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ORIGINAL PAPER

Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem

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Abstract The trap-tube problem is used to assess whether an individual is able to foresee the outcome of its actions. To solve the task, an animal must use a tool to push a piece of food out of a tube, which has a trap along its length. An animal may learn to avoid the trap through a rule based on associative processes, e.g. using the distance of trap or food as a cue, or by understanding relations between cause and effect. This task has been used to test physical cognition in a number of tool-using species, but never a non-tool-user. We developed an experimental design that enabled us to test non-tool-using rooks, *Corvus frugilegus*. Our modification of the task removed the cognitive requirements of active tool use but still allowed us to test whether rooks can solve the trap-tube problem, and if so how. Additionally, we developed two new control tasks to determine whether rooks were able to transfer knowledge to similar, but novel problems, thus revealing more about the mechanisms involved in solving the task. We found that three out of seven rooks solved the modified trap-tube problem task, showing that the ability to solve the trap-tube problem is not restricted to tool-using animals. We found no evidence that the birds solved the task using an understanding of its causal properties, given that none of the birds passed the novel transfer tasks.

Keywords *Corvus frugilegus* · Trap-tube task · Tool-use · Physical cognition · Corvids

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Introduction

Animals act on their physical environment in various ways and must somehow encode information about its regularities in directing their behaviour. One of the most conspicuous forms of interaction with the physical environment is tool-use. This ability has been thought to require complex cognition because it involves manipulating at least two objects outside of the body. In humans, tool-use involves causally understanding the invisible forces such as gravity and observable physical rules such as connectedness that underlie interactions between objects. At the age of three, children already possess some knowledge of causal mechanisms, even those not directly visible (Gopnik and Schulz 2004). The discovery of tool-use in animals has raised the question of whether they show similar understanding. Research in monkeys and apes has revealed that some individuals of the species tested so far are able to solve physical tasks involving the use of tools, but that they do so by associative learning, in which cause and effect are associated through exposure to their contiguity without any understanding of causality (Tomasello and Call 1997; Visalberghi and Tomasello 1998; Povinelli 2000).

Habitual tool-use in the wild has also evolved in several bird species (Beck 1980). Woodpecker finches and New Caledonian crows, which use tools frequently (Hunt and Gray 2002; Tebbich et al. 2002; Hunt and Gray 2004), have been tested for their cognitive abilities in several physical tasks (Chappell and Kacelnik 2002, 2004; Tebbich and Bshary 2004). Tebbich and Bshary (2004) found no evidence that woodpecker finches use mental representations to solve physical problems, although one New Caledonian crow spontaneously shaped unfamiliar materials to create a functional tool for a specific task (Weir et al. 2002). This member of the corvid family is therefore

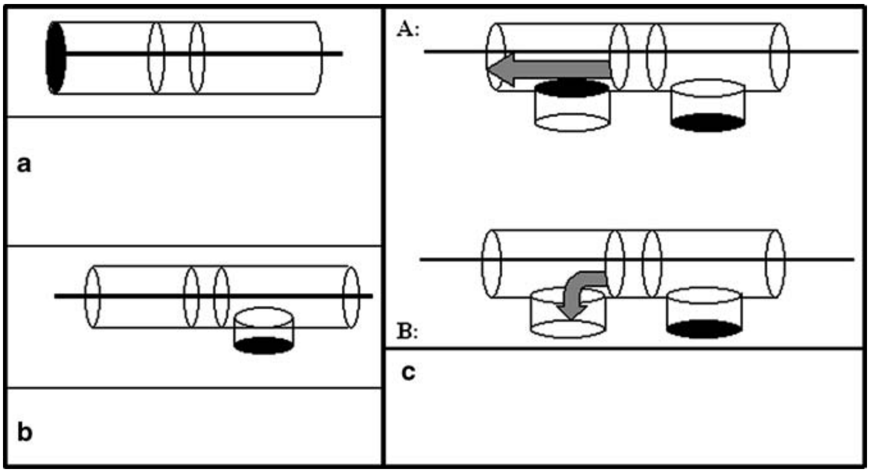


Fig. 1 **a** Training tube: A horizontal tube sealed at one end by a black perspex disc. The birds can only pull the stick from the open end; doing so yields a food reward; **b** The trap-tube task: A horizontal tube with a trap along its length. The birds must pull the stick away from the trap in order to get a reward and **c** Transfer tasks A and B. The *grey arrows* show the path the food will take in a successful trial. The birds must pull the stick from the side that the *arrow* is pointing to in order to get the reward

perhaps the most promising non-human candidate for advanced cognitive abilities in the physical domain.

However, only comparisons of the performance of non-tool-using and tool-using species on similar tasks can reveal whether the latter show better performance on physical tasks. Several studies have investigated physical cognition in non-tool-using primates. The majority of these studies have focused on the ability to detect and understand observable features of physical tasks, such as the necessity of physical contact between a food item and the object used to obtain it. Tamarins were able to recognise whether there was a connection between a cloth and a food item that was either on the cloth or beside it (Hauser et al. 1999). The same species was tested with a battery of raking tasks in which various functional and non-functional properties of the tools were altered (Hauser 1997). These experiments showed that tamarins were able to attend to the relevant features of tools and that this ability may arise as a consequence of generalizing from experience (Spaulding and Hauser 2005). A recent study carried out by Santos and colleagues (2006) has shown that both tamarins and vervet monkeys spontaneously chose to pull a rigid tool rather than a flimsy one. Furthermore, vervet monkeys (but not tamarins) preferred to pull a functional inverted rake rather than a non-functional one, an intact tool rather than a broken one, and avoided pulling food over a trap, in a performance comparable to that of chimpanzees on such tasks (Povinelli 2000). These results suggest that sensitivity to the functional aspects of an object is present in at least one non-tool-using primate.

Only a few studies have investigated physical cognition in non-tool-using birds. Funk (2002) showed that similar to the tamarins, yellow crowned parakeets prefer to pull a napkin supporting food rather than an empty napkin. Many birds show string pulling behaviour (reviewed by Seibt and Wickler 2006) but so far only some ravens and keas have been shown to respond to the functional connection between a string and a reward that is attached to it (Heinrich 2000; Werdenich and Huber 2006). A recent pair of studies tested whether rooks and bonobos were able to understand the concept of physical contact using a task comprising a clear horizontal tube containing a stick with a disc attached to it and a piece of food. The subjects had to choose which side to pull in order for the food to contact the disc and thus be moved by the stick to a position in which the subjects could reach the food. Although both species eventually learned to solve the task using external cues, neither the rooks (Helme et al. 2006b), nor the bonobos (Helme et al. 2006a) showed any understanding of contact. However, none of these tasks tested for the comprehension of unobservable forces such as gravity.

We therefore tested rooks, which have not been reported to use tools in the wild, on a modified trap-tube task (Fig. 1). In the original trap-tube task, which has been used to test tool-using primates and two tool-using bird species, animals are confronted with a reward located inside a clear tube with a trap off to one side. If a tool is applied from the wrong side of the tube, the reward falls into the trap and is lost. We modified this design such that a tool was already inserted into the tube before the trial began, thus allowing us to test a non-tool-using species. Active tool-use may place cognitive demands upon an animal, independent of those involved in processing object properties. By pre-inserting the tool, we were able to investigate what the birds understand about object properties without confounding this question with that of the cognitive demands of active tool-use. In studies carried out using the original trap-tube design, a total of three out of 12 chimpanzees (Limongelli et al. 1995; Povinelli 2000) and one out of four capuchin monkeys (Visalberghi and Limongelli 1994) eventually learned to solve the problem. However, in the traditional control condition, in which the trap is inverted and no longer functional, the successful primates showed the same behaviour as in the test, which suggests that they used a procedural rule (i.e. push reward away from the trap; Visalberghi and Limongelli 1994). One out of six woodpecker finches solved the trap-tube task and performed randomly (pulling the reward from both sides) in the transfer task with the inverted tube. However, more detailed analysis revealed that the bird solved the task by making careful observations of the effect of its action upon the reward (Tebbich and Bshary 2004). Consequently, these results do not provide evidence that this woodpecker finch had formed a mental representation of the task. This result also demonstrates the problem of using the inverted trap as a control task. Reverting to random responding is not conclusive proof for causal understanding, as animals that were using a rule specific to the exact configuration of the trap tube (with a trap beneath the horizontal tube) would also pass the inverted control. Likewise, as there is no cost in continuing to avoid the non-functional trap, it is misleading to assume that an animal that does this has understood nothing about causality. Even adult humans will avoid the non-functional trap in the inverted control task (Silva et al. 2005). We therefore designed two different ‘two-trap’ transfer tasks. Each tube contained both a functional and non-functional ‘trap’, circumventing the two methodological problems mentioned earlier. This series of experiments aimed to investigate whether rooks are able to learn to either avoid the trap using a rule based on associative processes or by representing some key features of the task, such as the function of the trap and the outcome of the pulling action.

Methods

Study animals and housing

The subjects were eight juvenile rooks, including two males (Conolly and Cleese) and six females (Monroe, Bussell, Fonteyn, Woody, Palin and Dowell). The birds were collected from two colonies in Cambridge on April 16th and 17th 2003, and hand-raised. Four individuals (Cleese, Bussell, Monroe, Conolly) received training and test-trials between October 2003 and February 2004, and four individuals (Fonteyn, Palin, Woody, Dowell) were tested during February and March 2005. The birds were not tested for tool-use abilities before the experiments, however in over 3 years of behavioural observations, we have never seen a rook use a tool, even when provided with a large number of sticks. Fonteyn participated in 2004 in another study (Seed et al. 2006), in which she was tested on two versions of the two-trap-tube task. These were the two transfer tasks in our study (Fig. 1c). Fonteyn performed randomly on both the trap-tube tasks (Seed et al. 2006). We cannot exclude that her previous experience affected performance in the current study where she also chose sides randomly. In 2003 and 2004, testing took place 5 days a week and the rooks remained in a side compartment during the entire test period. Due to new regulations for housing corvids in captivity (2005), testing was only possible on three successive days within 1 week. In between each test session, the birds were returned to the group in their housing aviary. All of the rooks were housed in a climate-controlled indoor aviary with a 12:12 h light:dark schedule. Each set of four subjects were housed in pairs in two side aviaries (each 2 m × 1 m) from the main housing aviary. During testing, a temporary opaque wall was erected to separate the rooks so that they were visually isolated from one another. Each test compartment contained several branches for perching and a wooden shelf was located at the front side of each compartment. Food was supplied *ad libitum* outside test sessions, water was always available. The daily feed included pasta, potatoes, meat, eggs, seeds, and fresh fruit. Food was removed 1 h prior to testing, and preferred foods (e.g. bacon, pork pie and meal worms) were not given as part of the regular feed. These food types were used as rewards, depending on the individual preference of each bird.

Phase I: training

A Plexiglas tube (175 mm long × 40 mm wide), open only at one end, was fixed horizontally onto a wooden block (200 mm long × 25 mm high; Fig. 1a). The side to which the open end pointed was randomised and counterbalanced across trials. A tool was inserted into the tube. It consisted of a wooden dowel with two Perspex discs attached to it, positioned in the centre of the dowel, 2 cm apart. A food reward was placed in the centre of the tube between the two discs. To obtain the food reward, rooks had to pull the tool towards themselves. The rooks had to perform 10 correct responses before proceeding to the test trials.

Phase II: trap-tube

The transparent trap-tube (Fig. 1b) contained a vertically oriented trap mounted lateral to the centre, 55 mm from the nearest end (Limongelli et al. 1995). We chose to position the food centrally because we wanted to prevent the birds from using asymmetry in the position of the food as a cue (Visalberghi and Trinca 1989). However, asymmetry in the position of the trap along the tube length could still have served as a cue to solve the task. As in the training trials, a tool was inserted into the tube with a food reward in between the two discs. The orientation of the apparatus changed trial by trial, so that the position of the trap was either right or left of the centre, according to a randomised, balanced schedule. The re-baiting procedure and change of orientation was performed out of sight of the rooks. Each trial lasted 10 min. Each bird had 10–20 trials per day. We set a criterion of 15 out of 20 correct in two consecutive blocks of 10 trials for them to advance to the transfer test. We used a criterion rather than an absolute number of trials for two reasons. First,

Table 1 Proportion of stick pulling from the left end of the trap-tube, irrespective of its orientation, per block of 10 trials

Block	Fonteyn	Palin	Woody	Cleese
1	0.5	0	0.7	0.5
2	0.7	0.1	0.2	0.7
3	0.7	0.2	0.1	0.6
4	0.5	0	0.4	0.8
5	0.3	0.1	0.9	0.8
6	0.6	0.1	1	0.5
7	0.7	0.2	0.9	0.8
8	0.6	0.4	1	1
9	0.3	0	1	1
10	0.9	0	1	1
11	0.9	0.3	1	
12	0.4	0.7	1	
13	0.5	0.3	1	
14	0.6	0.1	1	

Individuals show a significant side bias at values larger than 0.7 and smaller than 0.3 (Binomial test).

the rooks quickly became disinterested, and second, we did not want to facilitate habit formation. In 2003, we set the maximum number of trials to reach the criterion to 100, and in 2005 we set it to 140 trials.

Four of the seven birds developed a side bias during this test phase (Table 1). Palin, Cleese and Woody persisted in the side bias for more than 30 trials. We therefore revisited Phase I after 100 trials and gave Palin and Woody 10 additional trials with the training tube where the side from which the dowel could be pulled out of the tube was switched randomly. Animals that have developed a side bias may continue to use this strategy because they are rewarded in 50% of trials, and are therefore less likely to learn about the task associatively. It is therefore standard procedure in experimental psychology to correct for side biases.

During a trial, an experimenter baited the apparatus, placed it on the shelf in front of the bird and left the room. All trials were captured on video and scored as either successful (the subject obtained the food reward) or unsuccessful. All birds pulled the stick towards themselves, and no instances of pushing the stick were observed. One individual, Dowell, passed the training phase but stopped cooperating after three trials with the trap-tube and therefore was excluded from the analyses.

Phase III: transfer to a two-trap tube

Half the subjects were presented first with task A and then with task B, and half were presented with the tasks in the opposite order (Fig. 1c). Each design had both a functional and a non-functional trap. In task A, the non-functional trap was open. If a rook pulled the tool from the side of the open trap, the food reward fell through the opening onto the shelf and was accessible to the bird. In task B, the non-functional trap was blocked at the top with a black disc and the food was accessible by pulling it (the food) over this non-functional trap. Before starting the test trials, all birds had four exploration trials in which the tube was presented without a tool in different orientations (traps facing downwards, upwards and to the side). One food reward was placed inside the tube and another one on top of it. We conducted these exploration trials in order to give the birds an opportunity to become familiar with the new physical properties of the task, especially the new positions of the black discs. The non-functional trap appeared twice on the left and twice on the right. In two out of four exploration trials, the traps were inverted. The rooks then received 50 test trials, in blocks of 10 per day, with both tasks A and B.

Data analysis and statistics

The criterion for successful performance was set to 15 or more correct trials within two consecutive blocks of 10 trials. Specifically, the number of correct responses in one of the two blocks had to be at least seven and in the other at least eight. We used a Monte Carlo simulation (see Adams and Anthony 1996; Manly 1997) rather than simple binomial statistics to analyse our data because the probability to reach the above-mentioned criterion by chance increases markedly with each additional block of trials. This inflates the likelihood of type-I errors.

We used the Monte Carlo simulation to calculate the probability of reaching the above-mentioned criterion by chance within the total number of blocks performed by the subjects. To do so, we simulated the performance of subjects that choose randomly, i.e. each of the two alternative outcomes (correct vs. incorrect) occurred at equal probabilities. We simulated the behaviour of these subjects in blocks of 10 trials until two consecutive blocks reached the above-mentioned criterion. This simulation was run repeatedly (1,000,000 permutations) and resulted in the probability distribution of number of blocks required to reach the criterion by chance. The *p*-values associated with the performance of our study animals were calculated by comparing their performance to the probability distribution of our simulation.

In the second analysis, we used a corresponding Monte Carlo simulation to test the seemingly bad performance of one individual in a transfer test. It differed from the previous simulation in that the criterion was set to seven or less correct trials in three consecutive blocks of 10 trials. The number of correct trials in two of the three blocks had to be two or less while in the third block three or less correct choices had to be made. If the corresponding measure for this individual revealed significance, this would imply a below chance performance. All values were obtained by performing 1,000,000 permutations. The level of significance was set to $\alpha = 5\%$.

Results

Phase II: single trap-tube task

Three individuals, Bussell, Monroe and Conolly, reached the criterion within 50, 40 and 30 trials, respectively (Fig. 2a). The Monte Carlo simulation revealed that the performance of Monroe and Conolly was significantly better than expected by chance (Monte Carlo simulation: Monroe $p = 0.043$; Conolly $p = 0.029$), while Bussell's behaviour was above the level of significance (Monte Carlo simulation: $p = 0.057$). In comparison to the acquisition rates for the tool-using species that have been tested on the original trap-tube task, these three birds learned surprisingly quickly; all four other individuals did not solve the task within 140 trials, however (Fig. 2b).

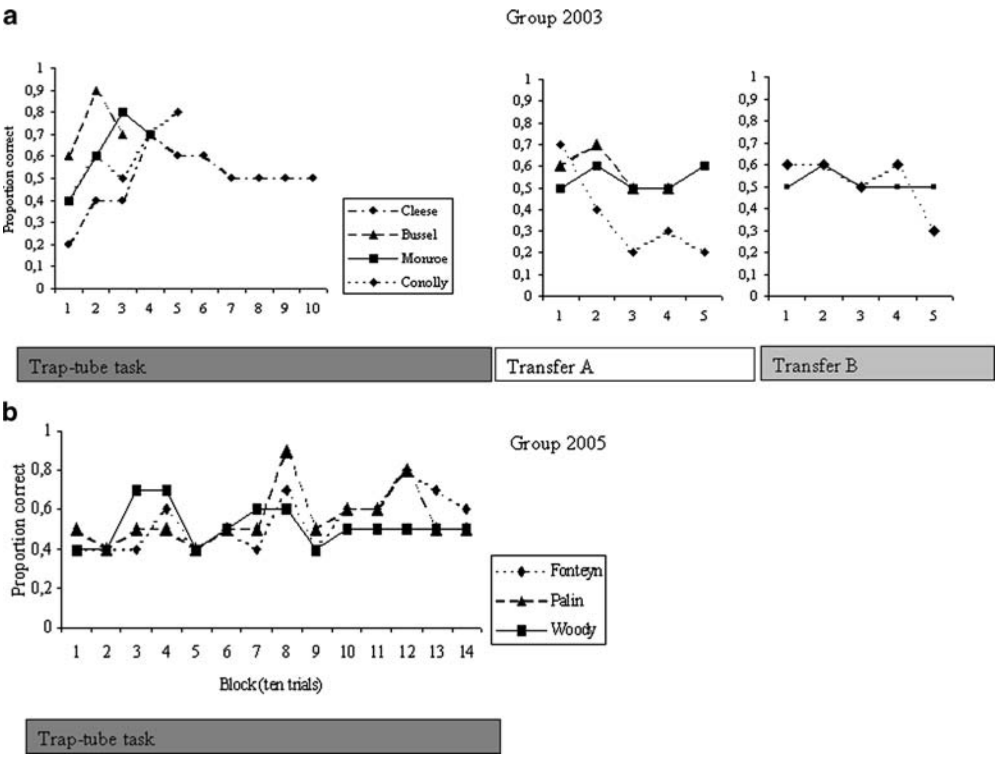
Phase III: trap-tube transfer task

Bussell, Monroe and Conolly proceeded to the transfer task since they reached criterion performance on the trap-tube. We aimed to give Bussell 50 trials on Tube A, then 50 trials on Tube B, and to give Monroe and Conolly 50 trials on Tube B, then 50 trials on Tube A. However, after 40 trials on Tube A, Bussell stopped approaching the apparatus and could not be tested further. None of the birds reached the criterion to successfully pass either transfer task (Fig. 2a). Conolly's performance dropped markedly in the last three blocks of the second transfer test. In the first two blocks, he developed a significant side bias for the right end of the tube but surprisingly switched to the left end after successfully retrieving food from the right end. After retrieving the reward once from the left end, he systematically chose the non-rewarded side closer to the functional trap and continued to use this strategy for 11 consecutive trials. It therefore appeared that Conolly's performance was not random. Our second Monte Carlo simulation showed that his behaviour in the last three blocks was significantly below chance (Monte Carlo simulation: $p = 0.003$).

Discussion

This study demonstrates that rooks, which do not spontaneously use tools, can solve the trap-tube problem. Our findings are in line with those of Hauser and colleagues (Hauser et al. 1999, 2002), who have found that non-tool-using primates are capable of learning the solution to other physical problems, such as those based on connectedness. Three out of the seven rooks solved the current task, but we found no indication that these birds were able to apply their acquired knowledge to the new transfer tasks. All the successful birds were in the first cohort and were tested a year earlier than

Fig. 2 **a** For the four individuals tested in 2003 and **b** for the three individuals tested in 2005. Percentage of correct pulls in the trap-tube task and in the transfer tasks A and B are given



the second cohort and under different conditions. We cannot be sure if this distribution was simply due to chance, to the difference in the age of the subjects, changes in housing conditions or to the fact that the second group had a larger break between consecutive days of testing sessions (four as opposed to two).

Surprisingly, the speed of learning seemed to be faster than that of any tool-using animals tested in the original trap-tube task (Visalberghi and Limongelli 1994; Limongelli et al. 1995; Povinelli 2000; Tebbich and Bshary 2004; Kacelnik et al. 2006). However, two features of our experiment which differed from the original trap-tube design could have facilitated learning. First, the rooks were not required to insert the tool, but only had to make a decision about which side to pull from. Using tools actively may require specific cognitive abilities such as the ability to foresee the effect of a tool on the displacement of the reward. Consequently, our modified trap-tube task may not impose the same cognitive demands as the original trap-tube task, although it still requires that the animals learn to avoid pushing the food into the trap. Second, pulling food towards themselves may be a more natural behaviour for animals than pushing it away and may be an explanation for the faster performance in rooks and woodpecker finches as compared to chimpanzees and capuchin monkeys. Indeed, a recent study with several primate species has demonstrated faster learning when comparing pulling sticks to pushing them (Mulcahy and Call 2006).

Interestingly, given the speed of their learning on the initial trap-tube task, none of the three individuals were able to learn to solve the transfer tasks within 50 trials. It is possible that this finer visual discrimination was more difficult for the birds, and one that they could not solve quickly. Alternatively, given that the rooks were likely to have learned the initial task using a procedural rule based on the asymmetrical position of a trap-like structure, learning the solution to the single trap-tube may have made it more difficult for the animals to attend to the features now relevant for solving the double trap-tube. A further experiment in which naïve birds were tested on the two-trap tube design from the outset lends support to this notion, as most of these birds (tested in October 2004) were able to solve this task within a similar range of trials (Chappell 2006; Seed et al. 2006).

The fact that none of the three individuals tested passed either of the two transfer tasks suggests that their learning on the trap-tube task was task-specific, although further control experiments would be necessary to determine the exact mechanism by which the rooks solved this task. The most parsimonious explanation is that they learned a distance rule, namely pulling the tool from the side furthest away from the trap. This would be in line with findings of all previous studies of animals on the original single trap-tube paradigm (Tomasello and Call 1997; Visalberghi and Tomasello 1998; Povinelli 2000). One bird (Connolly) performed significantly below chance in the second control task, i.e. he systematically chose the unrewarded side closer to the functional trap. It is plausible that this bird had formed another rule, based on the features of the trap tube and persevered without being reinforced. However, we are unable to explain why he adopted such a rule and which stimuli guided his behaviour.

Other experiments with both tool-using and non-tool-using primates have suggested that these species may understand something about the functionally relevant, observable features of problems, an ability distinguished from simple learning of arbitrary rules (Hauser et al. 1999; Mulcahy and Call 2006). The current task, however, was designed to probe understanding of the unobservable, causal elements of tool-related problems. It remains to be seen whether rooks can form mental representations of the observable features of problems, though this question is addressed in a separate study (Seed et al. 2006). In that study, one out of the seven rooks that learned to solve the two-trap tube task, was able to pass a series of transfer tasks. The performance of this one individual indicates that she could have abstracted a rule based on the observable features of the tasks, such as surface continuity and the inability of objects to pass through barriers.

There are two explanations for why some non-tool-using rooks perform well on the trap-tube problem. The first is that in rooks, the ability to solve physical problems reflects a more general cognitive ability that has evolved in a context other than tool-use. Their ecology comprises several factors that have been discussed as major forces driving the evolution of cognition. Rooks are generalists (Cramp and Perrins 1995), which may have driven the evolution of generalised knowledge acquisition (Sterelny 2003). A relatively large part of their diet requires them to extract food from a substrate (Cramp and Perrins 1995), which is believed to favour sensorimotor intelligence (Parker and Gibson 1977; Byrne 1995). This hypothesis gains support from the finding that corvids have the highest rate of feeding innovation of any family of birds (Lefebvre et al. 2002), which is likely to be due to the speed with which they learn. The demands made by a complex social life, may also favour the evolution of cognition in general (Humphrey 1976). Rooks are a colonial living species demonstrating sophisticated levels of social knowledge (Emery et al. in press) and may thus have evolved advanced general cognitive abilities in the social domain (Emery and Clayton 2004).

Alternatively, solving the single trap-tube task may be entirely explained by an associative account without any specific cognitive adaptations and can therefore be achieved by tool-using and non-tool-using species alike. The crucial ability, namely to apply acquired knowledge to a new situation, has not been demonstrated by either group, perhaps partly because of the lack of good test and control designs.

We think that our new control tasks overcome the problems of the inverted tube and provide a new method for testing generalised knowledge in both tool-using and non-tool-using species.

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