Metacognition across domestication: A comparison of dogs and dingoes

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Abstract

Metacognition refers to the ability to monitor one's own mental states. Using a simplified procedure based on prior work with non-human primates (Rosati and Santos 2016), we investigated whether domesticated dogs (*Canis familiaris*) and non-domesticated dingoes (*Canis dingo*) demonstrated metacognition by seeking information to remedy their own ignorance. In Study 1, we found evidence that dogs and dingoes were sensitive to the availability of information and only delayed their search for a hidden treat when doing so would provide increased visual access. Study 2 provided evidence that the information-seeking observed in Study 1 was indeed metacognitive. When information was always available to subjects in Study 2, dogs and dingoes only engaged in information-seeking when they did not already know where the treat was hidden. These results provide the first evidence to date that domesticated dogs metacognitively seek information in the face of ignorance, as well as the first evidence of metacognitive information-seeking in a non-domesticated canid.

Keywords: Metacognition, information-seeking, domestication, *Canis familiaris*

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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 and 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 and Wells 2003).

The role of metacognition in many seemingly sophisticated cognitive abilities compelled some researchers to hail it as a unique human cognitive capacity (Nelson et al. 1994) with a protracted period of development (Flavell 1979). However, a growing body of research in young children and non-human animals suggests that both of these claims are incorrect. Empirical research suggests that from a very young age, children are able to think about what they do and do not know. While the ability to accurately *communicate* one's own past mental states may have a more protracted period of development (Hogrefe et al. 1986; Wellman et al. 2001), children in their second year of life are capable of effectively indicating to others when they are ignorant by using physical gestures (e.g., shrugs and hand-flips) and stating "I don't know," (Harris et al. 2017). Perhaps more impressively, at 20 months of age, children use their metacognitive awareness to acquire information that they lack by looking back at their guardians when they are uncertain of the location of a hidden object, suggesting not only that 20-month olds can monitor and communicate their own ignorance to their guardians, but also that they have an appreciation of the knowledge state of their guardian and the information that the guardian can provide (Goupil et al. 2016).

Metacognition in Non-Human Animals: the uncertainty monitoring approach

In much the same way that developmental research has shown that the timeframe of metacognition begins earlier than previously thought, earlier claims about the uniqueness of metacognition have also been brought into question by studies of metacognition in non-human animals. The most common approach to investigating metacognition in nonhuman populations is a method widely referred to as *uncertainty monitoring*. In these uncertainty monitoring studies, researchers present subjects with a perceptual discrimination task in which subjects must categorize a visual display based on the density of its dots. The subject is trained to press one button if the visual display is dense, and trained to press a second button if the display is sparse (e.g., Smith et al. 1997). When subjects classify a stimulus correctly, they are given a reward; if subjects classify a stimulus incorrectly, they are punished with a timeout. However, subjects also have a third option that allows them to opt-out of the current trial and skip to the next trial without a timeout. If animals can track their own knowledge states, then they should use the opt-out option adaptively, namely, when they are faced with a stimulus whose density is not clearly dense or sparse. A growing body of research has shown that nonhuman primates (Hampton 2001; Smith et al. 1997; Suda-King 2008), dolphins (Smith et al. 1995), pigeons (Sole et al. 2003), and rats (Foote and Crystal 2007) succeed on variations of the uncertainty monitoring paradigm, using the opt-out option to skip trials that require them to categorize stimuli that are at the boundary of dense and sparse.

While uncertainty monitoring studies provide positive results suggesting the existence of metacognition in a variety of nonhuman animal species, many researchers have questioned what these successes actually reveal about subjects' underlying cognitive abilities (Carruthers 2008; Hampton 2009; Smith et al. 2014; Terrace and Son 2009). Although subjects' use of the opt-out option could indicate metacognitive representations, it is also possible that subjects' successes are indicative of lower-level cognitive processes. For example, the reward contingencies learned over many pre-training trials may motivate subjects' opt-out responses. Because subjects experience immediate feedback for their choices, they can readily form an aversion to middle density displays and use the opt-out option to escape the stimulus. Under this interpretation, subjects' behaviors are simply responses to three differently reinforced stimuli. Subjects push one button when presented with a sparse display to receive positive reinforcement and push the other button when presented with a dense display to also receive a reward; similarly, subjects push the opt-out button when presented with a medium-density display to avoid the punishment of a time-out. Therefore, a representation of "uncertainty" or lack of knowledge is not necessary in order to explain subjects' opt-out behavior.

Additionally, Carruthers (2008) argued that even in the absence of the possible reinforcement learning explained above, the competing strengths of subjects' beliefs may allow them to adaptively use the opt-out option without metacognition. In a typical uncertainty monitoring task, the subject possesses three basic beliefs when confronted with a stimulus that is ambiguously dense: the subject has a weak belief that the stimulus is dense, a weak belief that the stimulus is sparse, and the belief that pushing a button and being incorrect will result in a time out. Without the opt-out option, the subject randomly chooses which button to push, due to its competing weak beliefs. However, with the addition of the option to opt-out of the trial, subjects also have the belief that pushing the skip trial does not result in an aversive time out. Since the weak competing beliefs about the density of the stimulus do not perpetuate a desire to respond "sparse" or "dense," the subject's strongest desire is to avoid a timeout, which would motivate it to choose the skip option. Carruthers (2008) argues that this explanation is able to account for the behaviors of the subjects in uncertainty monitoring tasks without any appeal to metacognition.

Metacognition in Non-Human Animals: the information-seeking paradigm

Although there have been many variations and extensions of the uncertainty monitoring paradigm (see Terrace and Son 2009 for review), the unavoidability pre-training, risk of associative learning, and possibility of a non-metacognitive deflationary explanation of the opt-out behavior make it difficult to differentiate between true metacognitive ability and lower-level cognitive processes using this paradigm. Therefore, in order to circumvent these concerns, researchers have developed another paradigm to probe the existence of metacognition in nonhuman animals. The *information-seeking paradigm* builds on methods first used with chimpanzees and human children (Call and Carpenter 2001), in which subjects have the option to seek out information about the location of a hidden reward prior to choosing where to search. In this paradigm, a reward is hidden in an unknown location and subjects can either search randomly for the reward or perform a specific behavior that provides them with information about its location, thus allowing subjects to increase their accuracy. If subjects have metacognition, they can represent their own knowledge and therefore should take specific action to gather information when they are ignorant, but forgo information-seeking when they already know the reward's location. However, if subjects do not have metacognition, they should either randomly search for the reward without information-seeking or information-seek regardless of whether or not they have prior knowledge of the treat's location.

Evidence from the information-seeking paradigm suggests that some non-human primates—such as great apes and rhesus macaques—have the ability to metacognitively represent their knowledge states and selectively take action to remedy their ignorance (Beran et al. 2013; Call 2010; Call and Carpenter 2001; Goupil et al. 2016; Marsh and MacDonald 2012; Rosati and Santos 2016). One such study conducted by Rosati and Santos (2016), gave rhesus macaques the opportunity to approach the center of two adjacent tubes and visually check the location of a hidden food reward before approaching one of the distal ends of the tubes. Rhesus macaques checked the center location significantly more often when they did not observe the experimenter baiting the tubes than when they observed the baiting process. Furthermore, the subjects rarely approached the center when there was only a single tube present that provided no opportunity for information-seeking. Most impressively, subjects performed this information-seeking behavior with no prior training or exposure to the apparatus, showing that rhesus macaques in a naturalistic foraging context can spontaneously gather information to rectify their own ignorance.

Research using the information seeking task has also shown that metacognition is not restricted only to the primate line. Despite being phylogenically distant from primates, scrub jays (*Aphelocoma californica*) selectively seek out information when they are ignorant of the location of a hidden food reward (Watanabe and Clayton 2016), suggesting a species of bird may also have the ability to metacognitively represent their own knowledge states. This unexpected pattern of information-seeking across species indicates that metacognitive abilities may have evolved independently in several taxonomic groups. Therefore, additional investigations with a broader array of taxa are necessary to identify other species that possess metacognitive abilities and to understand what ecological challenges facilitate the emergence of metacognition.

Metacognition and Knowledge-Perception Tracking

Although non-human primates and scrub jays are phylogenically distant and face distinctive environmental challenges, these sets of species share one notable commonality: the ability to track the perceptual access and knowledge of other agents (hereafter referred to as *knowledge-perception tracking*). For example, when given the opportunity to steal food from two human competitors, one who has visual access to a piece of food and a second who does not, rhesus macaques selectively steal from the competitor who is visually inattentive even when the experimenter's sight is obstructed in a variety of nuanced ways (e.g., experimenter's back turned to the food, experimenter's head turned away from the food, experimenter's face blocked by an opaque occluder, experimenter's eyes blocked by a small opaque occluder; Flombaum and Santos 2005). Similarly, scrub jays strategically cache food in shadow when in the presence of a competitor, but show no such preference when caching in private (Dally et al. 2004). Additional evidence suggests that non-human primates and scrub jays use social cues to make inferences about what others see and know across a variety of experimental set-ups (non-human primates: Hare et al. 2001; Kaminski et al. 2008; Marticorena et al. 2011; Santos et al. 2006; Schmelz et al. 2011; scrub jays: Dally et al. 2004; Dally et al. 2005; Dally et al. 2006; Emery and Clayton 2001). Beginning early in life, human children are also very adept at tracking the knowledge and perceptual access of other agents (Onishi and Baillargeon 2005; Song and Baillargeon 2008; Southgate et al. 2007), and from as young as 13 months are able to make implicit predictions about the behaviors of other agents based on what the agents know and believe (Surian et al. 2007). Because of the parallels between the performance of human children and nonhuman primates, several researchers have suggested that these abilities may constitute a simple version of the more complex theory of mind abilities exhibited by adult humans (Call and Tomasello 2008; Marticorena et al. 2011; Whiten 2013).

While it is still unclear whether any animals possess the theory of mind abilities that adult humans possess (see reviews in Apperly 2010; Call and Tomasello 2008; Emery and Clayton

2009), this interesting overlap in knowledge-perception tracking and metacognitive abilities in scrub jays and non-human primates aligns with theoretical predictions about the cognitive mechanisms underlying these abilities in humans. Because metacognition and knowledge-perception tracking both rely on representations of mental states, several scholars have argued that the cognitive mechanisms underlying metacognition and those necessary for monitoring the knowledge states of others are dependent on one another (Carruthers 2009; Frith and Happé 1999; Goldman 2006). While these theories seek to explain the relationship between knowledge-perception tracking and metacognition in humans, in order to make claims about the phylogenetic roots of theory of mind, researchers' predictions must transcend species. These theories should predict that, to some extent, species that can think about and act upon the knowledge of others should show similar aptitude when thinking about and acting on their own knowledge and perceptual access.

Given the theoretical interdependence of theory of mind and metacognition and the observed overlap of knowledge-perception tracking and metacognitive information-seeking in scrub jays and non-human primates, it makes sense to test whether other species that exhibit similar knowledge-perception tracking also possess metacognitive abilities. One species that notably uses social cues to make inferences about what others see and know is the domesticated dog. Although it is unclear whether dogs' abilities reflect the same theory of mind mechanisms at work in other species (e.g. Bräuer 2014), domesticated dogs—like scrub jays and non-human primates—engage in sophisticated perspective-taking (Call et al. 2003; Bräuer et al. 2004; Kaminski et al. 2009; Kaminski et al. 2013) and seem to infer what agents know (Catala et al. 2017; Cooper et al. 2003; Maginnity and Grace 2014; Topal et al. 2004). Additionally, recent work suggests that dogs can integrate their understanding of a person's perspective with other information they learn from that person. For instance, dogs are more likely to follow the pointing gesture of someone who witnessed the location of a hidden treat than of someone who is ignorant (Catala et al. 2017; Maginnity and Grace 2014) and dogs prefer to approach someone who is willing to provide information over a person who is not attending to the dog (McMahon et al. 2010), demonstrating both a sensitivity to social cues and a preference for information. In this way, domesticated dogs are a particularly promising candidate species for exploring the extent of the relationship between knowledge-perception tracking and metacognitive information-seeking in nonhuman animals.

Failures of Canine Metacognition

Are dogs able to metacognitively represent their own mental states? Surprisingly, although several studies have found that dogs may track the knowledge and perceptual access of humans (e.g., Catala et al. 2017; Cooper et al. 2003; Maginnity and Grace 2014; Marshall-Pescini et al. 2014), previous work has shown that domesticated dogs fail to metacognitively seek out information. The first study to test canine metacognition investigated whether dogs would seek out information about which of two boxes held a hidden treat (Bräuer et al. 2004). Dogs could choose a box by pressing a lever to receive the food if the reward was inside. However, before choosing, dogs could seek out information about the contents of each box by looking through a window on the opposite side of the box. This study failed to find evidence of metacognition in dogs; when dogs were ignorant of the location of the treat, they almost never looked through the windows to check which box contained the treat. Only one dog consistently looked through the windows and it did so even on trials when it had seen which box was baited.

In another investigation of canine metacognitive information-seeking, dogs had the opportunity to gain information by reorienting themselves (McMahon et al. 2010). Prior to beginning the study, experimenters trained dogs to knock over boxes in order to get treats inside. Eventually, dogs were trained that a treat was always hidden under a particular box that was marked by a single white side. Specifically, 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 to rectify their own ignorance.

Although these studies failed to find evidence of metacognitive information-seeking, dogs' performance may not reflect their underlying cognitive competence. The existing studies relied on learned associations and required dogs to engage in costly behaviors in order to information-seek. Specifically, dogs had to walk beyond the location of the treat and inhibit a previously trained behavior (i.e. knocking over boxes in McMahon et al. 2010 and pushing levers in Bräuer et al. 2004) in order to information seek. Both of these features of past experimental designs may have taxed dogs' inhibitory control, and thus led to performance issues that impeded their ability to information seek.

A New Investigation

To address some of these potential issues, we utilize a naturalistic information-seeking paradigm based on a procedure previously used with rhesus macaques (Rosati and Santos 2016).

Importantly, this new task allowed dogs to information-seek at a relatively low cost. As with rhesus macaques in Rosati and Santos (2016), dogs 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 a transparent 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 towards the possible locations of the hidden treat, therefore reducing the inhibitory control required to successfully information-seek.

In addition to investigating whether dogs show evidence of metacognitive information-seeking in a simplified task, we also examined how domestication may have affected metacognition in canines. Across domestication, dogs faced selection pressures for cognitive traits favorable for working cooperatively with humans (Hare and Tomasello 2005; Johnston et al. 2015; Topál et al. 2014), such as a sensitivity to human communicative signals (Bräuer et al. 2006; Prato-Previde and Marshall-Pescini 2014; Soproni et al. 2002; Udell et al. 2008) and a tendency to look back at humans (Miklósi et al. 2003; Passalacqua et al. 2011). These artificial selection pressures may have also resulted in the ability to track the knowledge (Catala et al. 2017; Cooper et al. 2003; Maginnity and Grace 2014; Topál et al. 2004) and goals of others (Marshall-Pescini et al. 2014). If the cognitive mechanisms underlying metacognition are truly linked to knowledge-perception tracking, then metacognitive abilities may have also developed in dogs over the course of their domestication, but not in closely-related non-domesticated canids. Thus, we would expect that non-domesticated canids, like wolves and dingoes, would be less likely to exhibit metacognitive information-seeking than dogs.

In the current study, we directly compare a population of Australian dingoes to a population of domesticated dogs. Dingoes are a close, but non-domesticated relative of domesticated dogs (Ardalan et al. 2012; Cairns and Wilton 2016; Savolainen et al. 2004; for review see Fillios and Taçon 2016 and Smith 2015). Although there have not been any direct investigations into dingo knowledge-perception tracking, dingoes are less prone to follow human social cues than dogs (Smith and Litchfield 2010), less likely to look back at familiar humans (Smith and Litchfield 2013), and generally less likely to make eye contact with familiar humans (Johnston et al. 2017). These findings suggest that, compared to dogs, dingoes are less sensitive to the social cues that are important for tracking the knowledge and perceptual access of other agents. If dingoes are less likely to metacognitively seek information than domesticated dogs, this would suggest that metacognitive abilities may have developed in dogs during their history of domestication, possibly in relation to knowledge-perception tracking.

Study 1

Methods

Dog subjects. Twenty domesticated dogs 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 (1), experimenter error (1), and camera failure (1). Subjects were pets whose guardians entered their information into our online database and volunteered for participation. Prior to 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 7 genetically pure dingoes from the Dingo Discovery Research Centre in Victoria, Australia. Nine additional dingoes were tested and excluded for not approaching the apparatus during the familiarization (2), and failure to pass the warm-ups (7). In order to participate, subjects had to be comfortable leaving their living quarters and walking on a leash to the grassy testing paddock.

Apparatus and testing setup. Subjects were allowed to approach a fence apparatus to obtain hidden food. A 0.74 m high section of fence 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 sometimes present. During some parts of the study (i.e., the information-seeking impossible trials), a bent occluder was placed in front of the center portion to block the center opening. Behind the fence there was also a second rear occluder (40” x 29.5”) that prevented subjects from seeing where the experimenter hid the treat when the front bent occluder was absent. Additionally, 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 received daily exercise. Subjects of both species began the study approximately 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 in front of the paddock’s 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 highly familiar sanctuary staff member for the dingoes.

Dogs received 1 cm cubes of Natural Balance Beef sausage as their reward throughout the study and dingoes received 1 cm pieces 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 a 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 are sensitive to the availability of information, they should approach the center of the fence only when it is unoccluded in the information-seeking possible trials and, subsequently, choose the correct side more often in information-seeking possible trials compared to 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, 5 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 in order to give the subject experience with the increased visual access they could get 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 prevent the placement of the bucket from making any noise. The experimenter then stood back 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 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 twice, 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.

If the subject put its nose behind a side of the fence, this was considered a choice of that side. “No choice” was recorded if the subject did not put its nose behind a side of the fence within thirty seconds of being released. 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 2 trials in a row. 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. This second day of testing was added with dingoes 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 which they sometimes had the opportunity to information-seek 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. Specifically, 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 thirty seconds to choose a side.

Trial type (information-seeking possible, information-seeking impossible) and treat location (right side, left side) were pseudo-randomized 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. One dingo only completed five test trials before ceasing to approach on two successive trials. All other subjects completed all eight test trials.

Coding and data analysis. The first author and an additional coder who was blind to the study's hypothesis coded information-seeking and accuracy. Information-seeking 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 record for both variables in which the subject did not choose a side within 30 seconds. Reliability was high for both variables (r = 97% for information-seeking, r = 100% for accuracy).

Statistical analyses were conducted with R statistical software (version 3.2.1, R Foundation for Statistical Computing, Vienna, Austria). Information-seeking was analyzed with a generalized linear mixed model (GLMM) coded as a binary response term (performed information-seeking = 1, did not perform information-seeking = 0). Predictors of interest were species (dog or dingo), trial number, and trial type (information-seeking possible or information-seeking impossible). The mixed models were conducted using R package ‘lme4’ (Bates et al. 2012). We first tested a null model that used only subject identity as a predictor of information-seeking, which we then compared to full models with all predictor variables and interactions. Based on the initial results of the GLMM, we conducted follow-up *t*-tests looking at information-seeking across the two different trial types (information-seeking possible vs. information-seeking impossible) for both species. Additionally, choice accuracy was analyzed with a GLMM coded as a binary response term (chose the side where the treat was hidden = 1, chose the side where the treat was not hidden = 0). Predictors of interest were species, trial number, and trial type.

Results

Our model for information-seeking revealed that subjects’ tendency to approach the center portion of the apparatus was marginally predicted by species (LRT: $x^2 = 3.5$, $p = .061$) and significantly predicted by trial type (information-seeking possible vs. impossible; LRT: $x^2 = 18.3$, $p < .001$). No other factors or interactions were significant predictors (LRT: *p*s > .176).

Given that we found main effects of both species and trial type, we conducted follow-up *t*-tests comparing performance on information-seeking possible vs. impossible trials for each species separately. First, we examined dogs’ likelihood to approach the center portion of the fence across the two trial types. Dogs were more likely to information-seek during the information-seeking possible trials when the center was open ($M = 1.00$ out of 4) compared to the information-seeking impossible trials when the center was closed ($M = .15$ out of 4), $t(19) = 4.34$, $p < .001$ (see Figure 3).

Next, we conducted follow-up *t*-tests with dingoes to investigate their information-seeking behaviors across the two trial types. We examined dingoes’ likelihood to approach the center portion of the fence across the two trial types. Dingoes, like dogs, were more likely to information-seek on trials when the center of the fence was open in the information-seeking possible trials (*M* = 1.43 out of 4) compared to trials when it was closed in the information-seeking impossible trials (*M* = .71 out of 4), *t*(6) = 2.5 , *p* = .047 (see Figure 3).

Finally, given that we saw a main effect of species in our GLMMs, we also conducted a direct comparison of how likely the two species were to information-seek across the two trial types. Dingoes were no more likely than dogs to information-seek on information-seeking possible trials, *t*(9) = .89 , *p* = .395. However, dingoes were marginally more likely than dogs to information-seek on information-seeking impossible trials, *t*(7) = 1.90 , *p* = .099. This suggests that dingoes may have been more likely to approach when the center was closed because they were trying alternative strategies of information-seeking, such as smelling, even though these strategies did not make them more accurate.

Our model for accuracy showed that subjects' tendency to choose the correct side was not significantly predicted by species, trial number, trial type, or their interactions. The full model with all predictor variables and interactions did not outperform a null model that used only subject identity as a predictor of accuracy (LRT: $x^2 = 8.67$, $p = .277$). This finding suggests that subjects did not perform more accurately in the information-seeking possible trials compared to the information-seeking impossible trials even though subjects performed more acts of information-seeking in the information-seeking possible trials.

Discussion

Our results provide the first evidence to date that canids engage in nonsocial information-seeking. Using a simplified design with minimal task demands, we found that domesticated dogs and non-domesticated dingoes delayed their search for a hidden treat in order to approach a location that could provide them with information. Crucially, subjects approached the information-seeking location significantly more often on trials when doing so would yield useful information compared to when that same behavior did not provide information.

It is particularly surprising that subjects independently sought out visual information in the current study because two prior studies suggest that domesticated dogs do not engage in this behavior (Bräuer et al. 2004; McMahon et al. 2010). However, our method was designed to give dogs and dingoes the best chance possible of demonstrating information-seeking. Unlike prior studies of canine information-seeking, subjects in the current investigation received prior 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 could see if they walked up to the center portion of the fence. In addition to lessening the task demands, the 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 in order to pass the warm-up trials, subjects had to attend to the treat while at the center of the fence and remember its 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 both the time-cost and inhibitory control required to information-seek. Therefore, this method of information-seeking presented the lowest cost of all the information-seeking behaviors required in previous studies of canine metacognition (Bräuer et al. 2004; McMahon et al. 2010).

However, it is important to note that in order to information-seek, subjects did have to inhibit their desire to immediately approach and search for the treat behind a random side of the fence. This may explain why the information-seeking exhibited in the current study was still somewhat rare in both dogs and dingoes – on average, dogs approached the center portion of the fence in 1.00 out of the four information-seeking possible trials, while dingoes approached the center in 1.43 out of four possible information-seeking trials.

While Study 1 failed to find a significant interspecies difference in information-seeking for the information-seeking possible trials, dingoes did information-seek during the information-seeking impossible trials marginally more often than dogs. This result could suggest a possible interspecies difference in olfactory metacognitive information-seeking when visual information is unavailable. Future work utilizing other modalities—such as sound or smell—may find additional evidence of metacognitive information-seeking in canids.

Even though Experiment 1 provides preliminary evidence that domesticated dogs engage in information-seeking and presents the first indication of a similar level of information-seeking in a species of wild canid, it is unclear whether this behavior reflects metacognition or simpler cognitive processes. Namely, subjects' information-seeking behaviors may be due to a general tendency to explore and information-seek in a non-metacognitive way. Non-metacognitive exploratory behavior, often referred to as "curiosity" (for a short summary see Byrne 2013) is theorized to be a general-purpose behavior in which animals explore without any obvious stimulus or reinforcement for that behavior. 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). Much like keas, dingoes and domesticated dogs may fail to represent anything about their own knowledge states or the information that they can gain by examining a location, and instead may just instinctually explore the visual affordances of an environment.

In order to gain insight into the motivation behind subjects' information-seeking, we conducted a follow-up study in which subjects already knew the location of the treat, but still had the option to information-seek. If the information-seeking in Study 1 was driven by non-metacognitive exploratory behavior, then subjects in Study 2 should information-seek regardless of whether or not they already know where the treat is hidden. However, if subjects' information-seeking is driven by metacognition, then they should information-seek more often when they do not know where the treat is hidden.

Study 2

Although both dogs and dingoes information-seek more when doing so will provide them with visual information compared to when their visual access is blocked by an occluder, it is possible that subjects are simply exploring features of the environment without any representation of their own ignorance. Study 2 investigates the possibility that the differences in information-seeking across trial types in Study 1 were not due to metacognition, but rather due to general exploratory behavior. Specifically, Study 2 established subjects' baseline levels of exploration of the unoccluded fence section when this behavior did not provide subjects with new information.

Unlike Study 1, subjects in Study 2 always had the opportunity to information-seek by approaching the unoccluded center portion of the fence. However, during half of the trials subjects already knew where the treat was hidden, making any information-seeking redundant. If canids possess metacognition, then subjects in the current study should information-seek when they do not already know the location of the treat, but should forgo information-seeking when they have prior knowledge of the treat's location. However, if subjects are instinctually drawn to explore the affordances of the environment even when doing so will provide them with no new information, then subjects in Study 2 should information-seek regardless of whether or not they have prior knowledge of the treat's location.

Methods

Dog subjects. Twenty domesticated dogs participated in this study. Dogs were tested and recruited as they were in Study 1. Twelve additional dogs were excluded for not passing the warm-ups (10), owner interference (1), and not eating the treats during the warm-ups (1). In an effort to match our dog sample to our dingo sample, we did not exclude dogs that had participated in Study 1; therefore 5 of our 20 dog subjects also participated in Study 1.

Dingo subjects. Nine genetically pure dingoes 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 (2), and failure to pass the warm-ups (7). 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 9 dingoes included in our final sample, four needed a second day of testing due to failure to approach during the familiarization phase (1), and failure to pass warm-ups trials on day 1 (3).

To achieve the maximum sample size possible, we tested dingoes in Study 2, regardless of whether or not they had participated in Study 1. In our final sample of nine dingoes, four participated in Study 1 and five did not. As described in more detail in the supplementary materials (see Supplementary Figure 1), the pattern of results that we observed remained the same regardless of whether we examine the data of all nine dingoes, or the five dingoes that participated only in Study 2.

Testing setup and design. Subjects were tested with the same apparatus and testing conditions (dogs: large testing room; dingoes: familiar outdoor paddock) used in Study 1. However, the bent occluder that was placed in front of the center portion to block the center opening in Study 1 was not included in Study 2.

All subjects participated in a familiarization phase, warm-up trials, and test trials, which were identical to Study 1 with two exceptions. First, during the familiarization phase, the front occluder was not present, therefore allowing subjects to sniff and examine the unoccluded center portion of the fence. Secondly, and most importantly, in test trials, instead of manipulating the informativeness of information-seeking, as we did in Study 1, we manipulated necessity of information-seeking by showing subjects where the treat was hidden in half of the test trials.

Specifically, during the test trials, the rear occluder was positioned such that the center portion was 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. In half of the trials, the experimenter crouched down so that she and the bucket were hidden behind the fence. She then moved the bucket behind the fence towards one of the ends of the fence so that the subject did not know on which side the bucket was hidden (ignorant trials). In the other half of the trials, the experimenter crouched down behind the fence, but kept the bucket raised above the fence so that she was hidden from the wrist down, but the bucket was fully visible to the subject. Then, the experimenter moved the bucket over the fence and around one side of the fence until it right above the ground at which point the bucket was placed down behind the fence (knowledgeable trials). 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; therefore, in all trials, the subjects could approach the center portion of the fence and gain visual information about the location of the treat. The experimenter then instructed the handler to release the subject and the subject was given thirty seconds to choose a side.

Trial type (knowledgeable vs. ignorant) and treat location (right side, left side) were pseudo-randomized 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. The exclusion criteria for the subjects were identical to Study 1.

Coding and data analysis. Using the same guidelines as in Study 1, the first author and a second coder who was blind to the study's hypothesis coded information-seeking and accuracy. No choice was recorded for both variables in which the subject did not choose a side within 30 seconds. Reliability was high for both variables (r = 99% for information-seeking, r = 100% for accuracy). As in Study 1, information-seeking was analyzed with a generalized linear mixed model (GLMM) coded as a binary response term (performed information-seeking = 1, did not perform information-seeking = 0). Predictors of interest were species (dog or dingo), trial number, and trial type (knowledgeable or ignorant). Similarly, choice accuracy was analyzed with a GLMM coded as a binary response term (chose the side where the treat was hidden = 1, chose the side where the treat was not hidden = 0). Predictors of interest were species, trial number, and trial type.

Results

Our full model of information-seeking with all predictor variables and interactions outperformed our null model that used only subject identity as a predictor of information-seeking. 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: $x^2 = 18.4$, $p < .001$). No other factors or interactions were significant predictors (LRT: *p*s > .115). According to our model, subjects were more likely to information-seek when they did not already know the location of the treat (*M* = 0.72 out of 4) compared to when subjects were knowledgeable about the location of the treat (*M* = 0.14; see Figure 4).[1] This finding suggests that subjects' information-seeking behaviors were contingent upon their own knowledge state.

Similarly, our full model for accuracy that included all predictor variables and interactions outperformed our null model that used only subject identity as a predictor of accuracy. Our model for accuracy showed that subjects' tendency to search behind the correct side of the apparatus was significantly predicted by trial type (knowledgeable vs. ignorant; LRT: $x^2 = 11.4$, $p < .001$). No other factors or interactions were significant predictors (LRT: *p*s > .251). According to our model, subjects were more likely to choose the correct side when they already knew the treat's location (*M* = 3.03 out of 4) compared to when subjects were ignorant about the treat's location (*M* = 2.24 out of 4). The significant effect of trial type on choice accuracy suggests that subjects were able to use the information given to them during the hiding presentation of the knowledgeable trials to help them to choose the correct side.

Discussion

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[1] Due to the limited availability of dingoes, some of the dingoes in our sample for Study 2 also participated in Study 1. Additionally, in an effort to make our samples comparable, we did not restrict the participation of dogs based on prior participation in Study 1. In order to make sure that those subjects that had already seen the task were not driving our observed effects, we reran our analysis of information-seeking, excluding subjects that also participated in Study 1. In this analysis, the pattern of information-seeking remained the same across trial types Therefore, the information-seeking observed in Study 2 was not driven by inclusion of non-naïve subjects (see Supplementary Figure 1).

Study 2 provides preliminary evidence for metacognitive information-seeking in domesticated dogs and non-domesticated dingoes. Both dogs and dingoes sought out information significantly more often when they did not know where the treat was hidden compared to when they had prior knowledge of the treat's location. This finding suggests that the information-seeking observed across Study 1 and Study 2 was not low-level exploratory behavior, but rather that the subjects were seeking out information to rectify their own ignorance.

Importantly, watching the placement of the bucket in the knowledgeable trials increased dingoes' accuracy when choosing which side to search compared to the ignorant trials when dogs were given no information about the location of the treat. This finding serves as manipulation check, suggesting that subjects retained the information about the location of the bucket during the short delay between seeing the bucket move behind the fence and being released.

General Discussion

Taken together, these two studies provide the first evidence that domesticated dogs and non-domesticated dingoes are able to track their own knowledge to seek out and use information to remedy their ignorance. Both dogs and dingoes performed information-seeking more often when they did not already know the location of a food reward, providing evidence that their information-seeking is contingent upon their knowledge state. Our results stand in contrast to two prior studies of canine metacognition, which failed to find evidence of information-seeking in domesticated dogs (Bräuer et al. 2004; McMahon et al. 2010). This discrepancy may reflect a difference in methodologies; while past studies required dogs to perform trained behaviors (e.g., knocking over boxes and pushing levers) and positioned the possible reward closer to subject than the information-seeking opportunities, the current studies utilized a more naturalistic foraging set-up that did not require any trained behaviors and minimized the cost of information-seeking.

Canids are not the only nonhuman animals that have exhibited significant differences in metacognitive information-seeking across different study set-ups. The use of a more naturalistic study design also generated the first evidence of spontaneous metacognitive information-seeking in rhesus macaques (Rosati and Santos 2016), whereas earlier research had only found evidence of information-seeking after extensive training (Hampton et al. 2004). Future investigations of metacognition in nonhuman animals should strive to utilize methodologies that more closely align with the types of behaviors that subjects naturally perform and the types of situations that subjects face in their daily lives. The use of more naturalistic study set-ups may help to close the gap between the performance of subjects in empirical studies and the underlying cognitive competence of nonhuman animals.

The Role of Inhibitory Control

Although our findings provide the first evidence of canine metacognition, it is important to note that information-seeking was a relatively infrequent behavior. For reference, across both studies, our dog samples had 155 trials in which they did not already know the location of the treat and they could engage in information-seeking because the center was unoccluded[2], but only performed information-seeking in 32 of those trials. The most likely explanation for the rarity of information-seeking in the current study is insufficient inhibitory control. In order to perform information-seeking, 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 utilized in

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[2] Specifically, we summed the number of information-seeking possible trials in Study 1 and the number of ignorant trials in Study 2.

our studies presented the lowest cost of the all the information-seeking behaviors required in previous studies of canine metacognition (Bräuer et al. 2004; McMahon et al. 2010), in order to information-seek, subjects did still have to exercise some inhibitory control in order to information-seek. Therefore, because our task required some limited inhibitory control, 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. Alternatively, a study design that increased the cost of an incorrect choice could lead to more instances of information-seeking as well. In the current studies, if a subject searched behind the wrong side of the fence, the subject did not receive the treat, but the next trial began almost immediately, giving the subject another opportunity to earn a reward. Introducing a delay for an incorrect choice would increase the cost of an incorrect choice, therefore increasing the value of information.

An Alternative Account of Information-seeking and Future Directions

Although many psychologists accept the information-seeking paradigm as a test of metacognitive ability, Carruthers (2008) offers a deflationary explanation of the behaviors required to pass this test. According to this account, information-seeking responses in non-human animals are not caused by representations of knowledge states, but rather emerge from conflicting desires to look for the hidden treat in two locations at once. This conflict of desires initiates a suite of general information-seeking responses such as walking forward and moving the head from side to side. These responses may cause the subject to look as though it is using metacognitive information-seeking, but these behaviors are best categorized as reflexive and are not done to amend a specific lack of knowledge.

In the context of the current studies, this non-metacognitive account would argue that the dogs approach the center portion of the apparatus in information-seeking possible trials in Study

1 and in ignorant trials in Study 2 not because they are intentionally seeking information about the location of the treat, but because they are executing a low-level reflexive response to conflicting desires. Although the current study may be subject to this critique, if this conflict-driven response is truly as low-level and non-specific as Carruthers describes it, then subjects should have also shown this behavior in the information-seeking impossible trials in Study 1. Therefore, because an indiscriminate approach response was not observed across information-seeking possible and information-seeking impossible trials, this suggests that the information-seeking behaviors exhibited in information-seeking possible trials in Study 1 and in ignorant trials in Study 2 trials were not simply rote responses to conflicting desires.

However, one could argue that the rote conflict-resolution information-seeking response is not so low-level as to cause dogs to approach barriers. Therefore, the subjects would only approach the center portion of the apparatus on information-seeking possible trials in Study 1, leading to a pattern of results that would coincide with our prediction of what metacognition would look like across our studies. In order to more fully refute this deflationary account, follow-up studies that require more novel information-seeking behaviors are required. Several non-human primate studies have elicited instances of more situation-specific information-seeking behaviors that are difficult to explain away as simple, instinctive responses to conflicting desires (e.g., Kornell et al. 2007; Beran et al. 2013). In addition, Call and Carpenter (2001) reported that on a subset of trials, chimpanzees would reach into one tube without checking its contents after they had looked into the other tube and found it to be empty. These spontaneous exclusion inferences made upon seeing the empty tube suggest that the chimpanzees are using some representation of the knowledge that they lack, rather than simply looking until they see food. Similar studies with canids that require more novel instances of information-seeking or that can more closely track subjects' looking behaviors while information-seeking will help to provide addition evidence that the representations underlying information-seeking in dogs and dingoes are truly metacognitive.

Future work on canine metacognition could also benefit from exploring whether dogs and other canids behave metacognitively in other contexts. For example, given that domesticated dogs are more adept at using social information than they are at utilizing physical information in treat findings tasks (Bräuer et al. 2006; Udell et al. 2008), this species may have even more success at information-seeking in social contexts. One human study that tested social information-seeking found novel evidence of metacognition in 20-month-old human children by measuring their tendency to selectively look back at their parents in order to gain information that they lacked (Goupil et al. 2016). Dogs naturally perform a similar behavior; they spontaneously look back at their guardians when confronted with an unsolvable task (e.g., Miklósi et al. 2003; Passalacqua et al. 2011). Therefore, a procedure measuring dogs' tendency to look back may provide new insight into canine information-seeking. Future studies should investigate whether domesticated dogs selectively look back in cases when they are ignorant in order to examine if looking back is performed metacognitively[3].

The Comparative Study of Metacognition and Knowledge-Perception Tracking

Taken together with existing comparative investigations of metacognitive information-seeking, the current study suggests a possible evolutionary link between metacognition and knowledge-perception tracking. Scrub jays, humans, and several non-human primates—heretofore, the only animals that succeed on tests of metacognitive information-seeking (Beran et al. 2013; Call 2010; Call and Carpenter 2001; Goupil et al. 2016; Marsh and MacDonald 2012;

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[3] Anecdotally, we did not see many instances of looking back in the current study. However, the design of our experiment was not developed to test this behavior directly.

Rosati and Santos 2016; Watanabe and Clayton 2016)—are known to exhibit knowledge-perception tracking (humans: Buttelmann et al. 2009; Kovács et al. 2010; Onishi and Baillargeon 2005; non-human primates: Flombaum and Santos 2005; Hare et al. 2001; Kaminski et al. 2008; Marticorena et al. 2011; Santos et al. 2006; Schmelz et al. 2011; scrub jays: Dally et al. 2004; Dally et al. 2005; Dally et al. 2006; Emery and Clayton 2001). Similarly, domesticated dogs behave in ways that are consistent with the ability to track the knowledge and perceptual states of humans (Bräuer et al. 2004; Call et al. 2003; Catala et al. 2017; Cooper et al. 2003; Kaminski et al. 2009; Kaminski et al. 2013; Maginnity and Grace 2014; Marshall-Pescini et al. 2014; Topal et al. 2004, although see Bräuer 2014 for a critical discussion of what mechanisms underlie these behaviors), and act upon their own knowledge in a metacognitive way. This interesting overlap provides support to the prediction originating from human psychology that, to some extent, species that can think about and act upon the knowledge of others should show similar aptitude when thinking about and acting on their own knowledge and perceptual access.

Additionally, the overlap between metacognition and knowledge-perception tracking in animals also makes exciting untested predictions about other species that should exhibit these abilities. For example, cleaner fish (*Labroides dimidiatus*) are able to track what their partner can see in order to strategically "cheat" without being punished (Drayton et al. in prep). If the ability to track perceptual access relies on the same mechanisms that underpin metacognition, cleaner fish may be an unexpected source of metacognitive information-seeking. On the other hand, we would expect the converse to be true for dingoes. Because the dingoes can metacognitively represent their own knowledge state, this theory would predict that dingoes will also exhibit knowledge-perception tracking. Although dingoes are less likely to follow human social cues than dogs (Smith and Litchfield 2010), less likely to look back at familiar humans (Smith and

Litchfield 2013), and generally less likely to make eye contact with familiar humans (Johnston et al. 2017), there have not been any direct investigations into dingo knowledge-perception tracking. Dingoes may nonetheless be able to track the knowledge and perceptual access of conspecifics. Additionally, this theory would predict that rats would not demonstrate knowledge-perception tracking because they fail tests of metacognitive information-seeking (Roberts et al. 2012).

Originally, we hypothesized that the artificial selection pressures faced by domesticated dogs may have resulted in their ability to track the knowledge (Catala et al. 2017; Cooper et al. 2003; Maginnity and Grace 2014; Topál et al. 2004) and goals (Marshall-Pescini et al. 2014) of other agents and that therefore closely-related non-domesticated canids would not exhibit these abilities. However, the presence of metacognition in a species of non-domesticated canid presents the intriguing possibility that even non-domesticated canids perform knowledge-perception tracking. Further investigations into knowledge-perception tracking in dingoes will not only elucidate the relationship between metacognition and knowledge-perception tracking, but also the effects of domestication on social cognitive abilities.

Conclusion

The findings of the current study highlight open questions about the relationship between metacognitive abilities and knowledge-perception tracking in nonhuman animals. While our studies provide the first evidence to date that domesticated dogs do perform metacognitive information-seeking and presents the first evidence of a similar level of information-seeking in a species of wild canid, it is highly unlikely that comparative psychology has found the extent of metacognitive abilities that exist in non-human animals. Although investigations in comparative psychology demonstrate that metacognition is not a uniquely human trait, further research is required to understand what social and environment factors facilitate the emergence of metacognitive abilities across taxa and how they may relate to the ability to represent the mental states of others.

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Author Contributions

AR completed Study 1 as part of two directed research credits in the fall of 2016 and the spring of 2017. Study 2 was done during the spring of 2018 in completion of the senior thesis requirement. AR designed the study with the guidance of AJ and LS; AR collected all of the dog data. AR assisted AJ in the collection of the dingo data for Study 1 and AJ collected dingo data for Study 2. AR and AJ analyzed the data together and produced the figures. AR wrote the manuscript and received feedback from AJ and LS.

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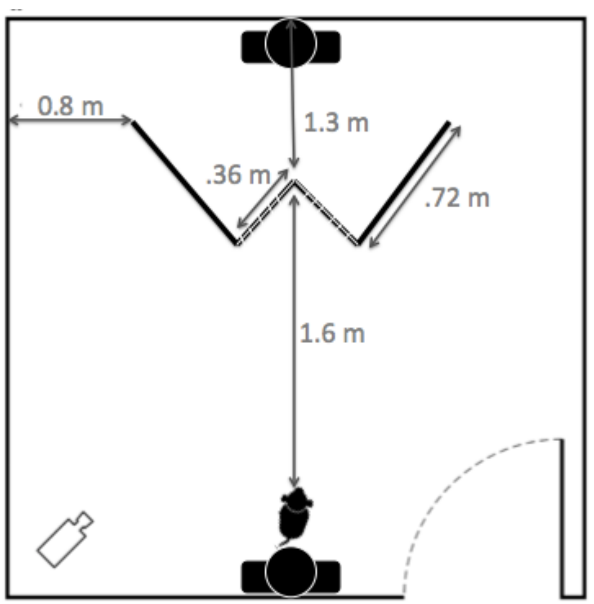
1a.



1b.

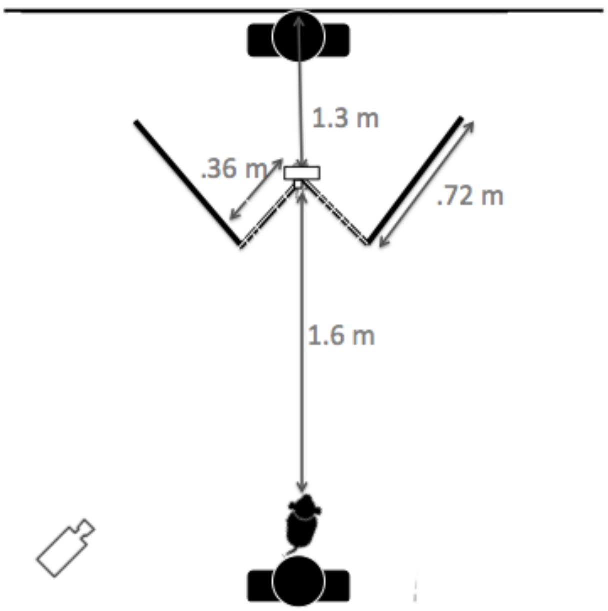
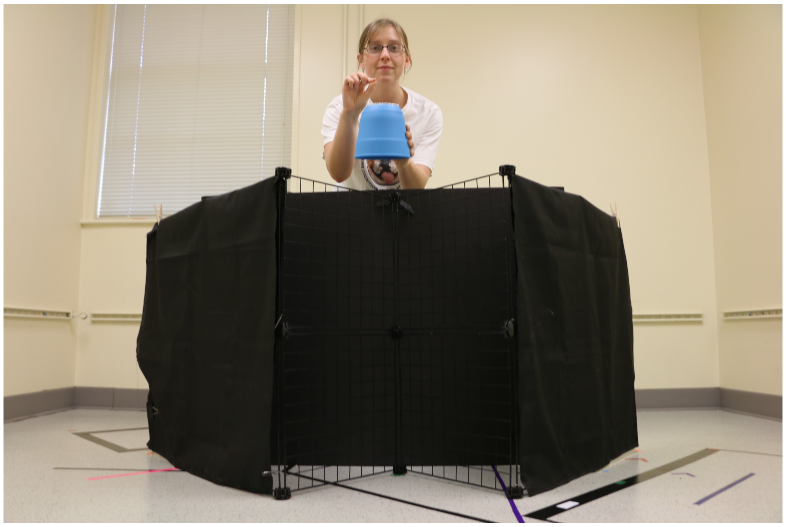


Fig. 1a and 1b Experimental set up for dogs (**Fig. 1a**) and dingoes (**Fig. 1b**). Subjects in both populations were positioned 2.2 m away from the center of the fence. Dogs were filmed from one camera overhead camera angle, while the dingoes were filmed from two camera angles, one to the left of the handler to capture accuracy and one positioned on top of the fence in order to capture information-seeking. 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.

2a.



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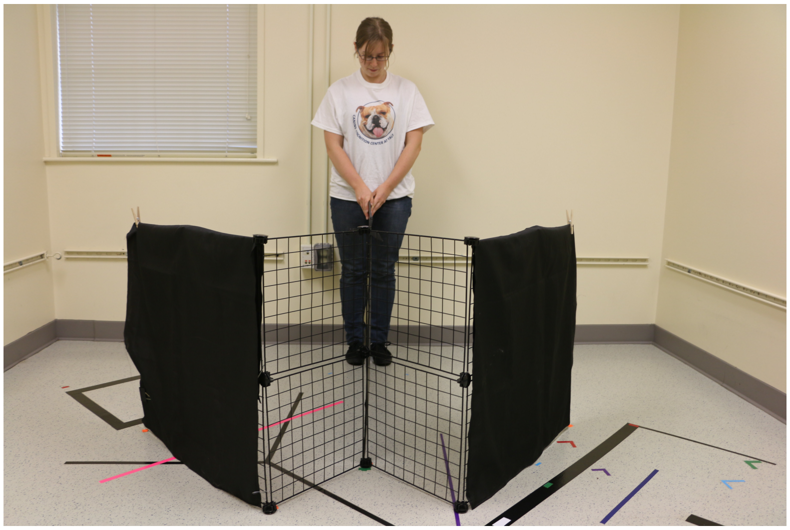

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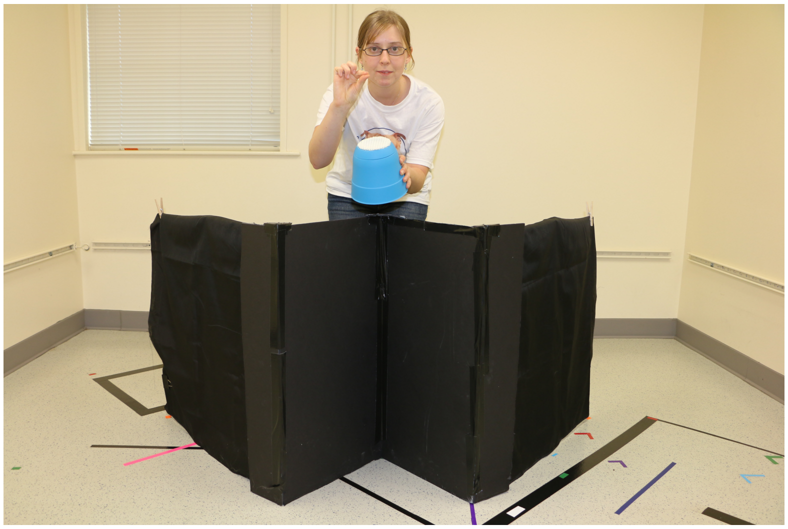


Fig. 2 During the warm-up trials, the front bent occluder was absent. At the beginning of each warm-up trial, the experimenter made eye contact with the subject, and then visibly placed the treat on the bucket (**Fig. 2a**). Then, she bent and hid the treat behind one of the two sides of the fence. The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

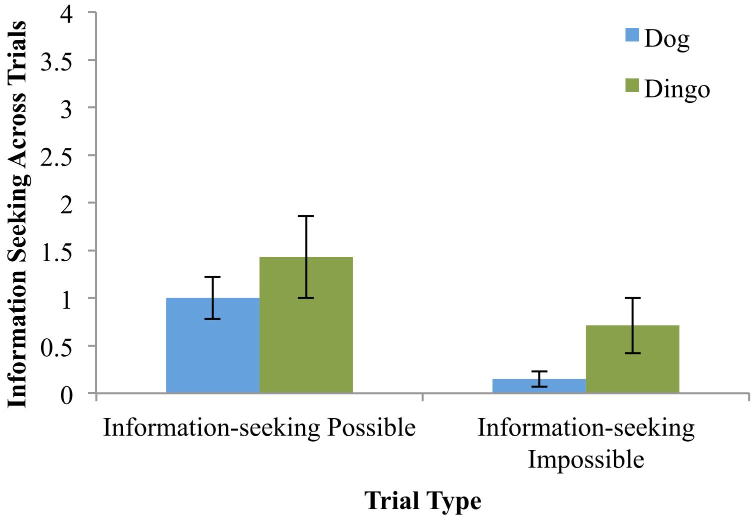


Fig. 3 Average number of trials in which subjects in Study 1 engaged in information-seeking broken down by trial type and species. Error bars indicate standard error.

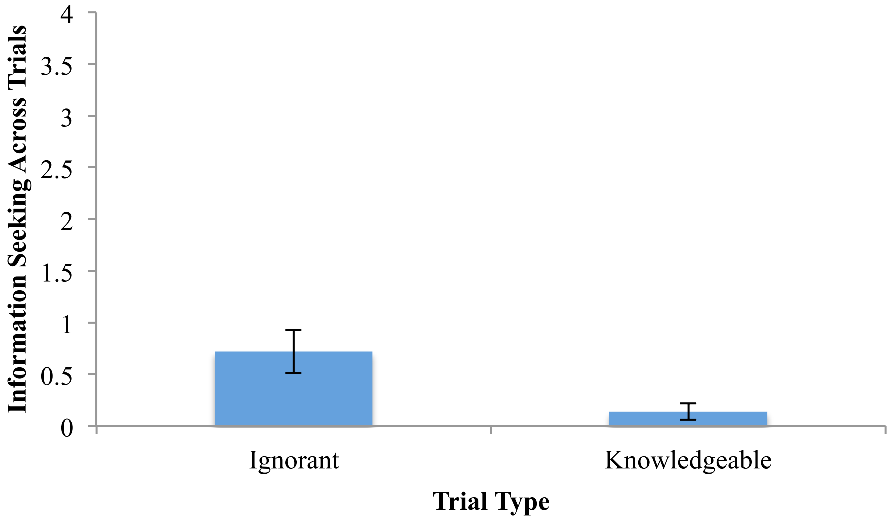


Fig. 4 Average number of trials in which subjects in Study 2 engaged in information-seeking broken down by trial type. Error bars indicate standard error.

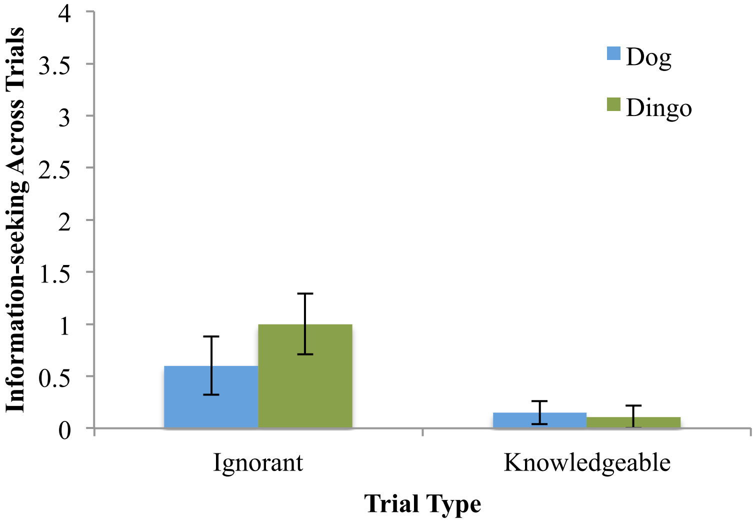
Name	**Species/Breed**	**Sex**	**Age**
Adina	Labrador Retriever	F	5 y
Archie	Yorkshire Terrier	M	1 y
Artie	Pembroke Welsh Corgi	M	2 y
Denver	Cocker Spaniel/Poodle Mix	M	11 y
Dora	Pembroke Welsh Corgi	F	7 y
Duncan	Labrador Retriever	M	4 y
Gracie	Collie/Labrador Retriever Mix	F	5 y
Harley	Terrier Mix	M	7 y
Harley	Beagle/Rottweiler Mix	M	6 y
Henry Jones	Dachshund/Jack Russell Mix	M	6 y
Isis	Rottweiler/Australian Shepherd Mix	F	5 y
Maggie	Labrador Retriever	F	6 y
Miles	Terrier Mix	M	8 y
Nutmeg	Labrador Retriever/Whippet Mix	F	4 y
Patty	Shetland Sheepdog/Border Collie Mix	F	2 y
Penelope Rose	Miniature Poodle	F	6 m
Ryder	Border Collie	M	5 y
Sadie	Labrador Retriever Mix	F	3 y
Sophia Maria	Corgi/Beagle Mix	F	7 y
Zeke	Labrador Retriever	M	3 y
Ernie	Dingo	M	7 y
Keke	Dingo	F	11 m
Kimmi	Dingo	F	2 y
Polly	Dingo	F	2 y
Saxon	Dingo	M	7 y
Snapple	Dingo	M	6 y
Wandji	Dingo	F	1 y

Supplementary Table 1. List of subjects, indicating species, owner-reported breed, sex (**M**ale/**F**emale), and age in years (y) or months (m) for Study 1.

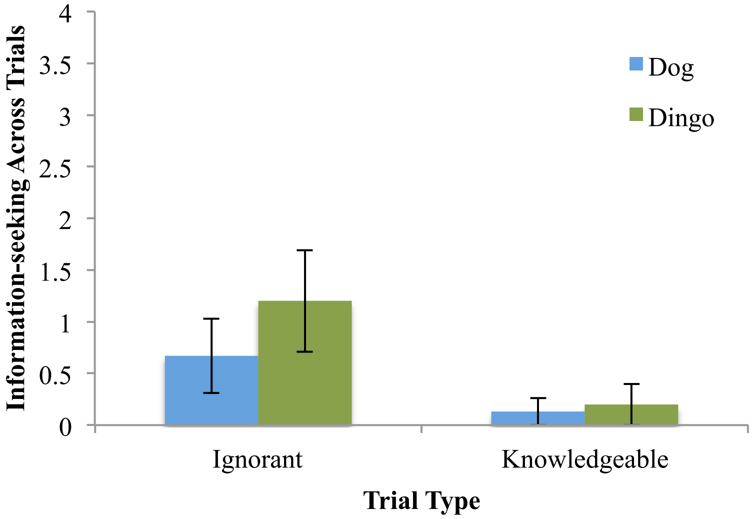
Name	**Species/Breed**	**Sex**	**Age**
Angus	Golden Retriever	M	10 y
Charlie	Boston Terrier/Chihuahua Mix	M	2 y
Chelsea	Australian Shepherd	F	7 y
Cooper	Labrador Retriever	M	5 y
Dallas	Cocker Spaniel	F	5 y
Elwood	Pembroke Welsh Corgi	M	2 y
Freja	Labrador Retriever/Whippet Mix	F	3 y
Giorgio	Havanese	M	12 y
Gobi	Labrador Retriever/Poodle Mix	M	4 y
Gracie	Border Collie/Labrador Retriever Mix	F	6 y
Hershey	Shuh tzu/Havanese Mix	M	7 y
Liam	American Staffordshire Terrier	M	7 y
Markl	Pomeranian	F	4 y
Oscar	Vizsla/Shuh tzu Mix	M	3 y
Sadie	Labrador Retriever Mix	F	4 y
Sidney	Norfolk Terrier	F	3 y
Tito	American Staffordshire Terrier	M	2 y
Topper	Labrador Retriever Mix	F	2 y
Winston	German Shepherd	M	1 y
Zoë	Labrador Retriever Mix	F	7 y
Aussie	Dingo	F	7 y
Berri	Dingo	M	7 y
Clyde	Dingo	M	7 m
Crikey	Dingo	M	1 y
Delilah	Dingo	F	7 m
Ebony	Dingo	F	7 m
Ernie	Dingo	M	8 y
Kimmi	Dingo	F	3 y
Saxon	Dingo	M	8 y

Supplementary Table 2. List of subjects, indicating species, owner-reported breed, sex (**M**ale/**F**emale), and age in years (y) or months (m) for Study 2.

SF1a.



SF1b.



Supplementary Figure 1. Average number of trials in which all subjects in Study 2 engaged in information-seeking broken down by trial type and species (**SF1a**) and the average number of trials in which subjects in Study 2 engaged in information-seeking broken down by trial type and species, excluding subjects that also participated in Study 1 (**SF1b**). Error bars indicate standard error.