

Knower–guesser differentiation in ravens: others' viewpoints matter

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Differentiating between individuals with different knowledge states is an important step in child development and has been considered as a hallmark in human evolution. Recently, primates and corvids have been reported to pass knower–guesser tasks, raising the possibility of mental attribution skills in non-human animals. Yet, it has been difficult to distinguish ‘mind-reading’ from behaviour-reading alternatives, specifically the use of behavioural cues and/or the application of associatively learned rules. Here, I show that ravens (*Corvus corax*) observing an experimenter hiding food are capable of predicting the behaviour of bystanders that had been visible at both, none or just one of two caching events. Manipulating the competitors' visual field independently of the view of the test-subject resulted in an instant drop in performance, whereas controls for behavioural cues had no such effect. These findings indicate that ravens not only remember whom they have seen at caching but also take into account that the other's view was blocked. Notably, it does not suffice for the birds to associate specific competitors with specific caches. These results support the idea that certain socio-ecological conditions may select for similar cognitive abilities in distantly related species and that some birds have evolved analogous precursors to a human theory-of-mind.

Keywords: raven; *Corvus corax*; knowledge attribution; perspective; competitive food retrieval; caching

1. INTRODUCTION

Predicting individuals' behaviour by integrating observable features from their current and past behaviours is a key element of social interactions [1,2] and provides the basis for any form of cooperation, competition and culture in human and non-human societies [3]. The level of sophistication non-human animals may reach in predicting others' behaviours has been linked to the degree of complexity in the species' social life (e.g. [4,5]). However, it is unclear to what extent this integration of information requires mental representations of others' mental contents [6–9].

The debate has recently gained momentum by the finding that, when tested in an ecologically meaningful context, some animals perform accurately in versions of the knower–guesser paradigm, i.e. a social problem-solving task considered to demand an understanding of others' perception. Specifically, non-human primates (chimpanzees *Pan troglodytes* [10,11], rhesus macaques *Macaca mulatta* [12]) and corvids (western scrub jays *Aphelocoma californica* [13,14] and ravens *Corvus corax* [15]) have been shown to instantly discriminate between potential competitors that differed in their visual access to food and/or in their experience of witnessing the hiding of food. Consequently, the results have been discussed as supportive evidence for an element of mental state attribution in non-human animals (concept ‘see’) and as a precursor step to a human-like understanding of others' minds [16,17]. Critics, however, have pointed

out that even the most recent studies lack the power to distinguish this mental interpretation from alternatives based on the assessment of observable cues: test subjects could have picked up on perceptual features during the experiment (e.g. subtle behaviours such as eye/head/body orientation, expression of emotions) and, by integrating this information with their knowledge about others' behaviour in competition for food or food caches, they could have acted according to rules like ‘do not go after food if a dominant has oriented towards it’ or ‘re-cache food in a site that is different from the one where it was cached when the competitor was present’ [18]. While studies have tried to counter this argument by controlling and/or estimating the animals' reliance on perceptual cues during experiments [11,14,19], the objection of an associative interpretation has yet remained untested.

Here I present new experiments on ravens (*Corvus corax*), exploiting the birds' tendency to remember and pilfer food caches they have seen others make. In the wild and in captivity, ravens readily compete against individuals that store food and also against individuals that could potentially pilfer caches [20,21], by flexibly adjusting when and where they approach observed caches [15,22]. This offers the possibility of testing bystanders at caching about their awareness of previous perception, and probably knowledge, of other bystanders. Furthermore, as scavengers, ravens show a natural tendency to attend to the behaviour of other species that are in possession of food, eventually trying to get hold of it themselves [23]. Hence, I used a human experimenter as storer, controlling the number and location of food caches being made in the presence of raven bystanders whose view of the caching area was manipulated by opaque curtains.

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Unlike previous studies [15,22], individuals varied not only in whether or not they acted as observers but when exactly they had visual access to the caching room, affecting their competitiveness for pilfering particular caches. Furthermore, the human experimenter positioned the cover material of caches in a way that allowed the competitor, but not the focal bird, to see both food pieces at testing. Thus, the competitor's motivational and knowledge state at testing was controlled irrespective of its treatment during caching (what it has/has not seen) and independently of the perception of the focal subject at testing (what it can and cannot see). I first addressed the ravens' ability to apply different behavioural responses to potential competitors with a varying degree of information about cache locations and then examined whether ravens base their pilfering decisions on a learned rule.

2. EXPERIMENT 1

(a) Hypothesis and predictions

Ravens that had witnessed a human experimenter making two food caches were confronted with a conspecific that had been visually present at both, none or just one of the caching events and thus would probably possess full, no or partial information about the cache locations. While fully informed competitors would pose a high risk of pilfering either cache, partially informed competitors would pose a risk to specific caches only, i.e. those they had seen being made. Accordingly, focal birds should hurry to pilfer the caches when confronted with fully informed conspecifics compared with non-informed subjects, but carefully select between caches when confronted with partially informed conspecifics, i.e. go for cache 1 with observer of cache 1 and for cache 2 with observer of cache 2.

(b) Methods

Ten hand-reared ravens (five males and five females) served as subjects (see also the electronic supplementary material). They were marked with coloured rings for individual identification and kept in one social group in a 240 m² aviary complex situated in the Cumberland Wildpark Grünau, Austria. The aviary consisted of four sections, arranged around a wooden observation hut [24]. Tests were carried out in section D, which was composed of five compartments: one central room (16 m²) and four observation rooms (each 6 m²; figure 1*a,b*). Birds that did not participate in a given trial were temporarily confined to sections from where visual access to D was blocked by wooden walls. When no tests were scheduled, birds were allowed to roam throughout the complex. They had ad libitum access to water and were fed twice a day with meat, milk-products and fruit.

For a trial, three birds were individually positioned in the observation compartments of section D. Two of these birds, the potential competitors for pilfering, were in adjacent compartments either on the right or left side of D; the focal subject was in one of the compartments on the opposite side (figure 1*a*). The focal subject had full visual access to the central room through a wire-mesh door and so did the competitor who was facing the focal subject. The door of the second competitor, in contrast, was covered by an opaque curtain, preventing him from seeing what happened in the room and the

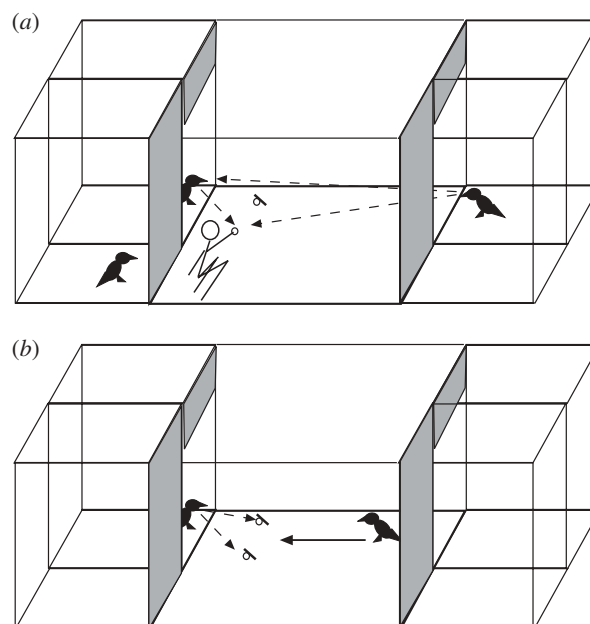


Figure 1. Sketch of the standard experimental set-up during caching and during testing. (a) E caches food in the presence of three ravens, two potential competitors on the left and the focal subject on the right. The opaque curtains on the doors of the back compartments are raised, allowing one competitor and the focal subject to witness the caching and to see one another (lines of sight are symbolized by arrows with dashed lines); the view of the other competitor towards the caching room remains blocked. (b) At testing, the focal subject heads in the direction of the caches (symbolized by arrow with solid line) while the competitor is still restrained in its compartment. The skewed positioning of the covers on the caches allows the competitor to see either of the 'hidden' food pieces (symbolized by arrows with dashed lines).

focal subject from seeing this competitor during caching. All three birds, however, were in full acoustical contact while a human experimenter made two caches. The focal subject stayed in its position during both caching events and thus was considered fully informed about the cache locations because it could observe both caches being made. Depending on the experimental protocol, the individual facing the focal subject stayed in its compartment during both caching events (stay-treatment) or switched position with the second competitor after the first cache has been made (switch-treatment). In the former case, one competitor (observer of both caches, OB) was fully informed about the cache location, whereas the second one (non-observer, NO) remained naive. In the latter case, both competitors were partially informed about the cache locations, observer 1 (O1) about cache 1 and observer 2 (O2) about cache 2. To reduce the likelihood of learning across trials to a minimum, birds received only two trials per condition presented in a randomized order and carried out over the course of a six months period (see also electronic supplementary material).

A human experimenter (E) was used to hide the food (two pieces of cheese, approx. 5 g per piece) to precisely determine the locations of the caches, the timing and order of caching, and the way of covering the cached food with substrate. The two food caches were made on the floor of the central room, 1 m from each other but

equidistant to the focal subject. They were generally closer to the competitor's side (approx. 2 m) than to the focal subject's side (approx. 4 m) to boost the latter's motivation to get the food first. To make a cache, E knelt down and dug a small hole (approx. 5 cm) into the substrate of the floor, which was made of gravel, small stones and wood chips. The experimenter made sure that both ravens with visual access to the central room were oriented towards the cache location (e.g. by calling their names and showing the food) before he put one piece of food into the hole and covered it with a flat stone (approx. $7 \times 10 \times 4$ cm). Stones of this type were scattered in the central room before the onset of the experiment. Importantly, E positioned the stone in a way that allowed a bird on the competitor's side, but not the focal bird, seeing (parts of) the hidden food peeping out beneath the cover.

After caching, the view of the focal subject was temporarily blocked by a pulled-down curtain. Depending on the protocol, one of the possible competitors, OB or NO in the stay-treatment and O1 or O2 in the switch-treatment, respectively, was placed in the compartment opposite the focal bird. The other potential competitor was rewarded with a small treat and released to the rest of the group (outside section D). The curtain in front of the focal bird was lifted and 15 s later, the door to the central room was opened so that the focal subject could enter the central room and go for one of the caches (figure 1b). After the focal bird had made its choice by touching the cover of a cache and/or retrieving the food, the door to the second compartment was opened, giving the competitor bird the chance to pilfer a cache as well. The crucial period was the head start of the focal subject, during which we measured the two core parameters: time (in s) between entering the room and pilfering a cache and which of the caches were chosen first.

The behaviour of the focal bird was recorded by a video camera from outside the central room and all data were analysed from tape. A second person who was blind to the hypothesis tested scored 25 per cent of the videos to assess inter-observer reliability. Concordance between raters was 99 per cent. I used Wilcoxon signed-ranks tests (calculated by hand owing to the small sample size) to compare the individuals' mean latency to pilfer caches between conditions OB and NO (stay-treatment) and O1 and O2 (switch-treatment). Similarly, I used the sign test on the birds' mean proportion of choosing cache 1 to compare their preference for a given cache between conditions OB and NO (stay-treatment) and O1 and O2 (switch treatment). Finally, I used binomial statistics to test whether the birds chose cache 1 (with O1) and cache 2 (with O2) above chance. In those tests only, results are given one-tailed because of the specific predictions. In all other analyses, results are given two-tailed. Alpha was set at 0.05.

(c) Results and discussion

As expected, ravens were quicker in pilfering the human-made caches when facing a fully informed competitor that had been visible at both caching events (OB) than when facing an uninformed competitor that had not been visible during caching (NO; Wilcoxon test: $n = 8$ (ties = 2), $T^+ = 33.5$, $p = 0.023$; figure 2a). However,

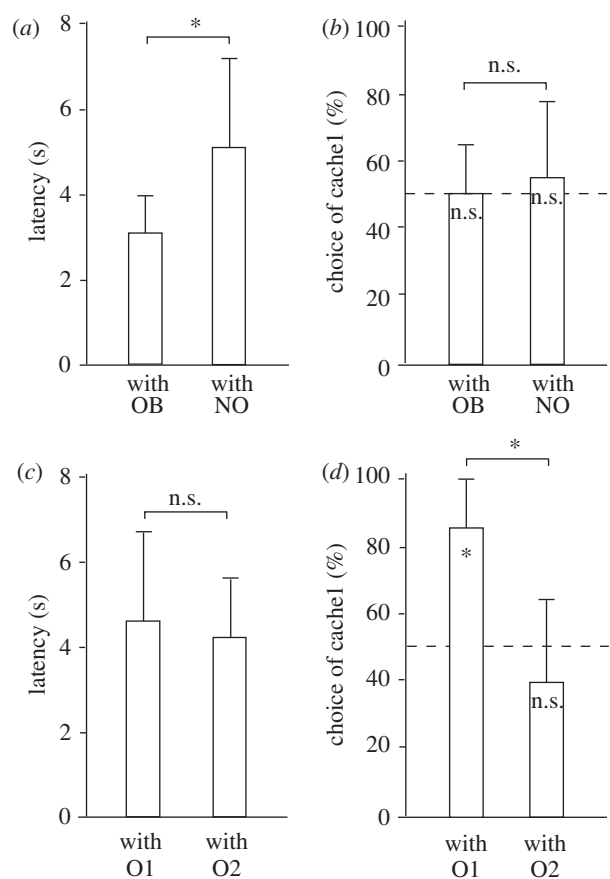


Figure 2. Pilfering speed and -selectivity (mean \pm s.e.m.) in the (a,b) stay-treatment and (c,d) switch-treatment. (a) Latency to pilfer caches with OB and NO, (b) Proportion of choosing cache 1 with OB and NO, (c) Latency to pilfer caches with O1 and O2, (d) Proportion of choosing cache 1 with O1 and O2. * $p < 0.05$, n.s., not significant; above bracket: comparison between conditions, within bar: comparison to chance (dashed lines).

birds did not show a preference for choosing a particular cache first during these tests in the stay-treatment (Sign test: $n = 5$ (ties = 5), $S = 3/5$, $p = 1$; figure 2b). Interestingly, ravens behaved differently in the switch treatment. When confronted with partially informed competitors, observer of cache 1 (O1) or observer of cache 2 (O2), they did not show a significant difference in pilfering latency ($n = 7$ (ties = 3), $T^+ = 15$, $p = 0.938$; figure 2c), but a significant difference in cache choice ($n = 6$ (ties = 4), $S = 6/6$, $p = 0.032$; figure 2d). Specifically, when facing O1, ravens were likely to choose cache 1 (eight out of 10 birds in the first trial, binomial, one-tailed: $p = 0.055$; nine out of 10 birds in second trial, binomial, one-tailed: $p = 0.011$). When facing O2, their choice of cache 2 was not significantly above chance (six out of 10 birds in first and second trials, binomial, one-tailed: $p = 0.377$). Note that the time between observing the cache and pilfering was shorter when birds were tested with O2 than with O1, potentially interfering with their performance (see electronic supplementary material for details).

Taken together, the findings support the assumption that ravens employ different behavioural tactics (hurry up or choose) according to the information their competitors had during caching. Unlike in previous studies [15,22], the birds' discrimination cannot be based on

the others' movements, since competitors were allowed to enter the room only after the focal subject had pilfered one of the caches. Furthermore, unlike in most other studies (e.g. [10,11,14,15]), motivational differences between different types of competitors can be ruled out because all but the focal subject had visual access to the 'hidden' food at testing. Thus, focal birds probably remembered who was visually present at which caching event and predicted the others' likelihood of pilfering the human-made caches accordingly. The failure of significantly matching O2 to cache 2 might indicate that the ravens' decisions were prone to certain errors, i.e. a primacy effect (see electronic supplementary material). The possibility of a primacy effect, however, could be seen as an additional support for the interpretation that the birds were relying on memory rather than on the others' subtle behavioural cues to decide upon a given tactic. Hence, the question remains how ravens represent knowledge about others, i.e. if they base their decisions on associations of observable features from others' past behaviours only or if they recognize the others' perceptual access and/or knowledge state.

3. EXPERIMENT 2

(a) *Hypothesis and predictions*

Experiment 2 examined the possibility that ravens differentiate between competitors according to learned rules without any understanding of the others' perception, i.e. 'compete with those that could be seen at the time of caching' as opposed to 'compete with those that have seen the caching'. As in experiment 1, birds were confronted with two potential competitors each of which were visible during one of the two caching events (O1 and O2). However, in half of the trials, a specially prepared curtain blocked the competitors' view towards the caches but not the view of the focal subject towards the competitors. If ravens were merely associating the others' visual presence with subsequent pilferage, their choice behaviour in the test should not be affected by the curtain at caching (because the focal subjects could always see the competitor) and they should consistently go for cache 1 with O1 and for cache 2 with O2. Alternatively, if ravens were responding to the others' perception, they should distinguish between conditions (because the competitors' view could be blocked by the curtain) and selectively pilfer caches only when the curtain had been pulled up during caching.

(b) *Methods*

For experiment 2, a wooden perch was installed in each of the observation compartments (1.5 m above ground; 2 m distance to the door to the central room) and all ravens were trained to wait on this to receive a small reward from the experimenter (piece of dry cat food). In addition, birds were habituated to a modified plastic curtain (195 × 85 cm) that could cover the wire-mesh doors to the central room. In each curtain, a rectangle of 35 × 50 cm was cut out 25 cm below the upper end, creating a transparent window in the otherwise opaque material. If the curtain was pulled down, the window allowed a bird sitting on the perch to see the focal bird sitting on the ground in the opposite compartment and, conversely, allowed the focal bird to see the competitor sitting on the



Figure 3. Focal subject's view of the competitor in the uninformed condition of experiment 2. Although the competitor's view towards caches made close to the door is blocked by the curtain, the competitor itself (sitting on the perch behind the window of the pulled down curtain) is in full view of the focal subject during caching.

perch (figure 3). However, the pulled-down curtain blocked the view of the competitor (sitting on the perch) towards the central room, specifically towards caches that were made less than 1 m next to the door. Thus, by pulling down the curtain with the cut-out window, the competitor's view and probable knowledge about cache locations could be manipulated *without* affecting the competitor's visibility to the focal subject during caching. Note that all birds had ample experience with visual barriers such as wooden walls and plastic curtains, which they routinely used to hide themselves for caching during daily feeding [21]. They thus might have experienced conspecifics that were visible during caching but, depending on their relative position, unable to see the food being cached. However, birds were never trained on any relationship between optical barriers, seeing and knowing in an experimental setting.

The observation phase consisted of the switch-treatment, with O1 being present during the making of cache 1 and O2 during the making of cache 2. In the informed condition, the curtain remained pulled up during observation, resulting in two partially informed competitors. However, in the uninformed condition, the curtain with the window was pulled down during observation, resulting in competitors that were seen at caching by the focal subject but were ignorant about the exact cache locations. To ensure that

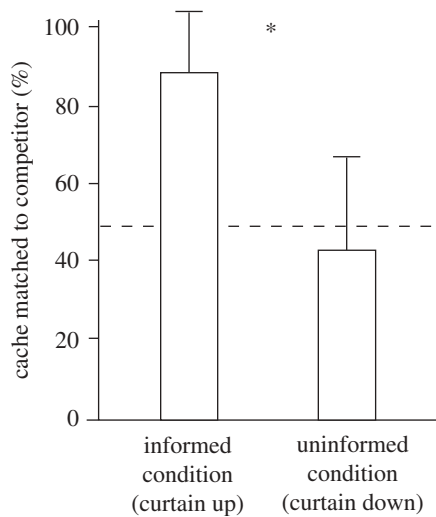


Figure 4. Selectively in pilfering caches, depicted as mean (\pm s.e.m.) proportion of matching caches 1 and 2 to O1 and O2, respectively, in the competitor-informed and -uninformed condition (i.e. curtain's position at caching). Dashed line represents chance level. * $p < 0.05$.

competitors were oriented in the direction of the food in either condition, E called their names before he started caching and, if necessary, during caching (see electronic supplementary material for a detailed description and a *post hoc* analysis of the competitors' behaviour during observation).

In either condition, the curtain was pulled up during testing and the competitor was allowed to sit on the ground of the observation compartment, directly next to the wire mesh door. Thus, focal subjects experienced the same situation as in experiment 1 during pilfering. Note that now the inclined placement of the covers allowed competitors to see both pieces of food. The crucial parameter measured was which cache the focal subjects chose first.

(c) Results and discussion

The ravens significantly differed in their selectivity of pilfering caches (% caches matched to competitors) between conditions (sign test: $n = 7$, $S = 7/7$, $p = 0.016$, figure 4). In the uninformed condition (when the curtain had been pulled down during caching), they did not show a preference for choosing a particular cache when confronted with O1 or O2 at testing ($n = 7$, $S = 4/7$, $p = 1$). However, in the informed condition (when the curtain had been pulled up during caching), they matched the caches to competitors ($n = 7$, $S = 7/7$, $p = 0.016$). Specifically, 6 out of 7 birds chose cache 1 when confronted with observer 1 (binomial, one-tailed: $p = 0.063$) and seven out of seven birds chose cache 2 when confronted with observer 2 (binomial, one-tailed: $p = 0.008$) in their first trials. Note that the curtain was always pulled up during testing so that its mere physical appearance cannot account for the results. Furthermore, all observers could see food in both caches at testing, i.e. their motivational and knowledge state was controlled irrespective of their experience during caching (what they had/had not seen). Ravens could still have picked up on differences in the others' visual behaviour during observation. However, analysis of the videos revealed that competitors

were always visually oriented towards E during caching, suggesting that observers' were behaving similarly in the informed and uninformed condition. Although we cannot exclude the possibility that ravens were using very subtle cues such as how long competitors looked in a given direction, the same birds completely failed in parallel experiments designed to explicitly test for their ability to use such looking cues given by conspecifics for finding hidden food [25].

Importantly, the current results do not support the assumption that ravens differentiate between competitors by applying a learned rule about who is seeing during caching. On the contrary, they indicate that ravens may take into account that the others' view can be *different* from their own, and informing the individual or not. Since we cannot rule out the use of subtle behavioural cues during observation, we cannot draw a firm conclusion about the underlying mechanism: the findings are consistent with the idea of recognising the other's perception and/or knowledge state, but also with the ability to memorize the other's line of sight.

4. GENERAL DISCUSSION

Taken together, the results of the two experiments support the assumption that ravens reach a high level of sophistication in predicting others' behaviour in competition for hidden food, adjusting their pilfering behaviour on the basis of their own and others' perceptual access at caching. These results corroborate previous findings on ravens from naturalistic experimental settings [15,20], indicating that spatial factors like the distance between food caches (more than 3 m in the previous studies, 1 m in the current setting) and the position of potential competitors (next to each other or facing each other) are of limited importance for the ravens' performance (but see results of chimpanzees, [19]). Furthermore, the results are in line with those obtained for western scrub jays [13,14], supporting the idea that some corvids may possess a 'who-component' of episodic-like memory and, possibly, psychological attribution skills. Finally, the results mirror the findings in great apes [11], providing a further hint for a convergent cognitive evolution between primates and corvids [26]. Still, to my knowledge, the highly controlled set-up and the explicit empirical elimination of a learned rule about who is visible at caching, are novel to the field. Hence, this study is one of the first to demonstrate that non-human animals can encode information that is 'unique' to the perspective of the competitor and the very first to show that it does not suffice for the test subjects to associate specific competitors with specific cache sites.

But do the results provide evidence for the ability of a bird to represent others' mental states? As with most studies on animal complex cognition, it is difficult to make such a claim on the basis of a limited set of experiments. What seems to be clear is that the ravens' behaviour in the current experiments was based on some mental representations about others. They apparently recalled past experiences from daily life, namely the behaviour of others when their view was/was not obstructed at caching and the behaviour of others when their view was different from their own view. Similarly, they might have recalled subtle differences in the

competitors' observing behaviour in the two conditions of the experiment. In either case the ravens need to have a sophisticated understanding of visual barriers, being capable of geometrically judging the other's view relative to their own. In the primate literature, such an ability has been referred to as '1 $\frac{1}{2}$ -order intentionality' [27] or 'third-kind explanation' [28] and in humans, the same ability is often considered as a pre-step for, or even as an element of, a theory of mind [6,29].

Support for the interpretation that ravens 'understand' others' perspectives, in the sense that they can follow others' lines of sight, comes from studies on gaze following involving a visual barrier positioned half-way between the cue-giver and the test subject. Similar to great apes [30], ravens are not distracted by the barrier but alter their position in order to look *behind* it after seeing a human experimenter looking there [31]. Interestingly, young ravens do not pass this barrier task nor do they use barriers to hide from others' view during caching until their first fall (6–8 months of age; [24,32]). Since ravens readily co-orient visually with others at earlier stages of development (2–3 months of age; [24]) and also rapidly learn about others' behaviour throughout their entire juvenile period (2 years; [33]), the speedy exploitation of barriers probably reflects some cognitive maturation. I thus speculate that young ravens reach a developmental stage at which they come to integrate associatively learned contingencies at a higher cognitive level, possibly reducing the complexity of social interactions by positing abstract 'intervening variables' that code for (some of) the others' mental states such as 'seeing' or 'knowing' [34]. On the basis of the current findings, I conclude that subadult ravens have already reached a stage in which they are capable of generalizing information about the others' visual behaviours (most probably acquired during daily life) to a novel, experimentally induced, situation.

The ravens' ability to precisely predict the others' behaviour and intentions during foraging goes along with a profound control of their own intentions, exemplified in the selective withholding of information and misleading attempts [21,22]. However, how far ravens come in applying their knowledge about different perspectives and/or knowledge states in a context other than food competition remains to be tested in future studies. The existing data support the idea that competition over hidden food selects for sophisticated mental representations about others in some corvids and that ravens are among those few non-human animals that might have evolved analogous precursors to a human theory of mind.

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