Kis, & Oláh, 2014), such as a sensitivity to human communicative signals (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Prato-Previde & Marshall-Pescini, 2014; Soproni, Miklósi, Topál, & Csányi, 2002; Udell, Giglio, & Wynne, 2008) and a tendency to look back at humans (Miklósi et al., 2003; Passalacqua et al., 2011). However, it is unclear whether these selection pressures had any impact on dogs' tendencies to seek information. In the current study, we directly compare a population of Australian dingoes (*Canis dingo*) to a population of domesticated dogs in a metacognitive information-seeking task. Dingoes and domesticated dogs last shared a common ancestor at least 5,000 years ago (Cairns & Wilton, 2016; Savolainen, Leitner, Wilton, Matisoo-Smith, & Lundeberg, 2004), and thus their comparison could provide insight into the impact of domestication on canine metacognition.

As discussed earlier, it remains unclear whether metacognition is an aspect of cognition that is shared widely across species (e.g., going back as far as the last common ancestor of primates and birds) or whether it has evolved independently in multiple species due to similar ecological pressures. To make headway in arbitrating between these alternatives, it will be particularly informative to identify species in which metacognitive information-seeking is fully absent or at least less robust. Given that domestication has influenced many other aspects of canine cognition (Johnston, Turrin, Watson, Arre, & Santos, 2017; Marshall-Pescini, Virányi, & Range, 2015; Range, Jenikejew, Schröder, & Virányi, 2014; Range & Virányi, 2014; Smith & Litchfield, 2010a), it is possible that domestication has shaped metacognition as well. In particular, dogs and/or dingoes may provide a valuable instance of a species that fails tests of information-seeking. If either or both species fail to seek information that they lack, this would provide (a) converging evidence with Paukner and colleagues (2006) and Roberts and colleagues (2012) suggesting that metacognition may have evolved independently in multiple species and (b) insight into the ecological pressures that may shape

metacognitive information-seeking. Alternatively, if both dogs and dingoes successfully seek information when ignorant about the location of a hidden treat, this would provide additional evidence that this kind of flexible information-seeking—and possibly metacognition—is shared widely across species. Thus, dingoes' performance on tests of metacognitive information-seeking—especially in relation to the performance of their domesticated relatives—will provide an informative step toward ascertaining the phylogenetic spread of this representational capacity and contribute further information about the potential homology of metacognitive abilities.

Study 1

Due to the rarity of information-seeking behaviors observed in past studies of canine metacognition (Bräuer et al., 2004; McMahon et al., 2010) and the lack of any existing data on information-seeking abilities in dingoes, we conducted an initial test of our information-seeking method in Study 1. Specifically, in Study 1, we examined whether subjects would (a) be willing to seek information in any context in our experimental paradigm and (b) be more likely to attempt to seek information when doing so would provide visual access to the reward than when it would not. If subjects never attempt to seek information in our experimental paradigm, then this might suggest that it is unclear to subjects how they can gain information about the reward's location in the context of this setup. To maximize the chance that subjects would understand how to seek information, all subjects were walked around the apparatus and completed warm-ups before beginning the test trials. Because we were primarily interested in confirming that subjects were willing to approach the apparatus, subjects were ignorant of the location of the food reward across all trials in Study 1. This was done to maximize their need for information. To investigate whether subjects would be more likely to seek information when it was accessible, we manipulated whether it was possible or impossible for subjects to seek information from the apparatus before making their choice. If subjects are sensitive to the availability of information, then they should be more likely to attempt to seek information when doing so will give them visual access to the reward's location compared with when the information-seeking behavior will not actually provide any information.

Method

Dog subjects. Twenty domesticated dogs of varying breeds (see Table S1 in the online supplemental materials) participated in this study. Dogs were tested at the Canine Cognition Center at Yale University. Fifteen additional dogs were excluded for not passing the warm-ups (12), owner interference (one), experimenter error (one), and camera failure (one). Subjects were pets whose guardians entered their information into an online database and volunteered for participation. Before running the experiment, all dogs visited the center at least once to make sure that they were comfortable in the center and had no aggressive tendencies.

Dingo subjects. Subjects were six genetically pure dingoes (see Table S1 in the online supplemental materials) from the Dingo Discovery Research Centre in Victoria, Australia. Ten additional dingoes were tested and excluded for not approaching the appara-

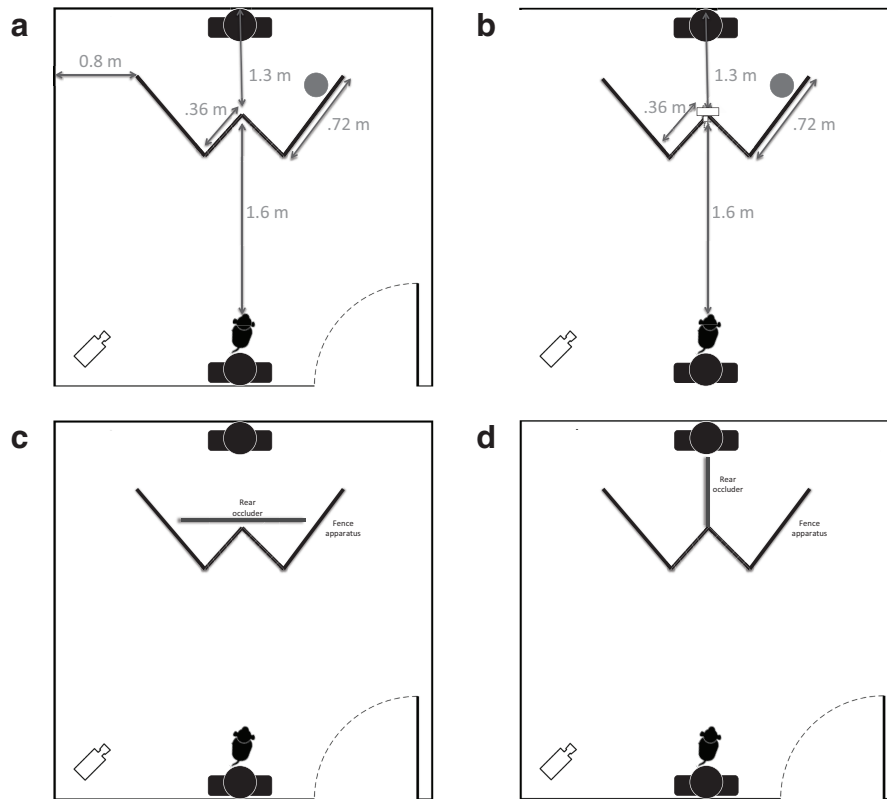


Figure 1. Experimental setup for dogs (a) and dingoes (b) for Studies 1 and 2. Subjects in both populations were positioned 1.6 m away from the center of the fence. Dogs were filmed from one overhead camera angle, whereas the dingoes were filmed from two camera angles, one to the left of the handler to capture accuracy and one positioned on top of the fence to capture information-seeking. The gray circle behind the fence represents one of the two possible hiding positions of the bucket on which the treat was placed. The dogs were tested in a room with their owners, and the dingoes were tested outside in a grassy paddock with a familiar sanctuary handler. A rear occluder was used in Studies 1 and 2 for all subjects. During the hiding presentation, the rear occluder was oriented such that it blocked the unoccluded portion of the fence apparatus from behind (c). After hiding the treat in all warm-up and test trials, the experimenter rotated the rear occluder such that it divided the area behind the fence apparatus while the subject made its choice (d).

tus during the familiarization (two), failure to pass the warm-ups (seven), and failure to approach the apparatus in two consecutive trials (one). We tested all available dingoes at this site that were comfortable leaving their living quarters and walking on a leash to the grassy testing paddock.

Apparatus and testing setup. A section of fence 0.74 m high in shape of a “W” served as the apparatus (see Figure 1). Opaque black sheets were draped over the far sides of the fence, such that only the center portion of the apparatus was unoccluded. In addition to the fence, two occluders were used to block subjects’ view through the unoccluded center portion of the apparatus at different times. During some parts of the study (i.e., the *information-seeking impossible* trials), a bent occluder was placed in front of the unoccluded portion to block the center opening. Behind the fence there was also a second rear occluder (40” × 29.5”) that prevented subjects from seeing where the experimenter hid the treat when the front bent occluder was absent (see Figure 1c). In both conditions, after the experimenter hid the food, she always rotated the rear occluder such that it prevented subjects from accessing both sides of the area behind the fence at once, but no longer blocked the

unoccluded portion of the apparatus (see Figure 1d). A small blue bucket (14.3 cm high, 15.9 cm in diameter) was used during both warm-up trials and test trials to make the location of the treat more visible.

Dogs were tested in a large testing room (3.5 m × 3.15 m). Dingoes were tested in a familiar grassy paddock where they exercised daily. Subjects of both species began the study ~1.6 m away from the center of the fence. During testing, the fence was positioned 1.3 m in front of a solid wall (dogs) or mesh wall (dingoes) that enclosed the larger testing area; the experimenter stood behind the fence with her back against the wall. All subjects were attached to a retractable leash held by the handler who was the owner in the case of dogs or a familiar sanctuary staff member for dingoes. Dogs received 1-cm cubes of Natural Balance Beef sausage as their reward throughout the study and dingoes received 1-cm disks of cooked chicken sausage.

Design. All subjects participated in a familiarization phase, followed by two to four warm-up trials and eight test trials. In the *familiarization phase*, the handler guided the subject around the fence to make sure that the subject was comfortable approaching.

This also established that the subject would not be distracted by the novelty of the fence or the front occluder during warm-up and test trials. During the *warm-up trials*, the handler walked the subject up to the unoccluded center portion of the fence so that the subject saw the location of the hidden treat before having the opportunity to choose which side of the fence to search behind. The warm-up phase exposed the subjects to the increased visual access they could get by looking through the center of the fence and highlighted the two possible locations of the treat. Finally, in the *test trials*, a treat was hidden behind the fence in one of the two previously established hiding locations. In half of the trials (*information-seeking possible* trials), the center portion of the fence was unoccluded such that subjects could go to the center of the fence to see the location of the treat before making their choice of which side to approach. In the other half of trials (*information-seeking impossible* trials), the center portion was blocked, such that going to the center of the fence no longer yielded any useful information. If subjects strategically seek out information, they should approach the center of the fence only when it is unoccluded in the information-seeking possible trials and, as a result, choose the correct side more often in information-seeking possible trials compared with occluded information-seeking impossible trials.

Familiarization phase. In the *familiarization phase*, the handler walked the subject from the starting position to both the left and right sides of the fence and then along the front of the fence. The experimenter stood centered behind the fence, holding the back occluder so that it served as a barrier between the two sides of the fence. This back occluder prevented the subject from accessing both wings of the fence at once when traveling behind the fence. During this familiarization, the front occluder was in place in front of the center portion so that the subject could sniff it. This positioning ensured that the front occluder did not distract subjects during later trials. All dogs were willing to explore the fence during the familiarization phase. However, five dingoes demonstrated hesitation to go behind the fence. All of these dingoes received a second attempt on an additional day, in which they were coaxed behind the fence with a piece of sausage. Three dingoes made it through the familiarization phase on the second day of testing, but two dingoes were excluded from further participation because they continued to demonstrate hesitation to go around the fence.

Warm-up trials. In the *warm-up phase*, the handler led the subject to the center portion of the fence to give the subject experience with the increased visual access they could gain by looking through the center of the fence. During this warm-up phase, the front occluder was absent from the front of the fence, but the rear occluder was positioned such that the center portion was still blocked during the treat hiding phase. The experimenter stood centered behind the fence while holding up the small bucket and said, “[Subject’s Name], look!” while making eye contact with the subject, and then visibly placed the treat on the bucket (see Figure 2a). Then, she bent down behind the fence so that she was not visible and placed the overturned bucket with the treat on it behind one of the two sides of the fence. At each of the two possible treat locations, there was a small foam pad on the ground to minimize the noise resulting from the placement of the bucket. The experimenter then stood up and rotated the rear occluder 90 degrees so that it was no longer blocking the center portion of the fence (see Figure 2b). The experimenter then instructed the handler

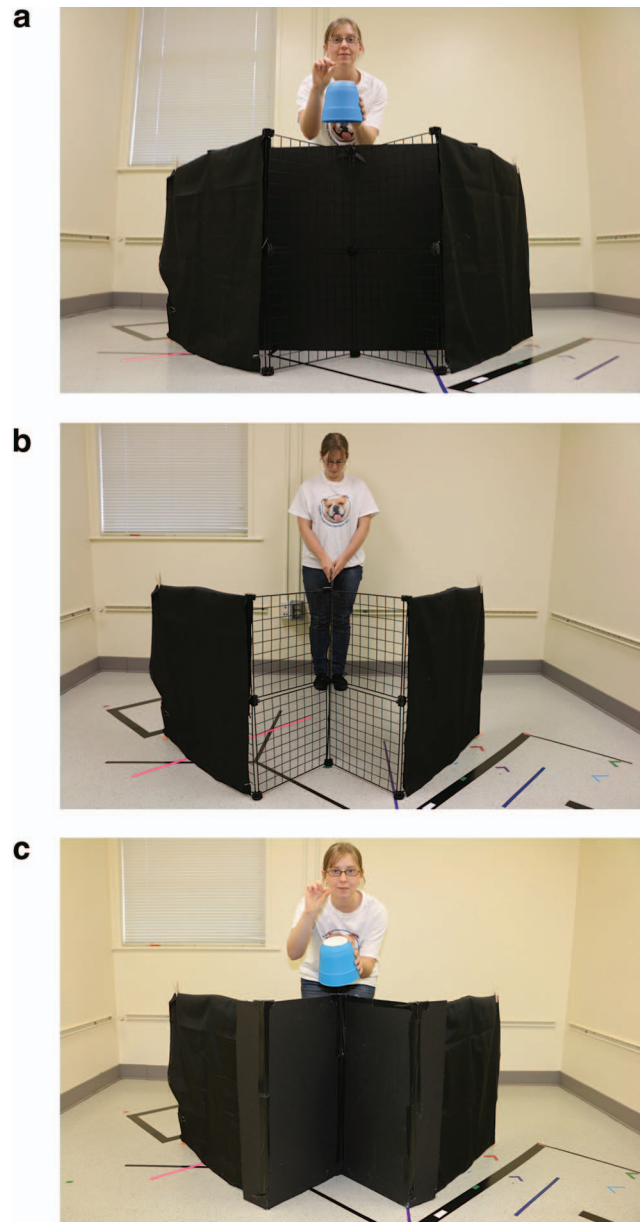


Figure 2. During the warm-up trials, the front bent occluder was absent. At the beginning of each warm-up trial, the experimenter made eye contact with the subject, and then visibly placed the treat on the bucket (a). Then, she bent and hid the treat behind one of the two sides of the fence. The experimenter then stood backup and rotated the rear occluder 90 degrees so that it was no longer blocking the center portion of the fence (b). In half of the test trials, the center portion of the fence was blocked from the front by the bent occluder (c). See the online article for the color version of this figure.

to walk the subject forward into the center portion of the fence so that it could see what was behind each side of the fence. Once the subject was positioned in the center portion, the experimenter bent down, lifted the treat off of the bucket, clicked her tongue, and replaced the treat on the bucket to highlight the treat’s location. She then told the handler to walk the subject back to the starting

position and then to release the subject by unlocking the retractable leash. These warm-up trials ensured that subjects had experience with the visual access that they could gain from the center of the fence. Moreover, given that subjects needed to remember the location of the treat after walking back to the starting position, these warm-up trials ensured that subjects could recall the location of the treat even after a delay, making this a higher criterion for memory capacity than was required for the actual test trials.

The experimenter would wait until the dogs ate the treat before she ended the trial. A priori, we decided that if the subject put its nose behind a side of the fence, then the subject had chosen that side. “No choice” was recorded if the subject did not put its nose behind a side of the fence within 30 s of being released. In practice, however, subjects always consumed the treat after choosing a side, such that the only time this operational definition was not met was on “no choice” trials.

If the subject chose the side of the fence with the treat behind it, they were allowed to eat the treat off of the bucket. If the subject chose the incorrect side, the experimenter lifted the bucket and treat to show them that the treat was on the other side but did not allow the subject to consume the treat. The location of the treat alternated left then right during the warm-up trials for four trials or until the subject chose the correct side for two trials in a row. Any subject that failed to approach the correct side for two trials in a row out of four was excluded from further participation in the study. Twelve dogs failed these warm-ups and were excluded from further participation in the study. Five dingoes failed the warm-ups and received a second attempt on an additional day, which we added to gather the largest sample of dingoes possible. Four of these dingoes failed the warm-ups again on their second attempt, but one dingo successfully completed the warm-ups on their second day of testing and was therefore included in our final sample.

Test trials. After passing the warm-up trials, subjects completed eight *test trials*. In half of the test trials, subjects had the opportunity to seek information by looking into the center opening of the fence before selecting a side. However, rather than having the handler walk the subject up to the center opening, the handler released the subject from the starting position immediately after the hiding presentation, which was identical to that of the warm-up trials. Therefore, subjects were ignorant as to the location of the reward in all test trials.

After the experimenter positioned the bucket and rotated the back occluder during the hiding phase, she stood centered behind the fence with her head down and instructed the handler to release the subject. Importantly, in half of the trials, the center portion of the fence was only blocked by the rear occluder during the hiding presentation (information-seeking possible trials) such that the subject could approach and check the location of the treat during the choice phase. However, in the other half of trials, the center portion was blocked from the front by the bent occluder for the entirety of the trial (information-seeking impossible trials) such that approaching the center portion yielded no useful visual information (see [Figure 2c](#)). Once released, the subject had 30 s to choose a side.

Trial type (information-seeking possible vs. impossible) and treat location (right side, left side) were pseudorandomized such that (a) subjects did not receive the same trial type more than two times in a row and (b) the treat was not on the same side more than two times in a row. If a subject made two consecutive “no

choice” responses in the test trials, the study session ended and the subject was excluded. One dingo only completed five of the eight test trials before making two no choice responses in a row and was therefore excluded.

Coding and data analysis. Amanda L. Royka and an additional coder who was blind to the study’s hypothesis coded center approach and accuracy. Center approach was defined as whether the subject entered the center portion of the fence before choosing a side on test trials. Accuracy was defined as whether the subject chose the side of the fence where the treat was hidden. No choice was recorded for both variables in which the subject did not choose a side within 30 s. Reliability was high for both variables (Cohen’s $\kappa = 0.96$ for center approach, 0.98 for accuracy).

Statistical analyses were conducted with R statistical software (Version 3.2.1, R Foundation for Statistical Computing, Vienna, Austria). Center approach was analyzed with a generalized linear mixed model (GLMM) coded as a binary response term (approached the center of the fence = 1, did not approach the center of the fence = 0). Predictors of interest were species (dog or dingo), trial number, and trial type (information-seeking possible or information-seeking impossible) with random intercepts included for subject. The mixed models were conducted using R package “lme4” (Bates, Maechler, & Bolker, 2012).

We began with a null model that used only subject identity as a predictor of center approach, which we then compared with a full model with all predictor variables and interactions. Once we confirmed that the full model was a better fit to the data than the null model, we used backward stepwise elimination from the full model to arrive at a final model such that only predictors and interactions that significantly improved the fit of the model were kept. Finally, we conducted follow-up binomial tests looking at center approach and accuracy across the two different trial types (information-seeking possible vs. information-seeking impossible) for both species.

Results

Our model for center approach revealed that subjects’ tendency to approach the center portion of the apparatus was significantly predicted by trial type (information-seeking possible vs. information-seeking impossible; LRT: $\chi^2 = 15.4$, $p < .001$, $R^2 = 0.24$); no other factors or interactions were significant predictors (Likelihood-ratio Test [LRT]: $ps > .108$; for reference, see [Figure S1a](#) in the online supplemental materials for results collapsed across species). The results of our model indicate that subjects were more likely to approach the center of the apparatus during information-seeking possible trials ($M = 1.08$ out of 4) than during information-seeking impossible trials ($M = 0.31$ out of 4; see [Figure S1a](#) in the online supplemental materials). Due to the size of our dingo sample, we wanted to confirm that this pattern held for both species when analyzed separately. Specifically, we conducted two additional GLMMs, one for each species, predicting center approach based on trial type with random intercepts for subjects. In line with our combined model, trial type significantly predicted dogs’ approach behavior (LRT: $\chi^2 = 17.3$, $p < .001$, $R^2 = 0.21$). Specifically, dogs were more likely to approach the center of the apparatus during information-seeking possible trials ($M = 1.00$ out of 4) than during information-seeking impossible trials ($M = 0.15$ out of 4; see [Figure 3a](#)). However, trial type was

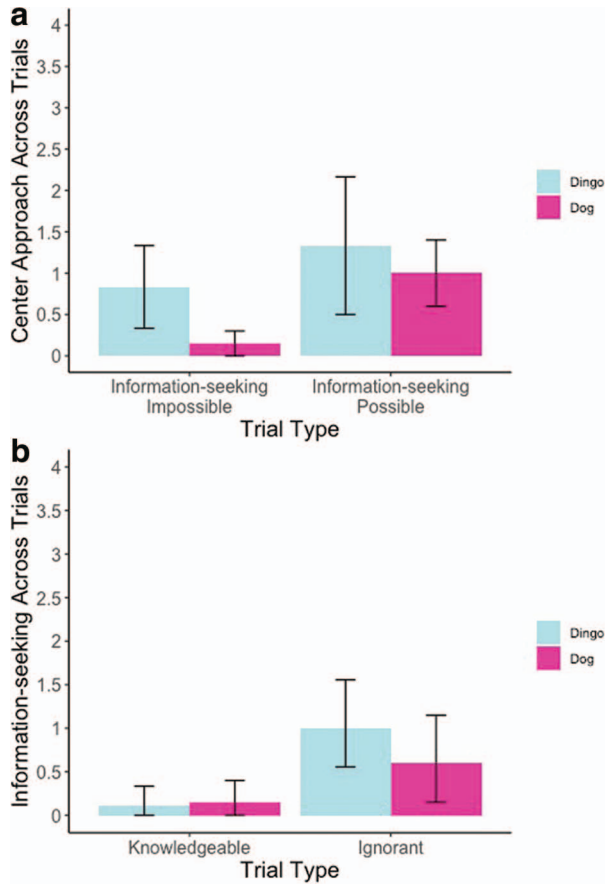


Figure 3. Average number of trials in Study 1 in which subjects approached the center portion of the fence (out of four) broken down by trial type and species (a). Average number of trials in which subjects in Study 2 engaged in information-seeking (out of four) broken down by trial type and species (b). Error bars indicate 95% confidence intervals. See the online article for the color version of this figure.

not a significant predictor of the dingoes' approach behavior (LRT: $\chi^2 = 0.88$, $p = .349$, $R^2 = 0.23$; $M = 1.33$ out of 4 in information-seeking possible trials, $M = 0.83$ out of 4 in information-seeking impossible trials; Figure 3a). Thus, although the pattern of results in dingoes mirrored that of dogs, it did not reach statistical significance in our sample of six dingoes.

To investigate whether subjects could successfully use the information available in the information-seeking possible trials, we used binomial tests with a Bonferroni correction for multiple comparisons¹ to examine how approaching the center of the fence affected subjects' accuracy across trial types. When subjects approached the center of the fence on information-seeking possible trials, they chose the correct side of the fence more often than would be expected by chance (22 out of 28 trials, $p = .004$). However, when subjects did not approach the center during information-seeking possible trials, they were not significantly more likely to choose correct side (subjects chose correctly in 34 out of 75 trials in which they did not approach the center, $p = .489$). For information-seeking impossible trials, subjects were not significantly more likely to choose the correct side when they did

not approach the center (subjects chose correctly in 50 out of 93 trials in which they approached the center $p = .534$). Similarly, when subjects *did* approach the fence during information-seeking impossible trials, they were not significantly more likely to choose correct side (subjects chose correctly in four out of eight trials in which they did not approach the center, $p = 1.00$). These findings suggest that dogs and dingoes were able to use visual information to increase their accuracy when they sought it out but were not using other cues (i.e., scent) to increase their accuracy when they entered the center portion of the fence on information-seeking impossible trials.²

Discussion

Our results in Study 1 demonstrate that both domesticated dogs and nondomesticated dingoes are willing to engage in information-seeking in the current experimental setup. Specifically, on the information-seeking possible trials, we found that both species approached a location that could provide them with information, rather than immediately searching for the hidden treat behind the apparatus. It is important to note, however, that subjects still approached the center relatively infrequently, even when information was available (on 25% of information-seeking possible trials for dogs and 33% of information-seeking possible trials for dingoes). The most likely explanation for the rarity of this behavior is insufficient inhibitory control. To seek information, subjects had to inhibit their desire to immediately search for the treat behind a random side of the fence and instead approach the center location where they could see the treat but not physically access it. Even though the method of information-seeking used in our studies presented a lower cost relative to other information-seeking behaviors required in previous studies of canine metacognition (Bräuer et al., 2004; McMahan et al., 2010), subjects still needed to exercise some inhibitory control to approach the center of the apparatus. Therefore, it is possible that dogs and dingoes would show even greater evidence of information-seeking in a task that completely eliminated the need for inhibitory control.

Notably, dogs approached the information-seeking location significantly more often on trials when doing so would yield useful information (i.e., when the front of the fence was unoccluded) compared with when that same behavior did not provide information (i.e., when the front of the fence was occluded). This finding is particularly surprising because two previous studies suggest that domesticated dogs do not engage in this behavior (Bräuer et al., 2004; McMahan et al., 2010, but see Belger & Bräuer, 2018, for findings more consistent with our results). However, our method was designed to give dogs and dingoes the best chance possible of demonstrating information-seeking behaviors. Unlike previous studies of canine information-seeking, subjects in the current in-

¹ Because we conducted four binomial tests, we used a Bonferroni-corrected p cutoff of $p < .013$ for these tests.

² Due to the small number of instances in which subjects approached the center in the information-seeking impossible condition, we did not conduct species-level analyses, examining the relationship between accuracy and information-seeking. See Table S2 in the online supplemental materials for contingency tables listing the raw numbers of trials in which subjects in Study 1 were accurate/inaccurate in their choice behavior based on whether they approached the center portion of the apparatus broken down by species.

vestigation received previous exposure to the increased visual access that they could get by looking through the center portion of the fence. During the warm-up trials, handlers guided subjects up to the fence; therefore, subjects did not need to make any spatial inferences about what they would be able to see if they walked up to the center portion of the fence. In addition to lessening the task demands, these warm-ups also allowed us to ensure that subjects had the visual acuity, attention, and memory necessary to succeed on the task when subjects were knowledgeable about the location of the treat. Specifically, to pass the warm-up trials, subjects had to remember the location while being walked back to the starting position, making this a higher criterion for memory capacity than was required for the actual test trials. Additionally, the information-seeking behavior in the current study was a natural action that only required a minimal delay in subjects' search, which reduced the inhibitory control required to seek information. Therefore, this method of information-seeking presented a much lower cost for subjects compared with the behaviors required in previous studies of canine metacognition (Bräuer et al., 2004; McMahan et al., 2010).

Unlike dogs, dingoes did not approach the center of the fence more often when doing so would provide them with information about the location of the hidden reward. Given that dingoes showed the same pattern of results as dogs, we think this is likely an issue of insufficient power in our dingo sample. However, it is also possible that dingoes approached on the occluded trials in an attempt to investigate olfactory cues, which may suggest a possible interspecies difference in olfactory information-seeking when visual information is unavailable. Future work using other modalities—such as sound or smell—may find additional evidence of metacognitive information-seeking in canids. Regardless of why we failed to see a difference between information-seeking possible and information-seeking impossible trials with dingoes, we found clear evidence that dingoes would seek information in at least some contexts in the current method. This served as a proof of concept and allowed us to progress to our primary question regarding whether dogs and dingoes would metacognitively seek information in Study 2.

Study 2

Study 1 provided preliminary evidence that domesticated dogs and nondomesticated dingoes will seek information from our novel apparatus. However, it remains unclear whether these canids will selectively seek information to rectify their ignorance. In other words, is information-seeking behavior in dogs and dingoes driven by metacognition? To examine this question, we conducted a second experiment in which we investigated whether subjects would seek information more often when ignorant of the location of a hidden treat than when knowledgeable.

Unlike subjects in Study 1, subjects in Study 2 could seek information by approaching the unoccluded center portion of the fence on every trial. However, we manipulated whether or not subjects *needed* to seek information: During half of the trials subjects already knew where the treat was hidden. Therefore, any information gained by approaching the center of the apparatus would be redundant. If canids possess metacognition, then subjects in Study 2 should approach the center of the apparatus when they do not know the location of the treat (i.e., in the ignorant trials) but

should forgo approaching the center when they have previous knowledge of the treat's location (i.e., in the knowledgeable trials). However, if canids lack metacognition, then subjects in Study 2 should approach the center at equal rates, regardless of whether they already know where the treat is hidden. This type of indiscriminate information-seeking behavior could suggest that subjects are instinctually drawn to explore the affordances of the environment without any representation of their own ignorance, often referred to as "curiosity" (for a short summary, see Byrne, 2013). For example, when faced with an inference by exclusion task in which food is hidden at one end of a tube, keas (*Nestor notabilis*) exhibit a tendency to redundantly inspect both ends of the tube even when doing so could provide no new information (Schloegl et al., 2009). Study 2 therefore tested whether dingoes and domesticated dogs fail to monitor their own knowledge states, and instead explore any available visual affordances of an environment.

Method

Dog subjects. Twenty domesticated dogs of varying breeds (see Table S3 in the online supplemental materials) participated in this study at the Canine Cognition Center at Yale. Twelve additional dogs were excluded for not passing the warm-ups (10), owner interference (one), and not eating the treats during the warm-ups (one).

Dingo subjects. Nine genetically pure dingoes (see Table S3 in the online supplemental materials) from the Dingo Discovery Research Centre in Victoria, Australia, participated in this study. Nine additional dingoes were tested and excluded for not approaching during the warm-up trials (two) and failure to pass the warm-ups (seven). As in Study 1, dingoes were given a second opportunity to participate in Study 2 if they were excluded on their first day for any reason. Of the nine dingoes included in our final sample, four needed a second day of testing due to failure to approach during the familiarization phase (one) and failure to pass warm-ups trials on Day 1 (three).

To achieve the maximum sample size possible, we tested dingoes in Study 2, regardless of whether or not they had participated in Study 1. Four dingoes in the final sample of Study 2 had previously participated in Study 1. Moreover, to ensure our dog sample matched our dingo sample, we recruited dogs for Study 2 regardless of whether they had participated in Study 1 or not. Five of the dogs in the final sample of Study 2 had previously participated in Study 1.

Design and procedure. The method of Study 2 was identical to that of Study 1, with two exceptions. First, given that subjects were able to seek information on all trials in Study 2, the bent occluder that was placed in front of the center portion to block the center opening in Study 1 was not included in any part of Study 2. Second, instead of manipulating the informativeness of the information-seeking behavior in test trials, as we did in Study 1, we manipulated subjects' knowledge of where the treat was hidden. In half of the trials, we prevented subjects from seeing where the treat was hidden (*ignorant* trials), and in the other half of trials, we allowed subjects to see where the treat was hidden (*knowledgeable* trials). The ignorant trials were identical to the information-seeking possible trials in Study 1 in which subjects could not see where the treat was hidden. In contrast, during the knowledgeable

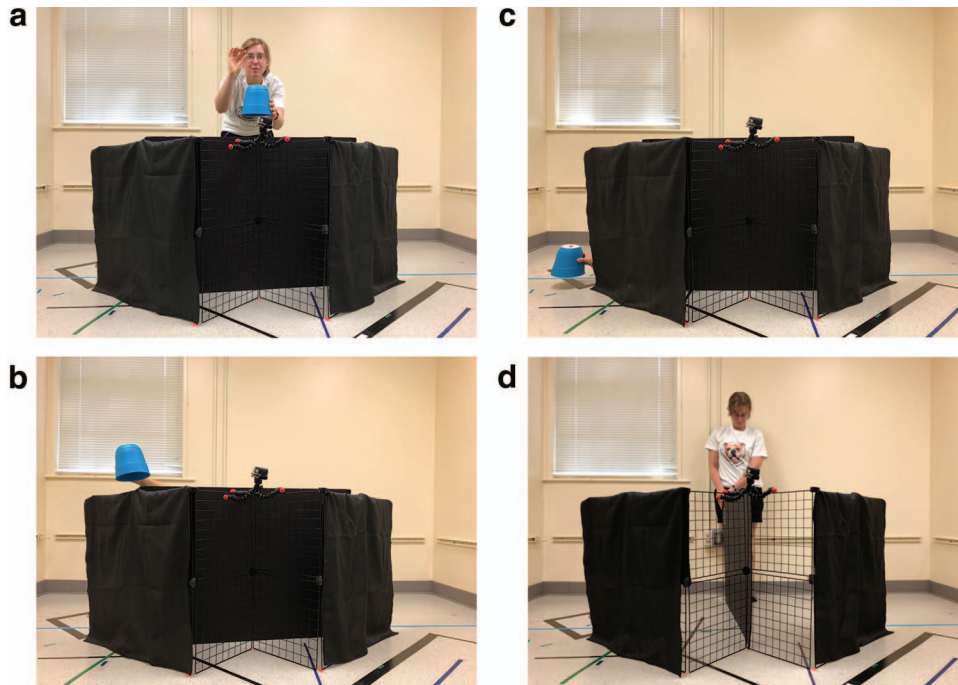


Figure 4. At the beginning of each trial in Study 2, the experimenter made eye contact with the subject, and then visibly placed the treat on the bucket (a). During knowledgeable trials, the experimenter moved the bucket to its hiding location by moving it above and around the fence (b and c). Then, in all trials, the experimenter stood up and rotated the rear occluder 90 degrees so that it was no longer blocking the center portion of the fence (d). See the online article for the color version of this figure.

trials, the experimenter kept the bucket raised above the fence throughout the hiding process so dogs and dingoes could see where the bucket was hidden (see Figures 4a–4d). Specifically, during the hiding process in the knowledgeable trials, the experimenter moved the bucket over and around one side of the fence until it was right above the ground at which point the she moved the bucket behind the fence and placed it down. If dogs and dingoes possess metacognitive awareness of their own knowledge states, they should be more likely to seek information on ignorant trials than knowledgeable trials, given that they already have the information they need to find the treat on the knowledgeable trials.

As in Study 1, trial type (knowledgeable vs. ignorant) and treat location (right side, left side) were pseudorandomized such that (a) subjects did not receive the same trial type more than two times in a row and (b) the treat was not on the same side more than two times in a row.

Coding and data analysis. Using the same guidelines as in Study 1, Amanda L. Royka and a second coder who was blind to the study’s hypothesis coded information-seeking behavior and accuracy. Information-seeking behavior was defined as whether the subject entered the center portion of the fence before choosing a side on test trials. No choice was recorded for both variables if the subject did not choose a side within 30 s. Reliability was high for both variables (Cohen’s $\kappa = 0.97$ for information-seeking, 1.00 for accuracy). As in Study 1, information-seeking behavior was analyzed with a GLMM coded as a binary response term (performed information-seeking behavior = 1, did not perform information-seeking behavior = 0). Predictors of interest were

species (dog or dingo), trial number, and trial type (knowledgeable or ignorant). Similarly, we conducted follow-up binomial tests looking at information-seeking behavior and accuracy across the two different trial types (knowledgeable vs. ignorant).

Results

Our full model of information-seeking behavior with all predictor variables and interactions outperformed our null model that used only subject identity as a predictor. Our model for information-seeking revealed that subjects’ tendency to approach the center portion of the apparatus was significantly predicted by trial type (knowledgeable vs. ignorant; LRT: $\chi^2 = 18.4$, $p < .001$, $R^2 = 0.32$). No other factors or interactions were significant predictors (LRT: $ps > .115$). According to our model, subjects were more likely to seek information when they did not already know the location of the treat ($M = 0.72$ out of 4) compared with when subjects were knowledgeable about the location of the treat ($M = 0.14$; see Figure S1b in the online supplemental materials). This finding suggests that subjects’ information-seeking behaviors were contingent upon their own knowledge state. Additionally, the main effect of trial type remains significant ($p < .001$) and the main effect of species remains non-significant ($p = .128$) even when excluding subjects that had previously been exposed to Study 1. To confirm that both dogs and dingoes seek information more often when ignorant, we conducted a GLMM for each species predicting information-seeking behavior based on trial type with random intercepts for subjects. Trial type significantly

predicted the information-seeking behaviors of both dogs (LRT: $\chi^2 = 11.2, p < .001, R^2 = 0.40$) and dingoes (LRT: $\chi^2 = 8.5, p = .004, R^2 = 0.18$; see Figure 3b).

We also conducted binomial tests with a Bonferroni correction for multiple comparisons³ to investigate whether subjects could successfully use the information from the hiding presentation in the knowledgeable trials and the information subjects gained by information-seeking in the ignorant trials.⁴ When subjects approached the center of the fence on ignorant trials, they chose the correct side of the fence more often than would be expected by chance (19 out of 21, $p < .001$). However, when subjects did not approach the center during ignorant trials, they were not significantly more likely to choose correct side (subjects chose correctly in 46 out of 94 trials in which they did not approach the center, $p = .918$). For knowledgeable trials, we were only able to examine accuracy using binomial tests for trials on which subjects did *not* approach the occluded center of the fence due to the limited number of trials subjects approached the fence on knowledgeable trials (four trials total). When subjects did not approach the center on knowledgeable trials, they were significantly more likely to choose the correct side (subjects chose correctly in 87 out of 110 trials in which they approached the center, $p < .001$). Although we were not able to run binomial tests on trials in which subjects *did* approach the fence on knowledgeable trials, it is worth noting that they chose incorrectly on three out of four trials for which they approached the center of the fence. These findings suggest that dogs and dingoes were able to use information that they gained from engaging in the information-seeking behavior to increase their accuracy during ignorant trials, and that subjects used the information from the hiding demonstration during knowledgeable trials to choose the correct side without attempting to seek additional information.

Discussion

Study 2 provides new evidence suggesting that domesticated dogs and nondomesticated dingoes change their information-seeking behavior based on their previous knowledge. Just as non-human primates (Call & Carpenter, 2001; Marsh & MacDonald, 2012a; Rosati & Santos, 2016) and scrub jays (Watanabe & Clayton, 2016) demonstrate metacognition by seeking information to remedy their own ignorance, both dogs and dingoes sought out information more often when they did not know where the treat was hidden compared with when they had previous knowledge of the treat's location. These findings suggest that dogs' and dingoes' information-seeking behaviors are not simply driven by general curiosity or general exploratory behavior, but rather by an ability to monitor their own ignorance.

General Discussion

Taken together, these studies provide positive evidence of flexible information-seeking behaviors in both domesticated dogs and nondomesticated dingoes. In the crucial test of this hypothesis in Study 2, both dogs and dingoes sought information more often when doing so would provide them with information they lacked. This adds converging evidence to recent findings of metacognitive information-seeking in domesticated dogs (Belger & Bräuer, 2018) and suggests that dogs' information-seeking behaviors are robust

even across changes in experimental design. Moreover, these studies provide the first evidence of information-seeking behavior in a nondomesticated canid. Our research—which used all the socialized dingoes that could be tested using this method—suggests that dingoes seek out information to remedy their ignorance much like domesticated dogs (Belger & Bräuer, 2018), nonhuman primates (Call & Carpenter, 2001; Marsh & MacDonald, 2012a; Rosati & Santos, 2016), and scrub jays (Watanabe & Clayton, 2016).

Interestingly, the findings presented here stand in contrast to the findings of two previous studies (Bräuer et al., 2004; McMahon et al., 2010), which failed to find evidence of information-seeking behaviors in domesticated dogs. This discrepancy likely reflects an important difference in methodologies. Although several past studies required dogs to perform trained behaviors (e.g., knocking over boxes, McMahon et al., 2010, and pushing levers, Bräuer et al., 2004) and positioned the possible reward closer to subject than the information-seeking opportunities, the current studies minimized the cost of seeking information and did not require subjects to execute any trained behaviors. Our methodology was based on investigations of nonhuman primate metacognition (Call & Carpenter, 2001; Rosati & Santos, 2016), which used naturalistic foraging designs to close the gap between the performance of subjects and their potential metacognitive competence. Furthermore, the one other study that found evidence of metacognitive information-seeking in dogs (Belger & Bräuer, 2018) used a similar setup in which dogs had to walk to a location where they could gain visual access to a hidden reward.

Notably, the amount of information-seeking behaviors observed in the current study was significantly less than the amount of information-seeking behaviors exhibited by dogs in Belger and Bräuer (2018). Subjects exhibited information-seeking behaviors relatively infrequently the current studies; across all of the trials in which it was possible to seek information in Studies 1 and 2, subjects only approached the center on 16% of trials. Although the designs of both the current study and Belger and Bräuer (2018) allowed dogs to seek information by walking to a central location along a fence, the designs differed in terms of where the demonstrators hid the rewards relative to the where the subjects could seek information. In Belger and Bräuer (2018), the reward was placed at the corner of one of two V-shaped fences, immediately *adjacent* to a location where dogs could seek information. However, in the current study, the treat was located behind one of the distal wings of the fence (see Figures 1a and 1b), not adjacent to the central information-seeking location. Thus, information-seeking opportunities in Belger and Bräuer (2018) may have been more attractive to dogs than in the current studies, as it brought them in closer proximity to the treat. Additionally, this may have also meant that the information-seeking behavior in Belger and Bräuer (2018) required dogs to exercise even less inhibitory con-

³ Because we conducted three binomial tests, we used a Bonferroni-corrected p cutoff of $p < .017$ for these tests.

⁴ See Tables S4a and S4b in the online supplemental materials for contingency tables of the raw number of trials in which subjects in Study 2 were accurate/inaccurate in their choice behavior based on whether they approached the center portion of the apparatus.

trol than in the current study. Despite these differences in the overall amount of information-seeking behavior, the fact that dogs succeed on both experimental designs provides even stronger evidence that dogs do in fact seek out information when they are unsure of the location of a reward.

The current studies also highlight the possibility that one of dogs' nondomesticated relatives—the dingo—may metacognitively seek out knowledge. It is particularly interesting and perhaps surprising that dingoes and dogs show similar performance in Study 2, given that previous work has highlighted a number of ways in which dogs differ from dingoes (Johnston et al., 2017; Smith & Litchfield, 2010a, 2010b). Future work on canine metacognition could benefit from exploring whether canids demonstrate similar flexibility when seeking information in other modalities. For example, nondomesticated canids may be particularly adept at exploiting olfactory information-seeking opportunities. This possibility is especially compelling in the case of the dingoes because their approach behavior in Study 1 was not significantly affected by the availability of visual information. However, because Study 1 did not manipulate the subjects' knowledge states and the scent cues seemed insufficient to locate the treat, these data do not provide direct insight into this question.

Our findings also suggest that dogs' information-seeking abilities are not the result of their history of domestication and that other closely related canids, such as gray wolves (*Canis lupus*), may likewise seek information to rectify their own ignorance. The addition of dingoes to the list of species that succeed on tasks of metacognitive information-seeking also raises further questions about the broader phylogenetic spread of this representational capacity. Given that researchers propose that metacognition may underpin humans' impressive learning (Vrugt & Oort, 2008) and cooperative (Frith, 2012) abilities, there exists an implicit assumption that metacognition is not shared widely across species. Under this theory, metacognition is present in species of primates, canids, and birds because it evolved independently, possibly due to similar ecological pressures. However, it is impossible to draw strong conclusions on this matter because there is only minimal evidence regarding species that do *not* metacognitively seek out information (Paukner et al., 2006; Roberts et al., 2012). Indeed, without further negative evidence, it is also possible that metacognition evolved before the last common ancestor of birds and primates (though see Paukner et al., 2006) and is therefore shared across species through common descent. To distinguish between these two possibilities, we need to continue to probe the metacognitive abilities of a variety of species.

The potential homology of metacognitive abilities across phylogeny may be further clarified through more nuanced investigations with species that have already succeeded at tests of information-seeking. Call (2010) examined the robustness of metacognition in great apes through additional variations on the classic information-seeking paradigm. In addition to manipulating whether subjects had previous knowledge of the location of the reward, this approach also tested how the cost of information, the quality of the reward, the availability of alternative information about the location of the reward, and the time delay between subjects witnessing the reward hiding and being released to search affected the frequency of information-seeking. In this way, the current studies represent just a first step toward understanding the metacognitive abilities of canids. Belger and Bräuer (2018) found

that dogs' information-seeking behaviors were not affected by the reward quality or the time delay between subjects witnessing the reward hiding and being released to search. Therefore, even though domesticated dogs seek out information about hidden rewards, their metacognition is likely to be somewhat fragile. It is unknown whether dingoes would show similar limitations.

Further investigations into the nuances of canine information-seeking behaviors would also clarify that the processes underpinning these behaviors are indeed metacognitive. Although the information-seeking paradigm circumvents many pitfalls of other tests of metacognition (see Carruthers, 2008; Crystal, 2019; Smith, 2009), several alternative explanations for information-seeking behaviors have been put forward (Call, 2012; Carruthers, 2008; Crystal & Foote, 2011; Hampton, 2009; Hampton et al., 2004). For example, individuals could rely on a generalized search response (Call, 2012; Carruthers, 2008) whenever they experience nonmetacognitive uncertainty about the location of the food. Under this explanation, in situations such as our ignorance condition (Study 2) subjects will use a suite of general, nonmetacognitive information-seeking behaviors until they see the reward. Similarly, the response competition hypothesis (Hampton et al., 2004) argues that nonhuman animals have two competing drives: to approach food and to search for food; the relative strengths of these desires then determine the behavior of the individual. When individuals are unaware of the location of the food, the search response wins out, therefore creating a search-when-ignorant behavioral pattern.

Although our data are consistent with a metacognitive account of information-seeking behaviors, they could also be explained by these alternative accounts. The current studies are an initial investigation of canid information-seeking behaviors and were not designed to robustly test these alternative explanations. However, research into nonhuman primate metacognition has produced a number of elegant studies that counter these alternative accounts to support a metacognitive interpretation of information-seeking behaviors and that could easily be adapted for future use with canids (Call, 2005, 2010; Hampton et al., 2004; Krachun & Call, 2009; Marsh & MacDonald, 2012a, 2012b). For example, chimpanzees and orangutans will not seek additional information after seeing that one of two potential reward locations is empty (Call, 2005; Call & Carpenter, 2001; Marsh & MacDonald, 2012a). These spontaneous exclusion inferences made upon seeing the empty location suggest that chimpanzees and orangutans are using some representation of the knowledge that they lack, rather than simply looking until they see food. Similar studies with canids should examine whether subjects move to retrieve the reward after only seeing that it is *not* in a potential location. Moreover, because domesticated dogs are capable of inference by exclusion (Erdőhgyi, Topál, Virányi, & Miklósi, 2007), tracking their exact looking behaviors may be a particularly promising way to provide additional evidence that the representations underlying information-seeking behaviors in dogs and dingoes are truly metacognitive. Similarly, neither a generalized search response explanation nor the response competition hypothesis predicts that subjects will perform redundant searches when the value of the food is high and the cost of the information-seeking behavior is relatively low. Yet, chimpanzees, orangutans, and rhesus macaques show exactly this pattern of behavior (Call, 2010; Hampton et al., 2004; Marsh & MacDonald, 2012b). Because subjects should have a stronger tendency to reach toward the known location of high-

value rewards, this finding provides evidence against the response competition hypothesis and suggests that these nonhuman primates seek information with a level of flexibility that is consistent with metacognition. By systematically titrating the cost of seeking information or the value of the reward for canine subjects, future work can provide new information about the flexibility of these species' information-seeking behaviors.

It will also be informative to test canine metacognition in social contexts, as seeking information from a human informant would test whether subjects still try to rectify their own ignorance when doing so will not give them visual access to the reward. If subjects approach sources of information that do not grant them perceptual access to the reward, then this evidence would counter the alternative explanations of information-seeking behaviors that are predicated on nonspecific exploratory behavior where the individual searches till it sees the reward (Call, 2012; Carruthers, 2008; Hampton et al., 2004). Additionally, domesticated dogs, in particular, may show even higher levels of information-seeking behaviors in social contexts because they are more adept at using social information than they are at using physical information to find a treat (Bräuer et al., 2006; Udell et al., 2008). Previous work has already demonstrated that dogs spontaneously look back at their guardians when confronted with an unsolvable task (Miklósi et al., 2003; Passalacqua et al., 2011). Future studies should investigate whether domesticated dogs selectively look back in cases when they are ignorant to examine if looking back is performed metacognitively. This methodology has already provided positive evidence of metacognition in 20-month-old human infants by measuring their tendency to look back at their parents selectively to gain information that they lack (Goupil, Romand-Monnier, & Kouider, 2016). However, because domesticated dogs are very sensitive to human social cues, it is also important to account for the Clever Hans phenomenon (Beran, 2012; Samhita & Gross, 2013) and limit possibility for human cuing—both in studies that directly investigate social information-seeking behaviors and in studies such as ours where humans are not meant to provide any social cues. It is notable that many studies of metacognition (Belger & Bräuer, 2018; Call & Carpenter, 2001; McMahan et al., 2010)—including the current investigation—rely on a knowledgeable experimenter to administer the task. Here, we minimized the potential for cues from the subjects' handlers by keeping the handlers blind to both the location of the reward during individual trials and the hypothesis of the experiment. Additionally, the experimenter kept her head down once the subject was released so that the subject could not see her eyes. Although these techniques can reduce the likelihood of unintentional cues resulting from eye gaze, completely eliminating the presence of the human experimenter would remove the danger of inadvertent cuing.

It may also be interesting to consider metacognition's relationship to other representational capacities in nonhuman animals. For example, several scholars argue that the cognitive mechanisms underlying metacognition and those necessary for monitoring the mental states of others are dependent on one another in some manner (Carruthers, 2009; Frith & Happé, 1999; Goldman, 2006). Although it is still unclear whether any animals possess the full set of theory of mind abilities that humans possess (see reviews in Apperly, 2010; Bräuer,

2014; Call & Tomasello, 2008; Emery & Clayton, 2009), nonhuman primates, dogs, and scrub jays all demonstrate an ability to track the perceptual access and knowledge of other agents, which is one component of what researchers have referred to as a *theory of mind* (nonhuman primates: Flombaum & Santos, 2005; Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Santos, Nissen, & Ferrugia, 2006; Schmelz, Call, & Tomasello, 2011; scrub jays: Dally, Emery, & Clayton, 2004, 2005, 2006; Emery & Clayton, 2001; domesticated dogs: Bräuer et al., 2004; Call, Bräuer, Kaminski, & Tomasello, 2003; Catala, Mang, Wallis, & Huber, 2017; Cooper et al., 2003; Johnston, Huang, & Santos, 2018; Kaminski, Bräuer, Call, & Tomasello, 2009; Kaminski, Pitsch, & Tomasello, 2013; Maginnity & Grace, 2014; Topál, Miklósi, & Manyik, 2004). Therefore, it is notable that, prior to the findings of the current study, the species that seem to think about and act upon the knowledge of others also show similar aptitude when thinking about and acting on their own knowledge.

Dingoes, however, provide an interesting counterexample to this overlap because, compared with dogs, dingoes are less sensitive to the social cues that are important for inferring others' mental states. For instance, even when heavily socialized to humans, dingoes follow human social cues significantly less than dogs, but more so than wolves (Smith & Litchfield, 2010a). Additionally, dingoes are less likely than dogs to look back at familiar humans (Smith & Litchfield, 2013), and generally less likely to make eye contact with familiar humans (Johnston et al., 2017). Although no one has directly tested whether dingoes possess theory of mind-like abilities in the context of inferring the perceptual states of humans or conspecifics, monitoring cues such as eye gaze is critical for mental state inference and is often discussed as a precursor to theory of mind (Bräuer, 2014). If dingoes fail to track the perceptual and knowledge states of others, but can represent their own knowledge state, then this raises the possibility that these representational capacities are separable in canids and possibly other nonhuman animals. Although there is still active debate about the exact interaction between theory of mind and metacognition in humans (see Carruthers, 2009, for review), the current findings open new questions about the relationship between these metarepresentational capacities in nonhuman animals and whether this relationship might differ from that seen in humans.

Although investigations from comparative psychology show that metacognition is not a uniquely human capacity, many open questions remain. Our studies provide converging evidence that domesticated dogs may perform metacognitive information-seeking and present the first evidence of a similar level of information-seeking in a species of nondomesticated canid. However, it is highly unlikely that comparative psychology has discovered the extent of metacognitive abilities that exist in nonhuman animals. Moreover, many questions persist about the flexibility of metacognition in nonhuman animals (Call, 2010). Further research is required to understand what social and environment factors facilitate the emergence of metacognitive abilities across taxa and how this flexibly representational capacity is deployed.

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