

An integrative approach to the study of 'theory-of-mind'-like abilities in ravens

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Abstract Due to new impressive results in primates and even non-primates such as dogs, dolphins, and corvids, the question whether or not non-human animals possess elements of a 'Theory of Mind' (ToM) has recently gained momentum. Indeed, attempts have been put forward to test species with ecologically relevant tasks, leading to the development of new test paradigms, such as the competitive conspecific or ignorant helper, and to run controls for behaviour-based alternatives. I here argue for strengthening this integrative approach and present preliminary data from our model system, the common raven *Corvus corax*. Based on observations of tactical manoeuvres of wild and captive ravens during foraging, we have tested the ability of hand-raised birds to differentiate between conspecifics that do and do not know about cache locations because they have or have not been able to see the caches being made. In addition to this version of guesser-knower experiments, we have been investigating (i) if the birds' performance is affected by the manipulation of observable cues, (ii) how likely the performance can be achieved by attending to observable cues, (iii) how flexibly birds can apply their skills across contexts, (iv) how the skills develop during ontogeny and (v) how they are affected by experience. The potential implications of incorporating tests for behavioural cueing and learning as well as the issues of ontogeny and flexibility to studies on ToM are discussed.

ToM in non-humans: a matter of methods or wishful thinking?

The ability to reason about others' mental states, i.e. the understanding that the behaviour of animate beings is guided by perceptions, attentions, intentions, and beliefs, has been considered as a hallmark in the evolution of mankind (e.g. Whiten 1991; Carruthers & Smith 1996). Possessing a 'Theory of Mind' (ToM, Premack & Woodruff 1978) may improve the

accuracy of predicting others' manoeuvres and adds a new quality in social interactions as it allows for role taking in cooperation, perspective taking in communication and in social learning, as well as intentional deception (Byrne & Whiten 1988; Tomasello & Call 1997). Interestingly, human children do not express the entire range of ToM-skills by a particular time of development but stepwise improve their abilities within their first years of life (e.g. Baron-Cohen et al. 1985; Charman et al. 2000). Such kind of development may indicate that a 'full-blown' ToM in humans does not represent one single mechanism but is composed of a set of skills (Stone & Gerrans 2006, see Leslie et al 2004 for a different view) some of which may be shared with our primate relatives (Tomasello et al. 2003; but see Povinelli & Vonk 2003).

Recent findings in apes, in particular

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chimpanzees *Pan troglodydes*, support this view: individuals seem to be capable of judging what others can and cannot see (Hare et al. 2000), respectively have and have not seen (Hare et al. 2001), respond to differences in the attentional state (Povinelli et al. 2003; Itakura 2004), follow others' gaze around visual barriers (Tomasello et al. 1999), distinguish accidental from intentional actions (Call & Tomasello 1998), and are capable of imitation (Whiten 1998), withholding information and misleading (Menzel 1973, Hirata & Matsuzawa 2001). In addition, they show clear evidence for mirror self-recognition (Gallup et al. 1995). Still, the performance of apes appears to be context-dependent and limited to particular test designs (e.g. competition vs. cooperation, Hare 2001; learning by apprenticeship vs. teaching, Matsuzawa et al. 2006). In this way, they hardly differ from monkeys such as capuchins *Cebus sp.* and macaques *Macaca sp.* that may show limitations in some ToM-related tasks (e.g. acquisition of tool-use by imitation, Visalberghi & Fragaszy 1990; understanding perception and attributing knowledge to conspecifics, Cheney & Seyfarth 1990; Kummer et al. 1996; Hare et al. 2003) but seem to do well with others (e.g. gaze following, Anderson & Mitchell 1999; Ferrari et al. 2000; understanding perception and distinguishing between human guessers and knowers, Kuroshima et al. 2002, 2003; Flombaum & Santos 2005; tactically deceiving others, Fujita et al. 2002).

Indeed, not only primates but also other mammalian taxa and even some birds show skills that may relate to building blocks of ToM. Domestic dogs *Canis familiaris*, for instance, differentiate between attentional states of humans (Gácsi et al. 2004; Schwab & Huber 2006), respond to human-given gaze cues in object-choice situations (Miklósi et al. 1998; Hare et al. 2002) and selectively communicate to ignorant rather than knowledgeable owners about the location of favoured items (Virányi et al. 2006). Similarly, bottlenose dolphins *Tursiops sp.* are capable of comprehending human pointing signals (Tschudin et al. 2001) and are able imitators (Herman 2002). Domestic pigs *Sus scrofa* and corvids, in contrast, have been

described to outwit competitors for food by withholding information (Bugnyar & Kotrschal 2002; Dally et al. 2005) and/or misleading attempts (Held et al. 2000, 2002; Bugnyar & Kotrschal 2004).

Notably, all of these species face a complex social life with strong affiliate bonds between particular individuals (kin, alliances, friend-/owner-relations) and/or strict dominance relations and fierce competition for resources (food, mates). In addition, all of these taxonomic groups have relatively large brains (Dunbar 1998; Emery & Clayton 2004). These characteristics raise the possibility that ToM-like skills could have evolved as a cognitive adaptation to specific socio-ecological problems, e.g. competitive foraging for enclosed or hidden food (Call 2001) and communication for forms of cooperation (Miklosi et al. 2003). Alternatively, selection could have acted on a refinement of responsiveness to others' behavioural cues that are associated with mental states such as seeing or knowing (e.g. presence of eyes, others' head orientation, emotional involvement; Heyes 1998). Hence, a socially complex environment could be responsible for both, the shaping of *existing* cognitive mechanisms (i.e. attending and learning about others' behaviour) *and* the cognitive break through of understanding (some of) others' mental states. The critical point is to distinguish which species/taxonomic group has, in evolutionary terms, opted for which of these scenarios.

Most, if not all, ToM-related studies on non-human animals can be potentially explained with attending to observables such as presence/absence of individuals or parts of their body (i.e. head, eyes), orientation of those body parts (towards/away from a target), or motivational states such as the involvement/disinvolvement in a task. Consequently, it may be due to our human ability of reasoning about mental states, that we are inclined to re-interpret sophisticated socio-cognitive skills of non-human animals in mental terms (Povinelli & Giambrone 1999). While this argumentation has its very right, putting it to the extreme may be counter-productive. Assuming that we are trapped in the fallacy to re-interpret behaviour-

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based mechanisms in mental terms, we may run into the problem where to draw the line (i.e. which type of performance *can* qualify as indication for a ToM?) not only in studies on non-human animals but also in studies on human infants and people with disorders.

I here argue for strengthening the idea of an integrated approach to the study of ToM-like skills in non-human animals. Similar to the research conducted on humans, we need to understand (i) when animals of a particular species show which types of skills, (ii) how flexibly they can apply those skills across contexts, (iii) if, and how much of, their performance is affected by the manipulation of observable cues, (iv) how likely the performance can be achieved by (learning to) attending to such cues, (v) how the skills develop during ontogeny and (vi) how they are affected by experience. In recent years, much improvement has been made in respect to some of these questions (e.g. i, iii) whereas others have, to my knowledge, been widely neglected (e.g. ii, iv, v). However, only the whole picture may allow us to understand what type of 'ToM' may be present in non-human animals, if there are differences between species, and whether or not any skills of non-human animals may be regarded as a precursor to a human ToM at all.

In the following, I present an overview of our ongoing research on social cognition in ravens, which in many points relates to the possibility of attributing mental states. According to the proposed integrated approach, we aim at testing individuals with ecologically relevant tasks and in different (i.e. more than one) contexts. Furthermore, we attempt to control for behavioural cueing and learning possibilities during (ToM-)studies but also test for the likelihood of attending to these cues and for learning in separate experiments. Finally, we address developmental issues and possible effects of play on the use of skills in juveniles and in adults.

Why ravens?

Recently, the interest in the bird family Corvidae (ravens, crows, magpies and jays) has gained momentum since some of its members

demonstrate intellectual skills that are in many domains comparable to monkeys and apes (Emery & Clayton 2004). A possible convergent cognitive evolution between corvids and primates would have important implications for our understanding of mental state attribution and elements of ToM because it allows for investigating these abilities as socio-ecological adaptations and *independent* of phylogeny. However, compared to primates, cognitive research on corvids is still in its infancy (Emery 2006) and only few species have been studied in detail, observationally and experimentally, in the lab and in the field (Marzluff & Balda 1992; Balda et al. 1996).

Common ravens *Corvus corax* have attracted humans' attention since ancient times, resulting in numerous stories in mythology and in a wealth of anecdotes in the scientific literature (Heinrich 1989). In the past 25 years, their social behaviour has been investigated intensively and experimentally (Heinrich 1999; Heinrich & Bugnyar 2007), revealing a complex social life with individuals forming partner-, kin- and friendship relations and a foraging biology that features high levels of cooperation, high levels of competition and the hiding of food for later consumption.

Ravens are basically opportunists that have specialized to live on the food other animals kill. This scavenging life-style pits them into constant interactions with predators (e.g. wolves, bears, humans) and with conspecifics that may be advantageous for diluting danger and gaining access to defended food (Marzluff & Heinrich 1991; Stahler et al. 2002), but also act as fierce competitors (Bugnyar & Kotrschal 2002b). Presumably as a consequence, ravens hardly consume food during crowd-foraging at carcasses but carry off loads of food for caching (Fig. 1) until the source is depleted. Caches are usually scattered at a moderate distance to the feeding site and revisited within hours (up to a few days) by remembering their exact locations (Heinrich & Pepper 1998). However, ravens tend to feed not only out of their own caches but also out of caches they have seen others make. This spatial memory for observed caches appears to be present in a



Figure 1. Raven with food in its throat pouch. It may just have pilfered the cache of another raven and/or is about to cache the food in the snow.

number of corvids (Bednekoff & Balda 1996a, b; Emery & Clayton 2001); in ravens, it is essential for efficiently finding and pilfering the caches of conspecifics (Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002a) which is a regularly used foraging technique, particularly for subordinate birds (Bugnyar & Kotrschal

2002b).

Due to the relatively high threat of pilfering, storing ravens could be expected to show counter-tactics to reduce the cache loss to conspecifics. Indeed, birds not only attempt to physically avoid others for caching (by leaving the commonly used feeding site; Heinrich & Pepper 1998) but sensitively respond to the *visual* presence of conspecifics (Bugnyar & Heinrich 2003). Depending on the situation (e.g. whether potential competitors appear in sight at the beginning or at the end of the caching), they may speed up caching (i.e. reduce the time of covering the cache with surrounding substrate), increase the camouflaging (i.e. prolong the time of covering with substrate, even leave the cache-site to get more/better cover material), interrupt caching and/or recover the food or refrain from caching at all (Tab. 1). Most interestingly, storers may even try to hide behind visual obstacles (e.g. wooden walls; Bugnyar & Kotrschal 2002a; Bugnyar & Heinrich 2003) or they make 'false' caches

Table 1. Summary of manoeuvres observed in wild and captive ravens during food caching and pilfering.

Role	Manoeuvre	Description
Storer	Leave others	Fly off the feeding site with food in the beak and/or throat pouch for caching away from conspecifics, with actual distance to others varying according to environmental conditions and number of ravens around
	Interrupt caching	Interrupt or stop caching when <i>visually</i> confronted with conspecifics
	Recover food	Recover food for later re-caching when others come <i>near</i> cache site
	Hide from view	Cache behind obstacles that obstruct the others' view
	Make false caches	Engage in caching behaviour without leaving the food inside the cache and/or cache non-edible objects while in the possession of food
	Defend caches	Return to caches and aggressively defend them against approaching conspecifics
	Retrieve caches	Return to caches and quickly recover the food before others arrive at the cache
Pilferer	Observe from distance	Do not approach the cache site while the storer is in the process of caching, but orient/reposition in a way that allows them full visual access to the cache site
	Delay approach	Do not approach the cache site as long as storer is nearby (ca. < 3 m distance)
	Interrupt pilfering	Stop approaching the cache and leave the site for later coming back in response to storer's re-appearance and/or defensive behaviour
	Misleading	Engage in searching at 'non-cache' sites when confronted with the storer
	Speed up pilfering	Outpace other potential pilferers by quickly going for the cache

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(Heinrich 1999). Further, they may aggressively defend their caches and/or quickly retrieve the food before a nearing dominant bird can gain access to it (Bugnyar & Kotrschal 2002a).

Potential pilferers, on the other hand, have been described to observe storers from distance and usually refrain from approaching the cache site until a storer has left (Tab. 1). Moreover, when storers attempt guarding the caches, potential pilferers may engage in apparent search at non-cache sites and/or leave for later coming back (Bugnyar & Kotrschal 2002a). However, in the wild and in captivity, ravens have also been found to compete among one another for pilfering caches (Bugnyar & Kotrschal 2002b), so that the timing when to

start a pilfer attempt may be crucial not only in respect to avoid eliciting the defence of storers but also in respect to outrace other bystanders for being at the cache first.

Taken together, the social context of food caching appears to be cognitively challenging. During caching and for pilfering the others' caches, ravens engage in sophisticated social manoeuvres that seemingly exploit the others' perception and intentions: storers act as if to avoid being seen by others and pilferers act as to conceal their intention and even attribute knowledge to fellow pilferers. Thus, understanding the mental states of others *could* give individuals an edge in outwitting conspecifics for caches and in maximizing their share.

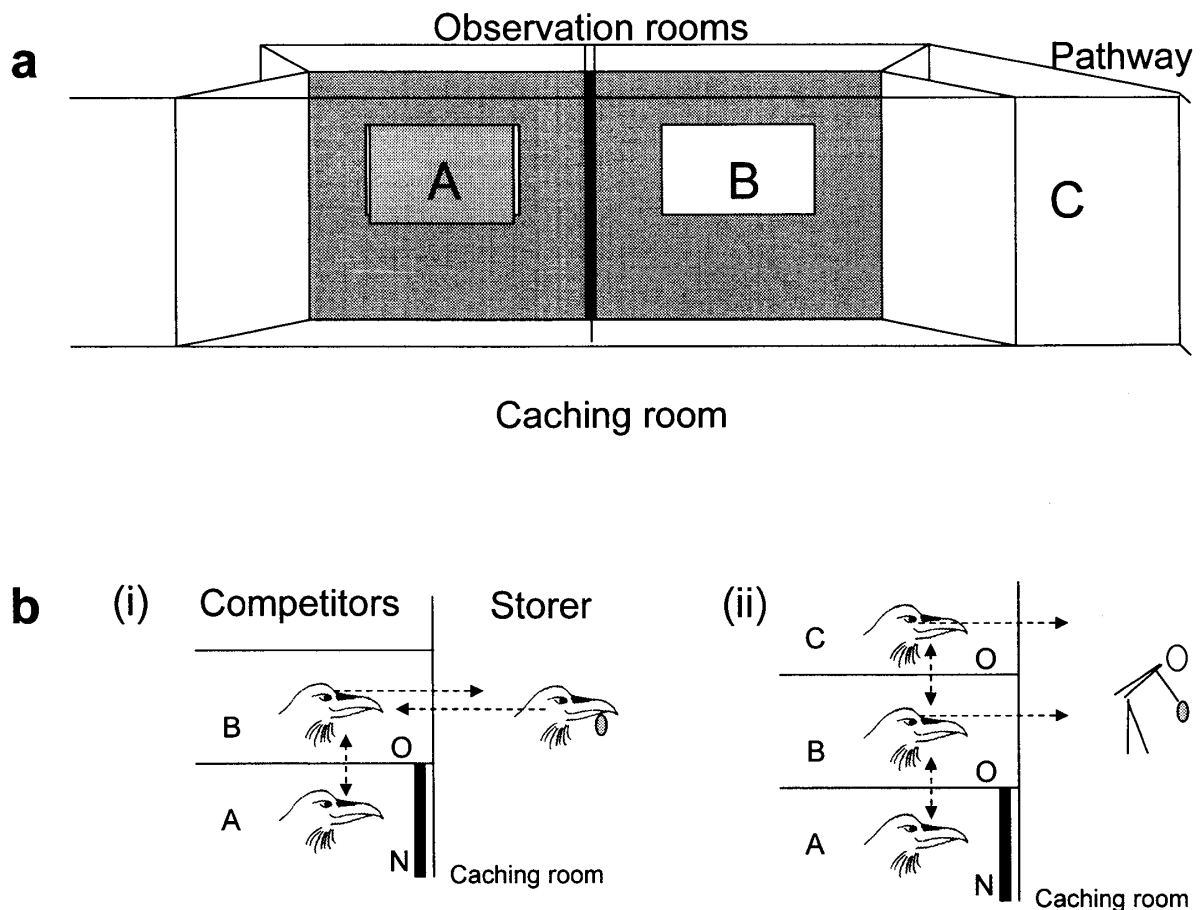


Figure 2. (a) Sketch of the experimental set-up in the studies of Bugnyar & Heinrich (2005, 2006), showing the storer's view of the observation rooms (A, B) and the connecting pathway (C) that could hold potential competitors for pilfer trials. The window towards A (and B) could be covered by an opaque curtain. Grey areas represent wooden walls; all other partitions were made of wire-mesh. (b) Sketch of the positions of ravens (O=observer, NO=non-observer) during caching trials when the focus in subsequent pilfer trials was (i) on the storer or (ii) on the bystander. Arrows with broken lines symbolize visual access. Black bar next to non-observer symbolizes the pulled-down curtain.

Testing ToM in ravens: guesser-knower experiments

To investigate the possibility for mental state attribution in ravens, we conducted a series of experiments with tame birds ($n=7$, $n=13$) that were hand-raised for this purpose and kept in social groups at the University of Vermont, USA, and at the Konrad Lorenz Forschungsstelle Grünau, University of Vienna, Austria. The principal logic of the tests was to manipulate the view of potential pilferers at caching and subsequently set (i) storers and (ii) observers of the caching in competition with those individuals that were also likely knowledgeable (previous observer) or ignorant (previous non-observer) about cache locations. Control of what ravens can or cannot see at caching was achieved by placing birds in rooms with a big transparent window that could be covered by opaque curtains (Fig. 2).

(i) Response of storers to conspecifics that had or had not 'seen' the caching

Ravens that had previously cached preferred food in the presence of two potential competitors, one that had and that had not had visual access to the caching room, were more likely to recover their caches when confronted with former observers than when confronted with former non-observers (Bugnyar & Heinrich 2005). Comparison with a baseline-condition (in

which storers were allowed to return to the caching room in private) revealed that this difference was due suppression of recovery behaviour when the birds were together with non-observers rather than to an increase of recovery behaviour with observers. Behavioural cues of the competitors such as the timing of approach, a direct or indirect approach to the cache sites, and little or much searching behaviour at non-cache sites were not reliable predictors for the storers' differentiation, since observers performed statistically indifferent from non-observers in each of those parameters in the tests with storers. Interestingly, observers did not show any delay, indirect approach to the cache or searching at non-cache sites when they were tested in private or, to control for effects of the mere presence of dominants, together with knowledgeable bystanders (Bugnyar & Heinrich 2006).

(ii) Response of observers to conspecifics that had or had not 'seen' the caching

Ravens that had witnessed a human experimenter hiding one piece of food in a 100-m²-room differentiated between competitors that also had visual access to the room at the time of caching and those that had not (Bugnyar & Heinrich 2005). Specifically, they directly flew to the cache when confronted with another observer (independently of its relative domi-

Table 2. Behavioural manoeuvres of ravens in guesser-knower experiments depending on the pairing with knowledgeable or ignorant conspecifics of high or low dominance rank. All behaviours are described in relation to baseline condition, in which birds were allowed to enter the caching room in private.

Focal subject	Competitors				
	Storer	Knower		Guesser	
		dominant	subordinate	dominant	subordinate
Storer	—	Suppress retrieval	Defend and/or Retrieve	Mislead if coming close	Defend if coming close
Knower dominant	Pilfer (no apparent response to other)	—	Speed up pilfering	—	Pilfer (no apparent response to other)
Knower subordinate	Delay and/or Mislead	Speed up pilfering	—	Delay pilfering	—

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nance rank) but delayed approaching the cache when together with a dominant non-observer (that could potentially displace them while digging for the food). Unlike to the behaviour ravens showed with (dominant) storers, birds did not engage in search activities at non-cache sites with non-observers but simply perched near the cache and waited for the dominant to move away from the cache site and/or to engage in non-foraging activities like preening or singing (Tab. 2).

Taken together, in both tests ravens discriminated between competitors whose view was and was not obstructed at caching and behaved as if they were knowledgeable and ignorant about cache locations. The fact that birds showed this performance also as bystanders (i.e. without being involved in the actual caching) discards the possibility that their decision was based solely on their own personal view (what they could and could not see at caching). Still, orienting on behavioural cues such as the others' approach behaviour could potentially explain the differentiation. Interestingly, the ravens seemed to be aware that their own behaviour could influence the others' disposition to defend or pilfer caches, as subordinate observers behaved differently when tested in private or with competitors. Only in the latter case, they opted for counter-tactics of providing no information (with dominant non-observer) or false information (with storer).

(iii) Ongoing experiments: controls for behavioural cueing and associative learning

Based on these encouraging results, we have been conducting a series of follow-up experiments on bystanders, aiming at replicating and extending findings in a rigorously controlled test-environment and confronting birds with probe trials that require them to infer cache-pilferage. Preliminary results indicate that ravens are capable of differentiating not only between observers and non-observers but also between observers that had visual access to the making of different caches. Moreover, their decisions appear to be unaffected by various controls for using behavioural cues and are still

accurate when required to infer pilferage of particular caches (i.e. in the absence of any conspecific at the time of testing). Finally, we are in the progress of investigating whether or not ravens base their differentiation between knowledgeable and ignorant conspecifics on learned rules such as 'compete with those conspecifics for pilfering that you have seen at the time of caching'. Preliminary results suggest that birds do not automatically go for caches that have been made in the visual presence of conspecifics, as would be predicted by such an associative account.

Testing for behavioural cueing: How likely can a skill be explained without a ToM?

ToM-experiments on non-human animals generally build on the logic of minimizing the possibility of using observable cues. However, the intrinsic problem with this approach is proving the 0-hypothesis, i.e. that no behavioural cues have been used (Povinelli & Giambrone 1999; Povinelli & Vonk 2003). Theoretically, experiments expanding on paradigms that are based on the logic of self/other mapping (triangulation) may be suited to avoid this problem (Heyes 1998). An alternative way may be to circumvent the problem and to determine the likelihood of behavioural cueing by actually testing for the use of observables in set-ups similar to those of the original ToM-studies.

This latter approach has been applied to ravens in a series of experiments, using an object choice paradigm (Schloegl et al., submitted). Naive individuals were allowed to search for food hidden in one of two cups after they had experienced a conspecific and/or human experimenter (=informed model) directing its head and eyes towards the baited cup. In addition to head- and eye-orientation of the informed model, birds could also orient on the other's position (sitting next to one of the 'caches' or between 'caches') and thus show local enhancement. Surprisingly, none of the ravens came to reliably use behavioural or position cues by knowledgeable individuals for guiding their search for hidden food within a total of 180 trials. These findings stand in stark

contrast to those of the guesser-knower experiments, in which the same birds instantly chose the caches that could have been observed by the individual present at testing.

Building blocks of ToM: Flexible use across contexts?

Based on the findings from the series of guesser-knower experiments, we may conclude that ravens can recall whom *they* have and have not seen at the time of caching and whether or not the *others'* view has been obstructed at caching. This information appears to be integrated with information about the competitors' role at caching (storer or bystander) and their relative dominance status. Altogether, this allows an accurate prediction of the others' behaviour and a high flexibility in performing tactical manoeuvres (e.g. speed up or delay pilfering, directly or indirectly approach cache, prefer one cache over the other, search at non-cache sites, etc.; Tab. 2). Hence, the high level of sophistication in interactions with conspecifics during food caching may indeed be linked with the ravens' ability of judging the others' view.

Interestingly, ravens also show some understanding of the others' view in experiments that do not directly relate to the food-caching context. When confronted with a human experimenter looking behind an opaque wall, they readily relocate themselves in a way that would allow them to look behind the visual barrier as well (Bugnyar et al. 2004). Thus, like apes and 1½ years-human infants (Butterworth 1991; Tomasello et al. 1999, Okamoto et al. 2002), ravens are capable of tracking the others line of sight geometrically around obstacles. Although this ability does not require an understanding of the others' perception (concept see), it has been considered as a pre-step or element in the development of a human ToM (Byrne & Whiten 1992; Charman et al. 2000).

The abilities to inhibit intentions and to understand that others can be manipulated by social means have been suggested as two further building blocks of a ToM, specifically for outwitting others to gain access to resources (Guzeldere et al. 2002). The performance of

ravens during food caching and for pilfering, strongly suggests that they possess these skills (see above; Bugnyar & Heinrich 2006). Moreover, a case study on tactical deception, in which one raven repeatedly leads a dominant bird away from food in a social foraging experiment (Bugnyar & Kotrschal 2004), indicates that ravens are capable of applying their deceptive skills in different foraging modes. The flexible use of food calls (e.g. production or suppression when faced with dominants; Heinrich & Marzluff 1991; Bugnyar et al. 2001) may be another hint in this direction. However, it is important to stress that none of these examples provides evidence for a ToM *per se*, because each of them can be explained by attending to observables and thus by understanding others as 'doers'. Still, if we assume ravens, based on the guesser-knower experiments, being capable of some elements of a ToM, then we would *expect* them to flexibly use this skill and show tactical manoeuvres in various situations — which appears to be the case.

Ontogeny and Experience

Given that the development of ToM in human children is probably one of the best studied fields in psychology (Perner 1991; Baron-Cohen 1995; Gergely & Csibra 2003; Tomasello et al. 2003), surprisingly little is known about the ontogeny of ToM-like skills in non-human animals (but see Matsuzawa et al. 2006), with most studies concerning the responsiveness to others' gaze. Young chimpanzees *Pan troglodytes* show the ability to follow an experimenter's gaze outside their visual field later in development than inside their visual field (Okamoto et al. 2002) and they may not reach the ability to stop following repeatedly given looks that lead to nothing of interest before late infancy (Tomasello et al. 2001). Likewise, ravens are capable of following others' gaze into distant space at an early stage of development (shortly after fledging) whereas tracking the others' gaze geometrically behind barriers does not appear to be possible before their first fall, which corresponds roughly to the time of total independence from their parents (Bugnyar et al. 2004). These findings indicate

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that cognitively more sophisticated skills are acquired later in ontogeny but they do not allow to specify the interplay between maturation and learning (Tomasello et al. 2001).

In respect to the ravens' tactical manoeuvres at caching, pilot studies indicate high levels of improvement in preventing others from pilfering, particularly during the birds' first summer (Bugnyar et al. in press). Moreover, the use of defensive tactics cross-correlates with the amount of pilfering shown, suggesting that young birds learn to protect their caches in interactions with others. Still, the temporal pattern of using visual barriers to obstruct the others' view seems to be different from other forms of cache protection since it does not show a steady increase but occurs abruptly in late summer/beginning of fall (Bugnyar et al. in press). Approximately at this time, young ravens come to geometrically follow humans' gaze around obstacles for the first time (Schloegl et al. in press), raising the possibility that individuals need a certain age (i.e. maturation state) to become capable of dealing with visual barriers. Which type of mechanism may underlie the sudden 'understanding' of barriers (e.g. concept 'see', learning to generalize across contexts etc.) remains speculative and calls for further experimental investigation.

Interestingly, the improvement of young ravens' cache protection and pilfer skills correlates with the amount of caching nonedible items such as small stones, twigs, flowers, and (preferably) coloured plastic items, but not with the amount of caching food. This difference may be due to the fact that ravens leave others for caching food whereas they may stay nearby, or even approach, others when caching nonedible objects (Kabicher 1996; Bugnyar et al. in press). Potentially, object caching could be used to actively stage pilfer interactions. If so, caching objects would not only qualify as play (Burghardt 2005) but provide ravens with plenty opportunities of learning about others' behaviour and intentions in daily situations without the risk of losing valuable food. Current experiments indicate that birds apparently have no problems to transfer social information acquired via object play into the food context.

Summary and conclusion

As predicted from their foraging biology, ravens show impressive skills in differentiating between conspecifics that face a high or low threat in competition for food caches and they flexibly adjust their manoeuvres according to the others' knowledge about caches (if competitors have or have not been visually present at caching) and intention (if competitors act as storers or pilferers and thus will protect or steal caches). None of our experiments provided an indication for learning across trials nor that manipulating the likelihood of using observable cues (presence/absence of individuals, head and eye orientation, involvement in task) had any effect on the birds' performance. To the contrary, parallel experiments requiring ravens to make use of behavioural cues (head and eye direction) proved to be difficult for the birds. In sum, our findings suggest that the birds' differentiation between competitors reflects their knowledge about others' visual experience rather than an orientation on observable cues or quick learning during the experiment. However, learning does play an important role during development, particularly during the birds' first year, and there is even some indication that ravens may utilize object play to gain learning opportunities. Hence, ravens likely acquire knowledge about others' behaviour during interactions over caches in daily life and they are capable of making flexible use of this knowledge in experimental tests. This means that our results are compatible with both, a mentalistic interpretation (that ravens know what others have or have not seen) and a '3rd kind explanation' (that ravens come to understand that visual barriers can block one's view and that this effect depends on one's exact position relative to the barrier). Future studies are needed to distinguish between these explanations and to clarify whether or not ravens really possess an element of a human-like ToM.

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