

# Do New Caledonian crows solve physical problems through causal reasoning?

A. H. Taylor\*, G. R. Hunt, F. S. Medina and R. D. Gray\*

*Department of Psychology, University of Auckland, Private Bag 92019, Auckland, New Zealand*

The extent to which animals other than humans can reason about physical problems is contentious. The benchmark test for this ability has been the trap-tube task. We presented New Caledonian crows with a series of two-trap versions of this problem. Three out of six crows solved the initial trap-tube. These crows continued to avoid the trap when the arbitrary features that had previously been associated with successful performances were removed. However, they did not avoid the trap when a hole and a functional trap were in the tube. In contrast to a recent primate study, the three crows then solved a causally equivalent but visually distinct problem—the trap-table task. The performance of the three crows across the four transfers made explanations based on chance, associative learning, visual and tactile generalization, and previous dispositions unlikely. Our findings suggest that New Caledonian crows can solve complex physical problems by reasoning both causally and analogically about causal relations. Causal and analogical reasoning may form the basis of the New Caledonian crow's exceptional tool skills.

**Keywords:** New Caledonian crows; causal reasoning; analogical reasoning; trap tube; trap table

## 1. INTRODUCTION

The eighteenth century philosopher David Hume (1711–1776) famously used the example of one billiard ball rolling into another to illustrate his argument that causal relations cannot be explicitly perceived (Hume 1739/1978). Instead, causal relations must be inferred from sensory information. Imagine a slight variation to Hume's example. At the moment of contact between the two balls, a third falls from above and lands next to the collision. How can an observer infer which ball causes the stationary ball to move? Associative learning involves the mental pairing of events that occur in close temporal and spatial proximity. This process cannot, therefore, identify the rolling ball or the falling ball as the cause. By contrast, causal reasoning, 'an understanding of 'how' and 'why' one event leads to another' (Visalberghi & Tomasello 1998), can discriminate between causal and arbitrary events occurring at the same time and place.

Studies have shown that non-human animals generalize along causally relevant features (Hauser 1997; Hauser *et al.* 1999, 2002), pay more attention to causal anomalies (O'Connell & Dunbar 2005; Hauser & Spaulding 2006) and are sensitive to the causal structure of events (Blaisdell *et al.* 2006). However, there is no conclusive evidence that non-human animals can use causal knowledge rather than associative learning to solve complex physical problems (Visalberghi & Limongelli 1994; Limongelli *et al.* 1995; Povinelli 2000; Fujita *et al.* 2003; Call 2004; Tebbich & Bshary 2004; Cunningham *et al.* 2006; Mulcahy & Call 2006; Santos *et al.* 2006; Seed *et al.* 2006; Penn & Povinelli 2007; Girndt *et al.* 2008; Martin-Ordas *et al.* 2008; Sabbatini & Visalberghi 2008). The absence of evidence

that non-human animals use sophisticated cognition when solving complex physical problems has led to suggestions that causal reasoning in humans is fundamentally different (Penn & Povinelli 2007; Penn *et al.* 2008).

The trap-tube paradigm has been used as the benchmark test for investigating whether non-human animals use causal reasoning to solve physical problems. In this task an individual must extract food from a horizontal tube in a direction that avoids a trap. The trap-tube contains two causally relevant features—the hole and the trap base. The hole is relevant because objects only move horizontally along continuous, not discontinuous, surfaces. The trap base is relevant because objects cannot move through barriers. These proximate causal relations, or regularities, operate in this way owing to a distal causal mechanism (gravity) that underlies these object interactions. Gravity pulls down all objects, but can only move those that are unsupported.

Early experiments tested for causal understanding by inverting the trap-tube after an animal had successfully learnt to avoid the trap. The continued unwillingness of subjects to push the food in the direction of the (non-functional) inverted trap led researchers to propose that capuchins, *Cebus apella*, and chimpanzees, *Pan troglodytes*, used associative cues rather than causal reasoning to solve the task (Visalberghi & Limongelli 1994; Povinelli 2000). A subsequent study showed that chimpanzees did not use an associative cue based on a distance rule, although they may have used a different rule such as 'always push away from the trap' (Limongelli *et al.* 1995). The primates in the above studies were restricted to using the tool to push the food out of the tube. When chimpanzees, orang-utans, *Pongo pygmaeus* and woodpecker finches, *Cactospiza pallida*, were allowed to pull the food out, they did not avoid the inverted trap after solving the initial problem (Tebbich & Bshary 2004; Mulcahy & Call 2006). This suggests that earlier results were confounded by

\* Authors for correspondence (alexhtaylor@gmail.com; rd.gray@auckland.ac.nz).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.1107> or via <http://journals.royalsociety.org>.

restrictions on the type of tool use possible (Mulcahy & Call 2006). The recent finding that humans also avoid the inverted trap, coupled with the fact that there is no cost in continuing trap avoidance, suggests that the inverted trap-tube control is conceptually flawed (Silva *et al.* 2005).

An alternative paradigm used to test causal understanding in primates is the trap-table task. In this task a subject must choose between raking in a reward behind a trap and raking in one on a flat surface without a trap. Primate success with the trap-table has been mixed. Capuchins (Fujita *et al.* 2003) and tamarins, *Saguinus oedipus*, (Santos *et al.* 2006) have failed to solve the trap-table problem. Vervet monkeys, *Cercopithecus aethiops*, performed above chance, but still failed in 35 per cent of trials (Santos *et al.* 2006). Hoorlock gibbons, *Hylobates hooleck*, solved the trap-table problem, with one subject performing successfully from the first trial (Cunningham *et al.* 2006). However, the authors suggested that this gibbon's success may have been based either on learning to associate the continuous surface of the table with reinforcement during training, or through viewing the trap as an obstruction and avoiding it. In all these studies, one tool was positioned in front of the trap and another in front of the flat surface. Recently it has been shown that apes make far fewer errors when they are only given one tool and can choose between the trap and surface (Girndt *et al.* 2008). The majority of apes (20 out of 24) when given a single tool avoided the trap on the first trial, suggesting that they were sensitive to the causal relations in the task. However, this study did not address the possibility that these apes had a previous disposition to avoid holes.

A rigorous method for identifying the cognitive strategies animals use to solve problems is 'triangulation' (Heyes 1993). Subjects first learn an initial discrimination task and are then presented with transfer tasks. In the transfer tasks arbitrary stimuli are changed, while the causal structure of the problem is kept constant. Successful performance across transfer tasks eliminates the use of associative cues and suggests the use of causal reasoning. A recent application of this method using novel trap-tube transfer tasks found that one rook, *Corvus frugilegus*, may have solved the trap-tube problem through sensitivity to causal relations such as 'surface continuity' (objects move along continuous surfaces) and 'object solidity' (objects cannot move through each other) (Seed *et al.* 2006). Primate studies have tested whether subjects can transfer knowledge between the trap-tube and trap-table. One chimpanzee that learnt to solve the trap-tube (but failed the inverted trap control) solved the trap-table in the first 20 trials (Povinelli 2000). This suggested that the chimpanzee understood something about the causality of the task. However, as the chimpanzees in this study were first given training on a trap-table without a trap, another possibility is that success was due to a learnt association between the reward and the continuous surface. In a recent study with four ape species, 20 individuals rapidly learnt to solve either the trap-table or trap-tube (Martin-Ordas *et al.* 2008). However, none of them successfully transferred between the trap-tube and the trap-table, or vice versa. This was despite the apes being able to pull rather than push the food reward and being given only a single tool to use. The authors suggested two possible reasons for the apes' failure to transfer. One was a lack of causal knowledge about the

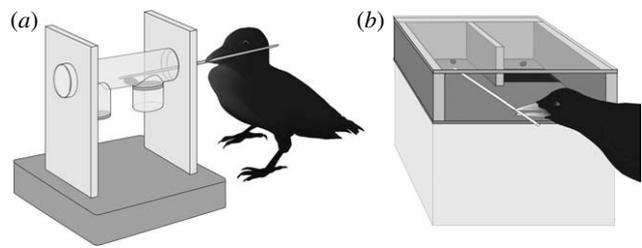


Figure 1. Drawing of the experimental apparatus. (a) The trap-tube. (b) The trap-table.

relations between the elements of the problem. The second was that causal knowledge was tied to specific actions, thereby preventing an analogy being established between the two functionally equivalent problems.

In the wild, New Caledonian crows, *Corvus moneduloides*, forage in holes for grubs and insects using a variety of tools with a level of sophistication sometimes surpassing that of the great apes (Hunt 1996, 2000a,b; Hunt & Gray 2004). Experimental work has suggested that their tool skills may be based on complex physical cognition (Weir *et al.* 2002; Weir & Kacelnik 2006; Taylor *et al.* 2007). If this is correct, New Caledonian crows might be expected to excel at physical cognition problems, such as the trap-tube task.

Here, we presented six New Caledonian crows with a two-trap-tube task similar to that used with rooks (Seed *et al.* 2006). In contrast to the rook study, we required the crows to use tools to extract the food (figure 1a). If a crow solved the initial trap-tube problem, we presented it with a series of transfer tasks. Rather than presenting trap-tube transfers that required the opposite response to familiar arbitrary features, as in the rook study, we removed features step by step across the transfers. This method was used to identify which feature a crow had used to avoid the trap. The use of causal features when avoiding the trap, rather than spatially and temporally contiguous arbitrary ones, would suggest the use of causal reasoning. However, crows might have associatively learnt about a causal feature such as a hole simply because they pay more attention to them due to their natural foraging behaviours. Associative learning has limitations that causal knowledge does not have. An associatively learnt cue can only be used to solve novel problems via stimulus generalization if the new problem contains features that share some perceptual similarity with the associative cue (Spence 1937; Shepard 1987; Ghirlanda & Enquist 2003). By contrast, causal knowledge can be transferred via analogical reasoning to novel problems that only share causal relations (Goswami & Brown 1989). For example, children with causal knowledge of the relation 'cutting' are more likely to solve analogies of the form: bread is to bread slice as lemon is to lemon slice (Goswami & Brown 1989). Therefore, the most compelling way to eliminate the possibility of associative learning is to present an animal with a visually distinct but causally equivalent task. For this reason we presented crows with a trap-table that differed from the trap-tube apparatus along three visual dimensions: shape, colour and material. If they could solve this visually distinct but causally similar problem, it would provide strong evidence that the crows' use of causal features was based on an awareness of the causal relations in the problem.

## 2. MATERIAL AND METHODS

### (a) Subjects

We carried out the experiment with six wild crows captured on the island of Maré, New Caledonia. Five of the crows (Batou, Slevin, Espanol, Egg and Obo) were adults more than 2 years old and one (Tiga) was a sub-adult less than 2 years old. Based on sexual size dimorphism (Kenward *et al.* 2004), only Obo and Egg were females. The crows were housed in a five-cage outdoor aviary close to the location of capture; the cages varied in size but were all at least 8 m<sup>2</sup> in area and 3 m high. After capture, a crow was left to habituate to the aviary and human presence for 3 days before experimental procedures began. The experiments here were carried out with one crow at a time in a separate cage; the other crows could not see into the experimental cage.

The crows were tested from January to March 2008. A trial started when a crow flew down to the table and ended when it left. Trials were recorded on video for later analysis. The crows were habituated to the initial trap-tube and trap-table by placing a meat block reward next to each apparatus. Ten trials were conducted for each apparatus. In the experimental phase, blocks of 10 trials were given, with no more than two blocks per day.

### (b) Experimental protocol

#### (i) Initial trap-tube

The initial trap-tube contained two traps: one functional with an opaque yellow disc at its base (arbitrary feature 1), and one non-functional with an opaque yellow disc at its mouth (arbitrary feature 2) (figure 2a). The upper rim of the functional trap was coloured blue in order to increase its visual salience (arbitrary feature 3). At the start of each trial, a small portion of meat was placed in the middle of the tube between the two traps and a tool was placed on the table in front of the apparatus (see clips 1–4 in movie 1 in the electronic supplementary material). The position of the functional trap (left or right) was randomized across trials. Crows were presented with 10-trial blocks. Crows solved the task if they obtained the meat in 17 trials across two consecutive blocks (binomial test with  $\alpha$  set at 0.01). A stricter criterion than  $\alpha < 0.05$  was used with the initial trap-tube task to ensure that the crows had developed a consistent method of trap avoidance. Testing ended if a crow failed to solve the problem after 150 trials.

#### (ii) Transfer tasks

Successful crows were given four transfer tasks. The crows solving the initial trap-tube could have used associative rules based on one or more of the arbitrary features. In transfer 1, the two yellow discs were removed, but the blue rim remained. The bottom of the traps rested on the wooden base (figure 2b). The removal of the discs prevented their use as cues to guide behaviour. Crows had to pull the meat over a continuous, clear Perspex surface and away from a hole with a blue rim. In transfer 2, we tested if the crows required the blue rim to solve the task. The transfer tube had high and low discs as in the initial trap-tube, but they were coloured black instead of yellow (figure 2c). The blue rim was removed. Success with transfers 1 and 2 would rule out a crow's use of a single arbitrary feature to solve the initial trap-tube. However, a crow could have solved these transfers if it had learnt to use multiple associative rules independently. For example, if the crows had learnt to both pull away from the blue rim when it was present or pull towards a high disc when it was present

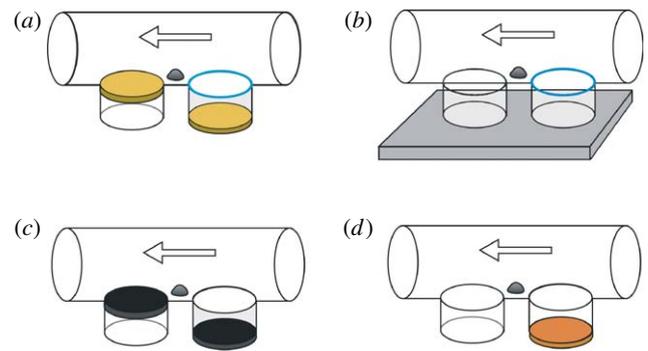


Figure 2. The trap-tube apparatus. (a) The initial trap-tube. (b–d) The three transfer trap-tubes. The coloured discs represent actual colours and solid surfaces. The left trap in transfer 1 was non-functional with a transparent solid surface. Transfer 1 was placed on a wooden base. The other three trap-tubes were suspended above the wooden base. The arrows show the direction in which the food must be extracted to avoid the trap.

(irrespective of its colour), then transfers where one of these features was absent would not lead to failure. Alternatively, the crows could have identified either the hole or the trap base as a causal feature.

In transfer 3, the trap-tube had one functional trap (with an orange disc at its base) and one non-functional trap (a hole without a base) (figure 2d). Success in transfer 3 would suggest that a crow was either using two independent associative rules based on the low disc and blue rim or the trap base as a causal feature. Failure in transfer 3 would suggest the use of two independent associative rules based on the high disc and blue rim or the use of the hole as a causal feature.

To discriminate between explanations based on multiple independent associative rules and those based on causal features, we presented the crows with a wooden trap-table apparatus (figure 1b). The crows had to choose between using the tool to pull a meat block behind a rectangular trap and to pull one resting on a continuous wooden surface. Given the lack of discs and a coloured rim, the crows could not use associative rules based on these arbitrary features. Furthermore, as this trap-table differed in colour, shape and material from the trap-tube, it was unlikely that any associative rules, even those based on the hole or the trap base, could be generalized from the trap-tube to trap-table. Successful transfer would instead suggest that analogical reasoning based on causal relations had been used to solve this perceptually distinct problem.

Crows were considered to have successfully transferred knowledge to a transfer task when they avoided the trap in a significant number of trials across two blocks of 10 trials (15/20 correct trials; binomial test with  $\alpha$  set at 0.05). If a crow's performance was significantly better than chance in the first block (9/10 correct trials), it moved onto the next transfer task.

### (c) Apparatus

All the trap-tubes were made of 40 mm diameter Perspex tube (see figure 1a). The horizontal tube was 175 mm long and held at each end by a vertical Perspex panel. The two Perspex panels were 150 mm apart and inserted into a wooden base 200 mm long  $\times$  25 mm high. The trap-table was a wooden platform 10 cm wide  $\times$  15 cm deep  $\times$  6 cm high (see figure 1b). It had 5 cm high wooden walls at the side and

back, and a wooden partition dividing the left-hand side from the right-hand side. The top of the apparatus was Perspex and chicken mesh. A rectangular trap 5 cm wide  $\times$  3 cm deep was located 2 cm from the rear of one compartment. The tool was a straight section of dowel 15 cm long  $\times$  0.3 cm in diameter.

#### (d) Data analysis

We recorded how the crows reacted to the trap-tube apparatus during a trial in three ways. We defined ‘inspection behaviour’ as a crow pausing in front of one end of the tube with its head orientated towards the entrance. ‘Trap probing’ was when a crow probed inside the trap with the tool. ‘Side switching’ was when a crow first probed one end of the tube with a tool then probed the other end.

Mann–Whitney *U*-tests that we carried out were one-tailed with exact probability values (Mundry & Fischer 1998).

### 3. RESULTS

Three of the six crows solved the initial trap-tube in less than 150 trials (figure 3*a*; see clip 1 in movie 1 in the electronic supplementary material). These crows (Obo, Tiga and Slevin) took over a 100 trials on average to solve the task (mean  $\pm$  s.e.;  $103.3 \pm 20.3$ ). The other three crows did not learn to avoid the trap (figure 3*b*). All the six crows preferred to pull the food out of the tube rather than push it out (91.2% of trials  $\pm$  2.7). The initial trap-tube trials of all crows were analysed to see if behaviours varied between the successful and unsuccessful crows. The successful and unsuccessful crows differed significantly in the proportion of trials where they switched the side they were probing (successful crows:  $22.1\% \pm 9.0$ ; unsuccessful crows:  $0\% \pm 0$ ; one-tailed Mann–Whitney *U*-test,  $U=9$ ,  $p=0.0318$ ). There was no significant difference in the proportion of trials where the crows inspected the tube prior to probing ( $22.0\% \pm 14.1$  versus  $13.7\% \pm 5.5$ ;  $U=5$ ,  $p=0.5$ ), or the proportion of the trials where the trap was probed ( $3.1\% \pm 2.7$  versus  $1.3\% \pm 0.7$ ;  $U=5$ ,  $p=0.5$ ).

There was variation between the successful crows in how much they visually inspected the apparatus before starting to probe. Obo usually inspected either one end (25.8% of trials) or both ends of the tube (37.1% of trials) before inserting the tool. Although Tiga often chose the correct end before probing, he only inspected one end of the tube in 17 per cent of trials and both ends in 6 per cent of trials. Slevin only looked down the tube once before probing. These differences may help to explain the variation in the rate at which the crows switched the side of the trap they were probing. Slevin switched sides in 40 per cent of trials, but the other two crows did so much less frequently (Obo, 14%; Tiga, 12%).

All three successful crows solved transfer 1 (figure 4*a*; see clip 2 in movie 1 in the electronic supplementary material), indicating that the yellow discs were not required for avoiding the trap. The crows also performed significantly above chance with transfer 2 (figure 4*b*), revealing that the blue rim was also not needed (see clip 3 in movie 1 in the electronic supplementary material). All the three crows failed in transfer 3 (figure 4*c*; see clip 4 in movie 1 in the electronic supplementary material). This indicated they had not used the trap base as a causal feature, or two independent associative rules based on the low disc and blue rim, to solve the initial trap-tube. During transfer 3, the crows often manoeuvred the reward

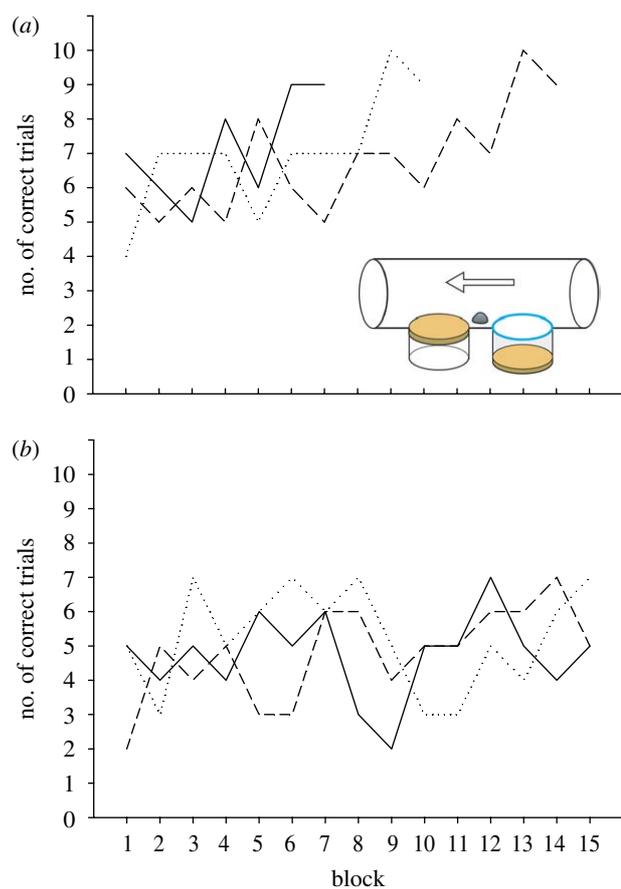


Figure 3. The performance of the crows with the initial trap-tube. (a) Successful crows (solid line, Obo; dotted line, Tiga; dashed line, Slevin) and (b) unsuccessful crows (solid line, Espanol; dotted line, Batou; dashed line, Egg). The *x*-axis gives the block number.

between each hole without pulling it into either, which suggested they were reluctant to pull the food into the holes (see clip 4 in movie 1 in the electronic supplementary material). To check whether the crows behaved differently in transfer 3 compared with the other trap-tube tasks, we analysed latencies and side-switching rates across tasks. We used the final block of trials with the initial trap-tube and the first block of trials in each of the three trap-tube transfer tasks. Interestingly, latency to trial completion and the number of times the crows changed the end they were probing were both the highest in transfer 3 (figure 5). For each of these measures, the probability that a crow has its highest score in transfer 3 is 0.25. The probability that all the three crows obtained the highest score in transfer 3 was significantly different from chance (binomial calculation,  $H_1: p=0.25$ ,  $n=3$ ,  $p=0.0156$ ).

Strikingly, all three successful crows rapidly solved the trap-table task (figure 4*d*; see clip 5 in movie 1 in the electronic supplementary material). The three crows also made the correct choice on their first trial. The performance in this task ruled out the use of two independent associative rules based on the blue rim and the higher disc during the trap-tube tasks. In case success was due to a prior disposition to avoid holes, we also tested the three crows that failed the initial trap-tube on the trap-table task. All three of these crows failed in the trap-table task, indicating that they did not have such a disposition (figure 4*d*).

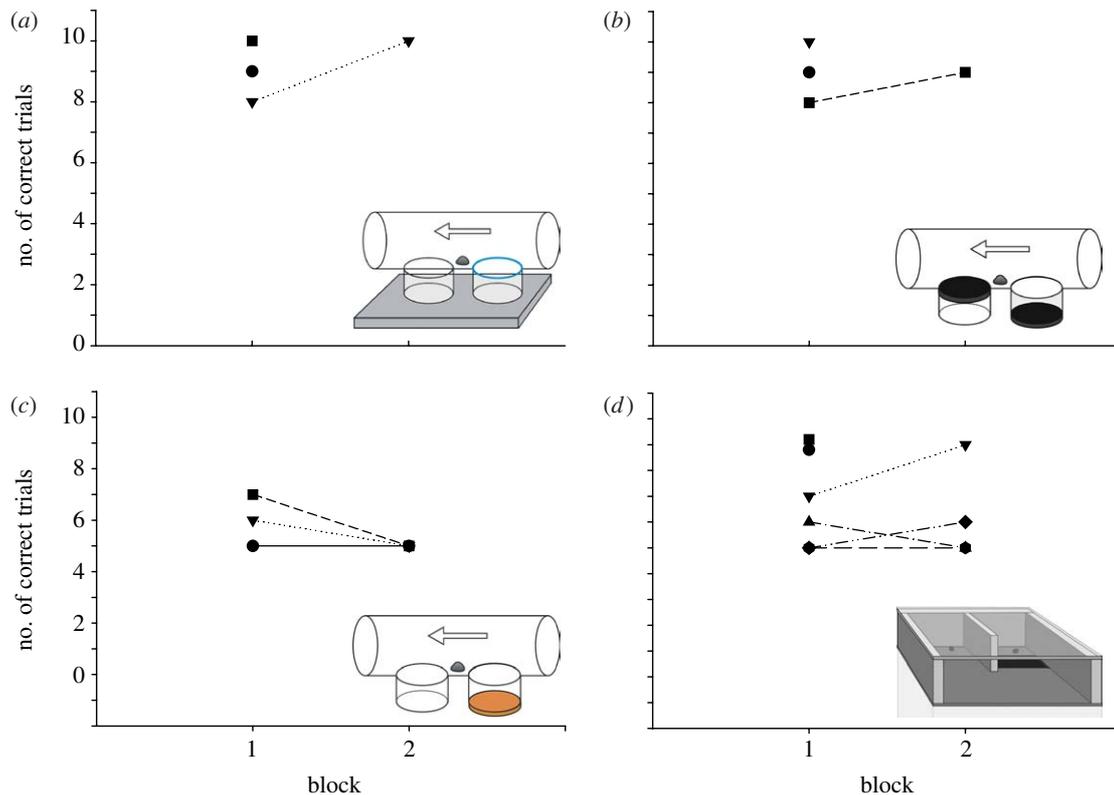


Figure 4. Results of the four transfer tasks. (a) Transfer 1: the only visual cue retained from the initial tube is the blue rim (circle, Obo; down triangle, Tiga; square, Slevin). (b) Transfer 2: the disc positions are the same as in the initial tube, but the discs are coloured black, and the blue rim is absent (circle, Obo; down triangle, Tiga; square, Slevin). (c) Transfer 3: the tube contains two holes, one with a base, making it a functional trap, and one without a base, making it a non-functional trap. Food can only be retrieved once it falls through the non-functional trap (circle, Obo; down triangle, Tiga; square, Slevin). (d) Transfer 4: the trap-table (circle, Obo; down triangle, Tiga; square, Slevin; diamond, Espanol; hexagon, Batou; up triangle, Egg).

#### 4. DISCUSSION

Three of the six crows learnt to solve the initial trap-tube. Their performance in the four transfer tasks demonstrated that they did not use one or multiple associative rules based on the arbitrary features in the trap-tube. The crows' success with the trap-table and failure with transfer 3, a tube with two holes, indicate that the three birds solved the initial trap-tube through sensitivity to the hole. The performance of the crows is consistent with that of one rook on the trap-tube problem (Seed *et al.* 2006). However, this rook was not tested on a functionally equivalent problem. The crows' performance in our experiments contrasts with a recent primate study where individuals from four ape species were unable to transfer knowledge from the trap-tube to the trap-table, or vice versa (Martin-Ordas *et al.* 2008).

Three crows failed the initial trap-tube task. Given that only the successful crows switched the side they were probing during the initial trap-tube task, inhibitory control may have been an important factor in their success. It would require strong inhibitory control for a crow to stop pulling meat towards itself and instead walk around the apparatus to probe from the opposite end. Inhibitory control is an important factor in problem solving by both children and non-human animals (Boysen *et al.* 1999, 2001; Passolunghi *et al.* 1999). The hypothesis that variation in inhibitory control might underlie the variation in crows' performance with the trap-tube task is supported by the way one crow failed the initial trap-tube. Espanol sometimes hesitated before pulling the meat into the trap; in 16.6 per cent of trials he momentarily halted pulling actions when the meat got to the edge of the trap, before

eventually pulling it into the trap. Despite his hesitancy, Espanol never switched to probing the other side of the trap during a trial. This suggests that although Espanol may have learnt when he would fail, he was unable to inhibit pulling the meat towards himself despite the presence of the trap.

A common dilemma in studies of animal cognition is that both high- and low-level explanations may account for apparently impressive performances. Before suggesting the existence of complex physical cognition in New Caledonian crows, several potential low-level explanations need to be eliminated. These include chance, visual and tactile generalization and prior dispositions. The first possibility is that the successful crows solved each transfer task by chance on the first trial, and then followed the rule 'do what was successful before'. This strategy would require spontaneous tracking of random switches in trap position. If the crows were capable of such tracking, it is unlikely they would have taken over a 100 trials on average to solve the initial trap-tube. Furthermore, analysis of the first-trial data in all four transfers shows that the three crows avoided the trap in 10 of the 12 first trials. Significantly, the first trial performances did not predict success in subsequent trials. For example, Tiga pulled the meat into the trap on the first trial of transfer 2, then significantly avoided the trap in the next 19 trials. Both Tiga and Slevin avoided the trap on their first trial of transfer 3, but then performed at chance levels in the next 19 trials.

The successful transfer to the trap-table indicates that the crows were sensitive to causal relations of the task only if this transfer was not possible through the generalization

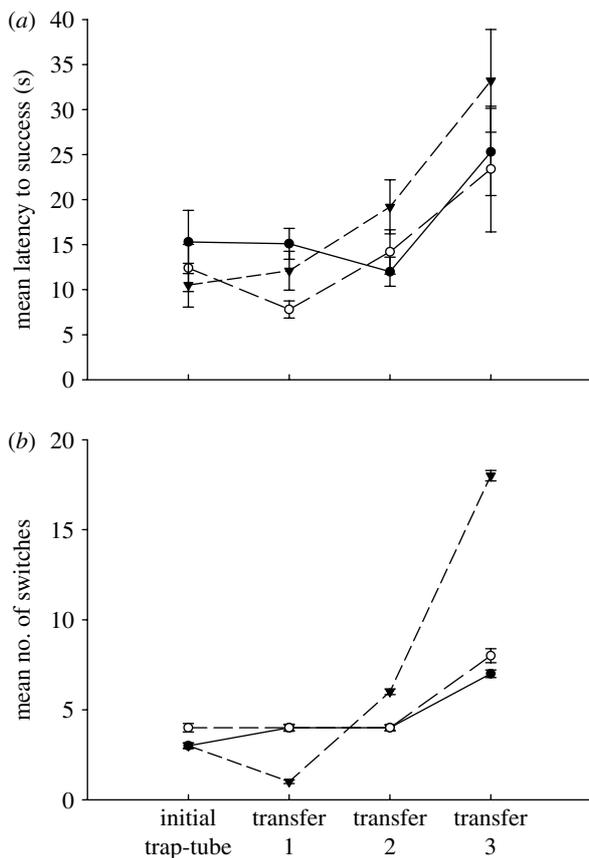


Figure 5. Comparison of latencies and switching rates ( $\pm$  s.e.) in four tasks with the trap-tube. (a) Comparison of latencies for the three successful crows in the initial trap-tube (final block only) and transfers 1–3 (first block only) (filled circle, Obo; open circle, Slevin; down triangle, Tiga). (b) Comparison of side-switching for the three successful crows in the initial trap-tube (final block only) and transfers 1–3 (first block only) (filled circle, Obo; open circle, Slevin; down triangle, Tiga).

of associative cues. Visual generalization operates through the identification of features that share similarities along one or more dimensions (Spence 1937; Ghirlanda & Enquist 2003). Shepard's law of generalization states that the probability of responding appropriately decreases exponentially with psychological distance between the test and novel stimuli (Shepard 1987). Therefore, the greater the perceptual differences between a previous and novel problem, the less likely it is that generalization can occur. The hole and continuous surface of the trap-tube differed from that of the trap-table in shape (circular hole versus square hole; concave surface versus flat surface), colour (transparent versus brown) and material (Perspex versus wood). The lack of perceptual similarities makes it unlikely that transfer to the trap-table could have occurred through the generalization of associative cues. Instead, it is more plausible that the crows transferred knowledge of the causal relations between the hole and the reward to the perceptually distinct trap-table problem. Mapping between visually distinct but functionally similar situations using causal relations is consistent with analogical reasoning (Gentner 1983; Goswami & Brown 1989; Gentner & Markman 1997).

Prior dispositions to avoid or learn about holes can be ruled out by the trap-table results. The failure of the three

unsuccessful crows with the trap-table indicates that the study birds did not have a predisposition to avoid holes. The trap-table transfer also excludes a related low-level explanation based on a prior disposition to have selective attention for holes. Search image biases developed in the crows' natural foraging might have caused them to associatively learn about holes simply because they were more salient. However, given the visual differences between the trap-tube and trap-table, the generalization of an associative rule based on the cue of hole position is an unlikely explanation for the successful crows' performances.

Tactile generalization can also be eliminated as an explanation. While the trap-tube and trap-table were visually distinct, the crows would have received similar tactile feedback from both problems, if they had probed the trap or continuous surface with the tool. However, there was little evidence of tactile searching behaviours during the first trial of each transfer. In 10 out of the 12 first trials, neither the continuous surface nor the trap was probed. Obo probed the trap on the first trial of transfer 3, and then pulled the meat into the same trap. Slevin probed the continuous surface on the first trial of transfer 2, although it was difficult to check whether this probing was directed at the surface or the meat close by. In a further four first trials, the tool tip very briefly touched the hole or continuous surface, before first contact with the meat, but the crows did not react to these contacts or repeat them.

Given the implausibility of the low-level explanations for the crows' behaviour, it appears that they solved the trap-tube and trap-table using the causal relationship surrounding object-hole interactions. This suggests that causal reasoning is a component of New Caledonian crows' cognition. However, compared with humans, this reasoning was slower and may have operated at a lower abstract level. The crows in our experiment required considerable experience with the initial trap-tube before they were able to regularly avoid the hole. They also failed in transfer 3 to switch spontaneously from using the hole as a causal feature to using the trap base as a causal feature. This suggests that the crows had knowledge of the meat's relation with the hole as a proximate causal regularity, but did not infer the existence of a distal causal mechanism (gravity). If the crows were capable of more sophisticated causal reasoning, they would have viewed the meat's relations with the hole and the trap base as two separate proximate causal regularities that were variants of the same distal causal mechanism (gravity). This would have led to a spontaneous sensitivity to the trap base as a causal feature. The crows' reasoning, therefore, appeared to be intermediate between 'weak causal knowledge' based on the associative learning of spatially and temporally contiguous events and 'strong causal knowledge' as seen in humans (Kummer 1995). The latter reasoning, through the inference of distal causal mechanisms, allows the rapid or *a priori* 'interpretation' of how events are related without multiple repetitions of these same events.

The results reported here provide the strongest evidence to date that non-human animals can use causal reasoning to solve complex physical problems. The crows identified a specific causal feature; they were sensitive to holes, not spatially and temporally contiguous arbitrary features. The crows also appeared to use the regularities in

how objects relate to surfaces; namely that objects only move horizontally along continuous, not discontinuous surfaces. Given the crows' success with the trap-table transfer task, our results also add substantial weight to the hypothesis that New Caledonian crows are capable of reasoning analogically (Taylor et al. 2007). Causal and analogical reasoning may form the basis of New Caledonian crow's exceptional tool skills (Taylor et al. 2007).

Our work was carried out under University of Auckland Animal Ethics Committee approval R602.

We thank W. Wardrobert and his family for access to their land and the Loyalty Islands Province for permission to work on Maré. We are grateful to M. Corballis, L. Hearne, S. Frisbee and R. Ross for helpful comments, D. Elliffe for statistical advice and V. Ward for the drawings. We also thank two anonymous reviewers for their useful suggestions. This work was supported by a Commonwealth Doctoral Scholarship (A.H.T.) and a grant from the New Zealand Marsden Fund (G.R.H. and R.D.G.).

## REFERENCES

- Blaisdell, A. P., Sawa, K., Leising, K. J. & Waldmann, M. R. 2006 Causal reasoning in rats. *Science* **311**, 1020–1022. (doi:10.1126/science.1121872)
- Boysen, S. T., Mukobi, K. L. & Berntson, G. G. 1999 Overcoming response bias using symbolic representations of number by chimpanzees (*Pan troglodytes*). *Anim. Learn. Behav.* **27**, 229–235.
- Boysen, S. T., Berntson, G. G. & Mukobi, K. L. 2001 Size matters: impact of item size and quantity on array choice by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **115**, 106–110. (doi:10.1037/0735-7036.115.1.106)
- Call, J. 2004 Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *J. Comp. Psychol.* **118**, 231–242. (doi:10.1037/0735-7036.118.2.232)
- Cunningham, C. L., Anderson, J. R. & Mootnick, A. R. 2006 Object manipulation to obtain a food reward in hooleck gibbons, *Bunopithecus hooleck*. *Anim. Behav.* **71**, 621–629. (doi:10.1016/j.anbehav.2005.05.013)
- Fujita, K., Kuroshima, H. & Asai, S. 2003 How do tufted capuchin monkeys (*Cebus apella*) understand causality involved in tool use? *J. Exp. Psychol. Anim. Behav. Process.* **29**, 233–242. (doi:10.1037/0097-7403.29.3.233)
- Gentner, D. 1983 Structure-mapping: a theoretical framework for analogy. *Cogn. Sci.* **7**, 155–170. (doi:10.1016/S0364-0213(83)80009-3)
- Gentner, D. & Markman, A. B. 1997 Structure mapping in analogy and similarity. *Am. Psychol.* **52**, 45–56. (doi:10.1037/0003-066X.52.1.45)
- Ghirlanda, S. & Enquist, M. 2003 A century of generalization. *Anim. Behav.* **66**, 15–36. (doi:10.1006/anbe.2003.2174)
- Girndt, A., Meier, T. & Call, J. 2008 Task constraints mask great apes' ability to solve the trap table task. *J. Exp. Psychol. Anim. Behav. Process.* **34**, 54–62. (doi:10.1037/0097-7403.34.1.54)
- Goswami, U. & Brown, A. L. 1989 Melting chocolate and melting snowmen: analogical reasoning and causal relations. *Cognition* **35**, 69–95. (doi:10.1016/0010-0277(90)90037-K)
- Hauser, M. D. 1997 Artifactual kinds and functional design features: what a primate understands without language. *Cognition* **64**, 285–308. (doi:10.1016/S0010-0277(97)0028-0)
- Hauser, M. & Spaulding, B. 2006 Wild rhesus monkeys generate causal inferences about possible and impossible physical transformations in the absence of experience. *Proc. Natl Acad. Sci. USA* **103**, 7181–7185. (doi:10.1073/pnas.0601247103)
- Hauser, M. D., Kralik, J. & Botto-Mahan, C. 1999 Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. *Anim. Behav.* **57**, 565–582. (doi:10.1006/anbe.1998.1032)
- Hauser, M. D., Pearson, H. & Seelig, D. 2002 Ontogeny of tool use in cottontop tamarins, *Saguinus oedipus*: innate recognition of functionally relevant features. *Anim. Behav.* **64**, 299–311. (doi:10.1006/anbe.2002.3068)
- Heyes, C. M. 1993 Anecdotes, training, trapping, and triangulating: do animals attribute mental states? *Anim. Behav.* **46**, 177–188. (doi:10.1006/anbe.1993.1173)
- Hume, D. 1739/1978 *A treatise on human nature*. Oxford, UK: Clarendon Press.
- Hunt, G. R. 1996 Manufacture and use of hook-tools by New Caledonian crows. *Nature* **397**, 249–251. (doi:10.1038/379249a0)
- Hunt, G. R. 2000a Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proc. R. Soc. B* **267**, 403–413. (doi:10.1098/rspb.2000.1015)
- Hunt, G. R. 2000b Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu* **100**, 109–114. (doi:10.1071/MU9852)
- Hunt, G. R. & Gray, R. D. 2004 The crafting of hook tools by wild New Caledonian crows. *Proc. R. Soc. B* **271**(Suppl.), S88–S90. (doi:10.1098/rsbl.2003.0085)
- Kenward, B., Rutz, C., Weir, A. A. S., Chappell, J. & Kacelnik, A. 2004 Morphology and sexual dimorphism of the New Caledonian crow *Corvus moneduloides*, with notes on its behaviour and ecology. *Ibis* **146**, 652–660. (doi:10.1111/j.1474-919x.2004.00299.x)
- Kummer, H. 1995 Causal knowledge in animals. In *Causal cognition. A multidisciplinary debate* (eds D. Sperber, D. Premack & A. J. Premack), pp. 26–39. Oxford, UK: Clarendon Press.
- Limongelli, L., Boysen, S. T. & Visalberghi, E. 1995 Comprehension of cause–effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **109**, 18–26. (doi:10.1037/0735-7036.109.1.18)
- Martin-Ordas, G., Call, J. & Colmenares, F. 2008 Tubes, tables and traps: great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Anim. Cogn.* **11**, 423–430. (doi:10.1007/s10071-007-0132-1)
- Mulcahy, N. J. & Call, J. 2006 How great apes perform on a modified trap-tube task. *Anim. Cogn.* **9**, 193–199. (doi:10.1007/s10071-006-0019-6)
- Mundry, R. & Fischer, J. 1998 Use of statistical programs for nonparametric tests of small samples often leads to incorrect *p*-values: examples from *Animal Behaviour*. *Anim. Behav.* **56**, 256–259. (doi:10.1006/anbe.1998.0756)
- O'Connell, S. & Dunbar, R. I. M. 2005 The perception of causality in chimpanzees (*Pan spp.*). *Anim. Cogn.* **8**, 60–66. (doi:10.1007/s10071-004-0231-1)
- Passolunghi, M. C., Cornoldi, C. & De Liberto, S. 1999 Working memory and intrusions of irrelevant information in a group of specific poor problem solvers. *Mem. Cognit.* **27**, 779–790.
- Penn, D. C. & Povinelli, D. J. 2007 Causal cognition in humans and nonhuman animals: a comparative, critical review. *Annu. Rev. Psychol.* **58**, 97–118. (doi:10.1146/annurev.psych.58.110405.085555)
- Penn, D. C., Holyoak, K. J. & Povinelli, D. J. 2008 Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behav. Brain. Sci.* **31**, 109–178. (doi:10.1017/S0140525X08003543)

- Povinelli, D. J. 2000 *Folk physics for apes: a chimpanzee's theory of how the world works*. Oxford, UK: Oxford University Press.
- Sabbatini, G. & Visalberghi, E. 2008 Inferences about the location of food in capuchin monkeys (*Cebus apella*) in two sensory modalities. *J. Comp. Psychol.* **122**, 156–166. (doi:10.1037/0735-7036.122.2.156)
- Santos, L. R., Pearson, H. M., Spaepen, G. M., Tsao, F. & Hauser, M. D. 2006 Probing the limits of tool competence: experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Anim. Cogn.* **9**, 94–109. (doi:10.1007/s10071-005-0001-8)
- Seed, A. M., Tebbich, S., Emery, N. J. & Clayton, N. S. 2006 Investigating physical cognition in rooks (*Corvus frugilegus*). *Curr. Biol.* **16**, 697–701. (doi:10.1016/j.cub.2006.02.066)
- Shepard, R. N. 1987 Toward a universal law of generalization for psychological science. *Science* **237**, 1317–1323. (doi:10.1126/science.3629243)
- Silva, F. J., Page, D. M. & Silva, K. M. 2005 Methodological–conceptual problems on the study of chimpanzees' folk physics: how studies with adult humans can help. *Learn. Behav.* **33**, 47–58.
- Spence, K. W. 1937 The differential response in animals to stimuli varying within a single dimension. *Psychol. Rev.* **44**, 430–444. (doi:10.1037/h0062885)
- Taylor, A. H., Hunt, G. R., Holzhaider, J. C. & Gray, R. D. 2007 Spontaneous metatool use by New Caledonian crows. *Curr. Biol.* **17**, 1504–1507. (doi:10.1016/j.cub.2007.07.057)
- Tebbich, S. & Bshary, R. 2004 Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Anim. Behav.* **67**, 689–697. (doi:10.1016/j.anbehav.2003.08.003)
- Visalberghi, E. & Limongelli, L. 1994 Lack of comprehension of cause–effect relations in tool-using capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **108**, 15–22. (doi:10.1037/0735-7036.108.1.15)
- Visalberghi, E. & Tomasello, M. 1998 Primate causal understanding in the physical and psychological domains. *Behav. Process.* **42**, 189–203. (doi:10.1016/S0376-6357(97)00076-4)
- Weir, A. S. & Kacelnik, A. 2006 A New Caledonian crow (*Corvus moneduloides*) creatively re-designs tools by bending or unbending aluminium strips. *Anim. Cogn.* **9**, 317–334. (doi:10.1007/s10071-006-0052-5)
- Weir, A. S., Chappell, J. & Kacelnik, A. 2002 Shaping of hooks in New Caledonian crows. *Science* **297**, 981. (doi:10.1126/science.1073433)