

Cognitive adaptations for tool-related behaviour in New Caledonian Crows

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Introduction

In the semi-tropical rain forest of the Pacific islands of New Caledonia, a crow detects the presence of a succulent grub (a beetle larva) deep in an inaccessible burrow in a tree. The crow flies to a nearby tree, breaks off a small branch, and removes leaves and minor twiglets, until a stick is left. The crow returns and, holding the twig in its beak, probes into the burrow until the grub has grasped the tip with its mouthparts. The crow then slowly withdraws the stick to expose and eat the grub. We know from laboratory studies that these crows can prepare twigs of different lengths or diameters, depending on their needs, and that they can also make tools of many different shapes for other purposes.

Elsewhere in the tree, a spider moves between the branches and the ground, releasing various mixtures of liquid proteins with different proportions to form different kinds of silk on its trail. The spider's movements are such that the trail of silk forms a perfectly designed web with a sticky spiral held by strong, non-sticky lines supporting the structure. This web building is achieved for an almost infinite variety of geometric configurations of the branches that provide potential support, thus creating a new solution to each problem. When the web is finished, the spider waits at its hub until an insect is trapped, when its own reward materialises.

Meanwhile, at a laboratory of artificial intelligence, a robot has been trained to select among a hammer, a spanner, and a screwdriver when presented with tasks involving nails, bolts, or screws, respectively. Using its experience, the robot recognises tools by decomposing images into segments of component shapes, somewhat like a cubist depiction of a natural object. On one occasion, the robot is presented with a nail and a piece of wood. The robot faces these materials and turns toward the tool panel; but, on this day, the experimenters have forgotten to hang the hammer in place. The robot "hesitates" in front of the panel, and finally picks the screwdriver, turns to the wood and nail and, holding the screwdriver by its blade, proceeds to hammer the nail into the wood by hitting it with the screwdriver's handle. The robot had never before done such a thing¹.

New Caledonian crows, spiders, and robots use and can construct objects outside their own body ("tools") to act on the outside world toward some goal. In all cases, each instance of tool making or use is different from previous ones, so that variability in the tasks' needs leads to variations in behaviour. Tool use is considered by many to be one of the defining features of advanced intelligence and to have played an important role in, or at least to have been correlated with, the specific features of human evolution. Quotes like the following are not rare:

"The first indications that our ancestors were in any respect unusual among animals were our extremely crude stone tools that began to appear in Africa by around two-and-a-half million years ago. The quantities of tools suggest that they were beginning to play a regular, significant role in our livelihood. Among our closest relatives, in contrast, the pygmy chimpanzee and gorilla do not use tools, while the common chimpanzee occasionally makes some rudimentary ones but hardly depends on them for its existence. [...] Clear evidence of a Great Leap Forward in our behaviour appears suddenly in Europe around 40,000 years ago,

coincident with the arrival of anatomically modern Homo sapiens from Africa via the Near East. At that point, we began displaying art, technology based on specialized tools, cultural differences from place to place, and cultural innovation with time.” (Diamond, 1992 p. 328)

To understand why tool making and use elicits such respect, and to form a judgement on whether this respect is justified, we need to examine nonhuman examples in some detail. We chose the spider and robot examples arbitrarily, to highlight the breadth of tool-related behaviours that may need to be considered and the reactions they generate in us as observers; but, as will become clear, our focus is on the crows.

Tools and cognition

Few people attribute high cognitive abilities to spiders in spite of their extremely sophisticated engineering achievements and the flexibility with which they tackle different geometric configurations of the support available. Few, again, would attribute complex cognition to the robot, in spite of its evident “creativity” in generating a new solution to a problem never faced before (for devotees of artificial intelligence, it is worth stating that we are not judging the correctness of these intuitions, but simply exposing them for analysis). The reasons for these presumed denials of cognitive respectability are varied, but they include arguments of the following kind.

Spiders have a complex, but rigid, built-in set of rules, shaped by evolution over many generations, and they respond to the spatial configuration of potential web supports with precisely pre-programmed behaviours. Spiders even have rules for how to behave if they happen to lose one or more legs. The fact that the list of such rules is large does not require the attribution of intelligence.

In the case of the robot, its behaviour can be explained by generalisation from its previous training, following a program devised by its human creators. Hammers are identified by an elongated “business end” shape attached perpendicularly by its middle to an elongated holding part (the “handle”). When in search of a hammer, the robot picks the shape that most closely resembles the compounds that have been successful before and uses it by assigning to each sub-component the role their model played in the training tool (the “handle” is the thinnest and most elongated shape in the compound). In this case, we can make explicit the robot’s internal mechanisms leading to innovative behaviour, even when the emergent behaviour itself was not pre-programmed and surprises its creators. For some people, this putative complete understanding of the mechanisms removes the need to invoke cognition and, for others, leads to re-defining the concept of cognition to make it equivalent to information processing.

Explanations such as the above are tempting, but problematic because, when faced with a human being performing any of the above tasks, our intuition leads us to assume that a process of planning, judgement, and decision-making involving emotions, unconscious and conscious representations, abstract thinking, and even language has taken place.

We do not believe that these double standards are necessarily wrong, because our intuition – deceptive as it may often be – is informed by much more than the sketches of behaviour we presented above. We rather believe that both intuition and explicit understanding may be improved by analysis of the formal and informal criteria that lead human observers to make such attributions. Here, we focus on one example, that of New Caledonian Crows (*Corvus moneduloides*), and air some views on what constitutes advanced tool-related cognition by relating and comparing our species' behaviour with that of other animals that make and/or use tools. We have no illusions of solving the problem of formulating a universally acceptable definition of cognition and then assigning each candidate to a well-defined category; we believe this is not possible. It should be possible, however, to inform the discussion and to identify which behavioural data can influence our judgement and which questions are more likely to offer some guide for future research.

The New Caledonian crow in the wild

Natural history

The New Caledonian crow is endemic to the Grande Terre island of New Caledonia, but it has also been introduced to the smaller island of Maré. It is common throughout the range of forest types found on Grande Terre (Hunt, 2000a; our personal observations) and it is also found in the Niaouli savanna (Hannécart & Létocart, 1980). This crow's diet is only partially composed of food obtained with tools, and includes insects and their larvae, snails, nuts, fruit, seeds, flowers, and other birds' eggs (Layard & Layard, 1882). It lives in social groups and there is a high level of parental care, with juvenile birds being fed by adults for at least 6 months after fledging, and (if the behaviour of captive birds reflects life in the wild) probably much longer (Kenward et al., 2004). The size of social groups varies, with some flocks reaching around 30 individuals. However, groups are usually of around three or four birds (Kenward et al., 2004), consistent with a breeding pair plus the clutch size of one or two eggs (Hannécart & Létocart, 1980); the larger groups are probably temporary conglomerations (Hunt, 2000b). Because field studies with marked individuals have not yet been carried out, it is not known how stable or closely related these groups are.

In addition to using tools, the New Caledonian crows display behaviours found in other corvids which are often thought to be associated with high cognitive abilities, such as breaking nuts by dropping them from branches (Hunt et al., 2002; Layard & Layard, 1882), and food-caching (Hunt, 2000b; our personal observations in the laboratory).

Tool use

Almost everything known about crows' tool use in the wild is from the work of Gavin Hunt and his colleagues. Tool use of several kinds is widespread throughout the crows' range. One sort of tool, cut from Pandanus leaves, has been found at 20 sites throughout Grande Terre and also on Maré (Hunt & Gray, 2003). Other kinds of hooked and straight tools have been found in at least 11 sites in the south of Grande Terre (Hunt & Gray, 2002). These tools are used and manufactured in different ways.

Stick-type tools are made from a variety of different materials, including tree twigs, fern stolons, bamboo stems, tree leaf midribs, and thorny vines (Hunt & Gray, 2002). In our laboratory, crows readily make similar straight tools by removing the barbs from long feathers and then using the stem formed by the quill and shaft (see Figure 1a, c-d).

Two issues are of particular interest: the method of manufacturing hooks and the way that Pandanus leaf cut-outs are made. The hooks sometimes occur naturally on the raw material, such as on lengths of thorny vines cut by the crows (Hunt & Gray, 2002). In other cases, however, the crows detach a secondary twig from the primary one by nipping at the joint with their beaks, leaving a piece of the primary twig to form a hook. After a twig is detached, crows typically remove leaves and bark, and have even been observed sculpting the shape of the hook with their beak (Hunt, 1996; Hunt & Gray, 2004a).

Figure 1 about here

The Pandanus leaf tool manufacture is interesting because it appears to require the use of a rule system which dictates a complex sequence of actions resulting in the finished tool (Hunt, 2000a; Hunt & Gray, 2004b). The edge of the stiff, barbed leaf is cut and torn in a sequence which results in the cutting-out from the leaf of a flat tool that may have various shapes, from long and rectangular to a tapering shape achieved by stepped cuts (see Figure 1b). The steps give the tool strength, because it is broad at the proximal end (where it is held), and also precision, because it is thin at the distal, probing end. Unlike, for example, the removal of twigs and bark from a stick, each action does not result in a progressively more effective tool: the final step is the removal of the tool from the leaf, so that until this point the tool is non-functional.

The design of the Pandanus leaf tools varies in complexity from area to area: in some areas, only unstepped tools are found, whereas across most of the island the more complex multi-step tools are made. There is no identified variation in availability of raw materials or in ecological correlates that could indicate different needs, so these design differences are suggestive of cultural transmission of tool design. If the more complex stepped tools are derived from the simpler rectangular tools, then social transmission may operate as a ratchet to preserve and accumulate design improvements (Hunt & Gray, 2003). This historical sequence is likely, as it seems improbable that the most complex tool design would have emerged at once.

At least two main techniques of tool use have been described. One method involves the use of tools (with or without hooks) to extract small invertebrates hiding under tree bark and crevices in the base of palm leaves (Hunt, 1996; Hunt & Gray, 2002). With Pandanus tools, a wild crow has been observed using the barbs on the leaf margin (which always point away from the tip of the tool) as hooks to facilitate the extraction of food from a hole (Hunt & Gray, 2004b). The other main technique is the beetle larvae fishing described in the opening paragraph. In this case, the tools are not hooked, but end in a straight tip (Hunt & Gray, 2002).

There remain many important gaps in our knowledge of these crows' behaviour in the wild. We know very little about:

- their sociobiology
- their dependency on the food provided by tools
- the development of individual skills
- the mechanism of cultural transmission
- the putative specialisation of individuals or family groups in tool variety
- the role of individual creativity
- the role of tool and food caching

It is crucial to know the answers to these questions if we are to make inferences about the cognitive processes that accompany this species' extraordinary behaviour. Equally crucial, however, is to compare what is known about these crows with the tool-related behaviour of other species.

Comparisons with other animals

We have seen in the preceding section that New Caledonian crow tool behaviour may be characterised by four striking features: it is *very common, possibly universal*, in that (as far as we know) all populations of this species hitherto studied show high levels of tool use; it involves a wide *diversity* of types of tool; it involves highly *complex* manufacture, most strikingly for the Pandanus tools; and (although this feature is still not fully demonstrated) the design of Pandanus tools may have been *cumulatively improved* through cultural transmission.

These characteristics all intuitively seem to be related to cognitive sophistication – so to what extent are they found in other animals? We are currently developing a framework for formal analysis of animal tool use within these and other categories; in this chapter, we will restrict ourselves to briefly discussing the extent to which other animals demonstrate similar behaviour.

Frequency

To our knowledge, New Caledonian crows and chimpanzees (*Pan troglodytes*) (McGrew & Marchant, 1997; Whiten et al., 1999) are the only nonhuman vertebrates where *all* populations show routine tool use. Woodpecker finches (*Cactospiza pallida*) (Grant, 1999; Tebbich et al., 2002) and orangutans (*Pongo pygmaeus*) (van Schaik et al., 2003) show high frequencies of tool use in some populations, but there are other populations that never use tools. In all other animal tool users, there is either insufficient data to assess tool use frequency or tool use is known to be absent from many populations.

Diversity

The diversity of tool types shown by New Caledonian crows is also rare. No other bird is known to routinely make more than one type of tool (tools are considered as being different 'types' if they are either used for different functions, or are acquired

or made in substantially different ways), and the only mammals, other than humans, that are known to use a diversity of tools are the great apes (chimpanzees and orangutans) (e.g. van Schaik et al., 2003; Whiten et al., 1999) and capuchin monkeys (*Cebus* spp.) (Moura & Lee, 2004; Frigaszy et al., 2004).

Complexity

Defining 'complexity' unambiguously is a philosophical challenge that goes beyond the scope of this chapter. However, a factor that seems closely allied to complexity is the degree of transformation necessary to produce a functional tool from the raw material. Using this as a working definition allows us to describe four levels of complexity in tool manufacture (levels 1 and 2 are modified from Beck, 1980).

- 0) *None*. Unmodified objects are used.
- 1) *Detach / subtract*. Severing a fixed attachment between environmental objects (or the substrate) or removing object(s) from another unattached object, so the latter is a more useful tool.
- 2) *Add / combine / reshape*. Connecting two or more objects to produce a tool; fundamentally restructuring material to produce a functional tool.
- 3) *Multi-step manufacture / fine crafting*. Involves either several (> two) manufacturing steps to produce a functional tool or fine, three-dimensional sculpting of the raw material (see Hunt & Gray, 2004a).

If wild tool behaviour only is taken into account, then no nonhuman vertebrates apart from New Caledonian crows have ever been reported to manufacture tools in a multi-step fashion or by fine crafting (Hunt & Gray, 2004a). Chimpanzees and orangutans have been reported to use crumpled leaves as sponges (Beck, 1980; van Schaik et al., 2003), which could be regarded as 'reshaping'; all other animal tool manufacture involves nothing more complex than detaching or subtracting objects from each other.

Cumulative cultural evolution

Human technology is entirely dependent on the transmission of techniques between generations and the resulting cumulative improvement in tool design. Although there is now reliable evidence for tool 'traditions' in chimpanzee and orangutan populations (van Schaik et al., 2003; Whiten et al., 1999), there is no evidence that their technology has improved cumulatively (Boyd & Richerson, 1996; Tomasello, 1999). This evidence contrasts with the observations that New Caledonian crows make Pandanus tools of differing complexity in different areas of New Caledonia in the absence of detectable habitat differences. The present geographical distribution of complexity and the fact that complex tools are likely to be modifications from simpler patterns is consistent with cumulative cultural transmission of improvements in design (Hunt & Gray, 2003). Experiments involving cross-fostering or hand-raising (e.g. Tebbich et al., 2001) are ultimately necessary to demonstrate that social learning is responsible for these differences, but the current evidence makes it plausible.

As the previous analysis illustrates, we can compare animals' tool using proclivities based on behaviour in the wild alone. However, many questions about the cognitive processes that underlie such behaviour are only answerable in the laboratory. The following section therefore outlines our programme of experimental work with New Caledonian crows.

The New Caledonian crow in the laboratory

We started our research using two subjects, Abel (a male) and Betty (a female), but we have since formed a colony of several groups totalling 21 subjects. All of the experiments described below were conducted with the original two subjects. Betty was captured from the wild in March of 2000, in Yaté, New Caledonia. We infer from her behaviour that she was probably a nutritionally-independent juvenile at the time of capture. Abel came from the Parc Forestier, a zoo in Noumea, New Caledonia, where he had been captive for at least 17 years (his age at capture was unknown). The pair lived together in a large room, with free access to an outdoor flight cage. They were fed *ad libitum* on a varied diet, but for the experiments we used their preferred food (pig or lamb's heart), which was not included in their daily ration.

The main issues we have tackled so far are the extent to which tool related behaviour showed anticipation ("planning") and the level of apparent "understanding" of the physical relations involved in the birds' actions. We have examined the degree of anticipation by testing whether, when facing a task that requires a tool, the crows pick a random available object within the range of shapes that can be used as tools or instead choose (or make) an object that is suited for the task being faced.

The question of understanding is more debatable – indeed the very term is not easy to define and we will not attempt to do so other than operationally. What we are addressing here is the level of abstraction of the rules that the crows use in performing their actions. Most tasks can be solved either by learning task-specific responses or by applying wider principles; this difference may be informative as to how sophisticated the cognitive mechanisms involved may be. For instance, Wilson and colleagues (1985) showed that, in a delayed matching (or non-matching) to sample task, pigeons formed specific associations involving precise sequences of stimuli, whereas corvids (jackdaws, rooks, and jays) seemed to use concepts of sameness and oddity. In another example, Povinelli (2000) has recently called attention to the fact that humans and chimps appear to solve similar problems using different concepts about physical interactions between objects. We replicated some experiments previously conducted with primates to examine whether the crows used the principles of gravity and rigidity or instead solved the problems by learning specific rules. Finally, we describe an experiment triggered by a serendipitous observation that gives an indication of the level of individual creativity these animals possess.

Selectivity

Tool length. Making or using a tool that is unsuitable to extract a given food item because of its size (too short to reach, too long to handle accurately) incurs costs in

terms of time and associated potential loss of the prey to another predator. It seems reasonable to expect that, having judged the geometry of a burrow, the crows may be able to show anticipation by selecting a tool that is well-suited for each case.

We tested the ability of our two original crows to select a tool of an appropriate length to obtain a piece of food in a horizontal tube (Chappell & Kacelnik, 2002). The birds were presented with food that, in 20 different trials, could be at 10 different distances from the open end of the tube (each distance occurred twice). The birds were also provided, in all 20 trials, with 10 sticks, each of a length matching the distances at which food was placed in the different trials.

Figure 2 about here

Our goal was to see if tool choice was determined by the food distance in each trial; Figure 2 shows the results. Both crows significantly avoided selecting tools shorter than the distance to food (and hence unsuitable). Furthermore, they selected tools that precisely matched this distance significantly more often than chance, thus reducing the frequency of use of tools that were longer than required. When, in a different experiment, the sticks were placed behind a screen so that the birds could not see both the tools and the food tube simultaneously, Abel still chose suitable tools more frequently than expected by chance, whereas Betty (who was still a juvenile at the time) seemed to lose motivation and did not perform the task.

Tool diameter. The diameter of tools is another dimension of size that affects suitability. In further experiments with the original two crows, we tested their ability to select and make tools with an appropriate diameter (Chappell & Kacelnik, 2004). For testing both selectivity and tool making, the task was to insert a tool through the end cap of an upside down 'L' shaped tube, and to push a small cup containing food along the horizontal leg, so that it would fall down the vertical leg of the tube (see apparatus in Figure 3). The diameter of the hole in the end cap was varied between trials.

In the first part of this study, we tested selectivity alone, using Betty. She was provided with three sticks of different diameters. The thinnest could be inserted through all of the holes, the medium diameter stick could only be inserted into the two widest holes, and the widest would only fit the widest hole. Even though she was capable of using all three diameters, Betty showed a strong preference for the narrowest tool, regardless of the diameter of the hole. When given a choice between two tools in a bundle and one loose one, she only dismantled the bundle when it contained the thinnest tool, thus paying the cost of disassembling the bundle only when required.

Figure 3 about here

In the second part of the experiment, both crows were exposed to the same apparatus, but they were not provided with tools. Instead, we placed tree branches into the aviary from which tools could be made. Both birds readily made tools by cutting segments of the branches and removing leaves and minor twiglets. The

diameter of the tools that were made increased significantly with the diameter of the hole (see Figure 3b). The birds made tools that were too thick to fit into the hole on only 2 (out of 29) trials; in both cases, they modified the tools by sculpting the thickenings that blocked their use immediately after first trying them, until they were suitable. Thus, in all but two cases, the birds made tools of appropriate final dimensions before actually trying to use them, correctly anticipating the hole size in that trial.

Specific associations vs. general principles

Rigidity. This experiment was inspired by similar experiments with chimpanzees by Daniel Povinelli (2000, Experiments 9-10). In it, we pre-exposed Betty to two rake-like objects with different levels of rigidity in a non-functional context, and then tested her in a situation where only one of the tools would serve (Chappell & Kacelnik unpublished data). The idea was to examine whether, when she needed to pick a tool among a set of objects that were familiar to her, but had not been used before as tools, she would choose according to the suitability afforded by the objects' properties.

The rakes differed in their business ends. One had a solid head made of wood, whereas the other had a flexible head made of thin plastic. Betty was allowed to freely manipulate the tools without the apparatus for several days prior to the start of the experiment. The rakes were then placed into a box with a transparent lid that was internally divided into two compartments (see Figure 4a). The two compartments each contained a food-filled cup placed in front of the head of each rake. The cup could be retrieved from the box by pulling the rake with the rigid, but not the flexible head. If Betty had learned the properties of the rakes and used this knowledge, then she should choose the rigid tool; otherwise, she might be expected not to pull at all or to pull both rakes with equal probability. Betty was 100% accurate on the first trial on each day, but she seemed to lose motivation quickly, and her accuracy decreased sharply over the course of each session (see Figure 4b). This drop in performance may be because if she made an error, then she could choose again without penalty; or she may have been inclined to explore the consequences of the alternative action. Betty's success on the first trial of each session contrasts with the results from Povinelli's chimpanzees, where six out of seven subjects performed at chance throughout the experiment (Experiment 9), and the only successful subject reverted to chance when a different experimental design was used (Experiment 10).

Figure 4 about here

Gravity. Here, we used another experimental design originally used with primates (Limongelli et al., 1995; Povinelli, 2000; Visalberghi & Limongelli, 1994) to test if the crows responded directly to the action of gravity or gave priority to local stimulus relations (Chappell & Kacelnik, in prep). The essence of the task was to expose the subject to a problem where to obtain the reward it was necessary to avoid a gravity trap (a blind-ending trap in a horizontal tube), and once the subject had learned this, to transform the task so that gravity was no longer a problem. If the subject was driven by local features of the trap, then the subject may continue to avoid it;

however, if the subject was using the concept of gravity, then it may ignore the now inconsequential stimuli associated with it.

After about 100 trials with the apparatus, Betty reached criterion (trap avoided on 8/10 trials or more on three consecutive blocks of ten trials). This performance is comparable to that shown by chimpanzees and capuchin monkeys (*Cebus apella*) (Limongelli et al., 1995; Povinelli, 2000; Visalberghi & Limongelli, 1994).

When the trap was inverted during the testing phase, responding did not return to random; instead, Betty continued to avoid the now irrelevant trap – a result which had previously been observed in chimps and capuchin monkeys, though one woodpecker finch did return to random responding on an inversion test (Tebbich & Bshary, 2004). Human infants have not been tested with an inverted trap to our knowledge; but, when children aged between 27 and 66 months were tested with the simple trap tube task, those under 3 years responded essentially at random, whereas those over 3 years learned to solve the task within a few trials (Limongelli, 1995; cited in Visalberghi, 2000).

This task is, however, difficult to interpret for all species, whatever the outcome. Even if subjects do return to random performance after inversion, then it may not be due to the use of gravity as a concept; subjects could be following local cues so narrowly that avoidance may not generalise to the inverted trap because it just looks different. The continued avoidance of the trap excludes the interpretation of a direct use of gravity, but it does not prove that Betty and the other nonhuman subjects tested in this task cannot use this concept. Nonhumans may use local cues rather than general principles when the former are effective. After all, subjects experience 100% success after the trap is inverted whatever they do, so there is no incentive to change the technique.

Innovation. We had an insight into the level of individual creativity of New Caledonian crows through a serendipitous observation that was made during the course of an experiment on selectivity. In the planned experiment, we were testing whether the crows would choose a hooked piece of wire over a straight piece, where the task was to lift a bucket containing food (using the handle) from a vertical tube. On one trial, Abel took the (suitable) hooked wire away, leaving Betty with an unsuitable straight wire. After attempting unsuccessfully to extract the bucket with the unsuitable straight wire, Betty spontaneously secured the distal end in a crevice and made a hook by pulling perpendicularly on the proximal end. With the hook thus made, she proceeded to retrieve the food.

To explore the phenomenon further, we repeated the task, but offered only the straight wire. Now, Betty bent the piece of wire and used it successfully on virtually every opportunity (occasionally she or Abel dropped the tool into the pipe, where it was out of reach) (Weir et al., 2002). She used at least two techniques and three locations to bend the wire (and has subsequently used a third technique), and she often corrected the shape of the tool several times before attempting to use it.

As far as we know, Betty did not have any experience with flexible wire or similarly pliant material prior to this episode nor were the techniques she used possible with natural materials. It is therefore clear that at least one member of this crow species is able to innovatively shape tools in anticipation of specific needs.

Discussion

The behaviour of New Caledonian crows both in the wild and in captivity conveys the impression that these animals' cognitive capacities are out of the ordinary. Indeed, they fashion and select tools according to apparently pre-conceived projects, to an extent not reported so far in any other bird and hardly in any other animal. They show inventiveness in solving new problems with flexibility. And they seem, in the case of the Pandanus stepped-cut leaves, to make tools to a design that is socially transmitted, so that regional differences are explained by cultural history. But, this impression of cognitive exceptionalism glosses over a deep uncertainty as to whether these birds are indeed genetically special, and if so why they have evolved these unusual traits. We turn now to discuss several angles of this problem. These comments are not aimed at providing mutually exclusive alternatives, but to indicate what issues lie ahead of us.

Ecological explanations

It remains possible that nothing is intrinsically special about New Caledonian crows' cognition, even if the behaviour is. This could be the case if the ecological circumstances in New Caledonia are so uniquely favourable for tool use (for instance, the absence of competitors exploiting beetle larvae hidden in tree holes) that any population of corvids or indeed other birds would develop similar behaviour under the circumstances. It is possible that not even the ecology is special. A fortunate accident could have led to an individual discovery that became culturally fixed in the population because of the nature of island life.

These hypotheses (unlikely in our view) can only be answered by developmental studies, including rearing individuals of this and other species under controlled conditions, including cross-fostering. Observation of experienced individuals from wild populations, even if transported to the laboratory, cannot disprove these 'killjoy' hypotheses, but they seem improbable to us. It is likely instead that special ecological circumstances led to unusual selective pressures, and this in turn led to the evolution of a heritable specialisation underlying the behaviour we see today.²

If the species does possess genetic peculiarities, then they could be at many different levels. The birds could, for instance, have particularly fine motor control of their beaks. An early manifestation of such a genetic specialisation could lead to reinforcing experiences with object manipulation and a further cascade of acquired skills through practice. Alternatively, the birds could simply be particularly confident and neophilic (as many island living birds are as a consequence of the scarcity of predatory mammals), so that they experience greater exposure to random manipulation of objects and consequent learning by reinforcement. Under this option, any genetic adaptations responsible for tool behaviour need not necessarily be associated with an unusual degree of cognitive sophistication.

Social learning

It is worth distinguishing the factors influencing the original emergence of the behaviour (and any subsequent 're-invention' by other individuals) from those influencing the spread of the behaviour through the population. Both are likely to play a role in the complexity and frequency of tool behaviour, but the latter is likely to be particularly important in determining both the proportion of tool users in the population and also the frequency with which tool behaviour occurs. Thus, if New Caledonian crows are particularly and heritably adept at social learning, then tool behaviour could be maintained in the population from an initial fortuitous invention, without the need for any heritable cognitive adaptations (other than possessing a tendency to learn socially).

It is well established that the behaviour of a single individual can spread and become established in a population. For example, a new song type spread and became established among a population of saddlebacks (*Philesturnus carunculatus*) in New Zealand as a consequence of one individual having an unusual vocalisation – probably due to a mistake in song learning (Jenkins, 1977). If juveniles live an exceptionally long period next to their parents and other relatives and forage close to them, then the transmission of such skills would be facilitated. New Caledonian crows do indeed live in groups that seem to be familial, so their social structure could provide opportunities for the social transmission of tool behaviour.

Rearing experiments may help to determine to what extent social learning is involved. Tebbich and colleagues (Tebich et al., 2001) found that young woodpecker finches developed proficient tool-using skills even when raised with non-tool-using adults. The young finches showed a strong spontaneous tendency to use sticks, and refined and consolidated the habit by their own experience. These observations suggest that social learning is not essential for the development and transmission of tool use in woodpecker finches.

However, in New Caledonian crows, the presence of geographic diversity in tool shape (Hunt & Gray, 2003) in the absence of detectable habitat differences strongly argues in favour of a cultural component, because geographic diversity can hardly result from purely individual acquisition in similar environments. In the context of the questions addressed in this chapter, the presence of a strong cultural component adds further uncertainty, because it opens the possibility that New Caledonian crows may simply be better at advanced forms of social learning than other corvids, rather than being particularly advanced in their cognitive abilities.

However, we know from our observations of hook-making (Weir et al., 2002) that New Caledonian crows do excel in creative problem solving. So, it seems unlikely that advanced social learning skills are a complete answer to the question, "What is special about this species?"

Cognitive adaptations: generalised or specialised?

Perhaps at the other extreme of the possibilities discussed above, New Caledonian crows might have an enhanced cognitive ability (compared, for example, to other

Corvidae) that is not specifically related to tool behaviour. They might have better general problem-solving abilities, be better able to deal with abstract or conditional rules, or have more accurate memories than other species. These abilities may explain tool behaviour, but they extend well beyond it. We have not yet had the opportunity to test these aspects of their cognition. An obvious route, that we are following now, is to compare behaviour of this and other species in tasks requiring problem solving, but not involving tools.

Alternatively, the crows may have cognitive adaptations strictly within the domain of tool behaviour. Even then, we can ask about the nature of the adaptation: do they learn specific solutions for each task they encounter or can they abstract more general principles? These abstractions could be very specific – for example, the individual might simply understand that pushing *that* object with *this* stick will cause it to move away from self; or fairly general – an object has an effect on another if and only if there is a direct, physical connection between them, regardless of the exact circumstances and objects involved. The latter allows for greater behavioural flexibility and improvisation in the face of variable availability of materials and differing tasks requiring tools.

For example, if a human finds herself in need of a screwdriver to remove a screw, but does not have one readily available, then she can attempt to use a blunt knife tip or a thin coin to serve the same purpose. She is able to do so because she “understands” the required physical forces involved and is able to generalise that knowledge to different objects. We all do something similar every time we try to use a new piece of computer software – with varying levels of success. The laboratory experiments described earlier suggest that New Caledonian crows have an impressive ability to generalise their tool expertise and to create new solutions. Making a hook out of an unfamiliar material and using a variety of different techniques that would not result in a working tool with natural materials seems even more impressive than loosening a screw with a blunt knife.

If New Caledonian crows do have a generalised cognitive adaptation, then it is most likely to be founded on knowledge about physical causality and object relations. But, is it conceivable that an organism without language would be able to deal with these rather abstract concepts? Neonatal human infants of 3 months of age have been shown to possess knowledge about physical causality (Spelke et al., 1992). They expect objects to move only on connected paths, rather than jumping discontinuously from one location to another (*continuity*), and they expect objects to move only on unobstructed paths, so that no parts of two distinct objects can occupy the same space and time (*solidity*). Other knowledge about the physical world (such as *gravity* and *inertia*) appears to develop at a much later stage. If such young infants possess this kind of knowledge – long before the acquisition of language, and before extensive motor exploration of the environment – then it does not seem impossible that nonhuman species might also be able to form some of these concepts. Time (and much more work) will tell.

References

- Beck, B.B. (1980). *Animal tool behavior*. New York, NY: Garland.
- Boyd, R., & Richerson, P.J. (1996). *Why culture is common, but cultural evolution is rare*. In: *Evolution of social behaviour patterns in primates and man: a joint discussion meeting of the Royal Society and the British Academy* (eds. Runciman, W.G., Maynard Smith, J., & Dunbar, R.I.M.). *Proceedings of the British Academy*, Vol. **88**, pp. 77-93. Oxford: Oxford University Press.
- Chappell, J., & Kacelnik, A. (2002). Tool selectivity in a non-mammal, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition* **5**: 71-78. DOI 10.1007/s10071-002-0130-2.
- Chappell, J., & Kacelnik, A. (in prep). Folk physics in New Caledonian crows: do crows understand gravity?
- Chappell, J., & Kacelnik, A. (2004). Selection of tool diameter by New Caledonian crows *Corvus moneduloides*. *Animal Cognition* **7**: 121-127. DOI 10.1007/s10071-003-0202-y.
- Diamond, J.M. (1992). *The rise and fall of the third chimpanzee*. London: Vintage.
- Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E.B., & de Oliveira, M.G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology* **64**: 359-366. DOI 10.1002/ajp.20085.
- Grant, P.R. (1999). *Ecology and evolution of Darwin's finches*. Princeton: Princeton University Press.
- Hannécart, F., & Létocart, Y. (1980). *Oiseaux de Nouvelle Calédonie et des Loyautés*. Noumea, Nouvelle Calédonie: Les Editions Cardinalis.
- Hunt, G.R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature* **379**: 249-251.
- Hunt, G.R. (2000a). Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society of London 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. (2002). Species-wide manufacture of stick-type tools by New Caledonian Crows. *Emu* **102**: 349-353. DOI 10.1071/MU01056.
- Hunt, G.R., & Gray, R.D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London B* **270**: 867-874.
- Hunt, G.R., & Gray, R.D. (2004a). The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society of London B (Suppl.)* **271**: S88-S90. DOI 10.1098/rsbl.2003.0085.
- Hunt, G.R., & Gray, R.D. (2004b). Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (*Corvus moneduloides*). *Animal Cognition* **7**: 114-120. DOI 10.1007/s10071-003-0200-0.
- Hunt, G.R., Sakuma, F., & Shibata, Y. (2002). New Caledonian crows drop candle-nuts onto rock from communally-used forks on branches. *Emu* **102**: 283-290.
- Jenkins, P.F. (1977). Cultural transmission of song patterns and dialect development in a free-living bird population. *Animal Behaviour* **25**: 50-78.

- 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. (in press). Development of tool use in New Caledonian crows (*Corvus moneduloides*): stereotyped action patterns and social influence. *Animal Behaviour*.
- Kenward, B., Weir, A.A.S., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature* **433**: 121. DOI 10.1038/433121a.
- Layard, E.L., & Layard, E.L.C. (1882). Notes on the avifauna of New Caledonia. *Ibis* **6**: 520-522.
- Limongelli, L. (1995). *Comprensione delle realzioni di causa-effetto nei Primati: uno studio sperimentale*. Unpublished PhD thesis, University of Rome, Rome.
- Limongelli, L., Boysen, S.T., & Visalberghi, E. (1995). Comprehension of cause-effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **109**: 18-26.
- McGrew, W.C., & Marchant, L.F. (1997). Using the tools at hand: Manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. *International Journal of Primatology* **18**: 787-810.
- Moura, A.C. de A., & Lee, P.C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science* **306**: 1909. DOI 10.1126/science.1102558.
- Povinelli, D.J. (2000). *Folk Physics for Apes*. Oxford, UK: Oxford University Press.
- Spelke, E.S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. *Psychological Review* **99**: 605-632.
- Tebich, S., & Bshary, R. (2004). Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Animal Behaviour* **67**: 689-697. DOI 10.1016/j.anbehav.2003.08.003.
- Tebich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society of London B* **268**: 2189-2193.
- Tebich, S., Taborsky, M., Fessl, B., & Dvorak, M. (2002). The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecology Letters* **5**: 656-664.
- Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology* **28**: 509-529.
- van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S., & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science* **299**: 102-105.
- Visalberghi, E. (2000). *Tool use behavior and the understanding of causality in primates*. In: *Comparer ou prédire: Exemples de recherches comparatives en psychologie aujourd'hui* (eds. Thommen, E., & Kilcher, H.), pp. 17-35. Fribourg, Suisse: Les Editions Universitaires.
- Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* **108**: 15-22.
- Weir, A.A.S., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science* **297**: 981. DOI 10.1126/science.1073433.

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature* **399**: 682-685. DOI 10.1038/21415.

Wilson, B., Mackintosh, N.J., & Boakes, R.A. (1985). Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Quarterly Journal of Experimental Psychology* **37B**: 313-332.

Figures

Figure 1



Figure 2

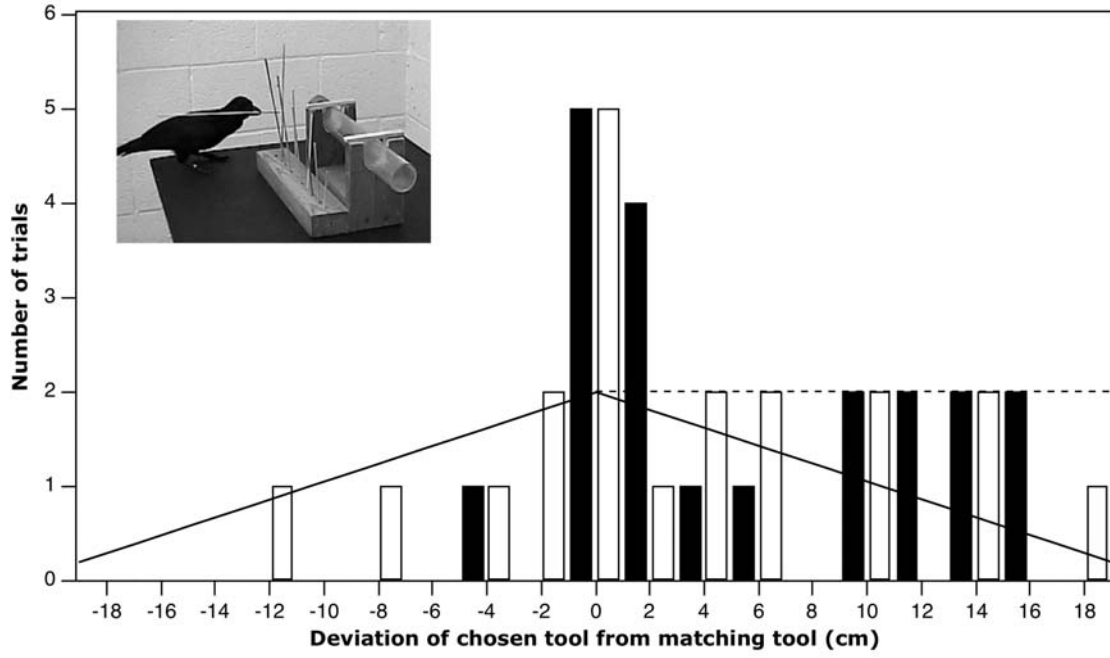


Figure 3

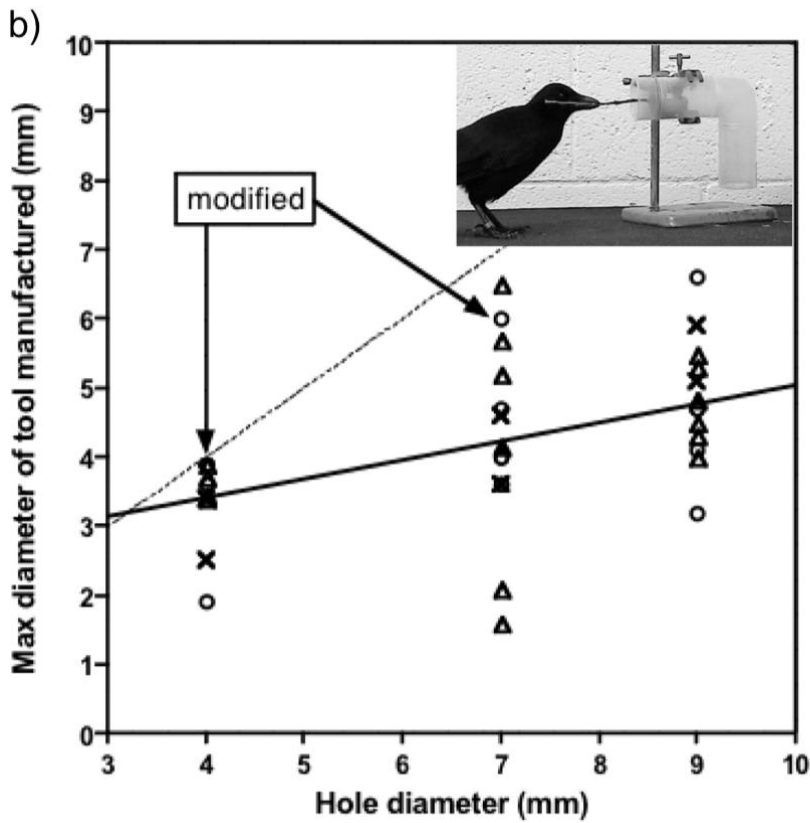
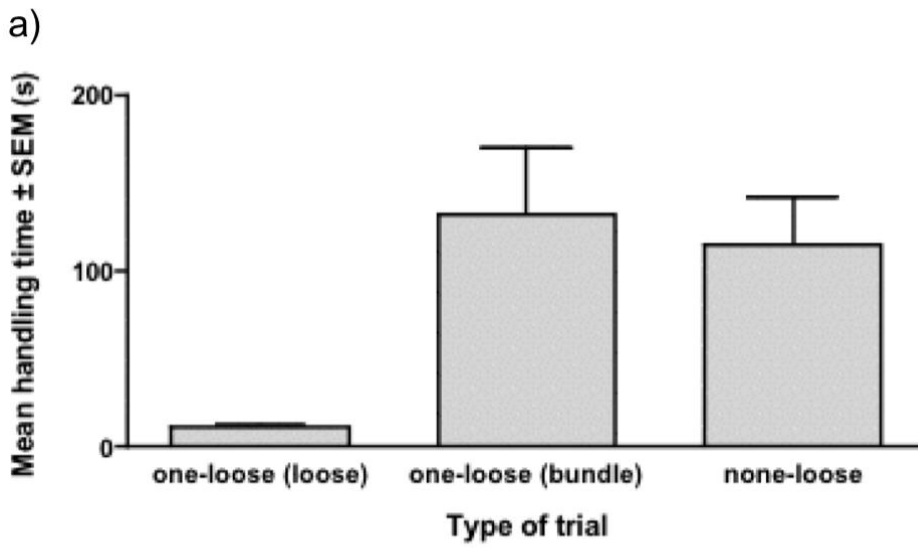
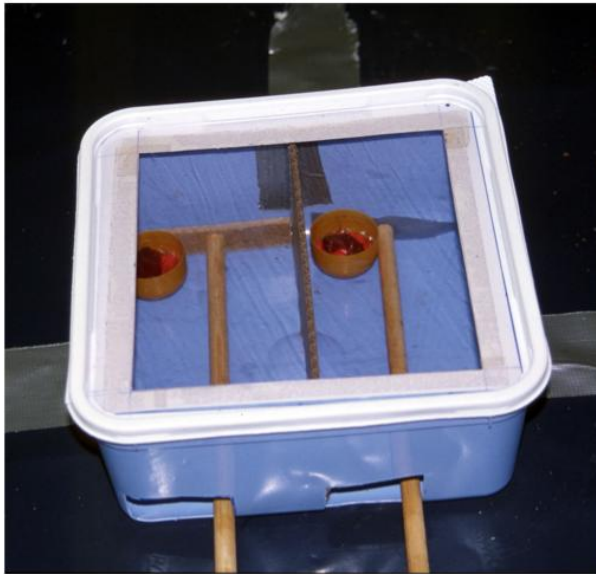


Figure 4

a)



b)

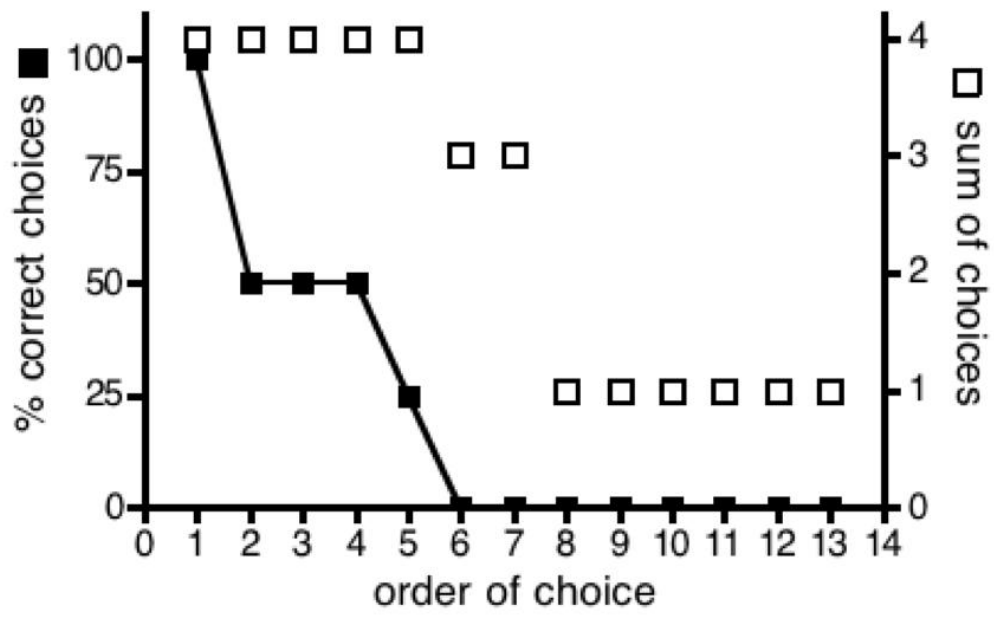


Figure captions

Figure 1. Tools made by New Caledonian crows in the wild and captivity. (a) Twig tools (captivity). (b) Pandanus tools (wild). Tools courtesy of Gavin Hunt. (c) Leaf petiole and cardboard tools (captivity). (d) Feather tools (captivity).

Figure 2. Choice of tools in a length selection experiment. Distribution of sticks chosen by Abel (filled bars) and Betty (open bars) relative to the matching tool (at 0). Solid line shows the expected distribution if the crows chose at random, and dotted line shows the expectation if they always chose the longest tool. The inset photograph shows Betty choosing a tool from the 'tool box'.

Figure 3. Choice and making of tools in relation to diameter. (a) **Cost of dismantling the tool bundle.** The left and central columns show mean time to obtain food in trials when one tool was loose and the other two were in a bundle. The leftmost column shows trials in which the tool used was the loose one and the central one trials in which the tool used was in the bundle. The rightmost column shows trials in which all three tools were in the bundle and hence the bundle had to be dismantled. Dismantling the bundle took substantially longer than using the loose tool. (b) **Diameter of manufactured tools.** Maximum diameter of tool manufactured as a function of the diameter of the hole. Open circles are tools made by Betty, open triangles are tools made by Abel, and crosses are tools that were made and then discarded. Significantly wider tools were made when the hole was wider. The photograph shows Betty inserting a tool into the apparatus.

Figure 4. Choice in a "rigidity" concept experiment. (a) **The 'rake box'.** The rigid tool is on the left and the non-rigid tool on the right. (b) **Tools chosen in the rake experiment.** The percentage of correct choices analysed by the within-session order of choice. In all sessions, Betty chose the correct tool on the first trial.

Endnotes

¹ We are grateful to Prof. M. Brady for this example.

² We have recently provided evidence supporting this hypothesis, by demonstrating that New Caledonian crows develop tool use even if reared in isolation without ever witnessing another individual using tools (Kenward, Weir, Rutz, & Kacelnik, 2005), and that successful tool use is preceded by non-functional, stereotyped 'precursor' behaviors (Kenward, Rutz, Weir, & Kacelnik, in press).