Downloaded from rspb.royalsocietypublishing.org on April 21, 2010

PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Complex cognition and behavioural innovation in New Caledonian crows

Alex H. Taylor, Douglas Elliffe, Gavin R. Hunt and Russell D. Gray

Proc. R. Soc. B published online 21 April 2010
doi: 10.1098/rspb.2010.0285

Supplementary data "Data Supplement"
http://rspb.royalsocietypublishing.org/content/suppl/2010/04/20/rspb.2010.0285.DC1.html

References **This article cites 31 articles, 7 of which can be accessed free**
http://rspb.royalsocietypublishing.org/content/early/2010/04/16/rspb.2010.0285.full.html#ref-list-1

P<P Published online 21 April 2010 in advance of the print journal.

Subject collections Articles on similar topics can be found in the following collections

behaviour (1184 articles)
cognition (294 articles)
evolution (1602 articles)

Email alerting service Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

Advance online articles have been peer reviewed and accepted for publication but have not yet appeared in the paper journal (edited, typeset versions may be posted when available prior to final publication). Advance online articles are citable and establish publication priority; they are indexed by PubMed from initial publication. Citations to Advance online articles must include the digital object identifier (DOIs) and date of initial publication.

To subscribe to *Proc. R. Soc. B* go to: **http://rspb.royalsocietypublishing.org/subscriptions**

This journal is © 2010 The Royal Society

PROCEEDINGS OF THE ROYAL SOCIETY B
FirstCite e-publishing
Proc. R. Soc. B
doi:10.1098/rspb.2010.0285
Published online

Complex cognition and behavioural innovation in New Caledonian crows

Alex H. Taylor*, Douglas Elliffe, Gavin R. Hunt and Russell D. Gray*

Department of Psychology, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

Apes, corvids and parrots all show high rates of behavioural innovation in the wild. However, it is unclear whether this innovative behaviour is underpinned by cognition more complex than simple learning mechanisms. To investigate this question we presented New Caledonian crows with a novel three-stage metatool problem. The task involved three distinct stages: (i) obtaining a short stick by pulling up a string, (ii) using the short stick as a metatool to extract a long stick from a toolbox, and finally (iii) using the long stick to extract food from a hole. Crows with previous experience of the behaviours in stages 1–3 linked them into a novel sequence to solve the problem on the first trial. Crows with experience of only using string and tools to access food also successfully solved the problem. This innovative use of established behaviours in novel contexts was not based on resurgence, chaining and conditional reinforcement. Instead, the performance was consistent with the transfer of an abstract, causal rule: 'out-of-reach objects can be accessed using a tool'. This suggests that high innovation rates in the wild may reflect complex cognitive abilities that supplement basic learning mechanisms.

Keywords: behavioural innovation; causal reasoning; New Caledonian crows

1. INTRODUCTION

Innovative behaviour is defined as '…the discovery of novel information, the creation of new behaviour patterns, or the performance of established behaviour patterns in a novel context' (Reader & Laland 2001). It has been shown that apes, corvids and parrots all innovate behaviours at higher rates in the wild than other primates and birds (Lefebvre *et al.* 1997*a*; Reader & Laland 2002). The reason for these higher rates is unclear (Lefebvre & Sol 2008). One possibility is that these three groups innovate using basic learning mechanisms just as other birds and primates do, but have 'more of the same'. That is, they can associatively learn rapidly. This allows them to learn the consequences of chance behavioural variants quickly, and so have increased rates of behavioural innovation. By contrast, slow associative learners will have greater difficulty innovating behaviours from accidental events because these events need to be repeated many times. An alternative possibility is that apes, corvids and parrots possess cognitive abilities more complex than simple learning mechanisms, which allow them to produce a greater variety of behavioural innovations.

Research on behavioural innovation has traditionally focused on the creation of novel behavioural patterns. Such 'linking' paradigms test whether an animal, having learned a number of behaviours in isolation, can then link them into a novel sequence during problem solving. This is different from training animals to carry out a novel 'chain' of different behaviours (Skinner 1953), where the links between behaviours are also trained. Linking paradigms have been solved by both chimpanzees (*Pan troglodytes*) and pigeons (*Columba livia*; Kohler 1925; Epstein *et al.* 1984). Both species can push a box under an out-of-reach reward and then jump on the box to get the reward. Crucially, spontaneous performances in both these species only emerge if a subject has previously learned each of the behaviours required for the solution (Birch 1945; Epstein *et al.* 1984). With such training, pigeons are able to link four behaviours together spontaneously to obtain a reward: opening a door, pushing a box from behind the door to under the reward, climbing onto the box and pecking at the reward (Epstein 1987). When presented with a problem requiring the use of a key to open a box to get the key to the next box and so on, chimpanzees are able to link up to 10 behaviours (Dohl 1968). Epstein *et al.* (1984) suggested that the linking of previously learned behaviours into a novel sequence was the product of simple, associative learning mechanisms such as competition between behavioural repertories, automatic chaining and functional generalization. He reached this conclusion because the production of behavioural sequences was dependent only on sufficient experience with each individual behaviour. Nevertheless, linking might be dependent on the ability of an animal to organize learned behaviours hierarchically into behavioural chains with goals and subgoals, although, to date, there is no conclusive evidence for this (Byrne & Byrne 1993; Byrne & Russon 1998).

Little is currently known about the cognition required for another type of innovation, the use of established behaviours in novel contexts. For a context to be different, the goal that the behaviour is directed towards must be sufficiently novel to rule out stimulus generalization as the cognitive mechanism involved in the behavioural innovation. For example, the use of a foraging behaviour on an unripe fruit that is slightly different in colour or shape to those usually eaten can be accounted for by stimulus generalization (Pavlov 1927; Spence 1937;

---

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

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2010.0285 or via http://rspb.royalsocietypublishing.org.

Received 10 February 2010
Accepted 31 March 2010

Shepard 1987) and thus cannot be considered a behavioural innovation. The use of a foraging behaviour, previously used for obtaining fruit, on a termite mound cannot be explained by stimulus generalization owing to the perceptual distinctness of the new goal, and therefore can be considered a behavioural innovation. Such behavioural innovation requires the flexible integration of the newly innovated behaviours, i.e. those behaviours that are being used in a novel context into a novel behavioural sequence. Therefore, it may also require the ability to organize behaviour hierarchically (Byrne & Byrne 1993; Byrne & Russon 1998).

A number of recent studies have shown that corvids and apes are able to use established behaviours in novel contexts (Mulcahy *et al.* 2005; Taylor *et al.* 2007). Other studies have even suggested that rooks and chimpanzees are capable of creating entirely novel behaviours (Weir *et al.* 2002; Mendes *et al.* 2007; Bird & Emery 2009), though in some of these studies, aspects of the novel behaviour could potentially have been derived from the transfer of tool manufacturing or nest-building behaviours to a novel context. For example, the ability of Betty, a New Caledonian crow, to bend a wire (a novel material) into a hook may have been based on the transfer of twisting and yanking motor patterns previously used for removing side branches from twigs. Claims that such innovative behaviours reflect the use of cognitive mechanisms other than associative learning are controversial (Emery 2006; Hunt *et al.* 2006; Clayton 2007; Lind *et al.* 2009; Shettleworth 2009). One area of debate surrounds the cognition required to solve metatool tasks. During a metatool problem, an animal that has previously only used tools to get food must use a tool in a novel context, to obtain another, functional tool. Although only a small number of metatool studies have been conducted, both apes and corvids have performed much better than monkeys. Metatool problems have been spontaneously solved on the first trial by 50 per cent of great apes (Kohler 1925; Mulcahy *et al.* 2005), 50 per cent of New Caledonian crows (Taylor *et al.* 2007; Wimpenny *et al.* 2009) and 100 per cent of rooks (Bird & Emery 2009), but only by 13 per cent of capuchins (*Cebus apella*) (Parker & Poti 1990; Anderson & Henneman 1994).

The transfer of the abstract, causal rule 'out-of-reach objects can be accessed using a tool', would allow an animal to solve metatool problems where one tool must be used to gain access to another tool (Taylor *et al.* 2007). New Caledonian crows have been shown to use such rules when solving other physical problems (Taylor *et al.* 2009*a*,*b*). However, it has also been suggested that animals can solve metatool problems through chaining and conditional reinforcement (Clayton 2007; Wimpenny *et al.* 2009). A recent study conducted by Wimpenny *et al.* (2009) found that after metatool use had been innovated by a New Caledonian crow, the bird continued to use a short tool to get the long tool in the absence of food. This behaviour showed that the long stick was a desirable object in its own right for the crow, probably owing to it being associated with food in the past. Therefore, it is possible that initial metatool use is because of New Caledonian crows having a natural tendency to '…attempt to retrieve attractive objects that are out of their reach…' (Clayton 2007). However, an alternative explanation is that the crow transferred a causal rule during initial metatool use but when the food was later removed the crow was unable to inhibit metatool behaviour owing to it having been associated with food in the past. Therefore, continued metatool use in the absence of food cannot be used to make conclusions about the cognition initiating this behaviour.

Here, we directly tested whether conditional reinforcement can provide a complete explanation for metatool use. A key feature of conditional reinforcement is that it is bidirectional: objects that have been positively rewarded are expected to be attractive to an animal, and objects that have been associated with negative consequences are expected to be avoided. Therefore, we added an additional step to the previous metatool problem we presented to New Caledonian crows (Taylor *et al.* 2007). Instead of placing the short stick in front of the toolbox containing a tool of sufficient length to extract food, we hung it from a string 1 m from the toolbox (figure 1). We expected this object to become a conditional punisher because in training the crows were unable to extract food from the hole with it. The short tool therefore would only have been associated with ineffective tool use and so should be an unattractive object. The crow's motivation to obtain the short stick could only be increased if it knew that the short stick could be used to get the long tool, and so the food. A conditional reinforcement account, therefore, predicts that a crow with no experience of metatool use should fail the problem. This is because the crow has never been rewarded for using the short tool to access the long tool, meaning there would be no reinforcement history to outweigh the crow's experience of the short tool as a conditional punisher. The punishing power of the short tool could only be negated *after* the solution of the problem, and until that occurred the crow should treat the short tool as an unattractive object. However, if crows initially carried out metatool use through the transfer of a causal rule, then they should be highly motivated to obtain the short stick and use it as a metatool because they know that it can be used to access the out-of-reach long tool. We presented this problem to two groups of crows. The 'innovation' group had only used string and tools to access food, and so needed to use both string pulling and tool use in novel contexts. The 'component' group had previously used string and tools independently to obtain other tools, and so simply needed to link six behaviours (1, pulling up the string; 2, removing the short tool; 3, transporting it to the toolbox; 4, extracting the long tool; 5, transporting the long tool to the hole; 6, extracting the meat) to solve the problem. This group was tested first to confirm that New Caledonian crows could link six behaviours together, which would allow us to rule out problems with linking as an explanation for any failure by the innovation group crows.

2. MATERIAL AND METHODS

We carried out the experiment with seven wild crows captured on the island of Maré, New Caledonia. Six of the crows (Djinn, Sam, Korben, Caspar, Lazlo, Chocho) were adults more than 2 years old and one (Maya) was a subadult less than 2 years old. On the basis of sexual size dimorphism (Kenward *et al.* 2004), Maya, Djinn and Sam were females. The crows were housed in a five-cage outdoor

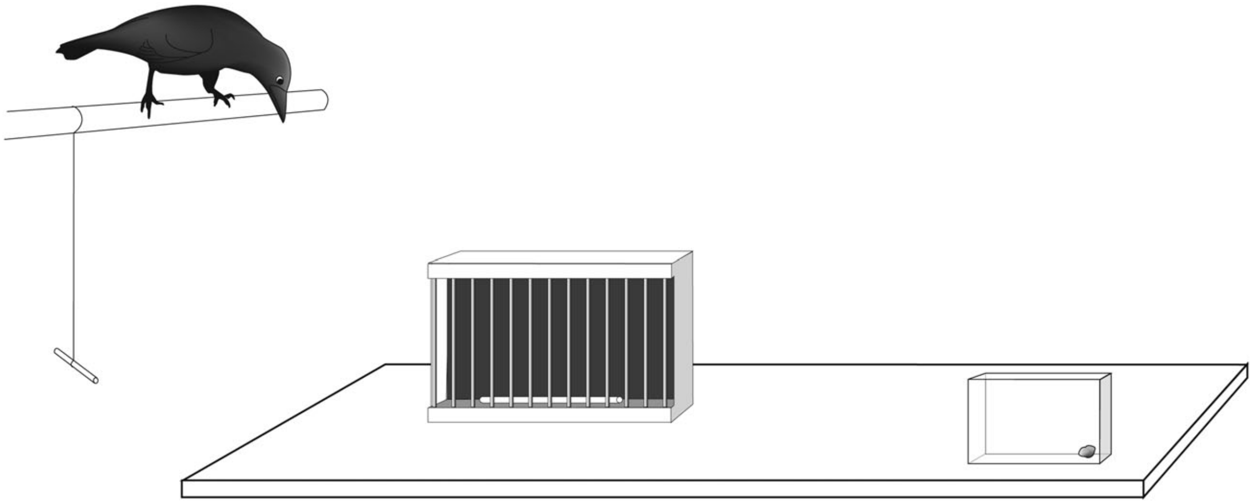


Figure 1. The three-stage metatool problem: crows had to pull up the string, remove the short tool, take it to the toolbox, extract the long stick, take the long stick to the hole and extract the meat.

aviary close to the location of capture; the cages varied in size but were all at least 8 m^2 in area and 3 m high. All crows were released at their site of capture after testing. On arrival into the aviary, all crows were tested for their tool preferences by presenting them with a 12 cm long stick tool and a 12 cm long pandanus tool, both of which could be used to extract food from a 7 cm deep hole in a log. After this experiment they started the metatool training.

The component group (Lazlo, Chocho and Korben) were given 10 familiarization trials in six tasks before testing began; each task was presented independently of the others. The six tasks were: (1) extracting meat from a 15 cm deep horizontal hole with an 18 cm long stick that we provided, (2) withdrawing an 18 cm long stick from the barred toolbox and extracting the meat from the hole (one end of the stick extended out between the bars making it easy for crows to see and extract the tool with their bills), (3) using a non-functional 5 cm long stick to try and extract the meat from the 15 cm deep hole, (4) pulling up a 40 cm long length of string with the meat tied to the end of it, (5) using the short tool to extract the long tool from the toolbox (metatool use), and (6) pulling up a 40 cm long string with the 18 cm long stick tied to its end and taking it to the hole to extract the meat. The familiarization trials were carried out in blocks of five, in the following task sequence: (1), (2), (3), (4), (5) (6), (1), (2), (3), (4), (5) and (6). The blocks of 10 familiarization trials given to the innovation group (Sam, Caspar, Maya, Djinn) omitted tasks (5) and (6); their task sequence was therefore: (1), (2), (3), (4), (1), (2), (3) and (4).

The experimental trials were 10 min long. Crows were given two blocks of five trials. To ensure that the birds were exposed to the problem for standardized blocks of time, the position of the short stick was reset if a bird moved and then discarded it before the 10 min trial period ended. Testing continued until a crow had solved the task in at least 80 per cent of trials across two consecutive five-trial blocks.

3. RESULTS

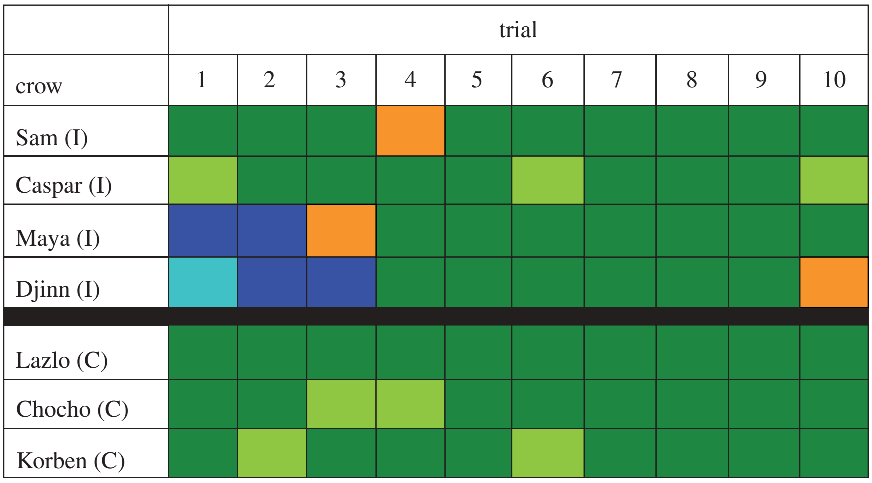
(a) *Training*

The behaviour of the innovation group during the training with the short stick was the same for each of the four birds. The crows first probed into the long hole with the short stick but could not get the food (mean of 5.25 trials: range 2–7, $n = 4$; time spent probing during any one probing event: mean of 3.9 s, range 1–7 s, $n = 4$). They then stopped probing into the long hole and instead approached the apparatus, picked up the short tool and then discarded it (mean of two trials: range 1–3, $n = 4$). Finally the crows approached the long hole, inspected the apparatus but did not pick up the short tool (mean of 2.75 trials: range 1–6, $n = 4$).

(b) *Three-step solutions*

All three crows in the component group solved the three-stage problem on the first trial without error (figure 2). That is, they inspected the apparatus then pulled up the string, removed the short tool and flew to the toolbox with it, extracted the long tool with the short one, then finally took the long tool to the hole and extracted the meat. These crows inspected the apparatus for a short time on the first trial before solving the problem (mean time ± s.e.m.: 29.6 s ± 4.4).

Two crows (Sam and Caspar) in the innovation group also solved the problem on the first trial (figure 2). Sam did so spontaneously without error after inspecting the apparatus for 110 s (her first trial performance is shown in the electronic supplementary material, movie S1). Caspar inspected the apparatus for 43 s, then pulled up and dropped the string. He then inspected the apparatus again for 40 s before solving the problem. After he obtained the short tool he inspected the hole, but did not use the tool in the hole. He then took the short tool to the toolbox, extracted the long tool and got the meat out of the hole. Maya solved the problem on her third trial and Djinn on the fourth trial. Maya pulled up and then dropped the string in her first three trials. In the first two trials, she pulled the short tool off the string and then dropped it. In her third trial, after first pulling up then dropping the string, she pulled up the string, took the short stick and used it in the hole, then took it to the toolbox and successfully solved the problem. Djinn pulled up and dropped the string in her first three, unsuccessful trials. She also pulled the short tool off the string and discarded it in the second and third



	trial									
crow	1	2	3	4	5	6	7	8	9	10
Sam (I)	🟩	🟩	🟩	🟧	🟩	🟩	🟩	🟩	🟩	🟩
Caspar (I)	🟢	🟩	🟩	🟩	🟩	🟢	🟩	🟩	🟩	🟢
Maya (I)	🟦	🟦	🟧	🟩	🟩	🟩	🟩	🟩	🟩	🟩
Djinn (I)	🔵	🟦	🟦	🟩	🟩	🟩	🟩	🟩	🟩	🟧
Lazlo (C)	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
Chocho (C)	🟩	🟩	🟢	🟢	🟩	🟩	🟩	🟩	🟩	🟩
Korben (C)	🟩	🟢	🟩	🟩	🟩	🟢	🟩	🟩	🟩	🟩

Figure 2. Trial-by-trial description of the experiment: innovation group (I) and component group (C). Colour bar: dark green, solves problem; light green, interacts with string, then solves problem; orange, takes short tool off string, probes hole, then solves problem; dark blue, interacts with string, takes short tool off string, drops; light blue, interacts with string, leaves.

trials. In the successful fourth trial Djinn solved the problem without error.

4. DISCUSSION

The success of the component group showed that New Caledonian crows can spontaneously link up to six learned behaviours into a novel behavioural pattern. Sam's performance showed that New Caledonian crows can also do this while using two behaviours in novel contexts. Her error-free performance was identical to that of the three crows in the component group. However, the performances of the other three crows in the innovation group were not spontaneous. Caspar solved the problem in the first trial, but only after first pulling and then dropping the string. The other two crows from the innovation group made several errors and took up to four trials to solve the problem.

The consistent pattern of behaviour during training sessions with the short stick shows that this object became a conditional punisher for the crows. Over the 10 training trials, the crows first stopped probing with the short tool then eventually stopped interacting with it in any way, despite the food being in close proximity and inaccessible. As the short tool had become an unattractive object for the crows, the conditional reinforcement hypothesis predicts that any behaviour directed towards it during initial problem-solving would extinguish very quickly. For the three crows other than Sam in the innovation group, this appeared to be the case because they dropped the string and/or short stick several times before solving the problem. However, all these crows subsequently retrieved and used the short stick as a metatool. The conditioned ability of the short stick to punish behaviour must therefore have dissipated, but what mechanism or new experience could have led to this? For the innovation group, the short stick was never paired with a conditioned reinforcer (the long stick), let alone with primary reinforcement until the successful solution of the complete problem (i.e. extracting the meat with the long tool). In other words, any new experience that could have lead to the short stick losing its punishing qualities could only have occurred *after* the crows had used the short stick, the very behaviour which should have been punished. In fact, the experience of the crows that initially pulled on the string before stopping and/or retrieved and then discarded the short stick should have increased, not decreased, the conditioned punishing power of the short stick. This is because any interaction with the short stick continued to be followed by negative consequences, rather than positive reinforcement. Therefore, conditional reinforcement seems an unlikely explanation for how the crows in the innovation group solved the metatool task.

Can the results be explained by other simple cognitive mechanisms? Epstein *et al.* (1984) suggested that the linking of learned behaviour into a novel sequence was owing to the competition between behavioural repertories, automatic chaining and functional generalization. While such processes may explain the performance of the component group, they cannot explain the innovation group's performance. Epstein's work showed that the crucial requirement for successful linking is the training on each specific component of the behavioural sequence. The crows in the innovation group had no experience of metatool use or of pulling up a tool tied to the string.

Resurgence has also been proposed as a potential candidate for the generation of behavioural innovation (Shettleworth 2009). When behaviour is extinguished before or while a second one is reinforced, it can reappear when the second behaviour is subsequently extinguished. Such an account would predict that when the crows could no longer obtain the long tool in the toolbox, the extinguished behaviour of probing the hole with the short tool should return. In our previous experiment (Taylor *et al.* 2007), six out of seven crows attempted to probe the toolbox containing the tool on their first attempt rather than the hole. In the current experiment, three out of four crows in the innovation group first probed the tool box rather than the hole. Resurgence cannot explain why the crows generated metatool use instead of the previously extinguished behaviour of probing the hole with the short stick.

A final possibility is that the crows' performance was based on a propensity to both pull up the string irrespective of the object at the end and to probe into dark places with tools. However, a recent string-pulling study conducted with New Caledonian crows (Taylor *et al.* 2010) showed that they rarely pulled up the string with a non-food item at the end when given the choice between string with meat on it and string with a rock. All 12 crows in the study significantly preferred to select the string with the meat attached rather than the string with the rock (in 90.8% of 240 trials). Eleven of the 12 crows chose the string with the meat rather than the one with the rock on their first trial. Therefore, string-pulling by New Caledonian crows is goal-directed because these crows do not pull up string irrespective of the object at its end. Early in their tool development New Caledonian crows probe with sticks into holes and on continuous surfaces where there is no food (Kenward *et al.* 2006). However, such behaviour does not explain why they would perform the metatool use. Kenward *et al.*'s (2006) study also showed that this behaviour disappears during tool development as the juvenile crows learn how to use their tools to obtain food. That is, crows appear to learn when and where to probe based on the reinforcement history of tool use. In our previous study (Taylor *et al.* 2007), crows were given the choice of a toolbox containing a tool and one containing a rock. If crows were simply following a disposition to probe into dark places, then they should have randomly chosen between the two tool boxes. However, all the crows in the study initially probed the toolbox with a long tool inside it. Unrewarded probing during metatool use is, therefore, directed only towards an appropriate goal, the long tool, unlike the early tool use of juveniles.

The results here show that the term 'spontaneous' should be more clearly defined in behavioural studies as it implies two properties: immediacy and lack of explicit training. These properties are not necessarily related. Sam's behaviour in the experiment was both immediate and untrained. The behaviour of the other crows in the innovation group (Caspar, Maya and Djinn) was not immediate (although it was strikingly rapid), but it was untrained. String-pulling by these crows during their first test trials was not reinforced, because it only resulted in obtaining the previously ineffective short stick, a conditioned punisher. However, the behaviour persisted and these three crows retrieved the short stick after only a small number of trials and used it to obtain the long stick, which they had never been trained to do.

This is not to say that operant conditioning plays no part in the solution of problems of this type, or in the innovation of behaviour. Clearly, behaviours that are followed by reinforcement—successful problem solution in this case—are more likely to be repeated than behaviours that are not, and reaching an intermediate stage in problem solution is likely to reinforce earlier steps. Also, it is well established that variability in behaviour—for example, innovation—is itself a conditionable property of behaviour. Morris (1987) and Page & Neuringer (1985) have shown that pigeons can learn to emit sequences of behaviour that they have never previously performed if reinforcement is contingent on such innovation. Finally, there is evidence for both conditional reinforcement and resurgence in the data presented here. Three innovation group crows pulled up the short stick and then discarded it, suggesting that they initially treated the short stick as a conditional punisher. However, conditional reinforcement does not explain the spontaneous, error-free solution by the fourth crow, or the eventual solutions by the other three crows. One of the four crows first took the short stick and probed in the hole with it, which is suggestive of resurgence. However, resurgence does not explain why three innovation group crows initially performed metatool use, or why this one crow subsequently did so. Therefore, the results show that a simple associative account alone is not sufficient to explain the successful behaviour of the innovation group crows.

Previously we suggested that New Caledonian crows use the transfer of a causal rule (out-of-reach objects can be accessed using a tool) to solve a metatool problem (Taylor *et al.* 2007). However, Wimpenny *et al.* (2009) claimed that metatool use does not require the transfer of such a rule because New Caledonian crows that had not previously retrieved tools from tubes with their bills failed a metatool problem. Furthermore, the crows also struggled to match the tool length to the task requirements. However, the inexperienced crows may have failed for several reasons: a lack of habituation to the apparatus, a lack of attention to the tool-tubes because of their previous irrelevancy, or individual variation in New Caledonian crows' cognitive abilities. Taylor *et al.* (2007) found that 43 per cent of crows solved the metatool problem on their first trial after all birds received the same training. In Wimpenny *et al.* (2009), 57 per cent of the crows solved the problem on the first trial, despite differences in training. Thus, it is possible that the failure of the inexperienced crows in Wimpenny *et al.*'s study may be owing to individual differences in cognitive ability rather than previous training experience.

The failure of the crows in Wimpenny *et al.* (2009) to match tool length to the task requirements may also be owing to reasons other than a lack of causal knowledge, such as inhibition, use of tools for depth gauging or conditional reinforcement. That is, the crows may not have been able to inhibit probing when close to the food, they may have used such probing to estimate distance and they may have been affected by the previous reinforcement history of a tool. Matching 'perceptual distance to food' and 'tool length' may well require different cognitive abilities to those required to form an abstract rule based on the functionality of tools in general. There is no theoretical reason why we would expect an animal that understands that tools can be used in a general way to obtain out-of-reach objects, to also be able to perfectly assess which tool it needs for a particular job. Indeed, not even humans match tool length to the distance to a reward, which suggests that it is unrealistic to expect New Caledonian crows to show such behaviour (Silva & Silva 2010).

Recent work has suggested that New Caledonian crows possess causal reasoning based on an understanding of object–object interactions (Taylor *et al.* 2009*a*,*b*). Three New Caledonian crows learned to solve a trap-tube problem where meat had to be extracted from a horizontal tube while avoiding a trap (Taylor *et al.* 2009*a*). The crows' performance with different configurations of the trap-tube apparatus suggested that they had used the position of the food relative to the hole to solve the problem. Sensitivity to this relation was conditional on the hole being in a functional position on the lower surface of the tube (Taylor *et al.* 2009*b*). After learning to solve the trap-tube the crows then spontaneously solved a perceptually distinct trap-table problem. These results show that after around 100 trials with the initial trap-tube apparatus, the crows had learned an abstract, causal rule: 'avoid pulling meat behind a hole, if the hole is in a functional position', which they then transferred to novel apparatus. The transfer of a causal rule could have also produced the metatool performances seen in our current study. That is, crows could have learned from prior experience of normal tool use that out-of-reach objects can be accessed using a tool. This rule was then transferred to the novel metatool problem and so increased the motivation of the crows to obtain the short stick. Thus the crows were able to stop treating the short stick as a conditional punisher. Such an explanation is plausible, given that the results here allow us to reject the null hypothesis that metatool use is produced by simple learning mechanisms. Further work on abstract rule learning in corvids is required to strengthen support for this hypothesis.

The crows' performance here shows that behavioural innovation, particularly the use of behaviours in novel contexts, can be underpinned by cognitive mechanisms that are more complex than, but supplement, simple learning mechanisms. This raises the intriguing possibility that the high rates of innovation seen in other corvids, parrots and apes may also reflect the presence of complex cognitive abilities that supplement associative learning mechanisms.

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 Province des Iles Loyauté for permission to work on Maré. This work was supported by the Cogito Foundation and a Commonwealth Doctoral Scholarship (A.H.T.) and a grant from the New Zealand Marsden Fund (G.R.H. and R.D.G.). We are grateful to V. Ward for drawing figure 1.

REFERENCES

Anderson, J. & Henneman, M. 1994 Solutions to a tool-use problem in a pair of *Cebus Apella*. *Mammalia* **58**, 351–361. (doi:10.1515/mamm.1994.58.3.351)

Birch, H. 1945 The relation of previous experience to insightful problem-solving. *J. Comp. Psych.* **38**, 367–383. (doi:10.1037/h0056104)

Bird, C. D. & Emery, N. J. 2009 Insightful problem solving and creative tool modification by captive non tool-using rooks. *Proc. Natl Acad. Sci. USA* **106**, 10 370–10 375. (doi:10.1073/pnas.0901008106)

Byrne, R. & Byrne, A. 1993 Complex leaf-gathering skills of mountain gorillas (*Gorilla g. Berengei*): variability and standardisation. *Am. J. Primatol.* **31**, 521–546.

Byrne, R. & Russon, A. 1998 Learning by imitation: a hierarchical approach. *Behav. Brain Sci.* **21**, 667–721. (doi:10.1017/S0140525X98001745)

Clayton, N. S. 2007 Animal cognition: crows spontaneously solve a metatool task. *Curr. Biol.* **17**, R894–R895. (doi:10.1016/j.cub.2007.08.028)

Dohl, J. 1968 Uber die Fahigkeit einer Schimpansin, Umwege mit selbststandigen Zwischenzielen zuuberblicken (The ability of a female chimpanzee to overlook intermediate goals). *Z. Tierpsychol.* **25**, 89–103.

Emery, N. J. 2006 Cognitive ornithology: the evolution of avian intelligence. *Phil. Trans. R. Soc. B* **361**, 23–43. (doi:10.1098/rstb.2005.1736)

Epstein, R. 1987 The spontaneous interconnection of four repertoires of behavior in a pigeon. *J. Comp. Psychol.* **101**, 197–201. (doi:10.1037/0735-7036.101.2.197)

Epstein, R., Kirshnit, C. E., Lanza, R. P. & Rubin, L. C. 1984 'Insight' in the pigeon: antecedents and determinants of an intelligent performance. *Nature* **308**, 61–62. (doi:10.1038/308061a0)

Hunt, G. R., Rutledge, R. B. & Gray, R. D. 2006 The right tool for the job: what strategy do wild New Caledonian crows use? *Anim. Cogn.* **9**, 307–316. (doi:10.1007/s10071-006-0047-2)

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)

Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A. 2006 Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Anim. Behav.* **72**, 1329–1343. (doi:10.1016/j.anbehav.2006.04.007)

Kohler, W. 1925 *The mentality of apes*, 2nd edn. New York, NY: Harcourt, Brace & Co. (transl. from German by E. Winter).

Lefebvre, L. & Sol, D. 2008 Brains, lifestyles and cognition: are there general trends? *Brain Behav. Evol.* **72**, 135–144.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997 Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560. (doi:10.1006/anbe.1996.0330)

Lind, J., Ghirlanda, S. & Enquist, M. 2009 Insight learning or shaping? *Proc. Natl Acad. Sci. USA* **106**, E76. (doi:10.1073/pnas.0906120106)

Mendes, N., Hanus, D. & Call, J. 2007 Raising the level: orangutans use water as a tool. *Biol. Lett.* **3**, 453–455. (doi:10.1098/rsbl.2007.0198)

Morris, C. J. 1987 The operant conditioning of response variability: free-operant versus discrete-response procedures. *J. Exp. Anal. Behav.* **47**, 273–277. (doi:10.1901/jeab.1987.47-273)

Mulcahy, N. J., Call, J. & Dunbar, R. I. M. 2005 Gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) encode relevant problem features in a tool-using task. *J. Comp. Psychol.* **119**, 23–32. (doi:10.1037/0735-7036.119.1.23)

Page, S. & Neuringer, A. 1985 Variability is an operant. *J. Exp. Psychol.: Anim. Behav. Process.* **11**, 429–452. (doi:10.1037/0097-7403.11.3.429)

Parker, S. T. & Poti, P. 1990 The role of innate motor patterns in ontogenetic and experiential development of intelligent use of sticks in Cebus monkeys. In *'Language' and intelligence in monkeys and apes: comparative development perspectives* (eds S. T. Parker & K. R. Gibson), pp. 219–243. New York, NY: Cambridge University Press.

Pavlov, I. P. 1927 *Conditioned reflexes*. London, UK: Dover Press.

Reader, S. M. & Laland, K. N. 2001 Primate innovation: sex, age and social rank differences. *Int. J. Primatol.* **22**, 787–805. (doi:10.1023/A:1012069500899)

Reader, S. M. & Laland, K. N. 2002 Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441. (doi:10.1073/pnas.062041299)

Shepard, R. N. 1987 Toward a universal law of generalization for psychological science. *Science* **237**, 1317–1323. (doi:10.1126/science.3629243)

Shettleworth, S. J. 2009 *Cognition, evolution and behaviour*. Oxford, UK: Oxford University Press.

Silva, F. J. & Silva, K. M. 2010 How do adult humans compare with New Caledonian crows in tool selectivity? *Learn. Behav.* **38**, 87–95. (doi:10.3758/LB.38.1.87)

Skinner, B. F. 1953 *Science and human behavior.* New York, NY: Macmillan.

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)

Taylor, A. H., Hunt, G. R., Medina, F. S. & Gray, R. D. 2009*a* Do New Caledonian crows solve physical problems through causal reasoning? *Proc. R. Soc. B* **276**, 247–254. (doi:10.1098/rspb.2008.1107)

Taylor, A. H., Hunt, G. R., Roberts, R. & Gray, R. D. 2009*b* Causal reasoning in New Caledonian crows: ruling out spatial analogies and sampling error. *Comm. Integ. Biol.* **2**, 311–312.

Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R. & Gray, R. D. 2010 An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PloS ONE* **5**, e9345. (doi:10.1371/journal.pone.0009345)

Weir, A. A. S., Chappell, J. & Kacelnik, A. 2002 Shaping of hooks in New Caledonian crows. *Science* **297**, 981. (doi:10.1126/science.1073433)

Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, R. & Kacelnik, A. 2009 Cognitive processes associated with sequential tool use in New Caledonian crows. *PLoS ONE* **4**, e6471. (doi:10.1371/journal.pone.0006471)