Cognitive psychology of tool use in New Caledonian crows (*Corvus moneduloides*)

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Thesis submitted for the Degree of Doctor of Philosophy
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ABSTRACT

Most studies into the evolution of humans' manufacture and use of tools have concentrated on non-human primates. Within the past decade, however, it has been reported that wild New Caledonian crows make and use tools as complex as those of chimpanzees, and that aspects of their behaviour may be culturally transmitted. In this thesis, I present work examining the cognitive basis of New Caledonian crows' tool-oriented behaviour.

I begin by reviewing the hotly-disputed issue of whether non-human animals are capable of 'reasoning' in the physical domain, and examining experiments designed to address this issue. It has often been claimed that naturally-occurring tool use and manufacture indicates special cognitive abilities, so I critically analyse this argument and propose a framework that might allow the question to be tested empirically.

After reviewing what is known of the ecology of New Caledonian crows, I address cognition directly, presenting results from two studies into their understanding of hooks and tool shape. I report that one subject showed remarkable innovation and flexibility by spontaneously making hooks out of wire when she needed a hooked tool, and by quickly transferring this ability to novel material requiring a different technique. However, it was not clear if her behaviour reflected a full and true understanding of the task and tool properties.

I also investigated whether the crows showed lateralised tool use, since wild crows have a population-wide bias for making tools using the left side of their bill. I found that individual captive crows almost always use tools with the same laterality, but there was no consistency across individuals (similar to observations in chimpanzees), suggesting that tool use and manufacture might have different neural underpinnings.

Finally, a study on hand-raised crows found that they reliably developed tool use and basic tool manufacture without ever observing others using or making tools, suggesting that they have a genetic propensity to use tools to retrieve food. However, none of the juveniles ever made tools as sophisticated as ones made by wild crows, so the possibility remains that social learning is important in the natural acquisition of tool-oriented behaviour.

Acknowledgements

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Author's contribution

Regarding Alex Weir's thesis submitted for the degree of DPhil, Trinity Term 2005, entitled "Cognitive psychology of tool use in New Caledonian crows (*Corvus moneduloides*)"

Chapter 1. Entirely my own work, apart from small parts of Section 1.3 which were adapted from two publications that I co-authored (Kenward, Rutz, Weir, Chappell, & Kacelnik (2004), *Ibis* **146:** 652-660; and Kacelnik, Chappell, Weir, & Kenward (in press), chapter in *Comparative Cognition: Experimental Explorations of Animal Intelligence*, eds. Wasserman & Zentall).

Chapter 2. Entirely my own work.

Chapter 3. Entirely my own work, apart from some sentences in the section describing Experiment 2, which were taken from a paper I wrote with two colleagues (Weir, Chappell, & Kacelnik (2002) *Science* **297:** 981 – see Appendix 5). The apparatus used in the experiments was designed and built by Jackie Chappell.

Chapter 4. Entirely my own work.

Chapter 5. I designed the experiment with input from the other co-authors. I collected and analysed the data and wrote the first draft of the paper. The co-authors were involved in editing and revising the paper.

Chapters 6. The crows were hand-raised by Ben Kenward and myself (with occasional help from other group members). The experiment was designed by all authors in collaboration. Ben Kenward conducted the demonstrations and collected detailed behavioural data (reported in Appendix 6); I helped with some of the video recording of sessions. Ben Kenward wrote the first draft of the paper, after discussion with co-authors, and all co-authors were heavily involved in editing and revising several drafts of the paper.

Chapter 7. Entirely my own work.

Note that chapters that have already been published are included in their published form (with permission from Prof. Ben Sheldon, Director of Graduate Studies, Department of Zoology), with the exception of an addition of a header and footer with the Chapter number, chapter title, and page numbers. Chapters not already published cross-reference by chapter number, but already-published chapters refer to published papers (i.e. in Chapter 1 [unpublished], I would say to "see Chapter 4", but in Chapter 3 [published] it would say "see Weir et al. 2002").

A CD-ROM containing Supplementary Movies is also enclosed. Movies are referenced as "Supplementary Movie X-Y", where X is the chapter number and Y the number of the movie within that chapter; where movies are mentioned in published chapters, refer to the appropriately-numbered movies on the CD-ROM.

for Betty

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Chapter 1

Introduction

1.1 INTRODUCTION

Since ancient times, humans have been fascinated by the question of “Are we alone?” – are there any other beings that have the same capacity for self-reflection and abstract thought? The first question that we would ask if we found life on other planets would undoubtedly be “Is it intelligent?”, but that question can also be asked about the animals we share this planet with – do any of them share aspects of our intellect? One key diagnostic feature of our intelligence is our technology – our ability to use natural objects as tools, and to modify them when necessary to solve new problems. This thesis examines the technology of one particular, and seemingly extraordinary, non-human animal: the New Caledonian crow. In particular, I ask whether and to what extent New Caledonian crows’ use and manufacture of tools reflects flexible cognition and an ‘understanding’ of the underlying physics, rather than simple rule-following, and what the crucial factors are that cause or allow this behaviour to develop.

There are two ways of addressing the question of whether other living beings have similar intellectual capacities to us. The first is to ask where our intellect comes from evolutionarily: can we identify what the building blocks of our cognition are by finding out what cognitive abilities our non-human relatives have? By doing so, we might be able to build up a picture of the cognitive abilities of our ancestors, and thereby understand what drove the evolution of our own abilities. This approach has been the more common one until recently, with a firm focus on studying the cognition of primates, and the great apes in particular.

The second approach is to ask whether a similar kind of intellect, or aspects of it, has ever evolved separately. By looking at the cognition of a wide range of animals, not closely related to humans, we might be able to work out firstly how rare our kind of intellect really is, and more broadly, which aspects of cognition can occur independently, which are dependent on each other, which are favoured by particular ecological and evolutionary conditions, and what kinds of neural architectures can support them. Since New Caledonian crows are clearly not closely related to humans, this will be the approach I am taking! I cannot hope to fully address all the issues just mentioned, but I hope the research I discuss sheds light on some of them.

Why the New Caledonian crow? Uniquely amongst birds, and perhaps all non-human animals, wild New Caledonian crows make a variety of tools from plant material, which they use to extract invertebrate prey from leaf litter and holes in dead wood (reviewed in Section 1.3 of this chapter). Several aspects of their wild tool-oriented behaviour are reminiscent of early human technology, so my research has concentrated on exploring the biology of this extraordinary behaviour in more detail, and in particular investigating whether assumptions that it reflects sophisticated cognition are warranted.

Although the work described in this thesis covers several fields (primarily ecology, cognition, lateralisation, and ontogeny), I devote much of this Introduction to the question of how to study cognition in animals, focussing on physical cognition in particular. There are two main reasons for this: firstly, two of the thesis chapters are devoted to experiments on cognition, some of which were inspired by the work with non-human primates I review below; and secondly, some of the conceptual issues (especially the thorny question of what we mean by ‘understanding’) are particularly difficult, and require in depth discussion. I then review what is currently known about New Caledonian crows’ tool-oriented behaviour in the wild, and the previous experiments into their cognition. Finally, I briefly outline the structure of the remainder of this thesis.

1.2 STUDYING PHYSICAL COGNITION IN ANIMALS

There is a long history of studying cognition in animals, and a wide range of methodologies have been used, including the collection of anecdotes (e.g. Romanes, 1886; Whiten & Byrne, 1988), recording and playing back vocalisations in an attempt to understand animal ‘language’ (e.g. Garner, 1892; Seyfarth et al., 1980), placing animals in ‘puzzle boxes’ (now ‘operant boxes’) and observing how they learn new behaviours (e.g. Thorndike, 1898; Powell & Kelly, 1975), and careful observation of the process by which behaviour is acquired (e.g. Morgan, 1930; Lonsdorf et al., 2004). However, following the ‘behaviorist revolution’ of the early 20th century (Watson, 1913), much of the psychological community came to see animal (and, Watson argued, human) behaviour as merely the product of associations between stimuli and responses, and the study of ‘complex cognition’ was largely neglected (although not entirely; see, for example, Klüver, 1937; Köhler, 1925; Yerkes & Yerkes, 1929; reviewed by Dewsbury, 2000). It took a number of surprising discoveries (e.g. cognitive maps: Tolman, 1948; one-trial food-avoidance learning: Garcia & Koelling, 1966; the importance of ‘play’ in problem-solving: Schiller, 1952; see review by Gould, 2004) and the publication by Donald Griffin of *The*

Question of Animal Awareness (1976) to re-establish the scientific respectability of investigations into complex cognition.

I focus here on research into animals' understanding of the physical world, since that is of most relevance to the experiments described in the rest of this thesis. There has, however, been a lot of research into other areas of so-called 'complex cognition', particularly language or symbolic communication and representation (e.g. Kaminski et al., 2004; Parker & Gibson, 1990; Pepperberg, 1999; Roitblat et al., 1993), and social cognition and intelligence (e.g. Byrne & Whiten, 1988; Call, 2001; Emery & Clayton, 2004; Hare & Tomasello, 2005; Whiten & Byrne, 1997) – as well as the links between these areas (e.g. Marino, 2002; Seyfarth et al., 2005). Without wanting to pre-empt the conclusions of the next section, the results from many of these studies have been similar: symbolic / communicative skill and social intelligence ability vary continuously among species, rather than showing large discontinuities, and despite initial presumptions that apes, and non-human primates in general, would outperform all other animals, this has not been the case. In fact, arguably the best evidence at the moment for elements of 'theory of mind' in non-human animals comes from corvids (Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002; Clayton et al., 2005; Dally et al., 2005; Emery & Clayton, 2001; Emery et al., 2004; Prior & Güntürkün, 2005) rather than the great apes (Heyes, 1998; Povinelli et al., 1999; Povinelli et al., 2002; Povinelli & Eddy, 1996a, 1996b; Povinelli et al., 1997; Reaux et al., 1999). Interestingly, in co-operative tasks similar to those the chimpanzees (above) were tested on, domestic dogs showed much greater sensitivity to the attentional state of humans than the apes had (Call et al., 2003; Gácsi et al., 2004; Hare & Tomasello, 2005); this might, however, be more due to domestication and the use of ethologically-relevant experiments, rather than true differences in mental state attribution (e.g. Virányi et al., 2006). Also, in more recent experiments where subjects had to compete over food, chimpanzees did show sensitivity to the visual perspective of conspecifics (Hare et al., 2000; Hare et al., 2001; Tomasello et al., 2003a, 2003b), although this could be explained by behaviour-reading (Povinelli & Vonk, 2003, 2004) or previously-established preferences in subordinates for avoiding food in the open (Karin-D'Arcy & Povinelli, 2002), rather than representation of the visual perspective of others.

I review naturally-occurring tool-oriented behaviour (i.e. tool use and manufacture) in non-humans, and its implications for cognition, in Chapter 2. In this section of this chapter I will instead discuss the general issue of 'understanding', and describe some of the experimental investigations that have been carried out into the physical cognition of other species.

1.2.1 What does 'understanding' really mean?

The issue of what constitutes 'understanding', or cognition and intelligence more broadly, has long been controversial, and there is still no clear concensus. Informally, the general idea is that to demonstrate understanding, an individual must react appropriately to a novel situation in a way that goes beyond instinctive responses, and cannot be explained solely by simple generalisation from previous experience. However, it has proved to be remarkably hard to make this informal concept more rigorous: obviously humans only come to understand how the world works through extensive experience, so how can we draw a clear line between simple 'generalisation' and true 'understanding'? The subsequent paragraphs outline my current (and still developing) view on what understanding is and how we can test for it. These ideas have been informed by reading a variety of texts (including but not limited to Dickinson, 2001; Evans, 2003; Hüber & Gajdon, in press; Kummer, 1995; Mitchell & Thrun, 1996; Povinelli, 2000b; Reboul, 2005; Sloman, 1996; Sterelny, 2003; Visalberghi & Tomasello, 1998; Vonk, 2005), as well as discussions with many people. For clarity and because the ideas are my own assimilation and evaluation of information from these sources, I do not cite references throughout the argument except to support specific points, but I do not intend to appear to take credit for ideas that have been proposed before.

In humans, the key difference between generalisation and understanding is our verbal explanation: we can say that the reason we, for example, pulled a chair over and stood on it to reach into a high cupboard to get food, is that we had worked out that the cupboard was out of reach, that the chair would support our weight, and that if we stood on the chair we could reach the cupboard (this is equivalent to one of the tasks that Köhler's (1925) chimpanzees are famous for performing, and that pigeons spontaneously solved after being trained on each element separately (Epstein et al., 1984)). However, in the absence of a verbal explanation, it would be very difficult to say whether the action of pulling the chair over and standing on it happened as a result of the knowledge described above, or instead was simply because we had learned through trial-and-error that similar actions allowed us to get the food (illustrating the importance of knowing how the behaviour was acquired, as emphasized by Morgan, 1930)[1]. We might argue, therefore, that to demonstrate understanding rather than generalisation from previous behaviour, we should carefully control all of the subject's previous experiences, and ensure that they had never had the opportunity to learn this action; but this might be too stringent a requirement to impose, since it is very unlikely that humans would instantly work out the correct solution if they had never had the opportunity to move objects around and stand on them. In fact, previous experience is crucial in order for us (and other animals) to develop understanding – as is nicely illustrated by Schiller's (1952; 1957) experiments showing that for chimpanzees to solve the kinds of problems that Köhler presented them with, previous opportunity to play with the objects was essential.

We appear to be left with a dilemma: we cannot infer 'understanding' if the individual in question had had previous opportunities to learn the behaviour through trial-and-error, yet it is unreasonable to expect them to behave correctly if they have never had any experience with the objects. One solution to this is to give individuals experience with objects in some contexts, but test them in completely novel circumstances where the behaviour needed to solve the task will never previously have been reinforced; if they perform perfectly from the first trial (since performance on subsequent trials may be influenced by learning on the first trial), we might then conclude they 'understand' the problem. There are still problems with this type of paradigm, though. Firstly, it does not really resemble the type of experience human children will have had, since non-human subjects will usually have several orders of magnitude less exposure to objects, materials, and problem-solving than human children, and it takes several years and explicit coaching on many different tasks before human children start to develop an effective understanding. Secondly, if despite these limitations subjects *do* perform correctly on the first trial, this might be due to the spontaneous 'chaining', or putting together, of previously separate (and associatively-learned) sequences of behaviour (e.g. Epstein et al., 1984; Epstein et al., 1981), a process that is usually not thought to be responsible for similar behaviour in humans.

Another way of approaching the issue is to use several 'transfer tests', in which aspects of the task are changed, to try to work out what is controlling subjects' responses.

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[1] Note that there is an argument that even for humans, what *causes* our behaviour is not our logical reasoning and understanding, but associations and habits learned previously (e.g. Evans, 2003; Oaksford & Chater, 2001). It is possible that our feeling that it was understanding and logic that caused our behaviour is actually *post hoc* justification (Nisbett & Wilson, 1977).

Using the example given above, we could see what humans would do if the cupboard was lowered to be within reach without use of a chair, if the chair's colour or texture was changed, or if it was replaced by, say, a flimsy cardboard box, a solid box, or a ladder. We could also ask if people could use different techniques to get the food – for example, a long stick to knock it down. We would predict that if people had a true casual understanding of the problem, they would only push the chair underneath the cupboard if it was necessary to reach the item, and they would readily use other objects capable of supporting them regardless of changes in colour or texture, but would avoid objects not capable of supporting them. In contrast, if they had merely learned the response of pushing the chair underneath the cupboard, they might continue to do the behaviour inappropriately if it was not necessary, fail to use other perceptually different but equally functional objects, and attempt to use perceptually similar but functionally inappropriate objects. In other words, if you understand the solution to a problem, your behaviour should be controlled solely by the causally-relevant features; if you have simply learned what to do, it is possible that by chance you may have learned about the causally-relevant features, but it is equally probable that you learned about causally-irrelevant, arbitrary features, such as the colour or shape of the chair. This approach is not without its problems either, since it is impossible to test *all* arbitrary cues that may be controlling behaviour (Visalberghi & Tomasello, 1998), and as mentioned above, subjects might have learned to respond to the causally-relevant cues even in the absence of understanding (e.g. Tebbich & Bshary, 2004). However, if it was consistently found that subjects responded on the basis of the causally-relevant features and never used arbitrary cues, we would probably have the most convincing evidence, in the absence of verbal explanations, that they 'understood' the underlying causality of the task.

In the following chapters of this thesis, I deliberately use the word 'understanding' in a somewhat vague, undefined manner. There are several reasons for this: it is frequently used this way in the literature, it should be fairly intuitive to readers what is meant by it, and as is apparent from the preceding paragraphs, the issue of definitions and how to distinguish between different explanations is controversial and unclear. Approximately, then, by 'understanding' I will be referring to the process(es) that remain(s) once simpler explanations – namely 'instinct', trial-and-error learning, and simple generalisation – have been eliminated. I return to this question in the discussion of Chapter 4, to ask whether and how our understanding of 'understanding' has changed in the light of the work I describe.

I now briefly review some work that has been carried out into the physical cognition of other species, which have employed some of the above techniques to try to address the issue of what understanding, if any, these species have of physical causality. This is not a fully comprehensive review – I have picked the experiments and research programmes that illustrate the points I want to make, and are most relevant to the experiments presented later. Moreover, I describe some of this research in detail in subsequent chapters, so do not discuss it below as well.

1.2.2 Experiments to date

There have been two broad classes of investigations into non-humans' physical cognition. The first is the Piagetian (Piaget, 1952) or neo-Piagetian (e.g. Case, 1985; Parker & Gibson, 1977) approach, which primarily consists of observing spontaneous behaviour and assessing the level of final performance that individuals reach on certain tasks, often from a developmental perspective. Piaget proposed that there were three 'stages' or 'periods' of intellectual development – the *sensorimotor*, *representational*, and *formal* stages – and within each stage six 'levels' or substages (reviewed in Case, 1985). Piaget suggested that human infants progress through these stages in parallel in a number of different domains of cognition, notably with his space, time, causality, sensorimotor intelligence, imitation, and object concept 'series' (which define the levels within each domain). Most Piagetian research with non-human animals has concentrated on assessing their performance in the sensorimotor stage within the different series (note that 'sensorimotor' is used to denote both a stage of development, and, as the 'sensorimotor intelligence series', a domain of cognition), since it develops earliest and describes the simplest forms of cognition. For example, level five of the sensorimotor period in the sensorimotor intelligence series is described as 'The Tertiary Circular Reaction or the Discovery of New Means by Active Experimentation', and is described as being characterised by repeated trial-and-error manipulation of object-object relationships, the use of different manipulation schemes in different contexts to meet varied ends, and the elaboration of a variety of means and a variety of ends (e.g. Gibson, 1990).

However, with the exception of Stage 6, none of the stages involve *understanding* in the sense I was discussing it above; instead, they concentrate on the variety of behaviours and manipulations that subjects engage in, and how well subjects can learn particular tasks (for example, Funk (2002) considered that pulling in a horizontal string to retrieve a reward on the end of it, regardless of how that behaviour was acquired, demonstrated Stage

5 performance) (but see Pepperberg, 2002 for arguments that the Piagetian approach is still relevant to animal cognition). Understanding is thought to develop in Stage 6: this is defined as 'The Invention of New Means through Mental Combinations', and is distinguished from Stage 5 on the basis of the origin of behaviours – Stage 5 behaviours are acquired by trial and error, whereas Stage 6 by 'insight' (which Piaget considered internalized trial and error, and is diagnosed (in humans) by the "Aha!" moment of sudden solution to problems; e.g. Bowden et al., 2005). Unfortunately, most of the purported demonstrations of Stage 6 performance in non-human animals are not well enough controlled to be accepted as proof of insight (itself usually poorly defined), so they will not be discussed further here. For example, Chevalier-Skolnikoff (1989) observed a (zoo-housed) capuchin monkey picking up a nut and a stick, carrying them to a rock, placing the nut in an indentation in the rock, and hitting it with the stick, and interpreted this behaviour as insightful, despite having no knowledge of the prior history of the subject, or of whether it had had previous opportunities to learn this behaviour by trial-and-error (as pointed out by several commentaries on the paper, e.g. Anderson, 1989; Bernstein, 1989; Gibson, 1989; Greenfield, 1989; Parker, 1989; Savage & Snowdon, 1989; Visalberghi, 1989).

The second approach relies less on a grand theory of cognition and cognitive development, and also lacks a formal name, although Daniel Povinelli (Povinelli, 2000b) labelled it investigation of 'folk physics', from similar studies with humans (e.g. Baron-Cohen et al., 1999). It has focussed on *how* (rather than *whether*) non-human animals solve problems, and has particularly made use of transfer tests to investigate what cues are controlling subjects' behaviour (as discussed above). Perhaps unsurprisingly, most of the studies have concentrated on non-human primates, particularly chimpanzees (*Pan troglodytes*), capuchin monkeys (*Cebus* sp.), and cotton-top tamarins (*Saguinus oedipus*). Most studies have also focussed on the use of tools, although not exclusively. Because this is similar to the approach I have taken, I expand on the research to date, describing primate and non-primate / avian folk physics experiments separately.

Primate folk physics

Some of the earliest, and certainly most famous, experimental investigations into non-humans' understanding of physical causality were carried out on chimpanzees by Wolfgang Köhler (1925) during the World War I, on the island of Tenerife. Köhler presented his group of seven chimpanzees with food made inaccessible in a variety of ways (e.g. a banana suspended from the ceiling), and objects in the room that they could use to retrieve it (e.g. a box that could be pushed to the spot beneath the banana and stood upon to reach it). Köhler found that his subjects could solve many of the problems in diverse ways, and concluded that their solutions were often ‘insightful’, in the sense that they appeared suddenly and without apparent trial-and-error based precursors (Thorpe, 1963). However, although his studies are still frequently cited as providing evidence that chimpanzees are capable of insight and the immediate solution to problems, several authors (e.g. Beck, 1977; Chance, 1960; Povinelli, 2000a; Schiller, 1952, 1957) have pointed out that in fact Köhler frequently demonstrated the opposite. Although his chimpanzees did occasionally show apparently insightful behaviour, more commonly they failed to solve very simple problems, and persisted in making some extraordinary errors over a long period of time. For example, “Grande tries to balance one box on its point on top of another repeatedly over a period two years, […] Chica tries to combine her stick with a box by placing it on the upturned edge of the box, again repeatedly, or […] Rana repeatedly tries to jump up sticks which are too short even to take her off the ground” (Chance, 1960, p. 132).

Similar types of problems have also been presented to zoo-housed orang-utans (*Pongo pygmaeus*; reviewed in Lethmate, 1982), who solved them all without difficultly. However, as with Köhler’s experiments, it is not always clear from the published descriptions *how* they solved the problems – whether the solution arose out of random manipulation, or understanding and reasoning. Lethmate does describe nine of the solutions as ‘insightful’, since the behaviour of the subjects was consistent with Beck’s (1967) idea of insight being characterised by a sequence of persistent but unsuccessful attempts, followed by a period of non-problem-directed activity, and then a sudden solution. It is unclear, though, whether these solutions actually reflected a sudden ‘understanding’ on behalf of the subject of how to solve the task, or instead occurred when the subject suddenly ‘recognised’ that (for example) the current tool would now be long enough to reach the target object. No transfer tests were described to try to ascertain what characteristics of the problems were determining subjects’ behaviour. Many of the same criticisms can be made of Klüver’s (1933; 1937) experiments into tool use and related problems with capuchin monkeys (*Cebus* sp.), although he was much more reluctant to claim that capuchins were capable of insight, and others have concluded that his experiments really demonstrated that capuchins’ problem-solving is entirely based on trial-and-error manipulation, rather than ‘mental representation’ (Visalberghi, 1993).

More recently, Daniel Povinelli has undertaken a systematic programme of experiments into the nature of chimpanzees' 'folk physics', using a group of seven subjects reared from an early age in his laboratory (Povinelli, 2000b). These experiments have systematically shown that Köhler's more informal observations were largely accurate: although chimpanzees are certainly frequent and proficient tool users in the wild (e.g. McGrew, 1992; Whiten et al., 1999), when presented with novel problems to solve in captivity they are rarely sensitive to the causal properties of the task. Povinelli's group presented their chimpanzees with a variety of different food retrieval problems involving tools: for example, (a) food is put in a tube with a 'trap' in the middle, and the subjects have to insert the tool in the end of the tube furthest from the food to retrieve it and avoid pushing it into the trap (the 'trap-tube' task); (b) food is available at the end of two channels, one of which contains a functional and one a non-functional tool (e.g. a rope tied around a banana, and one just resting on the banana), and subjects have to choose the correct one to pull; or (c) tools are provided that need modification (e.g. bending, or elements added / removed) to work. Every task was designed to pit a 'high-level' model of cognition against a 'procedural rules' model: for example, under the high-level model (which assumes that subjects understand causal features of the tasks), the chimpanzees were expected to always choose the tool that allowed *connection* with the food (for example, rope tied around a banana), whereas if they were using procedural knowledge (which assumes that subjects had simply learned what actions were successful, without understanding why) they might be expected to maximise *contact* between the rope and the banana, rather than the true connection. After pre-training on each task (and experience with the materials in their home range), subjects were given transfer tests for only a few trials, in order to test their *a priori* understanding rather than ability to learn the correct response(s).

For almost every subject and every task, Povinelli and colleagues found that the procedural rules model fitted the chimpanzees' behaviour better than the high-level model. Specifically, they concluded that "chimpanzees do not represent abstract causal variables as explanations for why objects interact in the ways that they do" (Povinelli, 2000a, p. 77). It should be mentioned that for a variety of reasons their findings are still very controversial, and not widely accepted. Criticisms include that their subjects were immature for almost the entire duration of their experiments (Anderson, 2001; Hauser, 2001)[2], the subjects had a relatively impoverished rearing environment since they were neither parent-raised nor enculturated (Whiten, 2001), previous experience and response biases might have affected the results (Hauser, 2001), and no direct comparisons with humans or human children are presented (Anderson, 2001; Silva et al., 2005; Whiten, 2001). These caveats mean that we should not interpret Povinelli and colleagues' results as proof that chimpanzees are incapable of understanding abstract physical causal relations, but the experiments remain interesting and thought-provoking.

Although Povinelli's work has been the most comprehensive of recent studies into the subject, his is by no means the only research group investigating primate folk physics, or even the first to use these techniques. Elisabetta Visalberghi and colleagues have carried out a number of experiments into folk physics with capuchin monkeys (now known to be proficient tool-users in the wild, like chimpanzees: see Boinski et al., 2000; Fragaszy et al., 2004; Moura & Lee, 2004; Phillips, 1998), great apes (primarily chimpanzees), and human children, pioneering the 'trap-tube' task (among others) described above. In the trap-tube task, they found that only one of their four capuchins learned to reliably insert the tool in the correct end of the tube, and by testing her with the trap moved to different positions or inverted, they found that she was using the rule of inserting the tool on the side furthest from the reward, rather than taking into account the position and function of the trap (Visalberghi & Limongelli, 1994). In contrast, they found that two of their five chimpanzees learned to insert the stick in the correct end of the tube, and carried on responding correctly even when the trap was moved to a different position (Limongelli et al., 1995; but see Reaux & Povinelli, 2000 for evidence that chimpanzees fail other transfer tests with an inverted trap and where the tool is pre-positioned in the tube). Human children under 3 years old apparently failed to learn the task, whereas those over 3 learned it very quickly, and did not use a distance strategy (reviewed in Visalberghi, 2000).

Visalberghi and colleagues have also carried out experiments into capuchins' and chimpanzees' understanding of tool shape and length. Visalberghi and Trinca (1989) presented four capuchins with food in a transparent tube (a task they were already familiar

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[2] Wild chimpanzees only become proficient at termite-fishing by 5-6 years old (Lonsdorf et al., 2004), and although they start nut-cracking between 3-5 years old, they continue to improve until 8-14 years old (Biro et al., 2003). Povinelli's experiments began when his chimpanzees were 5-6 years old, and ended when they were 10-11, so they might only have achieved full competence half-way through the experiments. Also, there have been suggestions (Biro et al., 2003) that there is a "sensitive period" for learning nut-cracking, and if individuals do not learn it during this period they will never acquire the skills; it is therefore possible that Povinelli's chimpanzees missed out on vital experience during the sensitive period.

with) and tools in a variety of configurations – sticks tied up in a bundle that had to be disassembled before it could be inserted into the tube (‘bundle’ condition), sticks with cross-pieces inserted through each end that needed to be removed before insertion (‘H-stick’ condition), or three small sticks each too short to reach the food, but if inserted in a sequence would be long enough (‘short tools’ condition). Although their subjects quickly solved the task in each of the conditions, their solutions only occurred *after* trying with the inappropriate tools, and they made frequent errors (such as inserting one short stick on one side of the tube and one on the other, or removing one of the cross pieces but attempting to insert the end with the cross-piece still attached) that suggested they did not understand the critical features of the task. Visalberghi and colleagues also tested three species of great ape (common chimpanzees *Pan troglodytes*; bonobos *Pan paniscus*, and an orangutan *Pongo pygmaeus*) with two of the same tasks (the bundle and H-stick conditions) (Visalberghi et al., 1995). They found that unlike the capuchins, on every trial of the bundle task the apes did unwrap it before attempting to use it; however, like the capuchins, the apes attempted to use the H-stick tools before removing the cross-pieces, and again attempted to insert the end from which they had not removed the cross-piece, and even attempted to use the cross-pieces themselves (which were much too short) to get the food. Visalberghi and colleagues concluded that there was a qualitative difference between the performance of the apes and the capuchins, although others (e.g. Povinelli, 2000a) disagree with this interpretation.

A third research group that has studied the physical cognition of primates in detail is Marc Hauser’s. His group have primarily studied a non-tool-using species, the cotton-top tamarin (*Saguinus oedipus*). Their main paradigm has involved training tamarins to pull one of two ‘tools’ (usually clay canes or pieces of cloth) towards them to retrieve a reward, and then to vary features such as the colour, texture, and shape of the tools, and the spatial relationship between the tools and rewards. Perhaps surprisingly, given that tamarins are not natural tool-users, he found that they tend to be relatively insensitive to (irrelevant) changes in the colour or texture of tools, whereas they are sensitive to (potentially relevant) changes in tool shape or the spatial relationship between the tool and reward (Hauser, 1997; Hauser et al., 1999; Santos et al., 2003) – in other words, they appear to be sensitive to the causally-relevant aspects of the task. Moreover, they found that these preferences appear in infancy (Hauser et al., 2002a), although aspects of them are dependent upon experience (Hauser et al., 2002b; Spaulding & Hauser, 2005). On first consideration these results appear surprising, as they seem to suggest that tamarins may be more sensitive to causal relations than natural tool-users such as chimpanzees and capuchins (indeed, Hauser, 2001 used exactly this argument as a criticism of Povinelli's experiments). However, there have been no studies with chimpanzees that have used exactly the same methodology, and recent studies with capuchins using Hauser's paradigms have found that they too seem to be sensitive to causal relations (Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003). The training conditions used in these studies may serve to explicitly condition the subjects to attend to the causally-relevant features, though, so it is unclear whether these results actually imply causal understanding or not. I discuss this issue further in Chapter 3, so will not examine it in more detail here.

Non-primate folk physics

In contrast to the extensive work on non-human primates' folk physics, there have been very few studies in other taxa. The most comparable to the work discussed above (and in subsequent chapters of this thesis), is the study by Tebbich and Bshary into the folk physics of Galapagos woodpecker finches (*Cactospiza pallida*; Tebbich & Bshary, 2004; see also Millikan & Bowman, 1967), which use twigs or cactus spines in the wild to forage for invertebrates in tree bark. They tested the finches on three tasks: the trap-tube and H-stick tasks, described above, and a length-selection task, where food was presented at different distances inside a transparent tube, and the birds were given a selection of tools of different lengths to choose from.

After four sessions of 20 trials each, none of their six subjects showed above-chance performance on the trap-tube task, although one subject ('Rosa') did show immediate success when then tested with an opaque tube (with a transparent trap, designed to maximise contrast between the trap and the tube), and maintained that success when transferred back to the transparent tube. Notably, in contrast to the chimpanzees and capuchins tested to date, Rosa did revert to random insertion when the trap was inverted (and therefore ineffective), which could be taken as evidence that she understood the function of it, although the authors believe that she was actually monitoring the moment-to-moment position of the food with respect to the trap, rather than using an *a priori* strategy of inferring the correct side to insert the tool (the suitability of this task and transfer test for inferring understanding has in any case been questioned; see Machado & Silva, 2003; Silva et al., 2005).

Three finches eventually became consistently successful in the H-stick task, although all continued to make errors until the end of the experiment (such as inserting the tool before modification, inserting the wrong end of the modified tool, and inserting the short pieces rather than the long ones). In the tool length task, three of the five subjects tested had a tendency to choose tools that were sufficiently long to reach the food on their first probe in each trial, although it seemed that this behaviour was acquired by trial-and-error, since one subject initially used the shortest tools most frequently, and the other two had a tendency to increase the length of the tools they first chose on trials immediately following failures.

1.2.3 In summary

It is hard to summarise the result of the many different studies into physical cognition in mammals and birds, primarily because few of them have used the same tasks or even general methodology, and because the results even within species often conflict, making inter-species comparison yet harder. Many of the experiments (especially the earlier ones) seem to have had an underlying assumption, perhaps based on an intuitive (but false) *scala naturae*, that primates (and apes in particular) must be the most intelligent non-humans, followed by other mammals, and then birds, reptiles, fish, etc. (Banks & Flora, 1977; Beck, 1982; Eddy et al., 1993). The results do not bear this out, and in fact there seems to be greater diversity in performance within taxa than between – within both Primates and Aves there are species that perform well on tests of physical cognition, and those that perform badly. Moreover, in almost every task, at least some bird species have been found to equal, or even outperform, the best-performing primates.

Another general finding is the elusiveness of ‘insight’, or causal understanding more generally. Despite over a century of research, there are still no experiments that prove beyond doubt that insight or understanding was responsible for the behaviour observed – but perhaps this inevitable, due to the nature of the phenomenon itself. Even more unsettling to our conception of ‘understanding’ as something that is either present or absent in an individual is the variation in performance: sometimes, subjects will perform very well on some tasks, but fail spectacularly others that appear to us very similar. This is a theme I will return to later in the thesis.

I now turn to New Caledonian crows: why they are an interesting species in which to study physical cognition, and what we know about them to date.

1.3 NEW CALEDONIAN CROWS

There have been anecdotal reports of tool use (or ‘pseudo’ tool use) in wild corvids for many years. For example, an American crow (*Corvus brachyrhynchos*) was seen to modify and use a sharp splinter of wood as a probe (Caffrey, 2000); another American crow apparently used a stone to smash an acorn (Duvall, in Boswall, 1978); ravens (*C. corax*) have been observed to drop rocks onto humans, possibly in nest defence (Heinrich, 1988); carrion and hooded crows (*C. corone / cornix*) are said in Eskimo mythology to pull up fishing lines to get fish under the ice (Holmberg, 1957, and Scott, 1974, cited in Lefebvre et al., 2002); an East African fan-tailed raven (*C. rhipidurus*) was seen to use a stone in an apparent attempt to break open a “false egg” (in fact, a ping-pong ball!) (Andersson, 1989); an Indian house crow (*C. splendens*) was said to “fish” for ants with leaves (Rajan & Balasubramanian, 1989, cited in Caffrey, 2001); two green jays (*Cyanocorax yncas*) were seen repeatedly probing with twigs and capturing insects (Gayou, 1982); and American crows and carrion crows (in Japan) are known to drop nuts onto roads and wait for cars to crush them (Grobecker & Pietsch, 1978; Nihei, 1995; note that Cristol et al., 1997, argue that this is not intentional, but this is refuted by Caffrey, 2001, and Nihei & Higuchi, 2001). Moreover, there have been a number of observations of spontaneous tool use (and manufacture) in captive corvids: an American crow used a small plastic cup to transport water to food to soak it (Beck, 1980); a northwestern crow (*Corvus caurinus*) used a stick to try and pry a peanut from bamboo (Jewett, in Boswall, 1983); ravens will readily pull up string with food attached (Heinrich, 1995, 2000; Heinrich & Bugnyar, 2005); a rook (*C. frugilegus*) repeatedly inserted a plug into a drain hole to retain rainwater for drinking and bathing, particularly on drier and warmer days (Reid, 1982); and several blue jays (*Cyanocitta cristata*) tore up strips of newspaper and used these (and other objects) to rake in out-of-reach food pellets (Jones & Kamil, 1973; similar behaviour has been reported in marsh tits, *Parus palustris*: Clayton & Jolliffe, 1996).

However, the examples above all involve occasional tool use by one or a few individuals – certainly the behaviours could never be said to be characteristic of the species. In contrast, tool use and manufacture in New Caledonian crows is widespread throughout their range (Hunt & Gray, 2002), and has been observed in all captive individuals (Chapter 5). In the next three sections, I review the current knowledge of New Caledonian crows’ ecology and their tool use and manufacture in the wild and in captivity.

1.3.1 Natural history

New Caledonian crows are endemic to the semitropical Grande Terre island of New Caledonia, but have also been introduced to the smaller island of Maré. They are common throughout the range of forest types found on Grande Terre (Hunt, 2000a; pers. obs. by myself, Ben Kenward, and Charlotte Burn), and are also found in the Niaouli savannah (Hannécart & Létocart, 1980) and in agricultural areas (Vuilleumier & Gochfeld, 1976; pers. obs. by myself, Ben Kenward, and Charlotte Burn). Their appearance is that of a 'typical' crow (*sensu* Goodwin, 1986), except for the unusually-shaped bill, particularly the maxilla, which has almost no downwards curve. In size, they are slightly larger than the Eurasian jackdaw (*Corvus monedula*), with a mean weight of 264g at capture reported for 43 crows, and a small but significant sexual dimorphism (with males larger than females; Kenward et al., 2004 (Appendix 1); Ross, 1988).

New Caledonian crows' 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 (Hannécart & Létocart, 1980; Layard & Layard, 1882); tool use seems exclusively directed at obtaining insects and other invertebrates (Hunt & Gray, 2002). They live in social groups, and there seems to be 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) possibly much longer (Kenward et al., 2004 - Appendix 1). The size of social groups varies, with some flocks reaching around 30 individuals. However, most commonly the crows are seen in groups of around three or four birds (Kenward et al., 2004 - Appendix 1), 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 possibly food and tool caching (Hunt, 1996; Hunt, 2000b; pers. obs. in the laboratory).

1.3.2 Tool use in the wild

Almost everything known about New Caledonian crows' tool use in the wild comes from the work of Gavin Hunt and his colleagues. The crows make and use several kinds of tool:

straight stick-type tools, hooked-twig tools, and pandanus-leaf tools. Pandanus-leaf tools have been found at 20 sites throughout Grande Terre and also on Maré (Hunt & Gray, 2003), and the other tool types have been found in at least 11 sites in the south of Grande Terre (Hunt & Gray, 2002).

The different tool types are made in different ways. Straight 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). Although their manufacture in the wild has not been described, it is likely that it involves simply detaching the tool from the substrate (e.g. branch or fern), possibly followed by the removal of additional material (such as leaves) from the tool. In our laboratory, crows readily make similar straight tools from oak branches, and by removing the barbs from long (moulted) feathers and then using the stem formed by the quill and shaft (pers. obs. by myself, Jackie Chappell, and Alex Kacelnik).

The way the crows make their hooked-twig and pandanus-leaf tools is of particular interest. 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 a primary one by nipping at the joint with their beaks, leaving a piece of the primary twig to form a hook. They then remove the secondary twig beneath the joint, remove leaves and bark, and sometimes actively sculpt the shape of the hook with their beak for several minutes, appearing to make it sharper by removing excess material (Hunt, 1996; Hunt & Gray, 2004a).

The manufacture of pandanus-leaf tools 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, 1996, 2000a; Hunt & Gray, 2004b). The edge of the stiff, barbed leaf is cut and torn in a sequence which results in a flat tool that is either rectangular and narrow, rectangular and wide, or tapered, according to the number and length of the cuts into the leaf. The crows make tapered tools by cutting and tearing into the leaf several times before removing the tool (see Figure 1), resulting in a series of ‘steps’ which 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 leaves and bark from a twig, each action does not result in a progressively more effective tool: the final step is the removal of the tool from the leaf, so until this point the tool is non-functional.

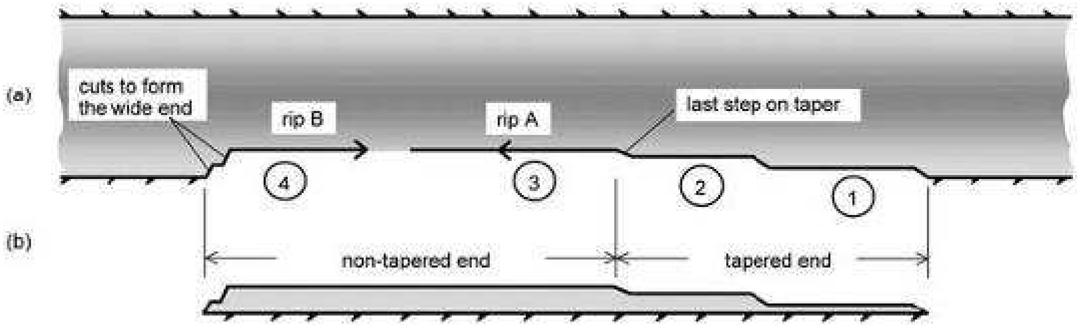

Figure 1: Schematic diagram showing how New Caledonian crows cut pandanus tools from the edge of pandanus leaves (reproduced from Hunt & Gray, 2004b with permission). The trunk of the pandanus tree would be on the right of the diagram. **(a)** The ‘counterpart’ left on the pandanus leaf after removal of the tool. The crows cut into the leaves (orthogonally to the edge of them), and then tear longitudinally. They start nearest the trunk, cutting in a tearing a number of times (three cut-tear sequences are shown here, ending with rip A), and then move beyond the last tear, cut in (twice in this diagram), and tear *back* towards the trunk again (rip B) to remove the tool. A movie clip of this sequence is provided as Supplementary Material to Hunt & Gray (2004b). **(b)** The tool removed from the pandanus leaf. The crows hold the wide end (on the left) in their beak, and insert the narrow end into holes when foraging, using the backwards-pointing spines as hooks.

The design of the pandanus-leaf tools varies in complexity from area to area: by examining the shapes left behind in pandanus leaves after tools have been removed (the tool ‘counterparts’), Hunt and Gray (2003) noticed that 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 identifiable variation in the availability of raw materials or ecological factors that could indicate different needs, so these shape 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). The improbability of the most complex tool design emerging *de novo* adds plausibility to this historical sequence. However, in the absence of cross-fostering studies and the translocation of adult crows between regions, it remains possible that genetic or ecological differences are responsible for the variation in tool shape.

There also seems to be population-wide lateralisation in the way the crows make pandanus tools: the leaves on pandanus trees spiral around the trunk in either a clockwise or anticlockwise direction, and on clockwise-spiralling trees 80% of tool counterparts are found on the left edges of the leaves (which are the most accessible), whereas on anticlockwise-spiralling trees counterparts are found equally on the left and right leaf edges (even though the right edge is now the most accessible) (Hunt, 2000a; Hunt et al., 2001).

Direct observations of the manufacturing process showed that when removing tools from the left edges of leaves, the crows use the left edge of their bill for the cuts at the tapered end of the tool and the right side of the bill for the wide end (see Figure 1); the inverse occurred when making tools from the right edges (Hunt & Gray, 2004b). However, the authors speculate that the right eye might be primarily guiding manufacture in both cases, since work with the bill tip is thought to involve binocular vision.

At least two different kinds of tool *use* have been described. One 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). The other is in the context of ‘fishing’ for Cerambycidae larvae (*Agrianome fairmairei*) from fallen trunks of the ‘bancoulier’ tree (*Aleurites moluccana*) using straight tools. Here, the crows mainly use “quick up and down actions in the probe hole through a vertical height of up to several centimetres, interspersed with quiet periods” (Hunt, 2000b p. 111), which the authors interpret as initially making the larva aggressive, and then (during the quiet periods) allowing it to grasp the tool in its mandibles; the tool is then carefully withdrawn with the larvae clamped onto the end of it. Occasionally Hunt and colleagues observed the birds moving the tool through a larger vertical height in a “pestle-like” manner, which often killed the larvae and prevented the crows from extracting them, although one crow did manage to extract a dead larva from a hole at a more horizontal angle (Hunt, 2000b), and another crow was able to extract dead larvae by levering them from an artificial box (Hunt et al., in press). Like pandanus-tool manufacture, tool use is lateralised, but possibly at the individual rather than the population level: crows often hold tools with the non-working end pressed against the side of their head, and four wild crows observed by Rutledge and Hunt (2004) almost always used the tools in the same orientation, although two were left- and two right-lateralised (see also Chapter 5).

1.3.3 Previous laboratory investigations

The following three experiments were carried out by Jackie Chappell and Alex Kacelnik on captive New Caledonian crows, before my DPhil started, and also took place in our laboratory (the Behavioural Ecology Research Group). They involved two subjects, Abel (a male) and Betty (a female), thought to be about 16-17 and 2-3 years old (respectively) at the time of the experiments.

The first experiment tested the ability of Abel and Betty 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 at different distances from the open end of the tube, and 10 sticks of different lengths. Both crows selected tools with lengths equal to or greater than the distance to the food significantly more often than would be expected by chance. Furthermore, they selected tools whose length precisely matched the distance to the food more often than expected. When, in a different experiment, the sticks were placed behind a screen so that the birds could not see the tools and the food tube simultaneously, Abel still chose suitable tools more frequently than chance, whereas Betty (who was still a juvenile at the time) seemed to lose motivation and did not perform the task.

The second experiment tested the crows' ability to select and make tools of an appropriate *diameter* (Chappell & Kacelnik, 2004). 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 out of the vertical leg of the tube. The hole in the end cap could be of three different diameters, which were varied pseudo-randomly across trials. In the first part of this study, only Betty was tested. 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 always used the thinnest tool, but only dismantled the bundle when it contained this tool, thus paying the cost of disassembling the bundle only when required. In the second part of the experiment, both crows were exposed to the same apparatus as above, but they were not provided with tools. Instead, oak branches were placed into the aviary from which tools could be made. Both birds readily made tools by breaking twigs off the branches and removing leaves and minor twiglets. The diameter of the tools they made increased significantly with the diameter of the hole, and on only two (out of 29) trials did they make tools that were too thick to fit into the hole; in both cases, they modified the tools by removing protrusions on the twigs immediately after first trying them, thereby making them narrow enough to fit through. 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.

Betty has also been tested using the trap-tube experiment described in Section 1.2.2 (Chappell & Kacelnik, in prep; summarised in Kacelnik et al., in press). She reached criterion (avoiding the trap on 8/10 trials or more on three consecutive blocks of ten trials) after about 100 trials with the apparatus, which is comparable to the performance of chimpanzees, capuchins, and woodpecker finches (Limongelli et al., 1995; Reaux & Povinelli, 2000; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994). When the trap was inverted during the testing phase, Betty did not return to random responses: she continued to avoid the now irrelevant trap, like all the chimpanzees and capuchins tested to date, but unlike the one woodpecker finch described above (Tebbich & Bshary, 2004). However, it has recently been shown that adult humans also continue to avoid the trap on inversion on over 90% of trials (Silva et al., 2005), which suggests that this is not a good test for ‘understanding’. Betty’s performance is described in more detail in Kacelnik et al. (in press), along with some other unpublished experiments into her and Abel’s folk physics.

In summary, in two of the three experiments to date into New Caledonian crows’ folk physics, both subjects showed sensitivity to causally-relevant features of the tasks (tool length and diameter). In the third experiment, the sole subject tested took many trials to learn how to solve the task consistently, and a transfer test suggested that she had not understood the physical principles involved. However, firm conclusions about the nature of New Caledonian crows’ folk physics cannot be drawn from these experiments: it is possible that previous experience had enabled the subjects to *learn* the relationship between hole length / diameter and tool length / diameter for the first two tasks, and conversely, adult humans make similar errors in the trap-tube task, even though they do understand the causal principles.

1.4 STRUCTURE OF THIS THESIS

The work described in this thesis examines various aspects of the tool use and manufacture of New Caledonian crows. I start (Chapter 2) by reviewing tool use and manufacture in other wild non-human animals, and asking whether (and if so, how) this relates to cognitive abilities. I next (in Chapters 3-4) describe a series of experiments designed to explicitly test New Caledonian crows’ folk physics, all focussing on the issue of tool shape and modification.

The issue of laterality is considered in Chapter 5. Lateralisation (or handedness) in humans is thought to be related to language and tool use, and as mentioned above, Gavin Hunt and colleagues (Hunt, 2000a; Hunt et al., 2001) had previously described population-level laterality in tool *manufacture* in wild crows. I studied laterality in their tool *use*, primarily focussing on the extent to which individuals, rather than populations, show lateral biases.

Chapters 6 is concerned with how tool-oriented behaviour develops in New Caledonian crows. Hunt and Gray (2003) had suggested that the shape of the pandanus tools they make is culturally influenced (described above), but nothing was known about how basic tool use developed. There were several possibilities, from complete reliance on social learning to a strongly genetically-canalized developmental 'programme', and we attempted to resolve some of these issues by examining the development of hand-raised crows that either did or did not receive demonstrations of tool use by their human foster parents.

In the final chapter (Chapter 7), I attempt to summarise the main findings from my DPhil research, discuss their implications, and suggest some directions for future research.

Additional data and papers published during my DPhil but not included as chapters, are presented as appendices. Appendix 1 is a paper describing observations of wild New Caledonian crow behaviour and ecology made by myself and colleagues, along with morphological measurements taken by us from captive crows (Kenward et al., 2004). Appendix 2 is the published version of Experiment 2 of Chapter 3 (Weir et al., 2002), and Appendix 3 presents trial-by-trial descriptions for this experiment. Appendix 4 has similar trial-by-trial descriptions from the experiments in Chapter 4, and Appendix 5 provides photos of the tools made by Betty in Experiment 1 of this chapter. Finally, a paper describing the detailed development of tool use in four hand-raised crows is attached as Appendix 5 (Kenward et al., in press).

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Chapter 2

Animal tool use reconsidered – a new framework for analysing tool-related behaviour in animals

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2.1 INTRODUCTION

Seeing an animal using a tool usually exerts a powerful effect on the observer. As Benjamin Beck (1980, p. xi) puts it, “there is an intuitive, sometimes mystical, appreciation of evolutionary continuity [when watching an animal use a tool] that is not elicited even by the most elaborate bird song or the most vigorous canid dominance interaction”. It is perhaps not surprising then, that early observers of animal tool use were particularly impressed by it, as shown by this quotation from William McDougall (1923, cited in Hall, 1963) discussing the discovery of tool use in solitary wasps:

> "Are we then to regard each of these two wasps as a lively *bahnbrechende* genius, leading their species onward to the use of tools; individual sports comparable to the man, or ape, who first took a stone in his hand to crack a nut and so foreshadowed the genius of Nasmyth? I see no other plausible interpretation of the facts" (p.91)

However, this assumption of special intelligence associated with animal tool use has also been heavily criticised, with several authors arguing that tool-oriented behaviour (defined to include tool use and manufacture, *sensu* Beck, 1980) is really no different from other types of animal behaviour, such as nest-building, which is explicable by standard genetic predispositions and simple learning mechanisms (e.g. Hansell, 2000). This chapter seeks to clarify the situation by considering how both tool use and ‘intelligence’ might be analysed in more detail, and thus whether there are any links between the two.

In the first section, I describe the historical interpretation of tool-oriented behaviour, and the existing empirical work on links between it and cognition. I then argue that in order to talk about the cognitive basis of behaviour, we need to consider what we really mean by ‘intelligence’. In the context of tool use, by ‘special’ or ‘intelligent’ most authors seem to implicitly mean “not instinctive or associatively learned”, although this point is rarely made explicitly. I attempt to formally define the three categories of behaviour (‘instinctive’, ‘simply’ learned, and ‘cognitive’), which is necessary before the issue of whether tool use is ‘special’ can be sensibly discussed (unless ‘special’ is used to mean “only performed by great apes and humans”, which is the implicit interpretation of some primatologists; e.g. Byrne, 2004). Obviously these are crude and simplistic distinctions, and the categories are in fact both continuous and hierarchical (for example, there will often be ‘innate’ rules that are modified by learning, or ‘cognitive’ behaviour that is dependent on learning and innate rules). However, these concepts may be useful for clarifying what is meant by arguments that tool using species should be more ‘intelligent’ than non-tool-users.

In the light of these distinctions, I consider whether there are any characteristics of naturally-occurring tool use that could be indicative of a greater or lesser involvement of ‘cognition’. I propose a framework that can be used to classify tool-oriented behaviour in wild animals into various levels in four categories that, although not necessarily individually linked to cognition, might in combination be more informative. It is not my intention that this should be used to conclude that a particular species is “more intelligent” than others – apart from anything else, there are a multitude of reasons why some species might or might not use tools, many of which have no relationship to cognition at all, and tool use is only one narrow aspect of any species’ behaviour. However, if tool-oriented behaviour is to be used as an index of cognition or postulated as a factor promoting the evolution of larger brains, as it sometimes has been (e.g. Lefebvre et al., 2002; Parker & Gibson, 1977; Reader & Laland, 2002), it seems sensible to take into account rudimentary information regarding the diversity and complexity of the behaviour within the species concerned.

I illustrate how the framework might be applied using a few selected examples. They are not intended to be comprehensive, but nevertheless demonstrate that the framework is realistic and practical. This new approach promises to be more powerful than the existing methods of analysis, and it can also act as a basis from which to study tool-related behaviour with more rigour.

2.2 A HISTORICAL VIEW

Technology, including tool manufacture and use[3], is considered by many to be a defining feature of advanced intelligence, and the appearance of sophisticated tool manufacture in humans appears to have coincided with other cognitive advances such as language and an understanding of causality. It is often argued that these three abilities are functionally linked (e.g. Gibson, 1993a; Oakley, 1949; Parker & Gibson, 1979; Washburn, 1959; Wolpert, 2003): for example, Wolpert argues that complex tool manufacture requires an understanding of cause and effect, and that it was the evolutionary advantage gained from the resulting technology that has driven human evolution, rather than social (e.g. Byrne & Whiten, 1988; Dunbar, 1996; Jolly, 1966; Premack & Premack, 2002; Whiten & Byrne, 1997) or sexual and reproductive (e.g. Lovejoy, 1981) factors.

Due to its prominence in human society and evolution, it is not surprising that tool use and manufacture in animals has been the subject of intense interest ever since it was first observed. Early authors assumed that tool use in animals must have the same cognitive basis as tool use in humans (e.g. Romanes, 1882) – and therefore implied ‘intelligent purpose’ and ‘perception of the relation of means to an end’ (Morgan, 1900). However, in the early part of the twentieth century, more and more examples of animal tool use, and even tool manufacture, were discovered. These ranged across phyla, from crabs waving stinging anemones in their chelipeds as defence against predators (Duerden, 1905, cited in Beck, 1980), to ant-lions and worm-lions (larvae of Neuropteran and Rhagionid flies) throwing grains of sand at ants or other insects that fall into their pits (Wheeler, 1930, cited in Beck, 1980). Tool use therefore came to be regarded by many as just another adaptation to ecological problems, or occasionally as the outcome of redirected ‘emotional’ responses or simple trial-and-error learning (e.g. Alcock, 1972; Beck, 1980, 1986; Hall, 1963; Hansell, 1987, 2000, 2005). Others argued that, for non-human primates at least, it is not tool use so much as manual dexterity that is ‘special’ and

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[3] I am using Beck’s (1980) definition of tools as “unattached environmental object[s]” that the user “holds or carries […] during or just prior to use and is responsible for the proper and effective orientation of the tool” and which are used to alter “more efficiently the form, position, or condition of another object, another organism, or the user itself” (p. 10). ‘Borderline’ (or ‘proto’) tools differ in that are not held or carried, and are generally attached at the time of use. Under this definition, hammers are considered to be tools, whereas anvils, which can serve the same purpose, are borderline (unless carried at the time of use – as sea otters do). Tool manufacture is defined as “any modification of an object by the user or a conspecific so that the object serves more effectively as a tool” (p. 11-12).

indicative of cognitive abilities (Byrne, 2004), and tool use and manufacture are simply an area where manual dexterity is expressed. Still others (e.g. Wynn, 1993) suggested that key cognitive abilities for tool-oriented behaviour, namely long-term memory and problem-solving abilities, evolved long before language: the "relatively simple and general kinds of thinking used in tool behavior suggest that it may well have been an older adaptation" (p. 404). Assailed from all sides, tool use in animals apart from the great apes lost its 'special' status, and was instead generally seen as qualitatively different from human technology, rather than a precursor to it.

Despite this, some authors have maintained that there is a link between tool use and cognition (e.g. Chevalier-Skolnikoff, 1989; Griffin, 2001; Parker & Gibson, 1977; Preston, 1998; van Schaik et al., 1999). For example, Donald Griffin argued that it was *one* category of behaviour where cognition was important, because the separation of the tool from the goal (usually food) meant that selecting or preparing the tool supposedly indicated awareness of whatever the tool served to accomplish: "It is appropriate to retain much of the commonsense view that tool use […] is rather special, although of course not uniquely indicative of conscious thinking on the animal's part." (p.114). Similarly, van Schaik and colleagues (1999) predicted that, in primates, "intelligent species […] are the only ones to show population wide tool use in the wild, and […] to manufacture tools in the wild" (p. 727).

There have been previous attempts to differentiate between different types of tool use based on cognition. For example, Sue Parker and Kathleen Gibson (Parker & Gibson, 1977) used a Piagetian analysis to define "context-specific tool use" and "intelligent tool use". The former was characterised by the use of only one "complex object manipulation schema" (a type of manipulation of two detached objects, such as hitting one object with another or raking in one object using another) with one object used for one purpose, and not much variation between individuals or groups. In contrast, "intelligent" tool use was diagnosed by the use of several complex object manipulation schemata, in several different contexts involving different objects, and acquired through trial-and-error or "insight"[4].

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[4] Incidentally, they propose that "intelligent tool use correlates with extractive foraging on seasonally limited embedded foods and an omnivorous diet, while context specific tool use correlates with extractive foraging on non-seasonal embedded foods and a narrow non-omnivorous diet" (p. 629), and that the seasonal availability of high protein foods selected for intelligence and explorative and manipulative propensities. However, this is a circular argument, since "intelligent tool use" is diagnosed by the use of different tools in

However, theirs was a purely theoretical analysis, and (as far as I am aware) there has been no empirical study into whether “context-specific tool use” really does indicate less intelligence than “intelligent tool use”. There have been some studies attempting to relate differences in tool-using propensities between species to the stages of “sensorimotor intelligence” they reach (e.g. Chevalier-Skolnikoff, 1989), but these have often been flawed by circular arguments, small sample sizes (in terms of species and individuals within species), and over-interpretation of the data (see the commentaries accompanying the above paper).

Two recent empirical papers have also taken the view that tool use *per se* is of interest, and have provided empirical evidence for this. These studies examined the relationship between tool use and relative brain size, in birds (Lefebvre et al., 2002) and non-human primates (Reader & Laland, 2002). Both used the occurrence of tool use within a taxon to derive an index that they correlate with relative size of the species’ brain (or regions of their brain). Both analyses found a correlation between occurrence of tool use and relative size of the neostriatum (in birds) (now called the nidopallium; Jarvis et al., 2005) and neocortex and striatum (in primates), as well as with other measures of behaviour flexibility.

The above studies are rare, though, in finding any link between tool-oriented behaviour and measures of cognition: most attempts to find correlations between the two have yielded nothing (e.g. McGrew, 1992b). I believe that even if such a correlation exists, current methods are unlikely to detect it for two main reasons. Firstly, they fail to precisely specify the hypothesis being tested. There are actually *two* possible relationships between tools and cognition: (1) that intelligent species should use tools; and (2) that to use tools requires intelligence. The first is clearly not correct: a species might well have the cognitive capacity to use tools, but its ecological circumstances (e.g. gorillas *Gorilla gorilla*: Byrne, 2004) and / or morphology (e.g. cetaceans: McGrew, 1993) might not favour the expression of this capacity (although note that tool use in wild gorillas (Breuer et al., 2005) and dolphins (*Tursiops* sp.; Krützen et al., 2005; Smolker et al., 1997) has just been described). Hypothesis (2) is what is (implicitly) being tested, but there is a general failure to recognise the implications of the first one not being true: the fact that many

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different contexts, which would by definition be unlikely to occur in a species that only eats one (or a few) different types of food (apart from in contexts other than foraging, where tool use is generally much rarer).

‘intelligent’ species may not use tools means that a general correlation between measures of cognitive ability and incidence of tool use is likely to be insignificant. What would really be predicted by the second hypothesis is that no tool-users should perform worse than the *worst* non-tool-users on general intelligence tests: if tool use requires a certain degree of intelligence, the distribution of scores on tests of cognition will be more constrained (at the lower boundary) for tool-users than non-tool-users, even though the average score might be similar.

The second reason for the difficulty researchers have had in detecting a correlation between tool use and measures of cognition, if one exists, may due to the lack of differentiation within the category of “tool use”. Most studies have considered purely the presence or absence of tool use reports for a taxon, and did not take into account any factors such as the frequency or complexity of the behaviours – for example, giving equal weight to a species where there is a single anecdote of one individual dropping a branch onto an intruder as to one where all individuals routinely make and use probing tools. As already mentioned, some researchers (e.g. Parker & Gibson, 1977) have proposed that tool-use be classified into “context specific” or “intelligent”, but their classification has never been taken into account in correlative studies, and in any case creates a false dichotomy when the reality is probably continuous. The authors themselves recognise this: “It seems likely that there is a continuum […,] and that context specific and intelligent tool use represent the extreme ends of the spectrum” (Parker & Gibson, 1977 p. 628); similarly, Gibson (1993a) suggested that we should consider the “degrees of development” (p. 8) of tool use and other characteristics, rather than adopting all-or-none definitions. There are a number of features of tool use that could be taken into account, which might help clarify when, and to what extent cognition is involved. However, before I discuss these I need to briefly consider the issue of what I mean by cognition or ‘intelligence’ in this context.

2.3 WHAT DOES ‘INTELLIGENT BEHAVIOUR’ MEAN?

In order to discuss whether tool-oriented behaviour is ‘intelligent’, we need to consider what we actually mean by the term. Defining intelligence is notoriously difficult, but perhaps the following thought experiment will help:

Imagine you watch an adult chimpanzee gather up several palm nuts and a stone and carry them over to a big flat rock; she carefully positions the nuts on the rock, repeatedly hits them with the stone until they break, and then picks out the edible pieces of kernel and eats them. Would you consider this to be 'intelligent' behaviour?

A naïve answer might be "yes", because the behaviour is complicated and resembles very much what humans would do in the same situation. However, imagine that you were now shown videos of the same chimpanzee when younger, which documented the development of the nut-cracking behaviour. When very young, she just randomly manipulated the nuts and stones; when a bit older, you see her bashing the various objects together – hitting the rock with the nuts, the stone with the nuts, the rock with the stone, and the nuts with the stone; older still, she carefully places nuts on the rock and hits them with the stone – but she also sometimes places the stone on the rock, and hits it with the nuts! Finally, three to four years after first showing interest in the nuts and stones, she manages to consistently put the objects in the right order of rock-nut-stone, and succeeds in breaking them (the details of this anecdote are fictional, but it broadly resembles the true pattern of development of nut-cracking in chimpanzees, although in the wild stimulus or local enhancement from conspecifics is thought to be important too; see Biro et al., 2003; Inoue-Nakamura & Matsuzawa, 1997). Your conclusion now might be that perhaps the adult behaviour is not necessarily 'intelligent', but instead the chimpanzee has simply learned the most effective sequence of actions for cracking nuts, and just repeats these without really understanding 'why' they work. (Although note that from the description above, it would also be possible that nut-cracking is an 'innate', genetically-encoded behaviour, and the apparent trial-and-error learning is no more than an epiphenomenon of maturation). Of course, it may be that having learned through trial-and-error, the chimpanzee might subsequently develop an understanding of why this behaviour works, but it is impossible to infer this solely from observing the nut-cracking behaviour described.

The above example illustrates that to attempt to deduce the cognitive basis of any behaviour, it is essential to know the history of how that behaviour came about in that individual – i.e., how it developed or was acquired (as emphasized as long ago as e.g. Morgan, 1930). It is still surprisingly common to see claims for cognition based on observations of just the final behaviour: for example, Boesch and Boesch (1993) observed that Taï chimpanzees selectively modify tools before using them, whereas Mahale chimpanzees modify them progressively during use, and the authors interpreted this as evidence that "the Taï chimpanzees seem to possess a better understanding than the

Mahale chimpanzees of the properties a tool should have for a specific task" (p. 164), a claim subsequently repeated by other primatologists (e.g. Visalberghi (1993 p.141): this shows “that chimpanzees can mentally represent what a familiar task requires, without trying out the different possibilities each time”). However, it is perfectly possible that the difference in performance between the two populations is a consequence of different frequencies with which they carry out the behaviour, and the Taï chimpanzees might simply have learned (associatively) over hundreds of occasions that it is more efficient to modify tools before using them rather than during use, without any “mental representation” or “understanding” at all (as discussed in Chapter 1). In general, any action in an adult animal whose history is unknown could result from several different processes, most of which we would not consider ‘intelligent’.

One way this problem has been tackled is using Piagetian concepts of object manipulation ‘schemata’ and the level a species reaches on the “Sensorimotor Intelligence Series”, as described earlier (Piaget, 1952; applied to non-human primates: Parker & Gibson, 1977). However, the application of Piagetian concepts to non-humans is problematic: they were developed to try to infer from the behaviour of human infants and children what concepts those children understood at that particular age, which can perhaps be justified by the argument that we know that adults definitely do understand the concepts (and for older children, we can ask them to explain their behaviour as well). Consequently, stages of the ‘Sensorimotor Intelligence Series’ are described in international terms: for example, stage 5 (“The Discovery of New Means Through Active Experimentation”; Piaget, 1952) is described as being characterised by “*purposeful* trial and error variation, differentiation and recombination of schemata in *experimenting to find* new means to old ends and new ends… [T]his involves manipulation of one object relative to another and/or relative to force/fields such as gravity or inertia, *in order to explore causality* or to solve a problem” (Parker & Gibson, 1977 p. 626, emphasis added). While this may be a sensible way of describing the behaviour of human children, it is unclear how you could determine whether a non-human was performing a behaviour *in order to* explore causality, or merely because it has a tendency to manipulate or destroy objects. The crucial element is what is learned as a result of the behaviour, but this is hard to ascertain in purely observational studies (similar points have been made by e.g. Adams-Curtis, 1989; Fragaszy, 1989).

Consequently, I prefer to keep things simple, and simply talk about three broad mechanisms that influence final behaviour. The first is genetic propensity, or **‘innateness’**:

some species-typical behaviours appear to emerge robustly and with little requirement for learning or practice (although this concept is extremely problematic, both in terms of theory and empirical demonstration; see Bateson & Mameli, in press). For the purposes of this chapter, when I refer to 'innate' behaviours I mean not simply behaviours that *emerge* without learning or practice, but those that *remain* fairly stereotyped, context-specific, and inflexible. It is quite common for behaviours to have innate components during development, but later to be used in a flexible and intelligent manner.

The second category is vast, and encompasses nearly all behaviour: that directly reliant upon learning, and in particular **associative learning** mechanisms[5]. Different behaviours might be reliant on learning to very different extents: for example, many species-typical ('innate') behaviours are slightly modified by learning (the basic components of nest-building behaviour in birds are thought to be relatively stereotyped and 'innate', but learning is involved for the handling of materials; Hansell, 2000), but entirely new behaviours can also be acquired through associative mechanisms (such as domestic cats learning to open doors by jumping onto door handles). Some forms of apparently social learning are also explained by these mechanisms: for example, stimulus or local enhancement simply involves an observer's attention being drawn to objects or places followed by standard associative learning (Heyes, 1994), which is thought to be the process responsible for blue tits (*Parus caeruleus*) acquiring the ability to open milk bottle tops to get cream (Fisher & Hinde, 1949; Hinde & Fisher, 1951; Sherry & Galef, 1984, 1990). Similarly, in 'observational conditioning' subjects learn about the associations between say stimuli and rewards, but 'vicariously', by watching others experiencing those associations – there is no requirement for a learning mechanism qualitatively different from associative learning (Heyes, 1994). Note that many 'special' kinds of learning (e.g. imprinting, song learning, taste aversion learning) would also fall into this category, since the underlying mechanisms are assumed to be associative in nature (reviewed in Hogan & Bolhuis, in press; Klosterhalfen & Klosterhalfen, 1985).

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[5] This discussion of learning is deliberately highly simplified. Clearly, there are many different forms of learning, including non-associative mechanisms (e.g. habituation, sensitisation, perceptual learning). Moreover, associative learning is usually divided into classical and operant conditioning (e.g. Domjan, 2003), and in the latter category people often distinguish between 'goal-directed' behaviour, which is driven by a representation of the goal, and 'habitual' behaviour, which is goal-independent, and often develops as a result of overtraining (Dickinson, 1980, 1985). While these differences are important and have profound behavioural consequences, the general point I am making applies to all of them: namely, learning occurs as a result of exposure to the occurrence of stimuli (including the individual's own behaviour) in proximity to each other.

The final category is what I believe most people mean when they talk about 'intelligent' behaviour: something that goes beyond what you have previously learned and are genetically predisposed to do – i.e. behaviour that **'emerges'** without any direct previous experience. Perhaps surprisingly, then, some researchers have included trial-and-error learning as being indicative of intelligence: for example, Parker and Potì (1990) say that "Most investigators agree that intelligence embodies an ability to learn to solve complex tasks through directed trial-and-error groping and insight" (p. 237), even though when reviewing definitions of intelligence in another paper, one of the same authors (Parker & Baars, 1990) states the common elements to most definitions are concepts of "understanding", "reasoning", and the "intentional adaptation of means to ends". Perhaps the reason for including trial-and-error learning is the very fact that it is so difficult to rule out, but since I believe that understanding problems and being able to design appropriate solutions to them are fundamental features of human intelligence, I will restrict this category to behaviour that can be demonstrated not to be an immediate consequence of previously learning. There are still different mechanisms that might be responsible for behaviours in this category: *generalisation* (or transfer of knowledge learned in different circumstances); learning by *imitation* (briefly, copying another individual's actions) and *emulation* (copying the *results* of another's actions) (e.g. Call et al., 2005); and some form of *reasoning*, based on an understanding of the task requirements (as discussed in Chapter 1).

The categories above are inherently hierarchical: for example, chimpanzees might have a genetic predisposition to play with stones and to bash objects together, but they might then learn socially to direct their attention to nuts and through trial-and-error how best to orient the stones and nuts to crack them, and finally generalise from their experience to use completely novel materials to achieve the same result if stones are not available. In contrast, it is implausible that any animal would be able to use reasoning to solve a problem, but unable to learn associatively.

Concerning tool use specifically, there are two questions: firstly, can we infer the involvement of any process beyond associative learning from the tool-oriented behaviour of wild animals? Secondly, are tool-oriented behaviours more likely than other behaviours to be the result of 'complex' cognitive processes? In the next section, I discuss several aspects of tool use that could or have been thought to relate to cognition, with a view to answering question one above. A comprehensive answer to question two is beyond the scope of this chapter, but it is possible that the framework proposed here would help in future investigations.

2.4 CATEGORISING WILD TOOL-ORIENTED BEHAVIOUR

So how can we tell whether a certain species' tool use is 'intelligent'? The only definitive way to assess a non-linguistic animal's 'understanding' of what it does is to present it with novel or transformed problems and examine how it solves them (as discussed in Chapter 1). However, in the absence of such controlled experiments, with all the logistical, monetary, ethical, and ethological difficulties they entail, can we infer anything from wild observations alone? This section examines one possible way of categorising tool-oriented behaviour in wild animals, and considers whether and how these categories might be related to cognition. I restrict this discussion to tools involved in foraging, since in non-human animals this is the most frequent mode of tool use observed (apart from unaimed dropping, which arguably is not tool use at all; Beck, 1980), it is the most comparable between species, and, as argued by McGrew (1993) and van Schaik and colleagues (1999), when considering tool use systematically it is best to analyse those aspects undeniably subject to natural selection, which is certainly true of subsistence technology.

What characteristics of wild tool-oriented behaviour might serve as diagnostic tools for inferring cognition? We can conceive of the problem in two stages: our first task is to distinguish between stereotyped, genetically-canalized behaviour and behaviour that involves some degree of learning or cognition. Having done that, we need to discriminate between behaviour reliant solely on associative learning, and that possibly involving more abstract processes.

There are perhaps four features of a species' tool-oriented behaviour that are relatively easy to observe, and might be relevant: (1) the frequency with which the behaviour is expressed; (2) the diversity of tools made and used, (3) the extent of inter-individual and inter-population differences ('variability') in tool-oriented behaviour, and (4) the complexity of the tools' manufacture. Whether and how performance within each category relates to cognition is discussed below.

2.4.1 Frequency

Perhaps the most fundamental question to ask when an instance of tool use is reported is how frequent the behaviour is in the species concerned (or possibly of even more significance, the extent to which the species is ecologically dependent on tools – but this is much harder to assess accurately). Surprisingly, perhaps, very few authors have even considered the frequency of tool use, often treating it as only present or absent in a species. To my knowledge, McGrew and colleagues (McGrew, 1992a; McGrew & Marchant, 1997) present the only formal categorisation of tool use by frequency, which has subsequently been used to classify putative cultural behaviours in chimpanzees (Whiten et al., 1999) and orangutans (van Schaik et al., 2003). Their scheme identified four levels of frequency: Anecdotal, Idiosyncratic, Habitual, and Customary. I have used this, slightly modified, as the basis for my levels below. As far as I am aware, no authors have attempted anything similar for ecological dependence on tools, although there have been studies that have attempted to measure this in particular species (e.g. woodpecker finches (*Cactospiza pallida*; Tebbich et al., 2002), burrowing owls (*Athene cunicularia*; Levey et al., 2004), and chimpanzees (Nishida & Hiraiwa, 1982; Yamakoshi, 1998)). Given the difficulty of assessing ecological dependence, the few studies into it, and the lack of obvious categories, I do not include it in the framework here.

One potential problem with determining the frequency of tool use is differences in research effort or ease of observation between species (for example, most mammals are nocturnal and cryptic). It is possible to develop a crude index of research effort using measures of the number of publications per species (e.g. Lefebvre et al., 2001), but it should still be noted that this category might be subject to substantial errors.

1) Anecdotal. Unique or rare events. These events may represent a latent ability in the species (that is just not seen very often), but they are not necessarily reliable: the behaviour might have been accidental on the part of the animal, or the observer might have been mistaken.
2) Idiosyncratic. Repeated events by only one individual. Such events are assumed to be reliable (i.e. not due to observer error) and non-accidental, but may not be a general characteristic of the species.
3) Habitual. Repeated events by several individuals over time. These may appear not to be universal due to methodological factors (e.g. a lack of sufficient observations or difficult observation conditions), or they may in reality not be universal because of local traditions of tool-related behaviour that have not spread to the rest of the species, or different ecological conditions.
4) Routine. Repeated events displayed by all appropriate members of the group or population. The tool use may not be universal within a population due to age or sex differences and/or seasonality of resources, or between populations due to ecological differences. It can be subdivided into (a) routine – population specific and (b) routine – species wide. The first would reflect a behaviour that was routine within one population, but not in other populations; the latter would characterise a species where all populations showed the mode of tool use under consideration, even if not all members of the populations showed the behaviour.

Is there any necessary link between the frequency of tool-oriented behaviour and cognition? Obviously, tool use can only be used as a sign of cognition if we can be sure that observations are reliable – so a single anecdotal report for a species should perhaps not be included in any analysis. At the other end of the scale, if the production of the behaviour is largely 'instinctive', we might expect that under similar environmental conditions, all individuals would show very similar or identical behaviour (unless there are genetic differences between them). However, the same outcome could also be due to advanced cognition or associative learning given a predicable environment: there are many examples of learned behaviour that is reliably performed by all members of a species (such as language learning in humans).

In other words, 'routine' tool use could be instinctive, learned, or cognitive, so there is no linear relationship between frequency of tool-oriented behaviour and cognition. In fact, observations of 'idiosyncratic' or 'habitual' tool use might be the best indication that it is not 'innate', although says nothing about what other processes might have caused that individual to develop the behaviour.

2.4.2 Diversity

Perhaps surprisingly, to my knowledge there are no reviews or meta-analyses that explicitly compare species in terms of the number of types of tools they make or use. However, this information would be relatively easy to extract from field reports, and might be important when considering cognition.

For the purpose of this classification, I consider tools as being different 'types' if they are either used for a different function (e.g. probing vs. hammering), or are acquired or made in substantially different ways (e.g. detaching leaves from a twig, vs. tearing strips from grass) (note that I am not restricting this to 'tool-kits' *sensu* McGrew, 1993, where different tools have to be used for different problems). A type is only included if it is used at a frequency that is at least 'idiosyncratic', since 'anecdotal' observations of tool use may be mistaken, or may not reflect the general ability of the species.

Unlike the other categories in this framework, the diversity of tools made or used by a species is a continuous variable. Specifying different levels would therefore require an arbitrary decision on how many types of tool represent level 1, level 2, etc…, which could potentially exert a significant bias on the overall classification. A better approach might be simply to use the number of different types exhibited as the measure (up to a maximum of, say, 10). If logarithms of this value are then taken to calculate total scores, the 'value' given to exhibiting an extra type of tool use will asymptotically decline, to a total of one for 10 or more. This makes intuitive sense, since it seems unlikely that using 8 tools requires significantly greater cognitive abilities than using 7, whereas there may a big difference between a species that only uses one type of tool and one that uses two or three.

1) One type only.
2) Two types.
3) Three types.
4) etc…
10) Ten types or more.

The number of types of tool used by a species does intuitively seem to be closely related to cognitive abilities. For example, individuals that can rapidly learn associations between events, or can flexibly apply previously acquired knowledge to new situations, might more frequently discover how objects can be used as tools than those without these abilities. However, on closer consideration, it is apparent that if evolution could genetically predispose a species to use one kind of tool, there is no reason why it could not equally easily select for using two or more kinds of tools – for example, some bird species use several different materials to make nests (Hansell, 2000), and this behaviour is usually assumed to be primarily under genetic control.

2.4.3 Variability

Individual differences in tool use are often taken as indicative of cognition, and population differences (interpreted as 'culture' or 'tradition') even more so. Both of these features can be diagnosed using information from the two preceding categories: the use of more than one 'type' of tool (or the same type used or made in different ways) at frequencies below 'routine – species wide' and in the absence of correlated ecological (and gender, age, and status) differences suggests individuals differ in their tool use. Similarly, if different populations use different types of tools (or use or make them in different ways), but the usage within the population is consistent, this would be considered as evidence for some form of 'culture'. However, humans illustrate that there is a fourth level as well: *cumulative* cultural differences, where there is evidence that tool design has improved across generations or between populations (this could be diagnosed by, for example, some populations making and / or using tools that were similar but superior to tools made / used by neighbouring populations).

0) None. No evidence for individual or population difference in tool-oriented behaviour (i.e. either all individuals use only one type of tool, or if they use more than one, all types are either used species-wide (4b), or the variation is explicable by ecological, age, gender, or status differences).
1) Individual flexibility. Different individuals use different types of tools or use tools in different ways (with no correlated ecological, age, gender, or status differences), but there are no consistent differences between populations.
2) Social learning / culture. Different tools are used in different regions (or they are used / made differently), and the variation is not explicable by correlated ecological differences.
3) Cumulative cultural evolution. Evidence for this is likely to be indirect, but may take the form of tool designs in different areas that are similar but between which there are functional differences (again, in the absence of correlated ecological differences).

Evidence for individual differences (i.e. level 1 above) in tool use certainly suggests that the behaviour is not entirely ‘innate’, and cultural differences even more so. However, both of these are theoretically explicable by genetic variation, either between individuals or populations: there may be polymorphisms in genes correlated with tool-using behaviour, leading to individual differences in tool use, and the use of different types of tool in different regions could result from evolution and genetic changes at a local level, which we now know can occur in morphological characteristics (body mass) in bird populations separated by just a few miles and inhabiting the same small woodland (Garant et al., 2005). However, given that it is often difficult or impossible to obtain explicit genetic information, the best evidence for the influence of individual learning or culture would be individual differences in, for example, tool use techniques, between individuals within the same population, as well as between individuals in different populations, as recently demonstrated in bottlenose dolphins (Krützen et al., 2005).

If genetic explanations can be discounted, is there any way to identify what processes are responsible for the tool use showing either inter-individual or inter-population variation? In the absence of any other information about the behaviour in question, it would be impossible to say whether inter-individual variation was due to associative learning mechanisms or ‘higher’ cognitive processes. Intuitively, it might be assumed that inter-population cultural differences must involve imitation or other forms of complex social learning, but this is in fact surprisingly hard to demonstrate in wild animals, and most supposedly cultural behaviours identified to date are probably transmitted by mechanisms such as social facilitation or stimulus enhancement, which are essentially based on individual associative learning rather than any form of 'higher' cognition (Heyes, 1994; Heyes & Galef, 1996). Tomasello (1999) argues that 'emulation' learning is responsible for transmission of some of putative cultural variants in tool use in wild chimpanzees, and gives as an example: "if a mother rolls over a log and eats the insects underneath, her child will likely follow suit. This is simply because the child learned from the mother's act that there are insects under the log[,…] not […] how to roll over a log or to eat insects; these are things she already knew how to do or could learn how to do on her own." (p.520). However, the example described above seems in fact to refer to stimulus enhancement, rather than emulation or affordance learning: the mother chimpanzee's actions just draw her daughter's attention to the log as a potential source of food, and the only learning involved is individual.

There are currently no convincing examples (except for vocal imitation, for example in birds (e.g. Enggist-Dueblin & Pfister, 2002; Jenkins, 1978), cetaceans (Rendell & Whitehead, 2003), and elephants (Poole et al., 2005)) of cultural traits in non-human animals that require a mechanism of social learning that is qualitatively different from individual associative learning (i.e. that fall into the 'Emergent' category in section 2.3) (Boyd & Richerson, 1996; Tomasello, 1999). Indeed, Tomasello (1999) argues that wild chimpanzees (and implicitly, other animals) do not have the ability to separately perceive the goal of a demonstrator and the means the demonstrator uses to achieve that goal, which is necessary for true 'imitative' learning. He goes on to argue that such imitative learning is required for cumulative cultural evolution: to learn and improve on a particular tool use technique requires learning the technique specifically and separately from the goal of obtaining food, rather than just learning generalities or an association between a particular object and food (for a related argument, see Boyd & Richerson, 1996). It is interesting that the only case where cumulative cultural evolution has been postulated in non-human animal technology is also one where, if proved, some form of imitative learning would be required: it concerns the stepped-cut pandanus tools made by New Caledonian crows (*Corvus moneduloides*; Hunt, 1996; Hunt & Gray, 2004b), where the particular manufacturing technique appears to differ between regions (Hunt & Gray, 2003), and it is hard to see how this technique could be learned other than imitatively (assuming specific genetic variation and / or ecological factors are not responsible for differences; see Kenward et al., in press (Appendix 6)).

In summary, evidence for inter-individual and / or inter-population differences in a species' tool-oriented behaviour can, indirectly, provide indications for the cognitive underpinnings, although only to the extent of (tentatively) ruling out purely 'innate' behaviour. Individual differences in tool-oriented behaviour are often apparent (usually to the extent of some individuals performing the behaviour and some not), but convincing examples of cultural differences are rarer, primarily confined to chimpanzees (Whiten, 2005; Whiten et al., 1999), orangutans (*Pongo pygmaeus*; van Schaik et al., 2003), dolphins (Krützen et al., 2005), and New Caledonian crows (Hunt, 1996, 2000; Hunt & Gray, 2002, 2003); there are also suggestions of cultural differences in tool use by capuchin monkeys (*Cebus* sp.; Anderson, 1990; Boinski, 2003; Ottoni et al., 2005a; Ottoni et al., 2005b), although this is still tentative and the best evidence is from captive or semi-wild studies. However, there are no species other than humans where there is strong evidence for cumulative cultural evolution, or for the involvement of social learning mechanisms beyond stimulus enhancement and social facilitation.

2.4.4 Complexity

The final aspect of a species' wild tool-oriented behaviour that might appear to be linked with cognition is the complexity involved in the manufacture of their tools. Beck (1980) defined four modes of tool manufacture – Detach, Subtract, Add/Combine, and Reshape – but did not state if he regarded them as differing in complexity[6]. One could perhaps consider complexity as being related to the degree of transformation involved in the production of the functional tool from the raw material. On this basis, it would seem that Detach and Subtract transform the raw material least, and Adding, Combining, and Reshaping material transforms it to a greater extent. I would add a third level

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[6] Oswalt (1976, cited in McGrew, 1993) also proposed a taxonomy for tool production in traditional human societies, consisting of 'Reduction' (reducing the mass or form of the raw material), 'Conjunction' (combining materials), 'Replication' (making two or more similar units to function as one part), and 'Linkage' (using physically distinct forms in combination), but these modes do not obviously differ in complexity. Likewise, Boesch & Boesch (1990) proposed six types of tool-making in chimpanzees ('break with hands', 'cut with teeth', 'pull (apart) while standing on', 'hit (and fracture) against hard surface', 'remove leaves or bark with teeth or hands', and 'sharpen ends with teeth'), but these also do not link with complexity, and are in addition very specific to primates. Note that another possibility, though, would be to consider the number of *different modes* of manufacture that a species uses, rather than simply the maximum level of complexity shown.

corresponding to multi-stage tool manufacturing and fine crafting: most human tool manufacture involves a far greater degree of transformation of the raw material than is characterised by any of Beck's categories (since 'Reshape' was defined as any fundamental restructuring of the raw material, such as the bunching up leaves in a non-specific manner). We therefore end up with four levels of 'complexity' (the first three based on Beck, 1980):

0) None. Unmodified objects are used (e.g. branches with leaves on, stones lying loose on the ground).
1) Detach / subtract. Severing a fixed attachment between two environmental objects (or the substrate), or removing object(s) from another unattached object so the latter is a more useful tool. E.g. removing a twig from a branch and/or leaves from the twig to use the twig as a tool, digging stones out of ground.
2) Add / combine / reshape. Connecting two or more objects to produce a tool, or fundamentally restructuring material to produce a functional tool. E.g. crumpling up a ball of leaves to make a sponge. (No examples of 'combination' or 'adding' of materials together have been observed in wild non-human animals.)
3) Multi-step manufacture / fine crafting. Involves either several (> 2) manufacturing steps to produce a functional tool, or fine, three-dimensional sculpting of the raw material, with detailed control over its final shape (see Hunt & Gray, 2004a). E.g. making multiple sequential cuts and tears in a leaf to produce a tapered tool, or refining and sharpening a hook on the end of a twig by removing small pieces of wood with the bill.

Does highly complex manufacture therefore indicate the involvement of complex cognition? It has often been implicitly assumed that it does: for example, the fact that chimpanzees do not make multi-component tools has been considered as evidence that they lack "hierarchical mental constructional skills" (Gibson, 1993b, p. 135), which implies that if the chimpanzees *did* make multi-component tools, that would show that they do have the associated cognitive skills. However, it is not clear that this intuitive assumption is true: is well known that many animals make complex structures (such as termite mounds and ant hills, the nests built a wide range of invertebrates, birds, and mammals (including chimpanzees), bowers built by bower birds, and dams by beavers; reviewed in Hansell, 2005), and there is compelling evidence that most of this building behaviour is largely genetically encoded, although learning may play a role in the selection and handling of materials (Hansell, 2000).

As with the previous category, though, it is possible that where other features of the tool-oriented behaviour (i.e. Frequency, Diversity, and Variability) lead us to believe that the details of the behaviour in question are not inherited, complexity may be relevant to cognition. Intuitively, this would seem to be the case: less complex manufacture should be easier to learn associatively (e.g. by trial-and-error) – particularly where it only requires small modification of behaviour already in the individual's repertoire, and where intermediate behaviours would also be advantageous. In contrast, if you see an individual performing highly complex behaviour that is not obviously similar to the normal behavioural repertoire of the species (particularly in multi-step manufacture when the intermediate steps do not produce a functional tool), it might be likely that 'higher' cognition is involved – either observational or 'insightful'. van Schaik and colleagues (1999) use precisely this logic to conclude that social learning is likely to be the predominant way in which tool using skills are acquired in wild apes, and Boesch (1993) has argued that the emergence of complex novel behaviours in chimpanzees at an age too young to be mastered cognitively would be evidence for imitation. Indeed, perhaps the very fact that chimpanzees do *not* make complex multi-component tools in the wild (McGrew, 1987) validates my suggestion that it is difficult to learn complex sequences through trial-and-error – even though we know that apes can make complex tools given appropriate training in captivity (for example, stone-flaking by an orangutan: Wright, 1972, cited in Toth & Schick, 1993).

2.5 THE FRAMEWORK

To be useful on a broader scale, there must be a way of combining the 'scores' in each category to give an overall measure for the species. There are several factors to take into account when doing this: for example, should different categories be weighted differently? It might be possible to make *a priori* arguments about which most closely relate to cognition, but with our current level of knowledge I do not believe it is possible to do so accurately (apart from *Frequency*, which beyond acting as a filter for possibly unrepresentative or inaccurate reports, is unlikely to be related to cognition at all). If different categories are not to be weighted differentially, the scores within each category must be transformed such that the totals for all categories are equal to each other. Another issue is whether the scores should be combined linearly (i.e. added together), multiplied, or joined in some other manner (such as thresholds defined for each category)? Other questions include how to deal with missing or uncertain values, and how to treat reports that do not distinguish between species (e.g. *Cebus* sp.). Which of these techniques is best may depend on the specific problems the framework is being applied to.

I have attempted this exercise with ten representative tool-using species in Table 1. This is not intended to be comprehensive, and for some species the classification may be wrong (due to lack of data or missed references) or controversial, but it illustrates the way in which the framework might be applied, and also some of the problems that might be encountered in its use. In terms of the questions just discussed, I have taken the simplest approach for ease of interpretation: I have not included Frequency in calculating any totals, and have calculated two scores for each species, depending on whether or not Variability was included (because the estimate of this for many species is very uncertain); I gave Diversity, Variability, and Complexity equal weight (details are in the table caption); the scores were combined additively; the mean was taken for uncertain values; and *Cebus* was treated as monospecific (since many of the references do not specify the species, and the taxonomy is uncertain).

What can we learn from the table? Considering only the scores that do not include *Variability*, visual inspection reveals three loose ‘groupings’ of species: chimpanzees, New Caledonian crows, orangutans, and capuchin monkeys have the highest scores (around 0.7 – 1.5), sea otters, dolphins, woodpecker finches, are next (0.25 – 0.30), and Egyptian vultures, green / green-backed herons, and ant- and worm-lions score the least (0). These groupings are reassuring, as they seem to make some intuitive sense. They also demonstrate the utility of this approach: without formal, multi-dimensional analysis, there is no clear way of differentiating between the examples given, as there is no ‘unique’ characteristic that defines each group (the differences are due to the degree to which species manufacture their tools and the number of tools they use).

Also reassuring is that the inclusion of *Variability* does not appear to change the rankings substantially. A few species swap places, but only within, not between groupings (although Egyptian vultures and herons now score 0.25, whereas ant- and worm-lions remain on 0). This suggests that *Variability* may be roughly correlated with *Diversity*, and

Complexity, as indeed would be expected if all are related to cognition. This result must of course be treated as being very tentative, based as it is on a small number of arbitrarily selected species, but it demonstrates possible uses of the framework.

With a more extensive dataset, many more questions could be asked. For example, to what extent are the levels in different categories correlated? Do species that score highly on these categories also score highly in folk physics experiments (i.e. do species that make and use many complex tools ‘understand’ the physics of tool use better than those that make and use fewer and simpler tools)? How do innovation rate, behavioural flexibility, and brain size (*sensu* Lefebvre et al., 2002; Lefebvre et al., 1997; Sol et al., 2005) relate to categories discussed here? Principal components analysis or similar techniques could be used to look for clusters and correlations in larger comparative studies.

A comprehensive dataset would also allow us to ask questions about relationships with cognition and behaviour in non-tool-related domains. For example, how do both overall and domain-specific scores in tool-related behaviours compare with performance in experiments involving social intelligence or concept formation? How does ecology and diet or social structure interact with scores in the framework? What is the influence of phylogeny? Many theories have been proposed that relate some or all of these factors to the evolution of tool use, but the lack of a system for formally classifying tool-related behaviours has hampered empirical analysis.

Table 1: The tool-oriented behaviour of ten tool-using species, analysed according to the proposed framework. Only species that use foraging tools in the wild at a frequency of 'habitual' or 'routine' have been included. The table has been sorted in descending order by the score in 'Totals (without variability)', since the score for Variability is very tentative or unknown for some species.

Frequency was excluded from the total scores, since it is not clear if this has any relationship with cognition – it is included in the table merely to filter out those species where there is only anecdotal evidence for tool use, or tool use by just 1-2 individuals. The formula for 'Totals (without Variability)' is $\log_{10}$('Diversity') + ('Complexity' / 4), whereas for 'Totals (with Variability)' it is $\log_{10}$('Diversity') + ('Complexity' / 4) + ('Variability' / 4).

Examples are not cited exhaustively: the references given are generally recent reviews, where available. The examples of tool-oriented behaviour in the second column are only included as an indication of the behaviours exhibited by that species: for detailed descriptions, see the original references. In some cases, the values assigned for a particular category represent a 'best guess' rather than a definitive answer, and it should be noted that for some categories (particularly Variability) and species there is substantial disagreement between researchers in the field. Citations corresponding to the numerical references are given beneath the table.

References from the table are as follows:

1: Whiten et al., 1999; 2: Whiten, 2005; 3: Hunt, 1996; 4: Hunt & Gray, 2003; 5: Hunt & Gray, 2002; 6: Hunt & Gray, 2004a; 7: van Schaik et al., 2003; 8: Moura & Lee, 2004; 9: Phillips, 1998; 10: Fragaszy et al., 2004; 11: Boinski et al., 2000; 12: Fernandes, 1991; 13: Beck, 1980; 14: Hall & Schaller, 1964; 15: Krützen et al., 2005; 16: Smolker et al., 1997; 17: Tebbich et al., 2002; 18: Tebbich et al., 2001; 19: Thouless et al., 1989; 20: van Lawick-Goodall & van Lawick, 1966; 21: Higuchi, 1988; 22: Sisson, 1974

(Table is on the following pages)

Species	Tool-oriented behaviour (wild)	Frequency	Diversity	Variability	Complexity	Totals		Refs
						(without Variability)	(with Variability)	
Chimpanzees (*Pan troglodytes*)	Many, including use of leaves as sponges, twig and grass probes for ants and termites, pestle-and-mortar for nut-cracking, etc.	4b	10	2	2	1.50	2.00	[1, 2]
New Caledonian crows (*Corvus moneduloides*)	Leaf stems as probes for Cerambycidae larvae. Straight stick tools for probing for invertebrates. Hooked stick tools for probing for invertebrates. Stepped-cut pandanus tools for probing for invertebrates.	4b	4	3	3	1.35	2.10	[3-6]
Orangutans (*Pongo pygmaeus*)	Leafy branch as sponge/scoop. Sticks as probes to extract insects / insect products from tree-holes. Sticks to extract seeds from *Nessia* fruits. Leaves as "gloves" to handle spiny fruits.	4a	3	2	2	0.98	1.48	[7]
Capuchins (*Cebus* sp.) (N.B. The different types of tool use may occur in different species or subspecies.)	Stone hammers and anvils to crack nuts and other types of food. Sticks to probe for insects, honey, or water. Stones to dig for tubers. Anecdotes of other types of tool use.	4a	3	2	1	0.73	1.23	[8-12]

Sea otters (*Enhydra lutris*)	Stones carried to seabed to hammer molluscs from the substrate. Rocks held on their chests while floating on sea surface, used as anvils to hammer molluscs open on.	4a	2	2	0	0.30	0.80	[13, 14]
Dolphins (*Tursiops* sp.)	Sponges broken off the seafloor and worn over their closed rostrums to apparently probe into the substrate for fish. (15 of 141 mothers in one population, and 7 of their offspring, have been seen to perform this behaviour.)	3	1	2	1	0.25	0.75	[15, 16]
Woodpecker finches (*Cactospiza pallida*)	Cactus spines and twigs to search for invertebrates.	4b	1	1	1	0.25	0.50	[13, 17, 18]
Egyptian vulture (*Neophron percnopterus*)	Stones thrown onto ostrich eggs to break them open.	3-4?	1	1	0	0.00	0.25	[13, 19, 20]
Green / green-backed herons (*Butorides virescens / Butorides striatus*)	Insects, worms, bread, etc. used to bait fish.	3	1	1	0	0.00	0.25	[13, 21, 22]
Worm-lions (larvae of genera *Vermileo* and *Lampromyia*) and ant-lions (larvae of neuropteran flies of genus *Myrmeleon*)	Grains of sand thrown at ants or other insects that fall into pits; not clear if this is directed at prey.	4b	1	0	0	0.00	0.00	[13]

2.6 CONCLUSIONS

In this chapter, I have proposed a framework for formal, multi-dimensional analysis of tool-related behaviour in animals, which may be more reflective of its underlying cognitive basis than simple ‘presence or absence’. I have shown how tool use and manufacture can be classified on four attributes – *Frequency*, *Diversity*, *Variability*, and *Complexity* – and have demonstrated how this analysis could be applied to selected examples. Even on a limited and rather arbitrary dataset, the framework classified species into roughly three groupings, which could not have been defined using any one dimension alone.

I do not believe that tool use is uniquely indicative of ‘special’ cognitive abilities: there are many reasons why an animal may not use tools (e.g. morphology, diet, or ecology) that have nothing to do with cognition, and there are many non-tool-related behaviours that are closely linked to cognition. However, I believe that some aspects of tool use may be correlated with highly developed cognitive abilities (in the physical domain), and that on this basis further investigation is warranted.

Since the discovery that tool use is displayed by animals ranging from crabs to chimpanzees, there have been many attempts to define unique features of human (and certain primate) tool behaviours that are considered to be ‘intelligent’. However, every time a unique attribute has been suggested (e.g. tool manufacture, culture, tool sets, tools as weapons …), further observations have revealed a non-primate species that shows this attribute, and the suggestion is rejected (which is incidentally revealing about attitudes that if a behaviour is shown by non-primates, it cannot be ‘intelligent’!). This framework is therefore proposed as a more sophisticated device for studying tool-related behaviour. For example, the occurrence of tool use in a taxon has been correlated with brain size in birds (Lefebvre et al., 2002) and primates (Reader & Laland, 2002), but these analyses might have been greatly enriched by consideration of aspects of tool using other than purely its presence or absence.

I hope that this chapter will inspire both reanalyses of existing data along the lines of this classification, and also future research to explicitly investigate tool use and manufacture in these terms. A comprehensive dataset might allow insights into the evolution and neural basis of tool use that would not otherwise be possible, and may shed light on the selective factors underlying the evolution of human technology. It is also noteworthy that New Caledonian crows were grouped with apes and capuchins on the basis of their tool-oriented behaviour in the wild, which suggests that they might be good candidates for investigating folk physics.

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Chapter 3

Hook choice and manufacture in two New Caledonian crows

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Unpublished manuscript.

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3.1 INTRODUCTION

As described in Chapter 2, many animals use tools, but from observations of wild behaviour alone it is very difficult to infer whether or not this involves an 'understanding' of physical forces or causal relations. None of the studies to date into non-humans' folk physics (reviewed in Chapter 1) have provided strong evidence for any understanding of causality: in general, subjects' responses seem to be guided by 'procedural rules' rather than 'high-level models' (*sensu* Povinelli, 2000). However, the strikingly diverse and complex nature of the tool use and manufacture shown by New Caledonian crows (*Corvus moneduloides*) in the wild (Hunt, 1996; Hunt & Gray, 2003; Hunt & Gray, 2004a; see Chapters 1 and 2 for more details; Hunt & Gray, 2004b) make these birds promising candidates for investigation of folk physics, and previous experiments on captive subjects indicate that they can select or make tools of appropriate dimensions for particular tasks (Chappell & Kacelnik, 2002, 2004).

As reviewed in Chapter 1, at least four of the tools (hooked-twigs, thorny vines, fern stolons, and Pandanus tools; see Hunt & Gray, 2002) that New Caledonian crows make in the wild include and are used as hooks. Indeed, it has been claimed that the crows' "hook use suggests an appreciation of tool functionality" (Hunt, 1996, pp. 250-251). If true, this would be especially significant as human children only become able to skilfully use hooks (or 'surround' tools in general) relatively late in development: they can *learn* to use hooks with prompting aged 13-18 months, and spontaneously use them at 24 months (reviewed in Brown, 1990), whereas they appear to understand how to use 'supporting' (e.g. cloths) or 'attached' (e.g. strings) tools much earlier (Bates et al., 1980; Schlesinger & Langer, 1999; van Leeuwen et al., 1994). However, experiments with chimpanzees and other primates have highlighted the need for controlled experiments into claims for 'understanding' based on behaviour in the wild – which could, after all, result from a number of non-cognitive processes (see Chapters 1-2).

No non-human primates are not known to spontaneously use hooks in the wild. Although several authors (e.g. Boesch, 1996; Boesch & Tomasello, 1998; Povinelli et al., 2000b) cite Sugiyama & Koman (1979) as reporting that wild chimpanzees in Bossou made and used hook-type stick tools to haul down branches of a fig tree, the paper actually describes chimpanzees *attempting* unsuccessfully to use hooked sticks as tools, and the authors conclude that the chimpanzees "failed to make an effective hook-type stick-tool"

(p. 523) (as pointed out by Hunt, 2000; Hunt & Gray, 2002, 2004b). Nevertheless, following reports of captive chimpanzees spontaneously using hooked sticks to haul in out-of-reach food (Köhler, 1927), there have been several experimental investigations into nonhuman primates' use of hooks in captivity.

Povinelli and colleagues (2000b) examined chimpanzees' ability to transfer their knowledge of hooks from one context to another. They first trained chimpanzees to use a hooked tool to retrieve a platform bearing food via a ring attached to the platform. Then, during testing, their subjects were presented with a choice of two novel platforms with no rings, but with posts (that could be used to retrieve them) either within or out of reach. Despite successful performance during training to retrieve the platform using the ring, all seven subjects chose randomly during the first eight test trials when the ring was replaced by a post. Further experiments showed that what seemed to be determining the chimpanzees' choices was *contact* with the platform, rather than any concept of 'connection' to it.

Marc Hauser and colleagues have conducted a series of experiments into hook use in cotton-top tamarins (*Saguinus oedipus*), who are not natural tool users, investigating what features tamarins use to select novel tools to retrieve food. In two studies (Hauser, 1997; Hauser et al., 2002a) they found that following training to choose between pulling hook-like tools with food 'inside' or 'outside' the hook, adult and infant cotton-top tamarins correctly chose novel tools that would lead to food over those that would not, even where the incorrect choice was more similar to the original tool than the correct one (although the tamarins were unable to alter the position of the tool if the original layout was not suitable). More recently, other researchers have found very similar results in (naturally tool-using) tufted capuchins (*Cebus apella*) (Fujita et al., 2003), who were additionally able to reposition tools that were not in an immediately usable orientation (Cummins-Sebree & Fragaszy, 2005), although their success following repositioning was initially very low (and improved with practice).

These results suggest that tamarins and capuchins may be able to learn some of the essential features of hooks that make them functional, and appear to indicate (counter-intuitively) superior performance than Povinelli's chimpanzees. However, it should be remembered there are some crucial differences between the experiments with the tamarins and capuchins, and those with the chimpanzees: firstly, the chimpanzees were required to pay attention to the nature and relative positions of three items – a tool, a platform (which itself had an additional element, the post / ring), and the food – whereas the capuchins and tamarins only had to consider two items, the tool and the food (interestingly, in experiments 6 and 7 of Fujita et al., 2003, capuchins were at chance when obstacles or traps were introduced between the tool and the subject, which was interpreted as an inability to understand the spatial relationship between three items). Secondly, it was the nature and location of the *tool* that was varied in the capuchin and tamarin experiments, whereas it was the platform, post, and position of food with respect to these that were varied for the chimpanzees. Thirdly, and perhaps most importantly, there were differences in the amount of previous experience the subjects had in the different studies: Hauser's (1997) tamarins and Fujita et al.'s (2003) capuchins were previously trained on many configurations of tool and reward (it is unclear whether the capuchins in Cummins-Sebree & Fragaszy, 2005 were trained with different configurations or not), whereas Povinelli's chimpanzees only had prior experience of one configuration of hook and reward (which was different from that used in the test sessions). Moreover, other experiments by Hauser's group (Spaulding & Hauser, 2005) explicitly showed that in the absence of previous experience and training, tamarins and common marmosets (*Callithrix jacchus*) are not sensitive to the functional features of hooked tools, validating a criticism of Povinelli's experiments made by Machado and Silva (2003). It is therefore very possible that the apparent differences in performance between the monkeys and apes result from these task differences, rather than true cognitive differences.

In this chapter, I report the results of two experiments into New Caledonian crows' understanding of hooks. The first experiment investigated whether captive New Caledonian crows had an *a priori* preference for a hooked tool over a straight tool when they needed a hook. The task was an extension of some earlier (unpublished) experiments by Jackie Chappell, which involved the same apparatus but provided a stick tool with a small hook projecting at 90° from one end; these experiments were not completed because the crows turned out to be capable of retrieving the bucket with either end of the stick, by using it to pin the handle of the bucket against the sides of the tube and thereby pull it up. In Experiment 1 here, the crows had to choose between two wire tools, one straight and one hooked – in this case, the straight wire was designed to be unsuitable for retrieving the bucket, because it is smooth and non-rigid, so the bucket would just slip off it. Although wild New Caledonian crows naturally use hooks, the tools presented to them here were perceptually very different from their natural ones (where the hooks consist of either small spines on the edge of Pandanus leaves, or small V-shaped ends on twigs resulting from the removal of a side-twig). Since the task presented here was also very different from any natural foraging problems, and wild crows use straight tools as well as hooked ones, the crows should not have had any automatic preference for the hooked tools: any preference found would therefore be best explained by some degree of ‘understanding’ of the task requirements.

The second experiment investigated the ability of New Caledonian crows to *make* hooked tools from novel material (the same wire as used above). It was designed to follow up observations of apparent hook-making in Experiment 1, and involved simply presenting the subjects with the same apparatus as above, but only one, straight, tool.[7]

3.2 EXPERIMENT 1

3.2.1 Methods

This experiment investigated whether New Caledonian crows would spontaneously choose a hooked piece of wire over a straight one in a task requiring a hooked tool. There were two phases (I and II) of the experiment, because after the first 9 trials the location and shape of the tools were altered (see Apparatus and Procedure, below) to solve limitations of the original design.

Subjects and housing

The subjects were two captive New Caledonian crows (*Corvus moneduloides*) held at the University of Oxford field station: ‘Abel’, a male, and ‘Betty’, a female. Both were wild-caught: Abel had been held for at least 15 years at the Parc Forestier zoo in Noumea, New Caledonia, and was estimated to be at least 17 years old at the time of the experiments, whereas Betty was caught by Jackie Chappell at Yaté, New Caledonia in March 2000, and was estimated to be around 3 years old. Both were brought to Oxford in April 2000.

The birds were housed together (free-flying) in an indoor room (4.29 x 2.94 x 3.00 m high), with access to an outdoor aviary (2.00 x 4.00 x 2.50 m high) during the day (see

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[7] Note that Experiment 2 has been published separately (Weir et al., 2002). This paper is included as Appendix 2.

Chappell & Kacelnik, 2002 for more details of housing and capture). During experiments they were confined to the indoor room, but were not separated as in previous experiments separation often resulted in unwillingness to participate. The aviaries always contained a variety of branches and twigs as enrichment, but the indoor room was cleaned and all visible twigs removed before experiments. The birds were maintained on a 12L: 12D lighting schedule.

The crows were fed ad-lib on soaked cat biscuits (Go-cat ®), an insect and fruit mix (Orlux® Universal and Orlux® granules), peanuts, mealworms, and occasionally small pieces of pig heart. Their normal food was removed 1 hour before experiments began, and replaced as soon as they were completed. Drinking and bathing water were permanently available.

Both subjects had participated in a number of experiments testing various aspects of tool use (Chappell & Kacelnik, 2002, 2004; Kacelnik et al., in press). One of these involved the same apparatus as in the present experiment, but with a different tool (see Section 5.1). Apart from one hour of free manipulation with flexible pipe-cleaners a year before this experiment, neither subject had had any experience with pliant material or wire since capture.

Apparatus

The apparatus consisted of a small bucket (made from a modified empty film canister) with a plastic ‘handle’ attached by sticky Gaffa® tape at opposite ends of the rim, placed at the bottom of a vertical transparent Perspex® tube. The bottom of the Perspex tube was held in a small ceramic dog bowl by wrapping Gaffa tape around the entire device. The tube/bowl were secured in the centre of a blue plastic feeding tray, again using Gaffa tape. A half brick was placed in the tray next to the tube/bowl to prevent the crows from pulling the apparatus off the table, and as a perch to enable them to probe inside the tube. See Figure 1 for more details.

The tools were made from plastic-coated garden wire (0.8 mm in diameter). One tool was always straight and the other one hooked; the hooks differed slightly between Phases I and II. In Phase I, the end of the hooked tool was bent into a U-shape (the hooked portion was 1 cm long) using a metal rod as a template. In Phase II, the end was bent into an L-shape (the L was again 1 cm long), because it appeared that the subjects occasionally had difficulty fitting the handle of the bucket into the U of the tool. The length of the tools as presented to the crows was 90 mm (note that the wire comprising the hooked tool was 100 mm long, since 1 cm was bent into a hook; the final tools were the same functional length). The position of the tools was also changed between phases: in Phase I, they were placed parallel to each other on top of the Perspex tube, either parallel or orthogonal to the brick perch (left / right and hook / straight-end orientation were pseudo-randomised across trials); in Phase II, they were placed on the brick parallel to the long sides of the tray (left / right and hook / straight-end orientation were again pseudo-randomised across trials), because frequently in Phase I the tools would be knocked off their position on top of the tube and subjects would thereafter not have a valid choice.

Figure 1: A photograph of the experimental apparatus. The handle of the bucket is visible at the bottom of the Perspex tube. A piece of straight wire is on top of the tube.

Procedure

Since the subjects had already had experience with the apparatus, and both were proficient at extracting the bucket using a wooden stick, no training was given. Outside of the experimental room, a small piece of pig heart (0.5 ± 0.1 g) was placed in the bucket, which was then dropped into the bottom of the tube. The tray containing the apparatus was then placed on a table in a corner of the experimental room, and the wires were positioned as described above. The experimenter immediately left the room and used a mini-DV camcorder (Canon DM-MV550i) to videotape all trials through a dark Perspex window (which was effectively one-way: it was not possible for humans, at least, to see through the window from the birds' side). Trials continued until the subjects had retrieved the bucket or dropped the tools irretrievably into the tube; no trial lasted longer than 10 minutes.

Nine trials were carried out in Phase I and 12 in Phase II (Phase I was ended after 9 trials because the position of the wires on top of the tube resulted in three invalid trials; the new position of the wires in Phase II allowed the completion of 15 valid trials in total).

There was a gap of 5 minutes between each trial. All trials took place on the same day (18 February 2002).

Scoring and analysis

All scoring was done from videotapes. For all actions, the subject performing them was noted (only one subject ever interacted with the apparatus at a given time). The following variables were recorded: the first tool picked up (and which tool was nearest the subject at the time it was picked up), the first tool the subject attempted to use (defined as inserting into the tube), the end of the tool used (in the case of the hooked tool), the tool the subject succeeded with, and the number of times the subject turned the tool round (defined as putting down a tool and immediately picking it up by the other end). The length of time spent probing (unsuccessfully) with the straight tool when the hooked tool was and was not available was also recorded. Any modifications the subjects made to the tools were noted. Note that because the data are 'censored' by success (i.e. probing obviously stops when the bucket is retrieved), the total number of probes and length of time spent probing with each tool would be meaningless, and were therefore not analysed. Similarly, the analysis of length of time spent probing with the straight tool depending on the availability of the hooked one is of dubious significance, since if the hooked tool was not available there was obviously no option of probing with it.

Since Abel occasionally picked up the tools before Betty first probed with them (on 5 trials in Phase I and 1 in Phase II), the tools were sometimes disturbed from their original location before Betty used them. Moreover, on 3 trials in Phase I only one of the tools was available when Betty first probed, since Abel had removed the other one or dropped it irretrievably into the Perspex tube. Consequently, in analyses of tool choice only "valid" trials where both tools were available and still near their original locations are included. It should be noted that they were not always exactly as originally placed, though, and it is possible that this may have affected Betty's choice.

Only Betty's behaviour was analysed statistically, because Abel interacted very little with the apparatus, and performed too few actions for analysis. Due to small sample sizes, non-parametric statistics were used on Betty's results pooled across both phases. One-tailed binomial tests (with chance = 0.5) were used to assess significance of tool choice. One-tailed tests were used as the question of interest was whether she used the hooked tool or hooked end of the tool more often than would be expected by chance. A two-tailed

Mann-Whitney U-test was used to compare the duration of probing with the straight tool under different conditions.

3.2.2 Results

Both subjects very quickly picked up the tools and attempted to use them to get the bucket. Since Betty interacted with the apparatus to a much greater extent than Abel over both phases of the experiment, Abel's results are summarised in Table 1, but are otherwise not discussed; only Betty's behaviour is analysed in detail. Overall, Betty retrieved the bucket on 6 of the 9 trials in Phase I and Abel on 1 on them; in Phase II, Betty retrieved the bucket on 10 of the 12 trials and Abel never successfully retrieved it. In one trial in Phase II Betty successfully retrieved the bucket with the unmodified straight tool; in all other trials, the successful tool was hooked. Notably, in three trials Betty bent the straight wire and used this to retrieve the bucket (see details below).

Tool choice

Betty was the first to pick up the tools in 5 of 9 trials in Phase I, and 11 of the 12 trials in Phase II (on 3 trials in Phase II she picked up both tools simultaneously; these trials are excluded from the first-picked-up analysis below). Over both phases combined, when she was first to pick up the tools she chose the hooked one first in 7 of 13 trials ($p = 0.50$; Figure 2a). On 9 trials, the tool she picked up first was the closest one to her, whereas on 3 trials she chose the most distant tool (on 1 trial the tools were equidistant from her; the tendency to pick the closest tool when the tools are not equidistant approaches significance, with $p = 0.07$). Because the birds could approach the apparatus from any angle, it was impossible to control which tool was closest to the subject on any particular trial. It is therefore possible that the subjects might have chosen to approach the tools from a particular side having already decided which tool to use, but this is unlikely given that the contrast between the tools and background was not great, and it would have been hard to see from a distance which tool was hooked and which straight.

On first probes in each trial, Betty used the hooked tool on 11 of 15 valid trials over both phases ($p = 0.06$; Figure 2b). On 6 trials Betty succeeded in getting the bucket with her first probe, and on 9 trials she succeeded without trying with the other tool (on the remaining 6 trials she probed for the bucket at least once with each tool).

She inserted the hooked end of the hooked tool significantly more often than the straight end, both when only first probes are considered (9 of 11 valid trials, $p = 0.03$; Figure 2c), and across all probes (17 of 22 probes, $p < 0.01$; Figure 2d). She also changed from holding the hooked end to holding the straight end of the hooked tool 5 times, whereas she turned it around the other way only once (N.B. all turnarounds happened before using the tool; the sample size is too small for statistical analysis). She never turned around the straight tool.

Figure 3 shows (a) which tool Betty first probed with on each trial, and (b) the sequence of probes with the hooked / straight end of the hooked tool across all trials. It is apparent from panel (a) that after using the hooked tool first on the first four (valid) trials, Betty then appears to choose randomly until Trial 14 (the 5th trial of Phase II). In contrast, panel (b) shows that she seems to consistently use with the hooked end of the hooked tool from her third probe, although there are 3 probes later on with the straight end.

Betty showed a tendency to probe for longer (unsuccessful probes only) with the straight tool when it was the only tool available than when the hooked tool was also available (Mann-Whitney U-test, $W = 229.0$, $p = 0.066$; Figure 2e). However, since she only probed 4 times with the straight tool when the hooked one was available, this needs to be interpreted with caution.

Tool modification

Betty modified the shape of the wire on 4 occasions. The trials where this occurred are described in detail below.

On Trial 5 (Phase I), Betty approached the apparatus and knocked both tools off the top of the tube, but Abel then displaced her. He spent a total of 14 seconds (in two bouts) probing with the straight end of the hooked wire, and then flew to a perch elsewhere in the aviary and retained the hooked wire. Betty then spent 8 seconds probing for the bucket with the straight wire, before she inserted the distal end of the wire into an opening in the Gaffa tape at the base of the tube, and pulled the end in her beak around the tube (for 3 seconds).[8] This resulted in a slight, broad bend in the wire, with which she attempted to get the bucket for 22 seconds. She again briefly (for 1 second) poked the end of the wire into the opening in the Gaffa tape, but did not pull it around the tube. She then took the wire to the edge of the tray, where she appeared (it is hard to see clearly on the videotape) to poke the end into Gaffa tape there, and pulled the other end orthogonally to the tape (for 4 seconds), resulting in a bend with an angle of 65° from straight. She spent approximately 10 seconds apparently attempting to remove the wire from the tape, where it had become stuck, and 6 seconds later used the bent end of the wire to retrieve the bucket (see Supplementary Movie 3-1).

On Trial 7 (Phase I), Betty picked up the straight tool and immediately flew away from the apparatus with it (the hooked tool was still on top of the tube). She spent approximately 2 minutes poking it into various holes and crevices around the aviary before returning to the apparatus and attempting to get the bucket with it for 3 seconds. She then poked it into Gaffa tape at the same corner of the tray as in trial 5 and bent it in a similar way, although the resultant bend was smaller (31°). She did not attempt to use it immediately, but again flew to other parts of the aviary and poked the wire into holes and crevices for around 1 minute. She eventually returned to the apparatus and retrieved the bucket successfully with the bent end of the wire. Notably, the hooked wire was available to her throughout this trial; Abel did not interact with the apparatus or tools at all.

On Trial 8 (Phase I), Abel was first to interact with the apparatus, and spent 9 seconds probing in the tube with the straight end of the hooked tool, and 7 seconds probing with the straight tool. He then flew to a perch elsewhere in the aviary with the straight tool. Betty very briefly (for less than 1 second) probed in the tube with the hooked end of the hooked tool, and then flew away with it and spent several minutes probing elsewhere in the aviary with both the hooked tool and the straight tool (which she had recovered from the aviary floor). When she returned to the apparatus carrying both tools, the hooked portion of the hooked tool was now L-shaped (it had a 90° bend), rather than U-shaped as before (with a 180° bend). She briefly probed for the bucket while holding both tools, and then discarded the straight tool and twice (for 5 and 7 seconds) probed with the straight end of

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[8] N.B. On the previous trial, Betty poked the Gaffa tape with the wire, resulting in a very slight bend, and also inserted it into a gap in the tape at the bottom of the tube, but then discarded the tool and tugged at the tape with her beak.

the hooked tool, before turning it around and retrieving the bucket with the hooked end of it.

On Trial 14 (Phase II), Betty probed for the bucket twice (for 2 and 6 seconds) with the straight tool, before almost retrieving the bucket with the hooked tool but ending up dropping the bucket and tool back into the tube (where the tool was now out of reach). She then had 3 more attempts to get the bucket with the straight tool (for 12, 2, and 4 seconds), interspersed with flying around the aviary and probing into other holes and crevices. After approximately 2 minutes, she returned to the apparatus with the wire slightly bent (how the bending happened was not apparent), and attempted to get the bucket for 25 seconds (partially raising it, but not completely). She again spent several minutes probing elsewhere in the aviary (the wire did not appear to bend any more), and had two more attempts to get the bucket (for 13 and 7 seconds). Finally, after 7 minutes she inserted the wire into Gaffa tape at a similar location to the previous two trials and pulled it orthogonally, which resulted in a bend of 91°. 10 seconds later she used the bent end of the wire to retrieve the bucket.

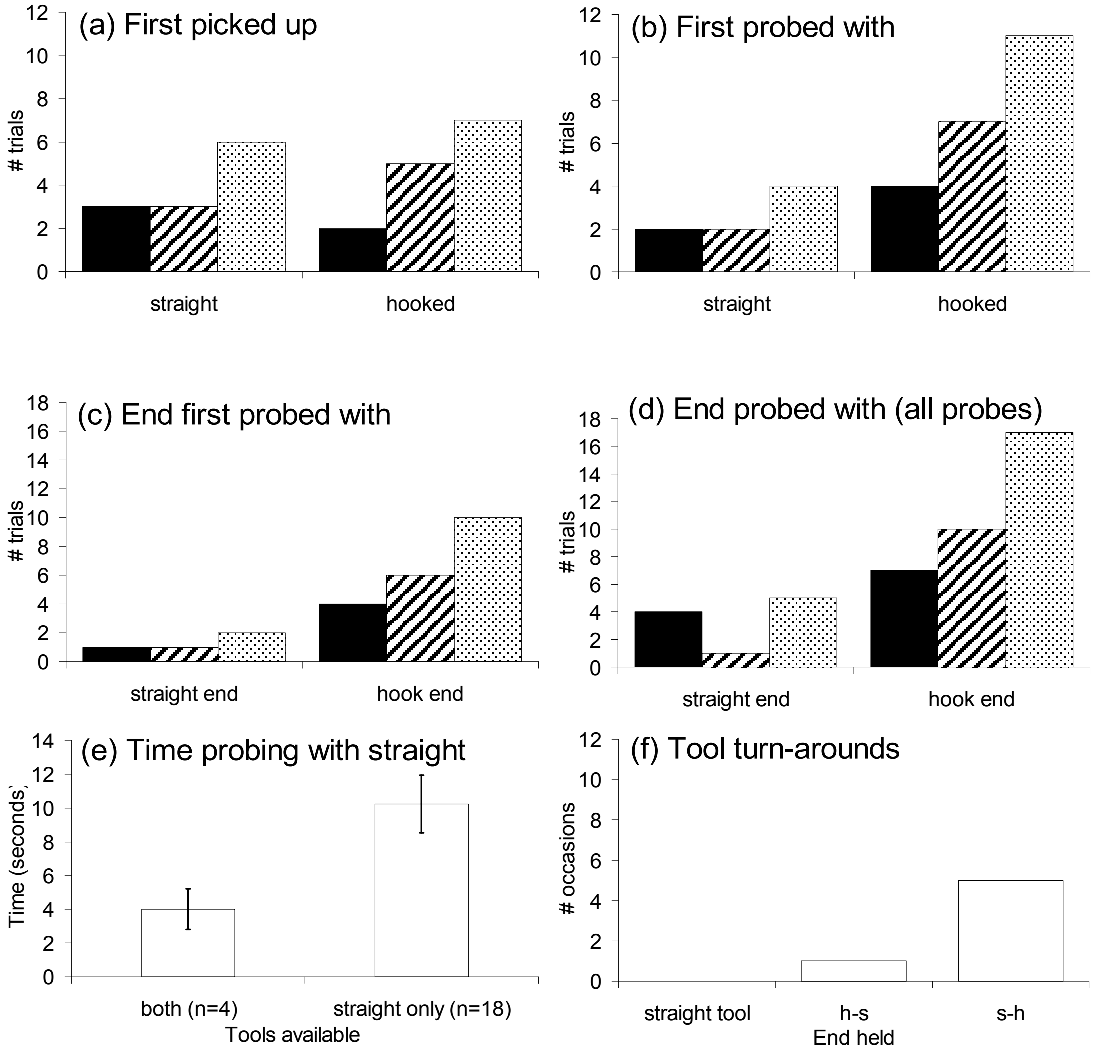

Figure 2: Tools chosen and used by Betty (filled bars: phase I; hatched bars: phase II; stippled bars: pooled data). **(a)** First tool picked up. **(b)** First tool inserted into the tube. **(c)** End of the hooked tool that Betty inserted into the tube on first probes on each trial. **(d)** End of the hooked tool that Betty inserted into the tube on all probes. **(e)** Average time (per probing bout) that Betty spent probing unsuccessfully with the straight tool when the hooked tool was and was not available. Error bars are standard errors. **(f)** Number of times Betty turned around tools. "h-s" indicates a change from holding the hooked end to holding the straight end of the hooked tool (i.e. the 'usable' end was previously straight, and subsequently hooked), while "s-h" indicates the reverse.

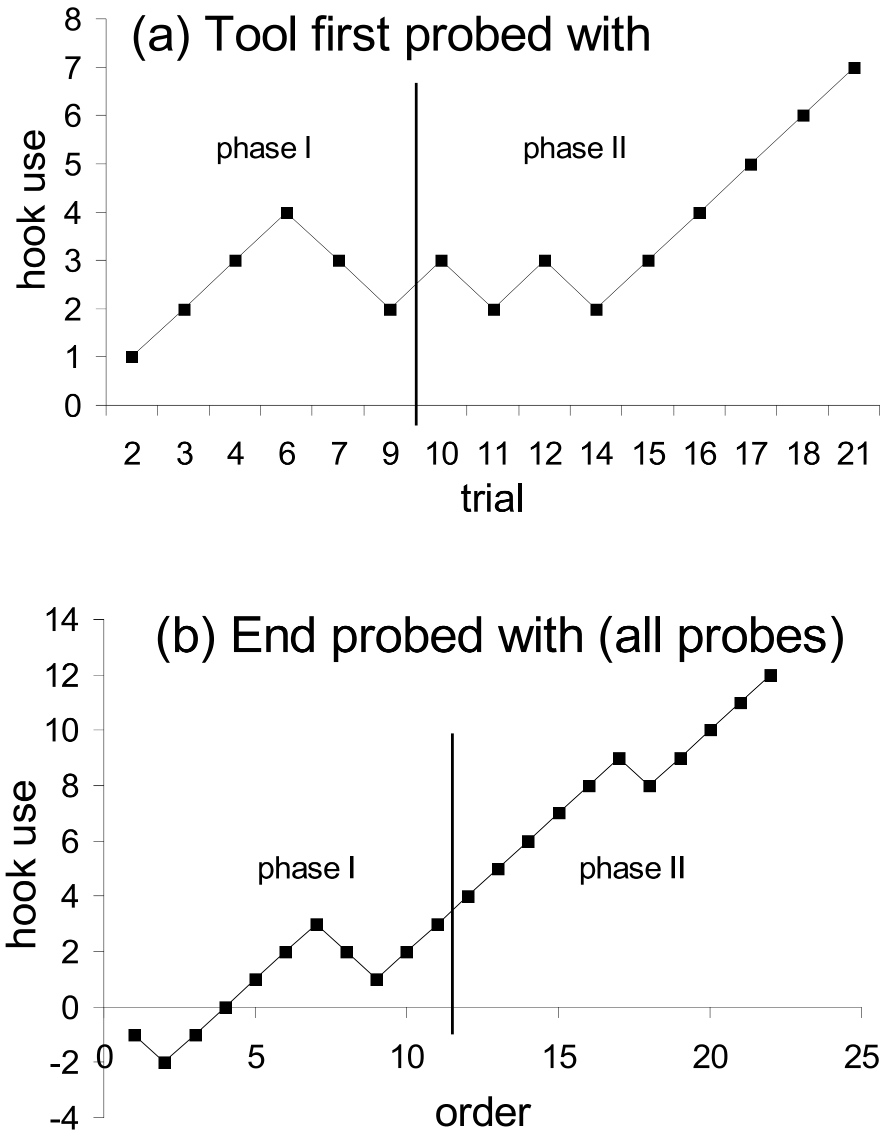

Figure 3: Time-course of tools used to probe for the bucket by Betty. Both graphs are modified learning curves: 1 is added for each ‘correct’ (hook or hooked end) action, and 1 is subtracted for each ‘incorrect’ action. The reason for preferring this format over standard learning curves is that random actions would result in a graph with no overall trend, whereas majority correct or incorrect actions would result in positive or negative slopes, respectively. **(a)** The tool Betty first used to probe for the bucket (valid trials only), by trial. The vertical line separates Phase I and Phase II. **(b)** The end of the hooked tool Betty used to probe for the bucket, in chronological order (all probes). Since there could be more than one probe per trial, the numbers on the x-axis do not correspond to trial numbers. The vertical line separates probes from Phase I and Phase II.

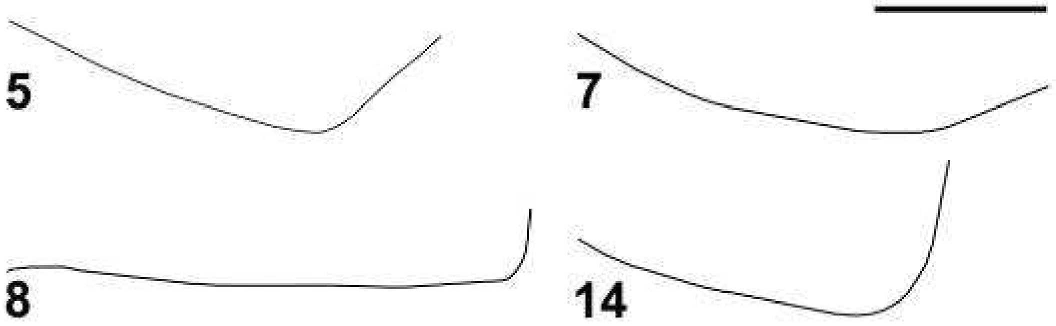

Figure 4: The final shape of four tools modified by Betty. The numbers next to each tool show which trial the tool was modified in. Tools 5, 7, and 14 were originally straight and were bent by Betty, whereas tool 8 originally had a U-shaped end, and Betty unbent it (note that it is therefore 1 cm longer than the others). Scale bar = 3 cm.

Table 1: Tools chosen and used by Abel (results pooled from both phases). 'Straight' and 'Hook' refer either to the tool chosen, or the end of the tool used, as indicated in the category column.

Category	Straight	Hook
Tool used when successful	0	1
End of hooked tool used when successful	0	1
Tool first picked up	2	3
Tool first probed with (in each trial)	2	3
End of hooked tool used (first probe of each trial)	2	1
End of hooked tool used (all probes all trials)	3	1

3.2.3 Discussion

The purpose of this experiment was to test the ability of two New Caledonian crows to choose appropriately between two tools, only one of which was usable for the task. This aimed to clarify their level of understanding of the function of hooks, in the context of prior work with apes and monkeys that yielded conflicting or inconclusive results (described before). It is apparent from the results that a detailed analysis is necessary to reach any conclusions. In general, both Betty and Abel were able to retrieve the bucket using the novel tools, but since Betty interacted with the apparatus the most and was responsible for all but one of the successful retrievals, the rest of the discussion concentrates on her performance.

Betty had no significant preference for which tool she picked up first – and it seemed as though her strategy may have been to pick up whichever tool was closest to her. She did have a tendency to preferentially *use* the hooked tool for her first probe, which implies that when she picked up the straight tool first, she often discarded it without using it – in other words, she became more 'choosy' as she approached the apparatus. However, it seems that this tendency was not established until she had completed 10 valid trials. These results are similar to those of Povinelli and colleagues (2000b, experiment 16 condition F): their chimpanzees showed no preference between a hooked and a straight tool in a task where they needed a hook. This was despite the chimpanzees having been trained to use identical hooked tools for a very similar task – whereas Betty and Abel had previously succeeded with both hooked and straight tools (of very different physical appearance to the wire tools here) on this task. Betty seemed to perform better than the cotton-top tamarins (Hauser, 1997; Hauser et al., 2002a) and capuchins (Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003), all of whom took several sessions of 10-12 trials before they reliably selected the correct tool, in contrast to Betty's consistent choice of the hooked tool after just 10 trials (although this conclusion should be regarded with caution, since she only received another 6 trials).

In contrast, when using the hooked tool Betty was much more likely to probe with the hooked rather than the straight end of it, and this preference appeared from her third probe. Moreover, she seemed to use the straight tool for longer if it was the only tool available, and she more frequently turned the hooked tool around so as to hold the straight end rather than *vice versa*. Here, Betty shows better performance than the chimpanzees: in two conditions (E and G) of Povinelli and colleagues' experiment 16 (Povinelli et al., 2000b) where the hooked tool was presented the wrong way round, the majority of retrieval attempts the chimpanzees made were with the wrong end of the tool, and they only reoriented the correct tool on 6 out of 28 trials – exactly the same number of times that they reoriented the incorrect tool (in condition E, this was also a hooked tool, but one that could not be used to retrieve the food; in condition G, this was a straight tool). Unfortunately Povinelli and colleagues did not implement a condition where they gave their subjects a choice between a hooked tool in the correct and incorrect orientations, so direct comparison of initial preference is impossible. Like Betty, cotton-top tamarins (Hauser, 1997; Hauser et al., 2002a) and capuchins (Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003; although the data are not broken down by tool type, so this is an assumption from pooled results) had a strong initial preference for tools oriented the right way (although tamarins without extensive previous experience with the tools in the correct orientation do not show this preference: Spaulding & Hauser, 2005), but unlike Betty (and like chimpanzees) tamarins never reoriented or repositioned non-functional tools (Hauser, 1997; Hauser et al., 2002b; Spaulding & Hauser, 2005), and capuchins only rarely did so successfully (Cummins-Sebree & Fragaszy, 2005; note that Fujita et al., 2003 do not report data on tool reorientation or repositioning).

These results are suggestive, but leave some uncertainty regarding Betty's 'understanding' of hooks. The first-picked-up and first-used results suggest that she did not have an immediate, *a priori* understanding that she needed a hooked tool for the task, and that perhaps she learned to use the hooked tool during the course of the experiment – i.e. she associated the hook with success. However, the fact that she preferentially used the hooked *end* of the hooked tool from her second probe suggests the opposite, that perhaps she did understand that it was better to use the hooked end than the straight end of tools. There is an alternative explanation, however: that she simply preferred (due to previous experience, or for ergonomic reasons) to hold the tool by the straight end. In a different experiment from the one described above, Povinelli and colleagues (2000a) found that some of their chimpanzees had a preference for holding the straight ends of tools – even though in that experiment it was the straight end that was functional, and the other end was not! Similarly, although Betty's trend to probe for a shorter length of time with the straight tool when the hooked one was also available could be taken as indicative of an understanding that the hooked one would work better, it is also consistent with a general tendency to probe for a shorter period of time when there are alternative options.

In the absence of further evidence, the most parsimonious conclusion is therefore that Betty did not have an immediate understanding that the task required a hooked tool, but instead quickly learned which tool and end of the tool were most appropriate. However, although it is right to be cautious about interpreting behaviour as the outcome of complex (or “higher”) cognitive processes if simpler (or “lower”) ones are sufficient explanations (Morgan, 1894), we should equally resist drawing hasty conclusions that animals are incapable of certain mental processes, solely on the basis of failure to perform ‘perfectly’ on one task. Humans are certainly capable of understanding highly complex concepts and mechanisms, but this does not prevent us making mistakes even on very simple tasks, due to lack or attention or motivation. Certainly, the best evidence for ‘perfect understanding’ would be solution from the first trial, occurring from the first manipulation of the tools and with no mistakes; the opposite extreme of entirely trial-and-error driven behaviour would be characterised by completely non-directional, random manipulations, with a gradual increase in the frequency of behaviour that is successful. Clearly, neither extreme explains Betty’s performance: experience is obviously necessary, but she also generalises very quickly to which aspects of the complex patterns of behaviour are appropriate, which is probably also the way that human learning or problem solving occurs much of the time. Moreover, in the current experiment, there was no penalty (apart from time) for initially probing with the incorrect tool, and the fact that on some trials Betty spent several minutes probing elsewhere in the aviary before attempting the task suggests that obtaining the food reward was not necessarily always her highest priority. The final note of caution is that Betty did on one occasion succeed in retrieving the bucket with the straight tool, so it is possible that even if she had a ‘full understanding’ of the task, she might still have considered it ‘worth trying’ with straight tools. Nevertheless, these observations do not provide evidence that she understands the function of hooks.

A separate issue is that of tool modification. Betty first bent the tool significantly on a trial in which the hooked wire was not available, which could be an indication that the bending was a deliberate, goal-directed act designed to produce a functional tool. The fact that she once (on Trial 7) bent the straight wire when the hooked tool was still available seems to imply that the bending was not specifically related to food retrieval, but instead happened accidentally and in the absence of any understanding. However, several lines of argument suggest that this conclusion may be premature. Firstly, on the two other trials when she bent the straight wire (including the first occasion), the hooked tool was *not* available, so bending the wire was an appropriate response. Secondly, despite on several trials spending many minutes probing with the tools in other parts of the aviary, and generally exploring and manipulating them in diverse ways, Betty never produced a significant bend apart from in the manner described above. All three of her bends occurred as a result of very similar actions – inserting the distal end of the wire into a gap in the Gaffa tape, and pulling the proximal end orthogonally with her beak – suggesting that bending was not an incidental result of probing with and manipulating the wire. Thirdly, Betty also probed the gaps in the Gaffa tape with the hooked tool five times, but never performed the insert-and-pull-orthogonally action except on the occasions described above, with the straight tool – also supporting the conclusion that the bending action was deliberate. Finally, on the penultimate trial of Phase I, Betty actually partially *unbent* the end of the hooked-tool, so that it was L-shaped rather than U-shaped. While this may have been accidental (it occurred out of camera shot), it is also possible that she had an aversion to the original U-shaped tool, which the subjects occasionally seemed to find difficult to fit under the handle of the bucket.

If Betty did bend the wire deliberately, then there is the question of how she ‘discovered’ that wire bends – clearly, she could not have known this *a priori*. One potential clue is that she did bend the wire very slightly by poking it at the Gaffa tape on the trial before her first significant bend. This suggests she might have discovered that wire bends as a result of probing near the base of the tube, possibly in an attempt to remove the tape there because that was the nearest location to the food. However, her first functional bending occurred in the tape at the side of the tray, and could not therefore be interpreted as simply an incidental result of attempting to get food.

The next experiment attempted to clarify whether or not her wire modification was deliberate by asking whether Betty would consistently bend straight wire when necessary.

3.3 EXPERIMENT 2

This experiment tested how the subjects would respond when only straight wire was available. If the wire modification seen in Experiment 1 was a chance outcome of tool manipulation, then it would not be expected to occur frequently in this experiment, even though a hook is required to retrieve the bucket. Moreover, if modifying the wire was (mentally) unconnected to retrieving the bucket, there might be relatively long gaps between modifying and using the wire. However, if Betty was 'deliberately' bending the wire to make a hook, then she should do so on every trial in the absence of the hooked wire, and use the wire immediately after modifying it.

3.3.1 Methods

The subjects and housing, apparatus, and procedure were identical to Experiment 1, except that only straight wire, 90 mm long, was provided (placed on top of the tube). All trials took place one day after Experiment 1 (on 19 February 2002). As in Experiment 1, trials continued until the subjects had retrieved the bucket, dropped the tools irretrievably into the tube, or failed to interact with the apparatus for 5 minutes; no trial lasted longer than 10 minutes. Seventeen trials were carried out in total.

For each trial, the following variables were recorded: the time since the start of the trial before Betty started modifying the wire ("latency to modification"), excluding time when she was not interacting with the apparatus; the length of time Betty probed with the unmodified wire ("probing unmod") on trials where she did modify the wire; the length of time Betty spent modifying the wire ("duration crafting"); the time between the end of wire modification and Betty's first subsequent probe with the modified wire, excluding displacements; and the time to successful retrieval of the bucket ("latency success") or to dropping the wire into the tube ("latency failure") for trials where Betty was the subject performing the final action (excluding time when she was not interacting with the apparatus). Additionally, the angle of any bend in the wire was measured after the end of the trial. A Spearman Rank correlation was used to examine the relationship between trial number and "latency to modification", "probing unmod", "duration crafting", and "latency success", and a two-tailed Mann-Whitney U-test was used to examine whether "latency success" differed significantly from "latency failure". Due to the small sample size, other measurements are only described, and not statistically analysed.

3.3.2 Results

The subjects retrieved the food on 10 trials, and dropped the wire irretrievably into the tube on the remaining seven. Betty bent the wire on 10 trials (her first bend occurring on Trial 2), and used it to retrieve the bucket on eight (Figure 6(a)); on one, she dropped it irretrievably into the tube after modification, and on the other Abel displaced her and used the bent wire himself to retrieve the bucket. Abel also retrieved the bucket on one trial with the unmodified wire. On the remaining six trials, Betty dropped the unmodified wire into the tube four times, and Abel twice (see Figure 5(a)). Betty only became consistently successful at retrieving the bucket from trial 10 (Figure 5(b)), although this was partly due to Abel's interference in three of the earlier trials. Trial-by-trial descriptions of the results are in Appendix 3.

Betty used two techniques to bend the wire. The first (similar to that used in Experiment 1, above) involved wedging one end of it in sticky Gaffa® tape (either at the base of the tube [5 trials], or at the side of the tray [4 trials]), and pulling the proximal end orthogonally with her beak (see Supplementary Movie 3-2). The second technique occurred on just one trial (Trial 13 – see Supplementary Movie 3-3): here, she held the wire in her feet along a perch 3 m from the food, and used her beak to bend one end.

The mean angle to which she bent the wire was 74 ± 9° (Mean ± SE[9]; range: 39 – 117°) (see Figure 6(b) for individual tool shapes; the angle to which each tool was bent is given in Appendix 3). Figure 5(c) shows an apparent bell-shaped relationship between the angle of a tool and the length of time she probed with it before retrieving the bucket (with the longest time probing being with intermediate bend angles), but the sample size is too small for (required) parametric statistical analysis. She started to bend the wire 35 ± 8 s (range: 11 – 83 s) after the start of each trial, which showed a non-significant tendency to decrease over trials ($r_s = -0.517$, $p = 0.126$), and used the resulting hook 6 ± 2 s (range: 1 – 19 s) after finishing bending. In all cases but one, she probed with the straight wire (for 15 ± 4 s; range 2 – 41 s) before starting to bend the tool (Figure 5(d)), which showed an almost-significant decrease across trials ($r_s = -0.565$, $p = 0.089$). She spent on average 6 ± 1 s (range: 3 – 15 s) bending the wire, which showed no change across trials (Figure 5(e); $r_s = -0.232$, $p = 0.519$). In all successful trials, the subjects retrieved the food within 2

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[9] Note that in Weir et al. (2002), the SD (of ± 30°) was erroneously reported, instead of the SE.

minutes (not including time spent away from the experimental apparatus); mean time to retrieval was 62 ± 9 s (range: 37 – 112 s). There was no significant change in latency to success across trials (Figure 5(f); restricted to trials where Betty performed the final action, $r_s = -0.228$, $p = 0.588$), and no significant difference in trial duration depending on whether the trial ended in success or failure ($W = 26.0$, $p = 0.213$).

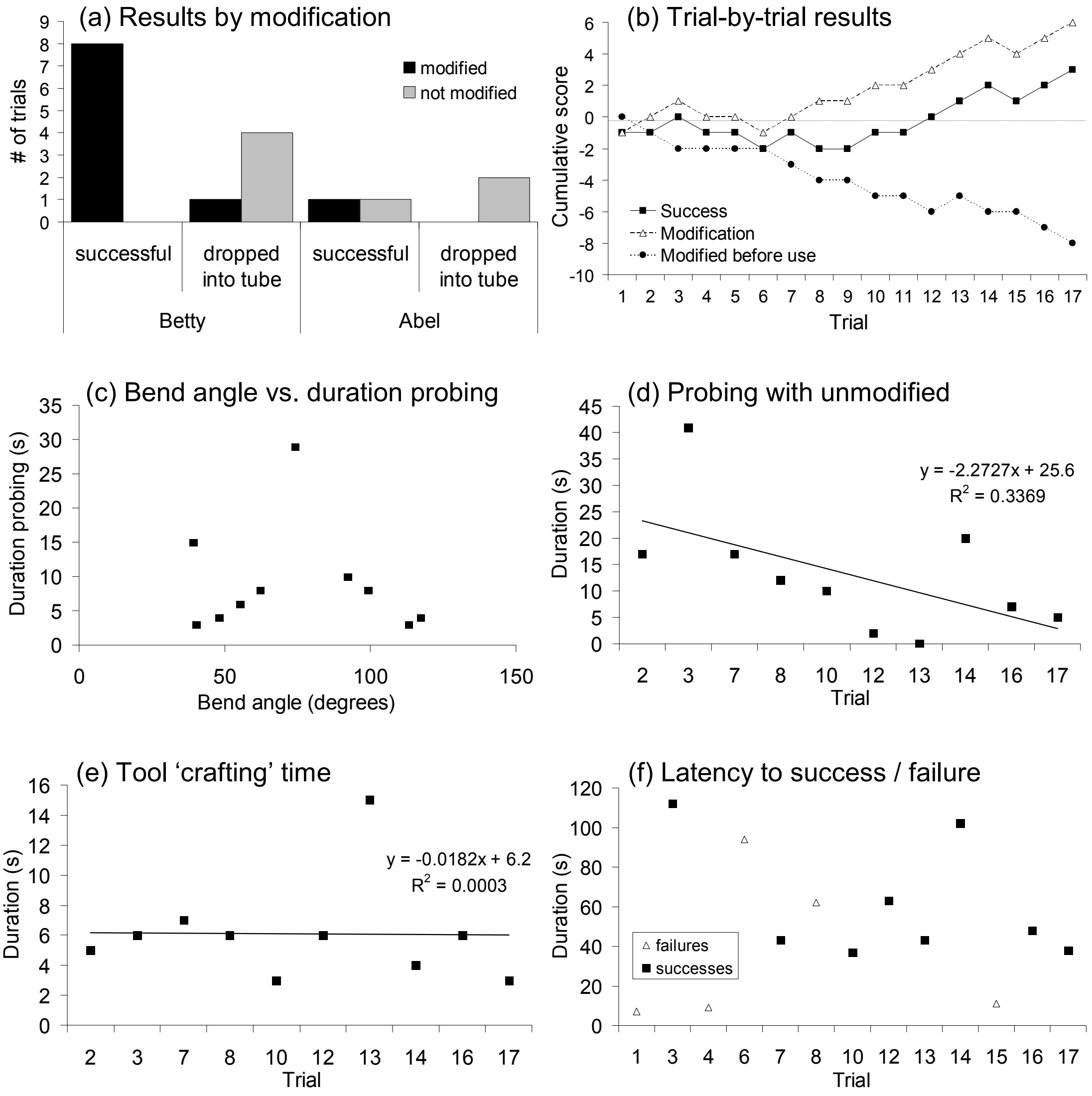

Figure 5: (a) The number of successful and unsuccessful trials for each subject in Experiment 2, according to whether or not the tool was modified. Note that one of the tools with which Abel retrieved the bucket was modified by Betty earlier in the trial. **(b)** Betty's cumulative success at retrieving the bucket, tool modification, and modification of the tool before first use in Experiment 2. The score for each measure is calculated by adding 1 for success / modification / modification before use, and subtracting 1 for dropping the tool in the well / no modification / modified after use. No change is made for the "Success?" series on trials where Abel performed the last action (i.e. retrieved the bucket or dropped the wire into the tube); no change is made for "Modification" if a tool was not modified and Abel performed the last action; no change is made for "Modified before use?" if no tool was modified. **(c)** The length of time Betty spent probing with a tool (after modification), plotted against the bend angle of the tool. **(d)** Duration of probing with the unmodified wire in each trial. This excludes trials where no tool was modified, and only includes time Betty spent probing with the unmodified wire. **(e)** The length of time Betty spent modifying tools. **(f)** Trial durations in Experiment 2. This shows the time from first interacting with the apparatus to either retrieving the bucket (filled squares) or dropping the wire into the well (open triangles), excluding time spent not interacting with the apparatus. Only data trials where the final action was performed by Betty are shown.

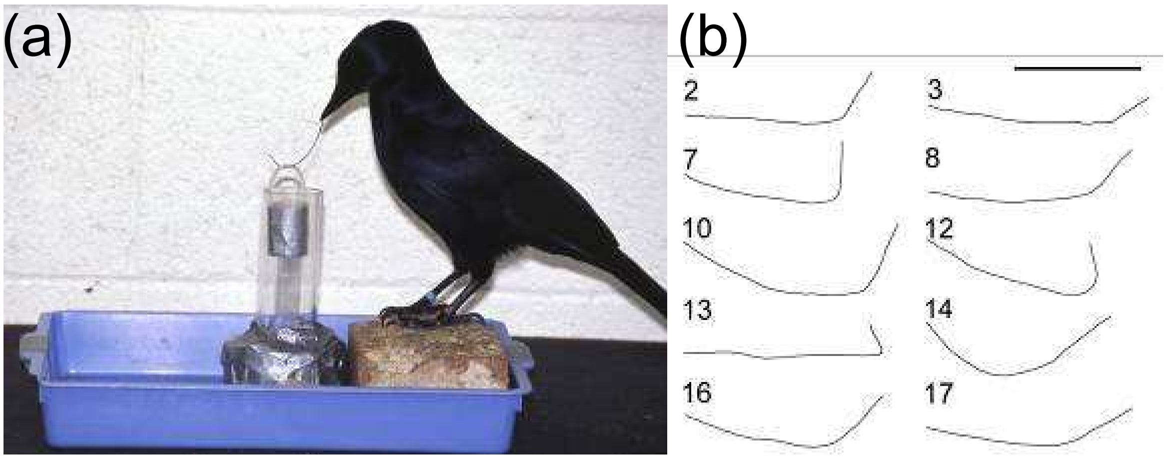

Figure 6: (a) Betty extracting the bucket containing meat using a piece of wire she had just bent. The photo was taken after the experiment was completed, but the hook and posture depicted are typical of experimental trials. **(b)** Outline tracings of all the bent wires, with the end inserted into the tube facing right. Numbers refer to trial number[10]. The wire bent in trial 8 was not successfully used to retrieve the bucket (it was dropped into the tube). Because of experimenter error, the wire in trial 10 was 2 cm longer than the wire in the other trials. Scale bar, 5 cm.

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[10] Note that in Weir et al. (2002), the tool for Trial 14 was erroneously labelled as “15” (whereas in fact, Betty did not modify the wire at all on Trial 15).

3.3.3 Discussion

Experiment 2 was designed to test whether Betty's wire modification in Experiment 1 was the result of chance actions, or if it was specifically related to the task requirements. When only straight wire was available, she bent it on the second trial and on nine subsequent ones (out of 14 in which she had undisturbed access to it). She used two techniques to bend it, and three different locations. On all trials apart from one, she probed for the bucket before attempting to modify the wire, although the duration of these probes declined across trials. She always used the wire almost immediately after modifying it.

These results suggest that the tool modification was not random, but was instead a specific response to the lack of an appropriate tool. It is hard to predict how frequently she would have bent the wire if it had been the outcome of random manipulation, and not task-related, but the fact that she bent it on so many trials (and note that on three of the four trials where she did not bend it she dropped it into the well after only probing for 5-6 seconds with it) makes it highly unlikely that this was the case. It is possible that modification could have occurred during 'play' or displacement behaviour, once she had abandoned unsuccessful attempts to reach the food, but the details of what happened on each trial do not support this argument: the mean latency to modification was only 35 s, of which she spent on average 15 s probing with the unmodified wire, which is less than half the average length of time she spent probing in each trial with the straight wire in experiment 1 (37 s). Moreover, the fact that she used the tools almost immediately after modification suggests that, at the very least, she recognised that they were then functional.

The use of different locations and techniques to bend the wire are also revealing. If the first occasion on which Betty bent the wire had been 'accidental' and she had learned about the positive consequences of this, we might predict that on later occasions she would simply repeat the behaviour that had led to this modification. Her use of different techniques and locations to produce similar results suggests that she was in fact intending to bend the wire, rather than simply performing previously-reinforced actions.

There are also, though, observations that suggest she did not have a full understanding of the task and the necessary modifications. Most strikingly, on nearly all trials she probed with the straight wire before modifying it, and the fact that the duration of these probes gradually reduced across trials suggests that she was *learning* to spend less time probing with the unmodified wire, rather than instantly ‘understanding’ that it was ineffective. Particularly revealing is the fact that on one trial (Trial 6) she only modified the tool very slightly (the bend was less than 10°, so this was not treated as “modified” in the analysis), and then probed with it for 62 s, eventually dropping it into the tube, suggesting that she perhaps did not ‘realise’ that the modification was not sufficient. However, it should be remembered that both Betty (in Experiment 1) and Abel (in Experiment 2) once managed to retrieve the bucket with the straight tool, so probing with the unmodified wire does not necessarily imply a lack of understanding.

Purposeful modification of objects by animals for use as tools, without extensive prior experience, is almost unknown. In experiments by Povinelli and colleagues (Povinelli et al., 2000a, experiments 24 to 26), chimpanzees (*Pan troglodytes*) repeatedly failed to unbend piping and insert it through a hole to obtain an apple, unless they received explicit coaching. Visalberghi and colleagues found that chimpanzees, bonobos (*Pan paniscus*), an orangutan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*) would remove transverse cross-pieces from a piece of dowelling, which allowed them to insert the dowelling into a tube to push food out (Visalberghi et al., 1995). However, the cross-pieces were inserted into the dowelling in such a way that they would fall out if the dowelling was rotated, and a similar experiment by Povinelli and colleagues (Povinelli et al., 2000a, experiment 27) found that chimpanzees had a general tendency to modify tools if they were not instantly successful, even if the modification served to make the tools less functional. Together with the fact that all the subjects in Visalberghi et al.’s experiments made at least one error (e.g. attempting to insert the tool before removing the cross-pieces), it therefore seems likely that the tool modification shown by them was not specific to the task, but the result of a general tendency to disassemble tools when possible.

There are numerous observations of wild chimpanzees appropriately modifying tools (e.g. Boesch & Boesch, 1990; Sanz et al., 2004; Sugiyama, 1985; Sugiyama, 1995), and wild capuchins have recently been observed to remove leaves or stems from their twig tools before using them (Moura & Lee, 2004). However, as discussed in Chapter 2, it is impossible to conclude anything about the cognitive processes involved in these behaviours, since the individuals will have had many opportunities to learn the appropriate modifications through trial-and-error or by observing others. In contrast, Betty had had little exposure to and no prior training with pliant material, and had never been observed to perform similar actions with either pliant or non-pliant objects. Moreover, the technique she used to bend the wire is distinct from that known to be used by wild crows to make hook tools (Hunt & Gray, 2004a, 2004b), and would be unlikely to be effective with natural materials. Undoubtedly, previous experience manipulating objects will have been critical to the development of her behaviour (just as human infants learn about everyday physics from their manipulative experience; e.g. Lockman, 2000), but she had no model to imitate and, to our knowledge, no opportunity for hook-making to emerge by chance shaping or reinforcement of randomly generated behaviour.

3.4 GENERAL DISCUSSION

The two experiments described in this chapter investigated the extent to which New Caledonian crows understand the function of hooked tools, which they naturally use in the wild. In Experiment 1, I reported that one of the two subjects, Betty, showed a tendency to preferentially use a hooked tool to retrieve a bucket (at least, from part-way through the experiment), and a strong preference to use the hooked *end* of the tool to probe with. Moreover, I found that on two occasions when the hooked tool was not available, she bent the straight tool into a hook and used this to retrieve the bucket. In Experiment 2, the same subject reliably bent straight wire when no hooked tool was available and used the resulting hook appropriately, and there was evidence that this bending was intentional and task-related.

Do these results show that New Caledonian crows have a full understanding of hooks, and of the task presented? For several reasons, I believe this conclusion would be premature. Firstly, only one subject performed enough trials for rigorous analysis, and the other subject made several mistakes in the few trials he performed; clearly, the results cannot therefore be considered to apply to *all* New Caledonian crows. Secondly, Betty made several errors in the hook choice experiment, particularly near the beginning of it, so the possibility that she rapidly learned which tool to use and which end to hold cannot be ruled out. Finally, she continued to unsuccessfully probe with straight tools throughout the experiment, and only gradually seemed to reduce this behaviour.

However, I believe the results also argue against a complete lack of understanding. In several respects, Betty performed better than chimpanzees, capuchins, and cotton-top tamarins tested under similar circumstances, and she certainly was not behaving randomly with respect to which end of the tool she used and when and how to modify the wire.

Perhaps, as is often the case when dichotomies are presented, the answer lies somewhere in between: Betty quickly learned that hooked pieces of wire were more effective than straight ones for retrieving the bucket, and on discovering that wire can be bent, spontaneously made use of this knowledge to make and use her own tools when necessary. Further experiments are necessary to reveal whether this is indeed the case, in particular focussing on the details of the acquisition of the behaviour. Also of interest, given that Betty did on one occasion slightly unbend the hooked wire, would be whether she would again unbend wire when that was required to solve a task. These questions are addressed in the next chapter.

Finally, there is the question of how the fact that the experiments involved just one subject limits the scope of the conclusions that can be drawn. Certainly, the use of a single subject means that it would be unwise to conclude that Betty's abilities are representative of New Caledonian crows. It also perhaps makes it more likely that her behaviour could be explained by idiosyncrasies of training procedures and prior history, and is consistent with procedural or inductive explanations, albeit with very fast learning. However, I believe that there can be advantages to the use of one or a few subjects in experiments: this forces the experimenter to focus on the details of their subject's behaviour, rather than glossing over this with statistics on overall performance. Ultimately it is an individual-level explanation of behaviour that is needed, since it is individuals who make decisions, learn, and (perhaps) reason, and each individual will have a different history and personality (e.g. Koolhaas et al., 1999). In a study involving many subjects, the 'outlier' that does not perform as expected will often be ignored, but if we are trying to develop general theories of cognition, every individual's behaviour should be explicable. This is not to deny the importance of repeating these experiments with other New Caledonian crows (which is take place at present), and with members of other species (both birds and mammals), but if those experiments showed different results they would not necessarily invalidate the need for an explanation of Betty's performance. It is also true, though, that other crows' behaviour could shed light on Betty's: if, for example, they all behaved in a purely procedural way and none spontaneously showed similar behaviour to Betty, this would make it more likely that Betty's behaviour was the result of an unlikely combination of factors in her previous experience. Furthermore, experiments with other crows might shed light on exactly what prior experience (such as using wire hooks) is necessary for appropriate wire manipulation to emerge.

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Chapter 4

What does Betty understand about manipulating tool shape?

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Unpublished manuscript

(Note that a version of this is in press at *Animal Cognition* as Weir, A.A.S., & Kacelnik, A. 'New Caledonian crows (*Corvus moneduloides*) creatively re-design tools by bending or unbending metal strips according to needs')

4.1 INTRODUCTION

In Experiment 2 of Chapter 3, I reported that Betty, a New Caledonian crow, spontaneously bent straight wire into a shape that she could use to retrieve a bucket from a well. Moreover, I found that this bending appeared to be 'deliberate', in that the bent wire was always used (successfully and appropriately) to retrieve the bucket immediately after modification, bending did not occur as a result of general manipulation of the tool, and the action used to bend the wire was highly distinct and not used except in that context. However, on a task where she had to choose between hooked and straight tools (Experiment 1, Chapter 3), the results were less clear-cut, and perhaps more consistent with a strategy based on learning to use the hook than an *a priori* understanding of its function. Consequently, some issues remain unresolved: in particular, did Betty's tool modification reflect a full comprehension of the task, in the sense of understanding that it required a hooked tool and one could be produced by bending, or was her behaviour governed by more "procedural" rules (*sensu* Povinelli, 2000)? It is hard to conclude the extent of understanding from one task alone: although we might try to infer the processes most likely to be governing subjects' behaviour, without testing how they perform under novel circumstances we cannot exclude the possibility that other mechanisms were responsible. For example, although I argue that it is hard to account for Betty's performance in terms of chance behaviour followed by reinforcement, it is impossible definitively to rule this out, since we cannot know what was really "going on in her head".

If Betty's behaviour really was controlled by some kind of causal understanding, she should be able to transfer that knowledge onto, say, different materials and different tasks. For example, to take two extreme possibilities: if Betty had simply learned (without understanding) that particular actions are effective at modifying wire to make it into a suitable shape, then given material that is equally pliant but requiring a different technique to bend it, I would predict that she would carry on using her old technique, and gradually and incrementally learn to modify this when it turned out to be ineffective. In contrast, if she 'understood' that she needed a hook, and was flexibly using appropriate techniques in a goal-directed manner to bend the wire, then given new material she should quickly adjust her technique to best make hooks from it. Similarly, the extent to which she was controlling the final shape of the tool, rather than simply performing a learned action with it, could be investigated by giving her a task for which she needed a different shape of tool.

Experimental investigations into how much control animals have over the shape of their manufactured tools are rare, primarily for the reason that few animals naturally make tools at all, and no non-humans apart from New Caledonian crows make tools with a precisely-determined final shape. Chimpanzees (*Pan troglodytes*) do adaptively modify the shape of their termite-dipping tools and leaf sponges, but the final shape does not appear to be controlled in detail – the modification is more a matter of chewing the ends of the sticks (Sanz et al., 2004; Sugiyama, 1985, 1997), removing leaves and twigs (Goodall, 1986), or chewing and crumpling leaves up (McGrew, 1992; Sugiyama, 1997). To my knowledge, the only studies that have examined the performance of non-human animals in tasks requiring tools to be shaped by bending or similar actions are one experiment involving chimpanzees (Povinelli et al., 2000b), and two involving capuchin monkeys (*Cebus* spp.; Anderson & Henneman, 1994; Klüver, 1937). I describe their findings in detail below.

Povinelli's group tested whether seven captive chimpanzees would unbend flexible piping to insert the end of it through a hole, and thereby dislodge an apple. Their subjects were first given extensive experience with the piping in their living enclosure, and all were seen to bend the material during this time. They were also given two trials with straight piping, which they could use without modifying to dislodge the apple – again, all subjects quickly and easily accomplished this. The subjects then received four test sessions, in which an experimenter bent the straight piping into an S-shape or a C-shape (neither of which would fit through the hole) in front of the subjects, and gave them the modified tool to freely manipulate and attempt to use for 2½ minutes. Only two of the apes ever modified the tools on the test trials, and did so only once each. However, one of them ('Kara') only attempted to use the *unmodified* end, and hence was not successful, whereas the other ('Jadine') did not successfully straighten the tool out, and hence also did not retrieve the apple (Povinelli et al., 2000b, Experiment 24).

The researchers subsequently attempted to 'scaffold' the chimpanzees' responses, by demonstrating how the tool could be modified so as to make it effective (Experiment 25). The subjects were given four sessions, each consisting of the following three trials: on the first trial, the experimenter unbent both ends of a C-shaped tool in front of the chimpanzee, and gave the resulting straight tool to the subject to use; on the second trial the experimenter unbent one end of the tool (in front of the chimpanzee) and again gave it to the subject; on the third (test) trial, the C-shaped tool was pre-positioned within reach of the subjects, and was unmodified by the experimenter. The results showed that the subjects had some difficulty even in trial 2: their success rate dropped from 100% on trial 1 to 60%, mainly because they preferred (69% of the time) to orient the hooked end of the tool towards the apparatus. On the test trial, there were five instances of tool modification by three apes (Kara, Candy, and Jadine), but none resulted in successful retrieval of the apple, and on 2 of the 4 occasions when they used the modified tool, they first directed the unmodified end at the apparatus. In Experiment 26, Povinelli and colleagues attempted to scaffold their subjects' responses to an even greater extent, by explicitly training them to bend the tool in the experimental chamber (but in the absence of the probing apparatus). When the sequence of trials from Experiment 25 was repeated after the scaffolding, they still preferentially tried to insert the hooked end of the tool in trial 2 (64% of the time). However, one subject (Jadine) did now modify the tool with her hands and successfully use it to retrieve the apple on every session of Trial 3. In Sessions 1 and 3 she immediately used the straightened end first, while on Session 2 she used the unmodified (and incorrect) end first (on Session 4, she modified both ends before using the tool). Three other subjects did modify the tools, but two of their modifications appeared to occur incidentally as they poked at the apparatus, and one used the modified end as a handle, and only attempted to probe with the unmodified (and ineffective) end; none managed to retrieve the apple as a result.

Klüver's (1937) and Anderson and Henneman's (1994) investigations were less detailed, and provided conflicting results. Klüver tested how one captive capuchin monkey performed on over 300 problems, mostly involving the use of various objects to retrieve food. One of these problems involved wire bent into a circular shape: to obtain food, the subject had to unbend the wire to make it long enough to rake the food in, but although he did (apparently unintentionally) open the wire slightly, this was not enough to retrieve the food. Anderson and Henneman tested two captive capuchins on eight experiments, all involving modifying or obtaining tools (mostly stick-type tools) for honey-fishing. In Experiment 8, the capuchins were provided with loops of soldering-wire, which had to be straightened out to fit into the honey-dipping apparatus. The description of the results is brief: "The male straightened out the wire after only a few seconds of the start of a given trial, and immediately honey-dipped with the tool. He did this on 100% of trials. The female, however, rarely contacted the wire […]." (p.358)

In summary, of the three investigations into control of tool shape in non-human primates, two provided evidence of apparently deliberate straightening of the tool.

However, the one chimpanzee that managed to do it only did so after extensive scaffolding of the response by the experimenter, and considering her performance on other similar tasks as well, the authors concluded that she "came to understand some very specific features of the tool configuration that was necessary to solve the tool-insertion problem, as opposed to reasoning about an abstract conception of 'shape'" (Povinelli et al., 2000b, p. 295). It should be noted, though, that several criticisms have been made of Povinelli's experimental protocols and the broad scope of the conclusions he draws from work with only seven subjects (Anderson, 2001; Hauser, 2001; Machado & Silva, 2003; Whiten, 2001), particularly given their relatively young age and impoverished rearing conditions, so these results should not be taken to prove that chimpanzees are incapable of solving these tasks. Anderson and Henneman (1994) do not provide enough details of the initial acquisition of the wire-unbending by their capuchin to allow conclusions to be drawn as to the extent of 'mental representation' involved in its behaviour. However, the wire was described as "soldering-wire", which is so flexible that it is possible that it would unbend without any deliberate, goal-directed attempt to modify it – the unbending might have happened solely as a consequence of grabbing the ends to use them.

At present, then, we do not have definitive evidence for goal-directed unbending of tools by non-humans, or (since no other experiments have been performed) for precise control over tool shape in experimental situations by any animals other than humans and New Caledonian crows. In the experiments reported here, I attempted to assess how flexible and precise Betty's control over the shape of tools was, and also to provide data more directly comparable with the experiments above. Specifically, I asked three questions: (1) how would she adapt to a change in the tool material, giving it different properties and changing the technique required to bend it; (2) would she spontaneously modify a bent tool to make it narrower (to fit through a small hole); and (3) would she *unbend* a tool to make it longer (to rake in distant food)? In each case, the issue of interest is not so much whether or not she eventually succeeds at the different tasks; rather, it is the process leading to the successful behaviour. It is hard to make specific predictions for how the behaviour would differ under different degrees of 'understanding', but in general terms I would expect that an agent whose behaviour is guided by comprehension of the causal properties of the task would make 'relevant' modifications to the tool, whereas one reliant solely on associative learning would make random modifications, and gradually converge on the correct solution. I discuss how these differences might be manifested for each task in the introduction to the relevant sections.

It would be very hard or impossible to unbend the kind of wire previously presented to Betty and Abel using only a beak, since the wire had a circular cross-section and would be likely to rotate in the beak on any attempt to unbend it. Instead, I used thin strips of aluminium as the tool material, since their wide rectangular cross-section would probably make it possible to hold and unbend them in a beak without slippage. However, these strips also had different mechanical properties from the wire Betty was previously familiar with: unlike wire, which can bend in any dimension, the aluminium strips were constrained to bending in the plane of the tool. It is not possible to bend them by pulling at right angles to the flat plane, and pulling at an angle to it causes the metal to twist and fold over on itself. Moreover, the tool cannot so easily be wedged in small holes, so a new modification technique is necessary, and the metal bends more easily (in the plane of the tool) than wire, which might make a wider range of manipulations possible. The wedge-and-pull-orthogonally action Betty used for the familiar wire would result in a twisted loop in this new material, which would not function as effectively as a hook.

The questions were addressed using three tasks, all of which Betty was familiar with: the well-bucket task (Chapter 3); a task involving pushing food out of a tube by inserting a tool through a small hole ("width task" hereafter; similar to that used in Chappell & Kacelnik, 2004); and a task simply involving raking in food from a long tube ("length task" hereafter; similar to that used in Chappell & Kacelnik, 2002). No previous exposure to the novel tool material was given – the first presentation was with the well-bucket apparatus.

4.2 EXPERIMENT 1: BENDING NOVEL MATERIAL

In this task I examined how Betty would adapt to the introduction of novel pliant material when faced with a task where she needed a hook. It had the potential to address three questions about Betty's previous performance in Chapter 3:

1. What did she know about the relationship between tool shape and success at retrieving the bucket (i.e. did she understand that hook-like structures are necessary / most efficient)?

2. What did she understand about the link between modification technique and tool shape (i.e. the specific effect(s) her actions had upon the resulting shape of the tool)?
3. To what extent was she aware of the connection between (1) and (2) above, namely, her manipulation of the tool, and the efficiency with which it retrieved the bucket?

Although it is hard to devise specific predictions for how her behaviour with the new material would differ depending on whether she understood these principles, or was merely following associatively-learned rules, we might be able to anticipate a few general features. Initially, whether she used understanding or procedural knowledge, we would expect her to repeat the behaviour that had led to success with the wire, since she would have no *a priori* way of knowing that the new material required a different technique to modify it. However, following this discovery, if she understood any of the principles above then she should be much quicker at learning to manipulate this new material in an appropriate manner than if she was merely using procedural rules. Using purely procedural knowledge, it would generally take many tens or hundreds of trials to learn the appropriate techniques to modify the material, since there are at least three separate associations to be learned (outlined in the questions above), yet only the last one is rewarded. When training an animal in an arbitrary operant task (where by design associative learning is the only tool at the animal's disposal) involving sequences of behaviour, it is essential to reward subjects at intermediate stages; otherwise, very large numbers of trials are required for subjects to learn the entire sequence based on feedback from final success alone (e.g. Mackintosh, 1994; Schwartz et al., 2002). For example, Epstein (1984) showed that pigeons spontaneously solve an analogous problem to Köhler's chimpanzees (Köhler, 1925) of pushing a box underneath a reward and standing on it to reach the reward, but only because they had been explicitly trained over hundreds of trials on each part of the sequence separately.

4.2.1 Methods

Subject and housing

The subject for all experiments was Betty, whose capture and previous housing and experimental experience were described in Chapter 3. At the time of these experiments she had been moved to aviaries in the Department of Zoology, University of Oxford. She was housed (free-flying) with four other crows (one of whom she had paired and mated with earlier in the year) with permanent access to an indoor room (4.00 × 2.50 × 2.50 m high) and an outdoor aviary (2.80 × 2.80 × 2.50 m high). Both indoor and outdoor accommodation contained many natural perches of varying widths and heights. Plastic children's toys provided environmental enrichment, and tree branches provided sources for tool-making. Drinking and bathing water were permanently available. The crows were fed *ad libitum* on soaked cat biscuits (Go-Cat®), an insect and fruit mix (Orlux® Universal and Orlux® granules), peanuts, and mealworms. They were encouraged to use tools regularly by making some of their preferred food otherwise inaccessible: mealworms were placed in holes drilled into tree stumps, and occasionally pieces of pig heart were placed in clear Perspex tubes that were left in the aviaries.

Experimental room

Experiments took place in a separate testing room (2.00 × 2.80 × 2.50 m high), which was accessed from the main indoor aviary via two openings (160 × 180 mm high) adjacent to each other, controlled by four hanging "bob-wires" (although it was therefore possible to see into the testing room through the wires, baffles erected inside prevented birds seeing the table where experiments were carried out until they had entered the room). The bob-wires were light aluminium tubes (200 mm long × 5 mm diameter, supplied by Boddy & Ridewood, UK) with moulded-plastic T-shaped tops, suspended from a rail; birds could push through them in one direction but not in another. One opening had wires swinging into the testing room, for entering it, and one had wires swinging into the main aviary, for leaving the testing room. The bob-wires on the entrance could be locked by means of a custom-built system (designed and built by myself and Ben Kenward), involving a magnetically-latched solenoid that when inactive held a barrier across the bottom of the bob-wires preventing them from moving, but when activated retracted and moved the barrier so that the wires could swing freely. The exit had no locking mechanisms, so birds were free to leave the testing room whenever they chose. A red LED in the main aviary positioned above the entrance was switched on when the solenoid was activated, signalling that the entrance was open so birds could enter the room. By locking the entrance after a subject had entered the testing room, it was possible to test birds individually without having to capture them, and without trapping them in the testing room since they were always free to leave. For a period of several months before experiments began, the testing room had been regularly provisioned with favoured food (primarily pieces of pig heart, mealworms, and waxmoth larvae (waxworms)) to encourage birds to enter, and the bob-wires were introduced progressively (by pinning all but one open, etc.) to habituate them to pushing through.

This system had the advantage that, due to voluntary participation and free exit, it was possible to be fairly sure that subjects were sufficiently motivated and unstressed to participate in the experiment (as it is known that stress can impair cognition in experiments; e.g. de Kloet et al., 1999). The use of preferred rewards but not excessive food deprivation was also designed to keep motivation levels optimal, since it is known that both excessive and insufficient motivation can impair performance on problem-solving tasks (e.g. Birch, 1945). However, the entry / exit system also had the disadvantage that the experimenter could not control which bird from the group would enter, so for all trials Betty was either isolated in the indoor main aviary, or kept there with two birds that never entered the testing room.

The experimental apparatus were placed on a table (1.00 × 1.15 × 1.00 m high) in the centre of the testing room, which had one side against a dark Perspex window. The experimenter was on the other side of this window; with the lights on in the testing room and off on the experimenter's side, it was impossible (for humans) to see through the window from the birds' side. The window could be slid up to allow the experimenter to position apparatus and arrange tools between trials.

Apparatus

The apparatus consisted of the bucket and well described in Chapter 3. The tool provided was a thin strip of aluminium (Trials 1-16: 90 mm long × 3.5 mm wide × 1.0 mm deep [apart from Trial 3, when it was 120 mm long, and Trials 4-5, when it was 105 mm long]; Trials 17-34, 90mm long × 5.0 mm wide × 1.0 mm deep [apart from Trial 23, when it was 3.5 mm wide], supplied by the metal workshop in the Department of Zoology); the corners of the strip were cut off and filed down until they were rounded, to minimise the risk of injury to the subject. The tool could only be bent in one plane, due to its rectangular cross-section; for humans, it bent without requiring the application of much force (less than for the wire previously supplied), but it would be unlikely to bend as a result of non-directed manipulation. For Trials 1-19, the tool was placed on top of the tube, with one end facing the brick. From Trial 20, a wooden block (10 cm × 6 cm × 6 cm deep) was provided (fixed to the table), which had several holes of varying diameters drilled into it to facilitate bending (if Betty chose to insert the distal end of the tool into one of the holes), and from Trial 27 the tool was placed in the holes in the wooden block (now fixed inside the tray with the apparatus) at the start of the trial. A new tool was provided for each trial.

Procedure

No training was given, since Betty was already familiar with the apparatus (she had been presented with the apparatus and ordinary wire several times since the experiments reported in Chapter 3, although not in the 6 months preceding this experiment; she had, however, been presented with the apparatus and straight, rigid tools in the 3 weeks preceding this experiment, in the context of habituation of other crows to the apparatus). Trials were performed between 20 August 2004 and 28 February 2005. Normal food was removed from the aviary 1-2 hours before experiments began, and was replaced immediately after the end of trials. Outside the testing room, a small piece of pig heart (0.5 ± 0.1 g) and / or a waxmoth larva (the reward was varied to maintain motivation) was placed in the bucket, which was then dropped into the bottom of the tube. The tray containing the apparatus was placed on the experimental table, and the tool positioned as described above. The experimenter then unlocked the entrance bob-wires and switched on the LED. All trials were videotaped through the dark Perspex window using a mini-DV camcorder (Canon DM-MV550i or Canon XL1); the final shape of the tool was also videotaped against a standard background, and all modified tools were numbered and retained for later analysis.

Trials were terminated 10 minutes after the subject first interacted with the experimental apparatus (defined as picking up or dislodging the tool), or if the subject left the testing room (a “trial” was only scored if the subject interacted with the apparatus). 31 trials were carried out before starting Experiment 2, and an additional three trials after the first two trials of Experiment 3 (all 34 trials are included in the analysis here). Twelve trials took place on 20 August 2004, two on 23 August, nine on 25 August, three on 27 August, five on 14 September, and three on 28 February 2005; the variation in the number of trials on each day is primarily due to the voluntary participation, since on some days Betty entered the testing room more frequently than on others.

Scoring and analysis

All scoring was done from videotapes. Each trial was summarised descriptively, and the following measures were recorded:

- success (whether or not food was obtained)
- trial duration (length of time from first contact with apparatus to success, excluding time when the subject was not interacting with the apparatus or tool)
- duration of probing with unmodified tool (probing defined as the tool fully inserted into the tube)
- whether or not the tool was modified
- latency until first modification
- the method of modification
    1) location of modification
    2) end that was modified (proximal, i.e. the end held in the beak; middle of the tool; and distal, the end furthest from the beak)
    3) technique used to modify (either ‘twist’, where the tool was held at an angle part of the way along its shaft and twisted around the beak, or ‘bend’, where the tool was held at one end in line with the shaft, and bent by moving the beak up and towards the tool)
- length of time spent modifying the tool (‘tool crafting time’: defined as the length of time from the first moment I could see the tool bending until the last)
- the end of the modified tool first probed with
- duration of probing with each end of the modified tool
- whether and on how many occasions the tool was turned around
- the final shape of the tool (photographed), scored according the following criteria: if the resulting tool had a bend of more than 90° at least 1/3 of the way towards one end (and was not grossly distorted, e.g. helical or with a circle on the modified end), it was scored as ‘1’; otherwise, as ‘-1’.

To check for learning effects across and within days, latency and duration measures (in seconds) were log-transformed (0.1 was added to all values before transformation, to eliminate errors due to zero values) and used as the dependent variables in separate general linear models (GLMs), with day (a number from 1-5, labelling all trials carried out on the same day; date was not used, as the highly variable spacing between trials caused the analysis to be unreliable) and trial-within-day and the interaction between them as continuous explanatory variables. For example, to look for learning effects on trial duration, a model was fitted of ln(trial duration) = day + trial-within-day + (day * trial-within-day). Residual plots were visually inspected to check that the assumptions of normality of error, homogeneity of variance, and linearity were satisfied. Due to non-orthogonality, if the interaction was not significant the model was re-fitted without the interaction, and it is these results that are reported.

Additionally, a GLM was used to assess whether time spent probing with the modified tool (modified end only, successful trials only) was related to the hook 'score' (as a categorical variable), and a Spearman Rank Correlation was used to examine whether cumulative hook score increased across trials. The other measures are only presented graphically and not statistically analysed, since formal analysis would not be any more informative than visual inspection.

4.2.2 Results

Betty adapted quickly to the new material and succeeded in modifying it to retrieve the bucket. She retrieved the bucket on 25 of the 34 trials using the new tool; out of the 9 trials scored as failures, in 3 she did retrieve the bucket using a twig tool she brought into the testing room with her, rather than the metal strip. In the remaining 6, she dropped the metal strip irretrievably into the tube or behind a brick. She developed a completely different technique for modifying the new material: she either twisted or bent the *proximal* end of the tool (i.e. the end held in her beak), whereas with wire she usually bent the *distal* end of it by levering it around the tube or other objects. Her general performance and detailed modification of the tool are discussed in the next two sections (her behaviour in each trial is described in Appendix 4, and the photographs of the final shape of each tool she modified are shown in Appendix 5).

Overall performance

Betty first modified the tool and successfully retrieved the bucket with it on Trial 3, and thereafter modified it on all but two trials (Figure 1(a)). However, on only six trials did she modify the tool before using it. The latency until she started modifying the tool and the length of time she probed with the unmodified tool dropped by a factor of 10 between

Trials 3 and 4 (Figure 1(b)). The latency before modifying the tool decreased significantly both across days and across trials within days, but the interaction between day and trial was not significant (day: $F_{1,27} = 9.29$, $p = 0.005$; trial within day: $F_{1,27} = 11.00$, $p = 0.003$; day*trial: $F_{1,26} = 2.50$, $p = 0.126$). The same was true for the duration of probing with the unmodified tool (day: $F_{1,27} = 36.38$, $p < 0.001$; trial: $F_{1,27} = 25.43$, $p < 0.001$; day*trial: $F_{1,26} = 0.06$, $p = 0.803$). This means that in general, at the start of each day's trials Betty probed for longer with the unmodified tool and started modifying it later than she did at the end of that day's trials, but both measures decreased as the experiment progressed. In total, there were only six trials where Betty probed for longer than 10 seconds with the unmodified tool, and the median duration of such probing was 3 seconds (mean = 12.2 ± 5.4 seconds S.E.). Frequently, she did not actually make contact with the handle of the bucket in these probes – it often appeared as if she was looking into the tube (while holding the tool), rather than actually probing for the bucket (see detailed descriptions for each trial in Appendix 4).

There was an interaction between the time to bucket retrieval (Figure 2(a)) across days and within days (day*trial: $F_{1,20} = 4.85$, $p = 0.040$, successful trials only), which was due to the fact that on the first day, the time to success fell very steeply with trial number, whereas on the other days it showed no trend. This effect was dependent on Trial 3: excluding this trial, the interaction was not significant (day*trial: $F_{1,19} = 2.86$, $p = 0.107$), and the model without the interaction showed that trial duration fell across days and within days (day: $F_{1,20} = 6.15$, $p = 0.022$; trial: $F_{1,20} = 5.10$, $p = 0.035$).

The 'tool crafting time' (Figure 2(b)) also decreased across days, but not within days, and there was no interaction (day: $F_{1,27} = 17.13$, $p < 0.001$; trial: $F_{1,27} = 0.49$, $p = 0.489$; date*trial: $F_{1,26} = 2.22$, $p = 0.148$).

Betty only started consistently turning the modified tool around before using it from Trial 11 (Figure 3(a)); since she primarily modified the proximal end of the tool, this means that for the previous 7 trials she initially probed with the unmodified end. The duration of probing with the unmodified end of the tool (Figure 3(b)) appeared to decrease up to the point where she started consistently turning the tool around, but the number of trials with non-zero durations is too small for statistical analysis. Across all 34 trials, she turned the tool around from holding the modified to holding the unmodified end on 30 occasions, whereas she turned it the other way only twice (and on four occasions she turned the unmodified tool around). Note that comparisons of the direction of tool turnarounds are of questionable interest, because Betty generally started by holding the modified end, since it was the proximal end that usually bent.

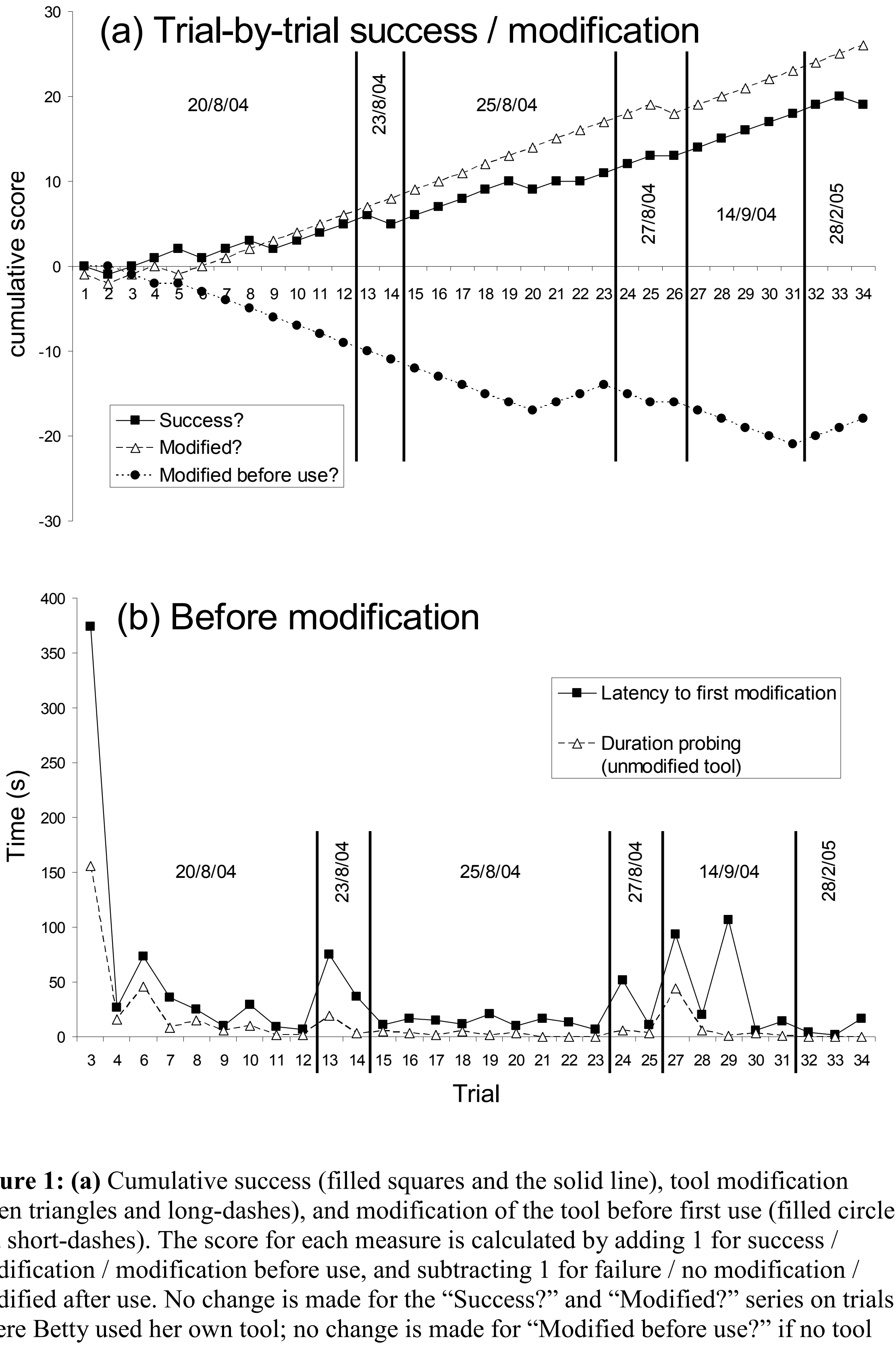


Figure 1: (a) Cumulative success (filled squares and the solid line), tool modification (open triangles and long-dashes), and modification of the tool before first use (filled circles and short-dashes). The score for each measure is calculated by adding 1 for success / modification / modification before use, and subtracting 1 for failure / no modification / modified after use. No change is made for the "Success?" and "Modified?" series on trials where Betty used her own tool; no change is made for "Modified before use?" if no tool was modified. Vertical lines and annotations show the date the trials were carried out. The graph shows that Betty started being consistently successful and modifying the tool from Trial 3, but very rarely modified the tool before use. **(b)** Duration of probing with the unmodified tool (open triangles and long-dashes), and the latency (measured from first touching the apparatus) until Betty modified the tool (filled squares and the solid line), for

each trial. Vertical lines and annotations show the date the trials were carried out. Note that this graph only includes trials where the tool was modified (so there are 30 trials in total). The graph shows that both duration of probing with the unmodified tool and latency until modification dropped by a factor of 10 between Trials 3 and 4; both measures continued to fall within and between days (see text for details).

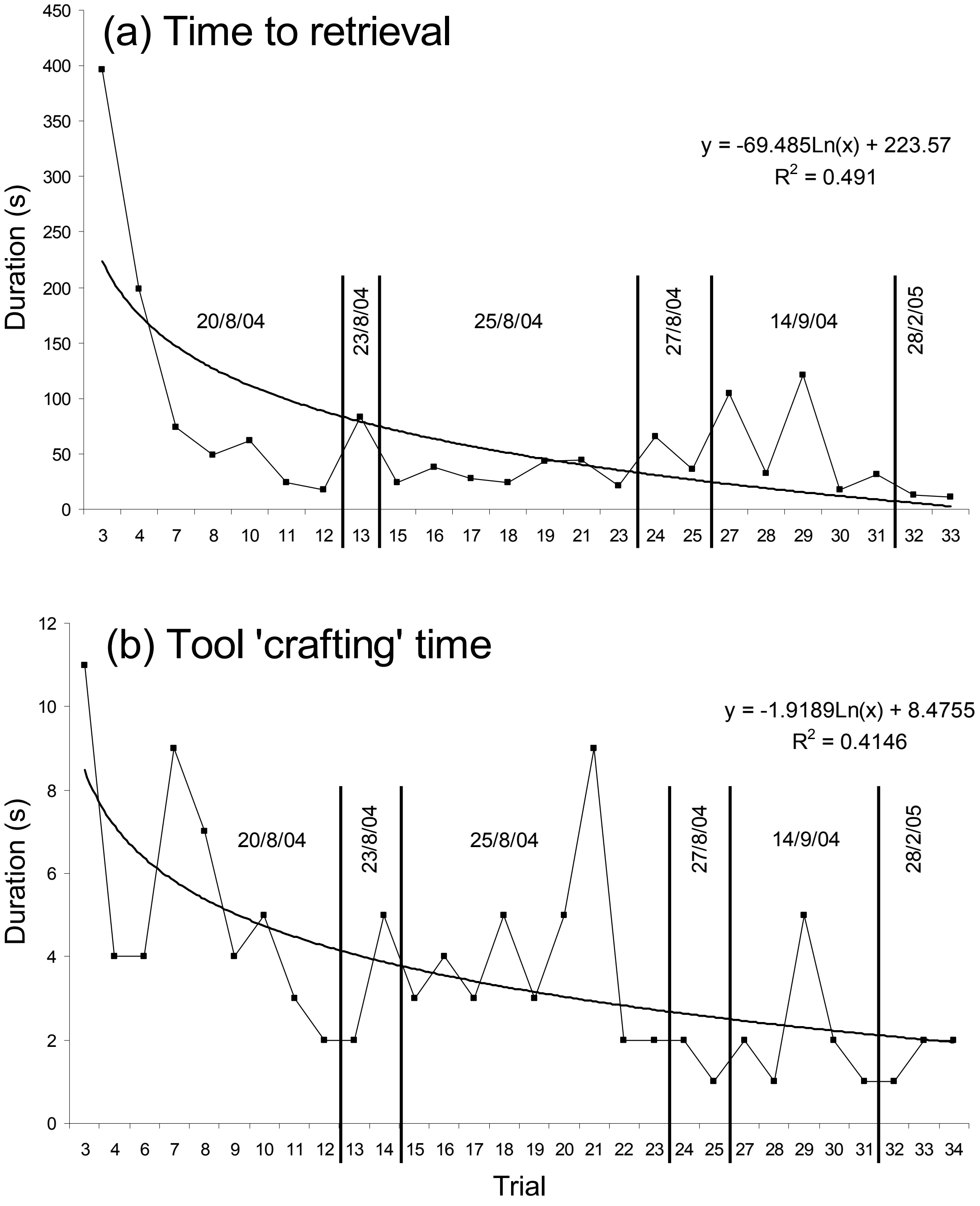
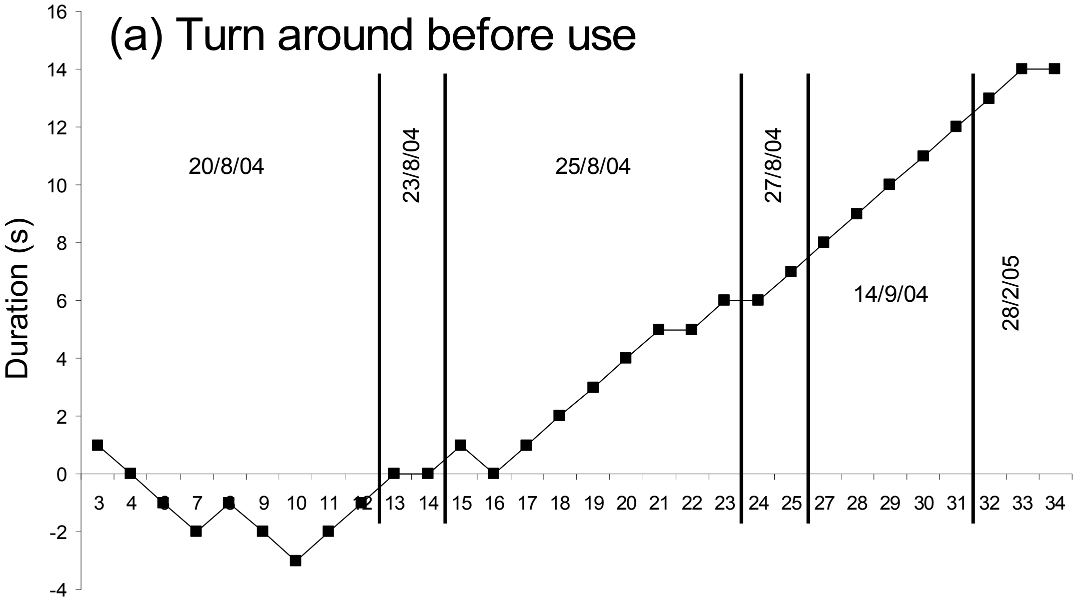


Figure 2: (a) Duration of successful trials in Experiment 1. A logarithmic trend line is fitted, and the equation and R^2 value are shown on the graph. Vertical lines and annotations show the date the trials were carried out. Note that since only successful trials are included, there are only 24 trials displayed. Trial duration fell significantly both across days and within days (see text for details). **(b)** Length of time Betty spent modifying tools in Experiment 1. A logarithmic trend line is fitted, and the equation and R^2 value are shown on the graph. Vertical lines and annotations show the date the trials were carried out. Note that only trials where Betty modified the tool are included, so only 30 trials are displayed. Modification duration fell significantly across but not within days (see text for details).



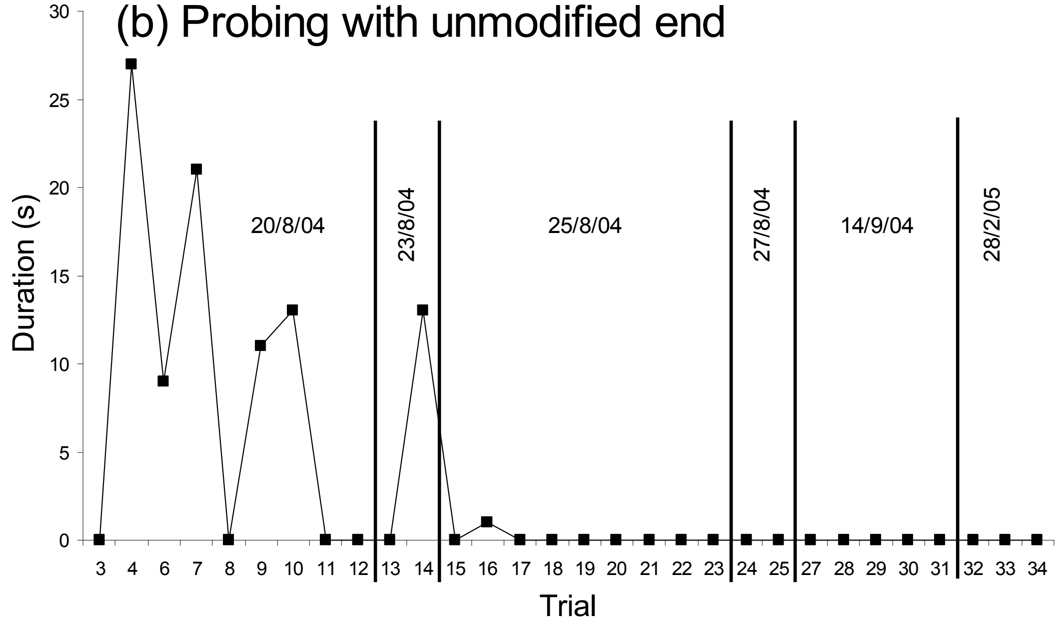


Figure 3: (a) Cumulative turning around the modified tool before using it. The score is calculated by adding 1 for each trial where Betty turned around the tool before using it, and subtracting 1 for each trial where she used the unmodified end first (no change is made for mistrials or trials where the tool was bent in the middle or at the distal end). Vertical lines and annotations show the date the trials were carried out. Note that only trials where a tool was modified at the proximal end are included, so only 30 trials are shown. After modifying the tool, Betty started to consistently turn it around before using it from Trial 11. **(b)** Duration of probing with the unmodified end of the tool (after modification). Vertical lines and annotations show the date the trials were carried out. Note that only trials where a tool was modified at the proximal end are included, so only 30 trials are shown. The duration of probing with the unmodified end appears to fall between Trials 4 and 17 (see text for details).

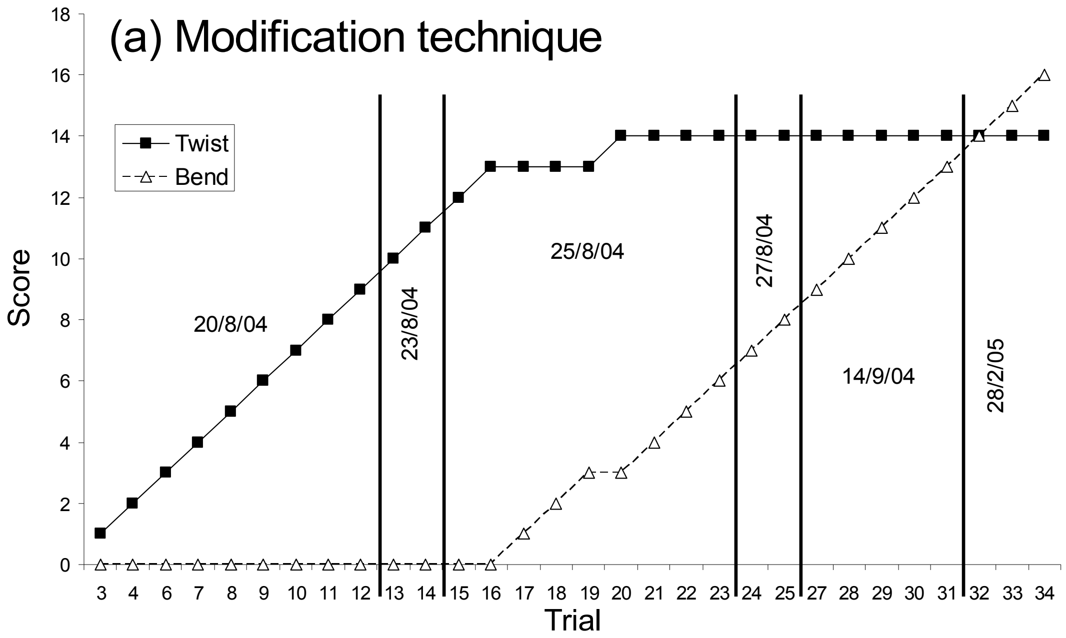
Details of tool modification

The first time Betty modified the new tool (on Trial 3) is of the most interest in terms of how she reacted to this new material (see Supplementary Movie 4-1). As described in Appendix 4 Table 1, she probed 9 times for the bucket with the unmodified tool (raising it almost all the way to the top of the tube once, and half-raising it several times), often poking the tool at the base of the tube in between probes (anthropomorphically, it sometimes looked as if she was ‘trying’ to insert the tool into the Gaffa tape the way she did with the wire previously, but since the metal has a larger cross-sectional area it did not puncture the tape). Over time these pokes seemed to become more vigorous, possibly as a result of frustration, and consequently after 3.5 minutes the tool bent slightly in the middle, although the bending itself did not seem ‘deliberate’. She carried on probing for the bucket and poking the tool at the Gaffa tape (once causing it to bend slightly more again) until 6.25 minutes into the trial, at which point she again poked the distal end against the Gaffa tape, but this time grasped the proximal end nearer the middle of the tool with her beak slightly sideways, and twisted her head so the metal bent around her beak (see Figure 4(a-f)). This is an action she had never performed with the wire, and did not perform on any of the previous ‘pokes’ in this trial. It caused the wire to twist into a large loop (see tool 3 in Appendix 5), which she then picked up (by the modified end) and proceeded to drop into the tube. Thanks to the loop she could still reach it, and picked it out of the tube, dropped it onto the tray, and picked up again by the unmodified end, and used the looped end to retrieve the bucket.

It is also interesting to see how she behaved on the trial immediately after first modifying the tool. On Trial 4, she probes twice (for 16 seconds) with the unmodified tool, and then pokes the end of the tool against the Gaffa tape and does a twisting head movement as in Trial 3. This does cause the tool to twist a little, but perhaps because the distal end was not so firmly wedged, the bend is far less than in the previous trial. She carries on probing with the unmodified end for almost 30 seconds, interspersed with another poke-twist movement, before turning the tool around and probing a further 7 times (for 1.5 minutes) with the modified end, interspersed with three poke-twist episodes, none of which were particularly effective. She eventually succeeds in getting the bucket, but the final tool is not modified very much from the original, and the modification attempts were clumsy and did not appear to be precisely controlled.

Figure 5(a) shows how Betty's modification technique changed across trials. From the figure, it seems that from Trial 17 she suddenly switched to using a 'bend' technique (e.g. Trial 32, shown in Supplementary Movie 4-2), rather than a 'twist' one, but it appears from the video footage that this was in fact a gradual transition: from Trial 12, she began to twist her head sideways less, and instead started pushing the tool away from her while raising the end of her beak, resulting in a bend rather than a twist. The effect of the different techniques is apparent in the final tool shapes (Appendix 5). Figure 5(b) shows how the 'score' (see 'Scoring and analysis' above) of the resulting tool shape changes across trials. A Spearman Rank Correlation across all trials shows that hook score does significantly increase ($r_S = 0.718$, $p < 0.001$), although from visual analysis it seems that apart from a period from Trials 10 to 13, she only started making consistently 'good' hooks from Trial 27. However, my score of how good a hook is does not necessarily correspond to what is functionally best: Betty was able to retrieve the bucket with almost all of the tools she made, regardless of how good they seem to us, and there is no relationship between hook score and time spent probing with the hook (GLM ln(time probing) = hook score, with Trial 4 excluded because it is 4.5 standard deviations away from the mean; $F_{1,21} = 0.35$, $p = 0.562$).

Figure 4(a-f): Stills from the movie of Trial 3 of Experiment 1, showing the moment Betty first ‘deliberately’ bent the new tool (using the “wedge-twist” technique). In (a)-(b) she moves her grip on the tool further down its shaft, and then in (c)-(d) she twists her head around, bending the tool in the process. In (e)-(f) the resulting bend in the tool is visible.



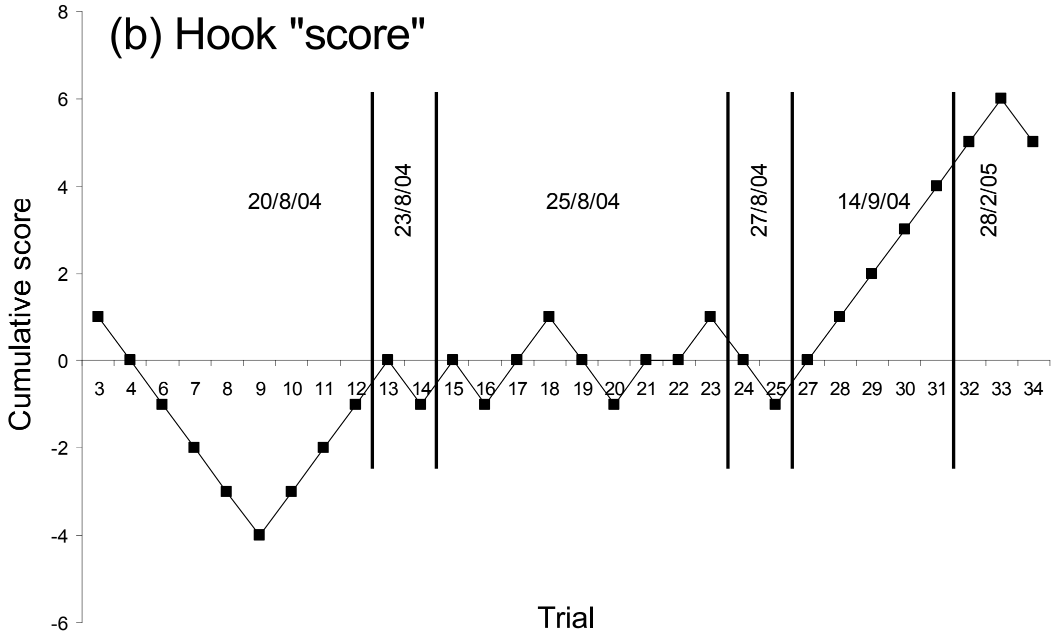


Figure 5: Betty's modification technique. **(a)** Cumulative use of the two modification techniques (only trials where the tool was modified). Filled squares and the solid line show use of the "twist" technique, while open triangles and the dashed line show use of the "bend" technique. 1 is added to the 'score' for use of the technique, while the score remains the same when the technique is not used. Note that although the techniques are analysed as separate categories, they are likely to have formed a continuum. **(b)** Cumulative hook shape 'score', by trial (only trials where the tool was modified). The score increased by one if the hook on that trial met the criteria mentioned in the Methods section, and decreased by one if the tool did not fulfil these criteria.

4.2.3 Discussion

From the third trial with the new material, Betty began to modify the aluminium strips, and was generally successful at retrieving the bucket. Are there any aspects of her behaviour that shed light on what she 'understood' about the causal features of the task?

The most striking result is the large drop in the latency until she modified the tool, and in the duration of probing with the unmodified tool, between Trials 3 and 4. Such sudden and large changes in performance have been attributed to 'insight'-like processes (e.g. Köhler, 1925; but see Spence, 1938), although a more likely explanation in this situation is simply that Betty had initially not 'discovered' that the new material was pliant, nor the best way to modify it. This conclusion is borne out by detailed analysis of her behaviour on the first trial involving modification: before successfully bending it, she repeatedly 'poked' the tool at the tape at the bottom of the vertical tube, which is the location where she most frequently bent the wire in previous experiments, but due to its larger cross-sectional area it did not poke through the tape and become wedged, as happened with the wire. Having discovered that the new material can be modified, she was subsequently much quicker to attempt to manipulate it (although note that on Trial 4 she modifies it much less effectively than on Trial 3 – and consequently it takes her far longer to retrieve the bucket with the modified tool than on any other trial).

Once she had learned about the properties of the new material, was her behaviour consistent with 'instant' understanding and appropriate behaviour thereafter? Two lines of evidence suggest not. Firstly, although the time she spent probing with the unmodified tool rapidly decreased across trials, she still nearly always attempted to probe for the bucket before modifying the material. However, this does not necessarily imply a lack of understanding, because there might be a cost (e.g. effort or discomfort) to modifying it, and she was once successful with the unmodified tool, so she might have perceived it as being 'worthwhile' probing without the hook. Secondly, for 5 of the first 7 trials (where she modified the tool) her first probes after bending the tool were with the unmodified end of it, probably because the new material generally bent at the *proximal* end (i.e. the end held in her beak), rather than the distal end like the wire. The duration of these probes dropped rapidly during these trials, and from Trial 11 she consistently turned the tool around before using it.

Was her behaviour, therefore, consistent with a complete lack of ‘understanding’, and suggestive solely of associative learning? Again, the results appear to suggest otherwise. Firstly, she learned very quickly how to effectively modify the tool, even though she had to use completely different techniques from with wire. In fact, from the sixth trial onwards, she only once spent more than 5 seconds modifying the tool. In addition, the ‘hook-ness’ of her tools rapidly improved and became more regular (see Figure 5(b) and Appendix 5), although even towards the end of the experiment there were the occasional malformed ones. This is despite the difficulty of modifying this kind of material with a beak as her only manipulative appendage, and the fact that the modification techniques she used are completely unlike any used by wild crows, or by Betty in other circumstances. As argued earlier, such rapid acquisition would be highly unlikely to occur in an agent reliant solely on associative learning, and if anything Betty’s previous experience with wire should have retarded the speed with which she learned about this new material, due to interference (e.g. Wilson et al., 1985).

How can we resolve the apparently conflicting results, suggesting that she both does and does not ‘understand’ the task? One possibility is that she understands *aspects* of the task, but not the entirety of it. In terms of the questions raised earlier, it seems that she did understand the relationship between her actions and the resulting tool shape, since she was able to devise entirely novel modification techniques very rapidly. It also seems that she understood (or had previously learned) that she needed hook-like shapes for the task, since she fairly consistently produced suitable shapes from the fourth trial (of those where she modified the tool). It is not clear how to work out a ‘null hypothesis’ for the likelihood of producing hook-like shapes versus all other shapes from random manipulation of the material, but just from the diversity of shapes Betty produced it is clear that there are several possibilities (and many more that she never made, and which would not even have fitted into the tube), yet she produced far more of the hook-like tools than the others. However, it appears that perhaps she does not understand *why* she needs a hook: it is very difficult to explain why she would ever probe with the wrong end of the tool after modifying it – which she sometimes did for over 10 seconds. She quickly learned to turn the tool around after modifying it (which, incidentally, she only did 4 times with unmodified tools, suggesting that she recognised it was only worthwhile turning around modified tools), but an agent who truly understood *why* they needed a hook should never probe with the wrong end of the tool.

4.3 EXPERIMENT 2: UNBENDING FOR TOOL SHAPE

This experiment began after Trial 31 of Experiment 1, so Betty was now very familiar with the aluminium strips and how to manipulate them. It tested whether, if presented with the tool bent at both ends and a task that required the tool to be inserted through a narrow hole, Betty would spontaneously modify the tool to allow it to fit through the hole.

4.3.1 Methods

Apparatus

The apparatus was one Betty was already familiar with from experiments by Stephen Barlow (unpublished) into selection of tool shape. The task was similar to that described in Chappell & Kacelnik (2004): to retrieve food, a tool had to be pushed through a small hole in the horizontal arm of the apparatus, which would push the food bucket along the tube and allow it to fall out of a vertical pipe. The apparatus was made from 5cm diameter Rotastack® components made for pet rodent housing (see Figure 6a). The tubing formed a 'cross' shape; the upper arm and one of the horizontal arms of the cross were blocked by solid (red) end-caps; the other horizontal arm had a (red) end-cap with a hole (7 mm diameter) drilled into it; for Trial 3, the vertical arm had an open semi-transparent section of tubing attached to it (as shown in Figure 6a). The reward (a small piece of pig heart or a waxworm, as in Experiment 1) was placed in a small plastic cup, which was positioned inside the horizontal arm of the apparatus, behind the end cap with a hole in.

The tool was a strip of aluminium (90 mm long × 5 mm wide × 1 mm deep) similar to that described in Experiment 1. Both ends of the tool were bent into small hooks (referred to hereafter as a "double-H" shape) using the body of a board marker (15 mm diameter) as a template; in its modified form, the tool was 60 mm long (see Figure 6b), and the hooks on each end prevented it from fitting through the hole in the end-cap (above). The tool was placed on top of the wooden block described in Experiment 1, which was fixed to the table about 30 cm from the front of the apparatus.

Procedure

The apparatus above was presented with unmodified, straight strips of aluminium in an experiment to familiarise other New Caledonian crows to the aluminium strips (Weir, unpublished data). As a result of the lack of control over which individual entered the testing room (see ‘Experimental room’, above), Betty had had 11 trials with the apparatus and straight tool before it was first presented in a bent form. These can be considered as training trials, although she had already had many trials with the apparatus and other (rigid) tools. On every training trial, she just picked up the tool and poked it through the hole, retrieving the food within seconds of the trial starting.

Food deprivation, rewards, and participation of the subject were as described for Experiment 1. The apparatus was prepared outside the testing room, and positioned on the experimental table before the subject was allowed to enter. All trials were videotaped as before. Trials were terminated 10 minutes after the subject first interacted with the experimental apparatus, or if the subject left the testing room (a “trial” was only scored if the subject interacted with the apparatus). Only three trials were carried out, for reasons that will become apparent from the results; all took place on 14 September 2004.

Scoring and analysis

All scoring was done from videotapes. Each trial was summarised descriptively, and only informal analysis was carried out, since only three trials were performed.

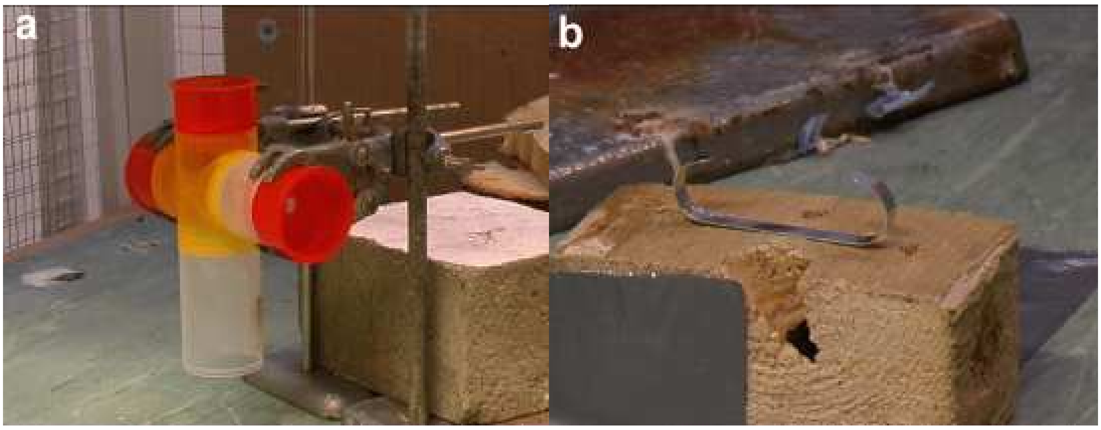


Figure 6: Equipment setup for Experiment 2. **(a)** The apparatus for the experiment; the food bucket (not visible) is in the horizontal arm facing towards the camera, just behind the red end-cap with the hole in. When a tool is inserted through the hole in the end-cap, the bucket gets pushed along the horizontal tube and falls out of the vertical one. **(b)** The tool for Experiment 2, positioned on a wooden block with holes drilled in to facilitate bending / unbending. The tool is a similar strip of aluminium to that used in Experiment 1, except that the both ends have been bent into small hooks. Without modification, the tool will not fit through the hole in the end-cap of the apparatus.

4.3.2 Results

Betty successfully retrieved the food on all three trials (described individually in Appendix 4 Table 2). This shows that on the first trial Betty got the food without using a tool at all. In the second and third trials, she did modify the tool by squeezing together one (Trial 2) or both (Trial 3) ends of the tool, effectively making it straight. On Trial 2, she used the unmodified (so still hooked) end to retrieve the food bucket by probing up the vertical arm, from underneath the apparatus. Consequently, in Trial 3 a semi-transparent vertical tube was added to vertical arm, to prevent this behaviour. In this trial, she tried once (for 4 seconds) to insert the unmodified (hooked) end of the tool through the hole to dislodge the food cup, and then immediately turned the tool around (modifying the other end in the process of picking it up) and poked the flattened end through the hole, dislodging and thereby retrieving the food.

4.3.3 Discussion

Betty quickly got the food in all three trials. Trial 3 was the only one where she performed the task as designed, and on it she obtained the food by squeezing together both ends of the tool and inserting one end through the hole in the end-cap, thereby solving the problem of "spontaneously modifying the tool to allow it to fit through the hole". However, this modification happened as a result of picking up the tool, as demonstrated by Trial 2 (when she did not need to modify the tool, but did so nonetheless). Moreover, she initially probed with the *unmodified* end of the tool on Trial 3, although she very quickly turned the tool around and used the modified end correctly.

In summary, these three trials do not provide evidence that she understood the task requirements and specifically modified the tool as a consequence. However, they also do not rule out this possibility. While probing with the 'wrong' end of the tool seems to indicate lack of comprehension, the duration of the probe was so short that it could be interpreted as Betty instantly 'understanding' that it would not fit. Turning it around is obviously the appropriate response; note that she did not turn around the tool in the other plane (i.e. rotate it around the axis of the tool shaft), as she has done in other tasks (when it is often appropriate; Chapter 3), nor did she repeatedly try to use the incorrect end. It is also informative to compare Betty's performance with Povinelli's chimpanzees tested on a similar tool insertion problem, given tools that had a straight end (that could be inserted into the apparatus) and an end that could not be inserted (two different designs). All of their subjects showed a strong preference for attempting to insert the “impossible” ends of the tools, and very rarely turned the tools around (Povinelli et al., 2000c, Experiment 12): out of 56 trials (8 per subject, 7 subjects), subjects only succeed in getting the food 3 times (despite many successful trials using straight tools previously). As mentioned in the ‘Introduction’, the chimpanzees had a similar preference for probing with the impossible end of the tool in experiments 25-26 (Povinelli et al., 2000b), although there they do appear to have turned the tools around more frequently (the number of reorientations is not explicitly presented, but 69 / 64% [Experiment 25 / 26 respectively] of first attempts were with the impossible end, yet the chimpanzees were successful on 61 / 80% of trials). In this context, Betty’s response of turning the tool around almost instantly seems impressive, even if not equivalent to a human-like understanding.

4.4 EXPERIMENT 3: UNBENDING FOR TOOL LENGTH

This experiment began after Trial 3 of Experiment 2. It tested whether, if presented with the tool bent into a broad U-shape (so that the ends would not pinch together when she picked it up) and a task requiring food to be raked out a horizontal tube, Betty would spontaneously modify the tool to make it longer and allow her to retrieve the food.

4.4.1 Methods

Apparatus

The apparatus was a horizontal tube made from clear Perspex (30 cm long, 4 cm diameter), mounted in a wooden stand with the centre of the pipe 12 cm high above the table (identical to that used in Chappell & Kacelnik, 2002). A piece of pig heart was placed inside the tube (10 cm deep for Trial 1, 13 cm deep for Trials 2-4).

The tool was a strip of aluminium (90mm long × 5.0 mm wide × 1.0 mm deep) similar to those used in experiments 1 and 2, bent into a broad U-shape. In Trial 1, the ends of the U were 2.5 cm apart (and almost parallel to each other – the angle between them was just 5°), and the tool was 4 cm long from the ends to the apex of the U-bend. Due to the results of Trial 1, the U-bend was made broader for Trials 2-4: the ends were now 5.5 cm apart (with an angle between them of 62°), and the tool was 3.4 cm long from the ends to the apex of the U-bend. The tool was placed on the wooden block with holes, as described for Experiment 1, which was fixed to the table about 30 cm from the opening of the tube.

Procedure

No training was given, since Betty was already familiar with the apparatus and tool (in its unmodified form). Food deprivation, rewards, and participation of the subject were as described for Experiment 1. The apparatus was prepared outside the testing room, and positioned on the experimental table before the subject was allowed to enter. All trials were videotaped as before. Trials were terminated 10 minutes after the subject first interacted with the experimental apparatus, or if the subject left the testing room (a “trial” was only scored if the subject interacted with the apparatus). Four trials were carried out: two on 14 September 2004 and two on 28 February 2005. To ensure Betty was still familiar with the properties of the tool on the second two trials, she was given three trials with the straight tool and well/bucket apparatus immediately beforehand (see Experiment 1).

Scoring and analysis

All scoring was done from videotapes. Each trial was summarised descriptively, and only informal analysis was carried out, since only four trials were performed.

4.4.2 Results

Betty successfully retrieved the food on 3 of the 4 trials (described individually in Appendix 4 Table 3). On the first trial, Betty managed to squeeze together the ends of the tool to create a flattened, straight tool 4.5 cm along (Figure 7 tool 1). Although the meat was 10 cm inside the tube, she just managed to reach and retrieve it by inserting her entire head and some of her neck into the entrance to the tube. For this reason, the U-shape was made broader and the meat positioned further inside the tube for Trials 2-4.

On Trial 2, Betty tried persistently to get the reward by probing inside the tube with the U-shaped tool (for 1.5 minutes), but did not succeed and never showed any ‘deliberate’ attempt to modify the tool (although, presumably as a result of repeated probing attempts inside the tube, at the end of the trial the tool was broader than at the beginning: the ends were now 7.5 cm apart, with an angle between them of 75°; see Figure 7 tool 2). On Trials 3 and 4, however, Betty did manage to get the reward as a result of modifying the tool.

Both trials involved a similar modification technique, which occurred several minutes into the trial: in the middle of a bout of probing in the tube, she raised her head and beak (still holding one end of the tool) in a very noticeable manner, causing the shaft of the tool to bend backwards against the lip of the tube (see Supplementary Movies 4-3 and 4-4). On Trial 3 this resulted in a bend backwards of ~40° (Figure 7 tool 3) and a tool 8.5 cm long, while on Trial 4 it was ~25° (Figure 7 tool 4) and 8.0 cm long. It is hard to judge whether the behaviour was 'deliberate', but it is not an action I have ever seen her perform with other tools, or with these tools on other occasions. On both trials she was then (just) able to get the meat with the tools.

Unfortunately, Betty died before I was able to complete any more trials; I was planning to continue with this experiment, and also to introduce a new apparatus to overcome the possibility that unbending occurred purely as a consequence of using the tool. These experiments will now be performed with other subjects.

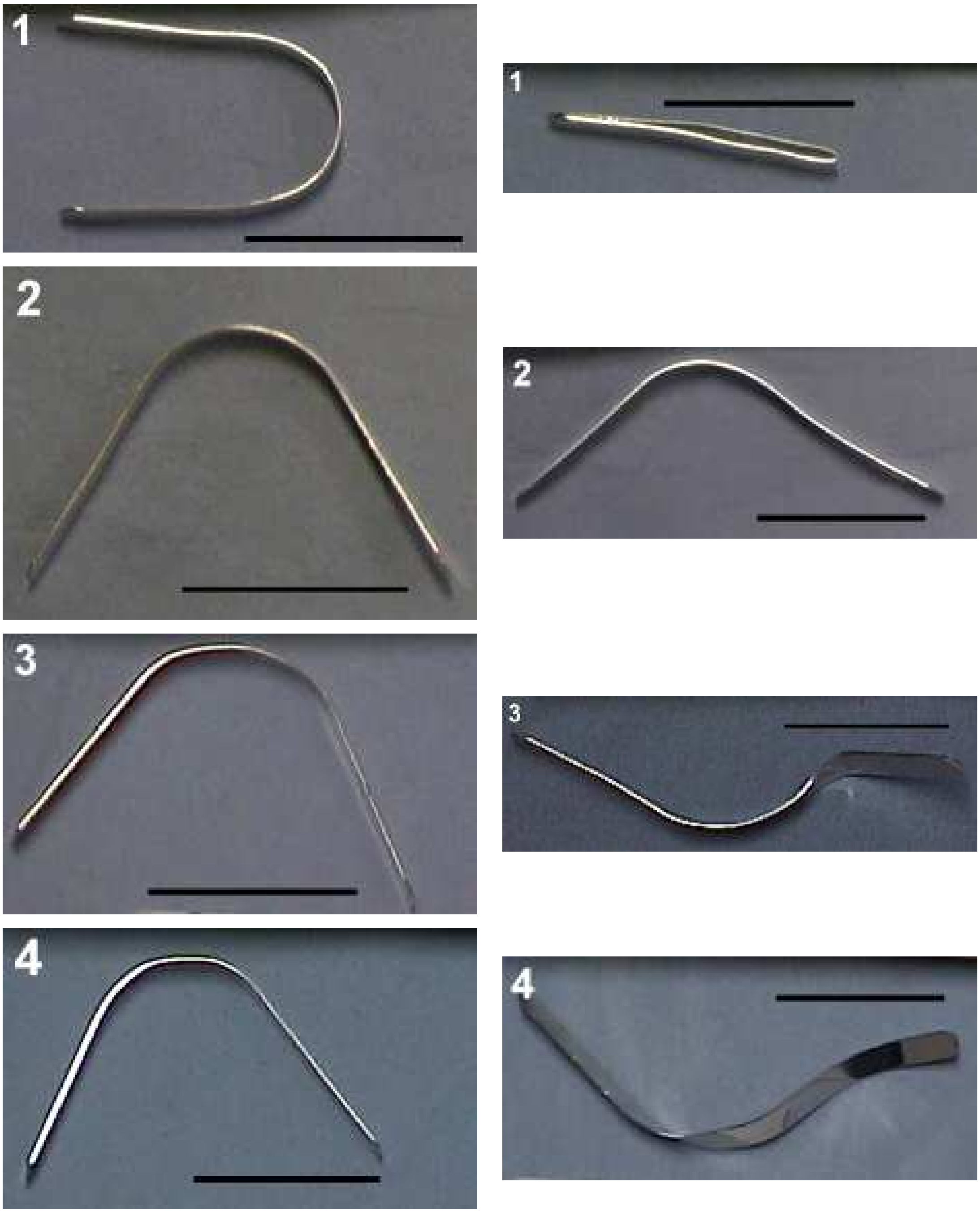


Figure 7: Before (left) and after (right) tools from Experiment 4. The number in the top corner shows the trial, and the scale bar is 3 cm.

4.4.3 Discussion

Betty again managed to get the food on 3 of the 4 trials, and as often is the case, on one trial solved the task in an unforeseen manner! Does her performance shed any light on her ‘understanding’ of the problem?

Trials 3 and 4 are particularly interesting: she did modify the tool in an appropriate manner, and the modification may have been ‘deliberate’ in the sense that the action is not one she has performed before. Moreover, she never modified the tool by bending or twisting it (and never appeared to attempt to), which were actions associated with success in Experiment 1 – so as a minimum she must have recognised that those behaviours would have been inappropriate. However, if she did ‘understand’ that the tools were not long enough in the original form, and she knew how to modify them, it is puzzling that she probed for so long with the unmodified tools (particularly since she probed for longer with the unmodified tool in Trial 4 than Trial 3, although she had already experienced the result of the modification). Again, her behaviour was not consistent with a complete understanding of the situation, but was also not random.

Here too, it is interesting to compare her performance with Povinelli’s chimpanzees (see ‘Introduction’ for a description of the experiments and overall results; the unbending experiments by Klüver (1937) and Anderson & Henneman (1994) are not reported in enough detail for comparison). In the first 56 test trials (7 subjects, 8 trials per subject) where they had to modify the tool to succeed, there were 7 instances where the tool was modified, but either the modification did not straighten the tool sufficiently, or the tool was not used appropriately after modification; no subject was successful in retrieving the reward. After explicit training in bending (note: not unbending) the tool out of the experimental situation, one subject (Jadine) did successfully modify and use the tool appropriately (although she still directed the unmodified end at the apparatus on one trial). There are many differences between the situation for the chimpanzees and Betty that make direct comparison impossible (including a different task (unbending for length rather than width); different material; different apparatus; and different species, with very different manipulative appendages and abilities!), but it is interesting to note that Betty’s modifications occurred after far fewer trials than Jadine’s, and without any explicit training by the experimenter. However, Betty had had extensive experience modifying the material for other tasks, which might have put her at a considerable advantage.

4.5 GENERAL DISCUSSION

These experiments aimed to delve deeper into the question of what Betty understood about hooks and tool shape, as revealed by Chapter 3. In particular, they asked how she would adapt to the introduction of a new material with different mechanical properties, and whether she would modify it in different and specific ways when faced with tasks that required different tools. In all three experiments, Betty had a high level of overall success (she only failed to get the food on 7 of 41 trials), adapted very quickly to the new material, and was able to modify the tools in different ways depending on the task requirements. However, examination of the details of her performance showed that it was neither consistent with a full, human-like understanding of the task, nor with what we would expect from purely following a series of procedural rules learned through trial-and-error. There are three general points I would like to make from these results.

Firstly, does the fact that Betty does not behave in the way we imagine we would necessarily mean that she does not understand the task? Although our logic tells us compellingly that we would never probe with the wrong end of the tool, a recent experiment has (re)emphasized the fallibility of intuition and introspection for making such assessments. Silva and colleagues (Silva et al., 2005) presented adult humans with both a physical and a schematic 'trap-tube' task, which has frequently been used to assess means-end understanding in non-human primates (as reviewed in Chapter 1). In this task, subjects are presented with a horizontal transparent tube containing a reward, with a 'trap' in the middle: if the food is pushed (or pulled) incorrectly, it falls into this trap and the subject cannot retrieve it. One of the critical tests for whether the subjects have learned about the causal properties of the task has been how they respond when the tube is inverted, so the trap is now oriented above the tube and therefore functionless: the argument has been that if they 'understand' gravity, they should no longer avoid the trap, but should start to insert the tool randomly with respect to the food/trap position, but most non-humans continue to avoid the trap (e.g. Reaux & Povinelli, 2000; Visalberghi & Limongelli, 1994). However, this assumption had never been tested with adult humans, who certainly should understand the causal basis of the task. In Silva and colleagues' experiments, the humans continued to avoid the inverted trap (36 / 40 trials in Experiment 1, 88 / 96 trials in Experiment 2), even though they reported that they understood that it was no longer effective. As Silva *et al.* point out, it is therefore critical to explicitly test how humans perform on tasks before interpreting a non-human animal's failure as evidence for lack of understanding. Therefore we should not be too hasty in concluding that, for example, initially using the wrong end of the tool after bending it necessarily implies that Betty did not 'know' what she should have been doing.

Secondly, regardless of how well humans would perform on the tasks, how does Betty's behaviour compare to other non-human animals' in comparable tasks? As already discussed, there are relatively few such experiments, but the most similar are those conducted by Povinelli's group (Povinelli, 2000). Compared to their chimpanzees, Betty seems to have learned more quickly and been generally more successful. It is impossible to rule out non-cognitive explanations for this disparity (such as previous experience, motivation, and task differences), but it is nonetheless interesting that she seems to outperform humans' closest relatives, who are often considered to be the most intelligent non-humans. Since tool use develops spontaneously in isolation-reared New Caledonian crows (Chapter 6), shows suggestions of being genetically well-canalised (Kenward et al., in press – Appendix 6), and is very widespread in the wild (Hunt & Gray, 2002, 2003), it may be that these birds have specific cognitive adaptations that make them particularly good at learning and possibly reasoning about physical tasks (we do not yet know how they perform on non-tool cognitive tests). In contrast, tool use in chimpanzees may be a product of more general learning processes, since it seems to be strongly culturally influenced (Whiten, 2005; Whiten et al., 1999, 2001; Whiten et al., 2005), and takes a long time for individuals to learn (Biro et al., 2003; Hirata & Celli, 2003; Lonsdorf, 2005; Lonsdorf et al., 2004).

Finally, what kind of model of cognition is suitable for explaining Betty's behaviour? Questions about understanding are frequently posed as all-or-nothing: either the subject fully understands the causal nature of the task (the "high-level model", in Povinelli's terminology), or is simply following procedural rules, with no causal understanding at all. This is also expressed in terms of whether or not subjects "seek explanations" (Povinelli & Dunphy-Lelii, 2001; Reboul, 2005; Vonk, 2005), or possess 'natural' (or 'strong') *versus* 'arbitrary' (or 'weak') causal knowledge (Kummer, 1995; Premack, 1995). However, the possibility that there may be a continuum seems rarely to have been considered (but see Hurley, 2003; Sterelny, 2003). Everyone is agreed that causal inference, even in humans, is based upon factors such as the spatiotemporal contiguity of cues, their priority, and their consistent conjunction (e.g. Castro & Wasserman, 2005; Dickinson, 2001), and that the associative learning mechanisms in human and non-human animals are specialised precisely for making these inferences (e.g. Rescorla, 1988). The key difference that seems to be postulated between humans and non-humans is that we are the only species that *represents* causal factors (particularly 'unobservable' or 'invisible' factors; Bering & Povinelli, 2003; Povinelli, 2000; Povinelli et al., 2000a) and forms theories about them – but obviously since we cannot ask the animals what they are thinking, it is difficult for us to know what, if anything, they are representing instead. Behaviourally, there seem to be two diagnostic features of human representation of causal factors. The first is transferability: we may learn about the causal relationship between two events (for example, removing a support from beneath an object and the object falling) in one particular situation, but we are able to generalise from that knowledge to completely different situations (a similar point has been made by Sterelny, 2003; he termed this "patchy generalisation" (p. 261)). The second is perhaps a consequence of the first: as a result of knowledge gained from other domains, when we observe a new event we tend to learn only about the causally relevant features of the event (for example in the trap-tube task, the position of the food and tool relative to the trap), rather than the many arbitrary details common to that specific situation (for example, capuchins incorrectly learn about the distance of the food from the end of the tube (Visalberghi & Limongelli, 1994), and in a modified version of the task, rooks incorrectly learn about the length of a stick protruding from the end of the tube (Helme et al., in press)). One possibility, therefore, for explaining behaviour like Betty's which seems to fall in between full understanding and no understanding, is that non-human animals are able to take into account knowledge gained in different circumstances to different extents. It should be possible to explicitly model this, using techniques borrowed from the field of machine learning and artificial intelligence (Mitchell & Thrun, 1996; Mitchell, pers. comm.). They have developed algorithms for 'analytical' (explanation-based) *versus* 'inductive' (purely statistical) learning, and it might be fruitful to seek to model animals' behaviour using algorithms which incorporate prior knowledge to a greater or lesser degree.

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Chapter 5

Lateralization of tool use in New Caledonian crows (*Corvus moneduloides*)

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Lateralization of tool use in New Caledonian crows (*Corvus moneduloides*)

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We studied laterality of tool use in 10 captive New Caledonian (NC) crows (*Corvus moneduloides*). All subjects showed near-exclusive individual laterality, but there was no overall bias in either direction (five were left-lateralized and five were right-lateralized). This is consistent with results in non-human primates, which show strong individual lateralization for tool use (but not for other activities), and also with observations of four wild NC crows by Rutledge & Hunt. Jointly, these results contrast with observations that the crows have a population-level bias for manufacturing tools from the left edges of *Pandanus* sp. leaves, and suggest that the manufacture and use of tools in this species may have different neural underpinnings.

Keywords: New Caledonian crows; tool use; laterality; handedness

1. INTRODUCTION

The predominance of right-handedness in humans, especially for tasks involving fine manipulation, has led some researchers to postulate a link between this asymmetry and other uniquely human traits, such as language (reviewed by Corballis (2003) and commentaries therein). Species-level rather than individual laterality is important because our closest relatives, chimpanzees (*Pan troglodytes*), show strong *individual* hand preferences in tool-use tasks, but no species-level laterality in the wild (McGrew & Marchant 1997, 1999; but see Hopkins *et al.* (2003) for evidence of right-handedness in captivity). However, the hypothesis of a link between species-level laterality and human uniqueness is challenged by work showing that many other vertebrates (from fishes to mammals and birds) show behavioural, motor and anatomical asymmetries, possibly reflecting a common evolutionary origin for laterality (e.g. Bradshaw 1991; Rogers 2002).

New Caledonian (NC) crows are notable for their frequent manufacture and use of tools, and appear to have many tool-related behavioural and cognitive adaptations (Hunt 1996; Chappell & Kacelnik 2002, 2004; Weir *et al.* 2002; Hunt & Gray 2003). They therefore represent an important case in which to establish whether tool use is associated with individual and/or species-level laterality. This possibility is supported by observations that throughout New Caledonia, NC crows leave more tool templates on the left than the right sides of pandanus leaves (Hunt 2000; Hunt *et al.* 2001), and that an individual wild crow made more tools from the left than the right edges of pandanus leaves (Hunt & Gray 2004). However, evidence for lateralized tool *use* as opposed to manufacture is only now becoming available. We are aware of observations of only four wild unsexed individuals have been reported (Rutledge & Hunt 2004). Here, we examine laterality in a larger sample of individuals of known sex under controlled experimental conditions.

2. METHODS

(a) *General approach*

We presented NC crows with a task similar to some that they face in the wild: retrieving larvae from holes in a tree stump. We provided them with symmetrical artificial tools and recorded the manner in which they held them when probing for food: that is, whether the end of the tool was held against the left or right side of the head.

(b) *Subjects*

The subjects were 21 NC crows held at the Department of Zoology, University of Oxford. Twenty crows had been trapped in two locations (near Tendéa (*ca.* 21°38′ S, 165°43′ E) and near Boulouparis (*ca.* 21°53′ S, 165°59′ E)) in July to August 2002, while another, 'Betty', had been trapped at Yaté (*ca.* 22°11′ S, 166°57′ E) in March 2000, and has already participated in laboratory experiments (for details of capture and housing see Chappell & Kacelnik (2002) and Kenward *et al.* (2004)). Neither trapping nor transportation caused any injuries to the birds. Capture was carried out with permission of the NC Parks Authority, and all relevant laws for trapping and transport were complied with.

(c) *Housing*

The birds were housed (free-flying) in two groups of nine and 12 individuals, each with permanent access to an indoor room (3.25 m × 4.10 m × 2.25 m high) and outdoor aviary (3.25 m × 0.86 m × 2.25 m high). Each group consisted of crows from only one area (except for Betty, who was housed with the Tendéa group). Both indoor and outdoor accommodation contained many natural perches of varying widths and heights. Plastic childrens' toys provided environmental enrichment, and tree branches provided sources for tool-making. Drinking and bathing water were permanently available.

The crows are fed *ad libitum* on soaked cat biscuits (Go-Cat), an insect and fruit mix (Orlux Universal and Orlux granules), peanuts, and mealworms. They were encouraged to use tools regularly by making some of their preferred food otherwise inaccessible: mealworms were placed in holes drilled into tree stumps, and occasionally pieces of pig heart were placed in clear Perspex tubes that were left in the aviaries. All individuals have been observed using tools.

(d) *Apparatus and procedure*

The probing apparatus was a tree stump (*ca.* 25 cm high × 30 cm diameter), with two holes drilled on its sides (*ca.* 10 cm deep × 2 cm diameter). The holes were slanted downwards, 20 cm apart and 10 cm from the stump's base, and both were visible from one side of the stump. Prior to the start of each session, the holes were almost filled with mealworms that had been chilled to reduce their activity and thus prevent them from crawling out.

The stump was placed on a table (41 cm × 77 cm × 75 cm high) in front of a dark Perspex observation window (roughly half of the sessions were conducted indoors and half outdoors), with the holes facing the window. A piece of dowelling (0.3 cm in diameter and 15 cm long, i.e. within the size range of natural tools) was placed on the table in front of the stump, equidistant from the two holes and parallel to the edge of the table.

Sessions were performed between February and May 2003, and lasted for 1–2.5 h, depending on the crows' level of activity. *Ad libitum* food was removed 3 h before observations began and replaced after the session finished. The dowelling was replaced whenever a bird removed it from the table and dropped it, and the mealworms were replenished when they became scarce. All sessions were recorded on video for later analysis.

(e) *Scoring and analysis*

Behaviour was scored by A.A.S.W. from the videos. Lateral tool use was defined as when the non-working tip of the tool projected on one side of the crow's beak or head. Thus, for example, if a crow held a tool with the non-working end against its left cheek, this was scored as 'left lateral' (see movie clip in electronic Appendix A). Note that although this is scored as 'left', the distal tip would be on the other side of the head's axis and hence it is probable that the contralateral (here, the right) eye would be monitoring the working end of

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Table 1. Laterality of tool use in NC crows (by hole).
(Bird, the identification of each subject (in terms of ring colour); % left, left lateral tool use as a percentage of total lateralized tool use; % straight, non-lateral tool use as a percentage of total tool use.)

		left laterality (bouts)			right laterality (bouts)						
bird	sex	hole a	hole b	total	hole a	hole b	total	total lateral	% left	total straight	% straight
BB	F	0	0	0	4	13	17	17	0.0	3	15.0
BK	M	0	0	0	24	15	39	39	0.0	51	56.7
YB	M	0	0	0	20	0	20	20	0.0	1	4.8
YK	F	0	0	0	9	31	40	40	0.0	0	0.0
PY	M	1	0	1	34	5	39	40	2.5	12	23.1
BG	M	29	1	30	6	0	6	36	83.3	49	57.6
GY	M	11	26	37	1	0	1	38	97.4	65	63.1
BP	F	1	39	40	0	0	0	40	100.0	1	2.4
KY	M	0	38	38	0	0	0	38	100.0	0	0.0
YY	M	1	39	40	0	0	0	40	100.0	0	0.0

the tool. Cases where the tip was inside the crow's beak were scored as 'straight'; this category conflates 'truly' non-lateral tool use with weakly lateralized cases where it was impossible to determine the direction of laterality, and for this reason was not formally analysed.

Laterality was scored for each 'bout' of tool use. A new bout was scored either when a bird released a tool and significantly changed its posture (to avoid counting as independent bouts occasions when crows momentarily released and re-grasped tools without moving their heads), or when a bird changed its hold on a tool (e.g. from straight to right, or from right to left). The hole that was probed during each bout was also scored.

Because there was variability in the number of bouts that different birds performed, we ceased scoring individuals after they had reached a total of 40 bouts of lateralized tool use in either direction: a power test showed that with 40 trials we would have a 90% chance of detecting an individual bias of 75% or greater. Individuals that performed fewer than 10 bouts of tool use were not included in the analysis. The experiment was terminated when 10 individuals had completed at least 10 bouts.

Binomial tests were used to determine whether individuals were laterally biased. A one-sample (two-tailed) t-test was used to examine whether there was a population bias in laterality over our sample: the proportion of birds that had a majority of left-sided bouts was tested against an expected mean of 0.5 (no bias).

To test whether the particular hole used biased the birds' laterality, we first calculated (for each individual) the proportion of left-lateral tool use in each hole relative to total left-lateral tool use, as in the equations below:

$$p(\mathrm{La}) = \#\mathrm{La} \,/\, (\#\mathrm{La} + \#\mathrm{Ra}),$$

$$p(\mathrm{Lb}) = \#\mathrm{Lb} \,/\, (\#\mathrm{Lb} + \#\mathrm{Rb}).$$

The first (capital) letter in each identifier indicates the laterality of tool use and the second (lower case) letter the hole being probed. Thus, $p(\mathrm{La})$ is the proportion of left lateral tool use in hole a (the left hole), $\#\mathrm{L}b$ is the number of bouts of left-lateral tool use in hole b.

To measure differences in laterality between the two holes, we subtracted $p(\mathrm{Lb})$ from $p(\mathrm{La})$ and did a one-sample (two-tailed) t-test over all individuals asking if this significantly differed from zero (individuals that used only one hole were excluded). A significant result here would indicate that the hole probed did affect the laterality of tool use.

3. RESULTS

Out of the 10 subjects, five were left- and five right-biased (all with $p < 0.0001$); thus, there was no overall preference (see table 1 and figure 1 for full results). Bilateral tool use was rare: only three birds ever used tools bilaterally, and the most bilateral individual used just 17% on its minority side. Seven out of the 10 subjects also showed at least one bout of straight tool use, ranging from 2.4% to 63% of total tool-use bouts. However, this should be interpreted with caution because (as noted above) this category might also include cases where laterality could not be determined.

Because only three birds were female, the sample is too small for statistical testing of an effect of sex. Inspection of the data shows that the ratio of right- to left-biased individuals was 2 : 1 in females and 3 : 4 in males, providing no suggestion for a sex difference in laterality.

The mean difference in proportion of left-lateral tool use between holes a and b was -0.0283, which was not significantly different from zero ($t_7 = -1.21$, $p = 0.267$; two subjects were excluded from this test because they exclusively used one hole), failing to demonstrate a difference in laterality as a function of which hole was probed.

4. DISCUSSION

We observed very strong individual laterality in tool use: only 2.3% (8 out of 348) of all bouts of tool use were on birds' less preferred sides. There was no evidence for a population bias in laterality: the numbers of left- and right-biased subjects were identical. Laterality did not obviously differ between males and females, but the sample size was insufficient for statistical testing. There was large variation in the extent to which individuals appeared to use tools non-laterally.

Our findings are similar to those reported by Rutledge & Hunt (2004), who found strong laterality in four wild crows in similar tasks, also split equally by side. Thus, there appears to be no species-level laterality in tool use, in contrast with the observations of Hunt *et al.* (2001) that 66% of tool templates had been cut from left edges of pandanus leaves. However, assuming that tool use and tool manufacturing are equally biased and pooling our 10 individuals with the four observed by Rutledge & Hunt (2004), a power test ($\alpha \geqslant 0.95$) shows that with 14 individuals there is only a 31% chance of detecting a population bias of this magnitude or greater, so we cannot confidently exclude a weak species-level bias in tool use.

As mentioned above, Hunt's (2000) and Hunt *et al.*'s (2001) discovery of population laterality in tool manufacture was based upon the templates of tools cut from pandanus leaves, which were consequently not attributable to individuals. However, in a recent paper, Hunt & Gray

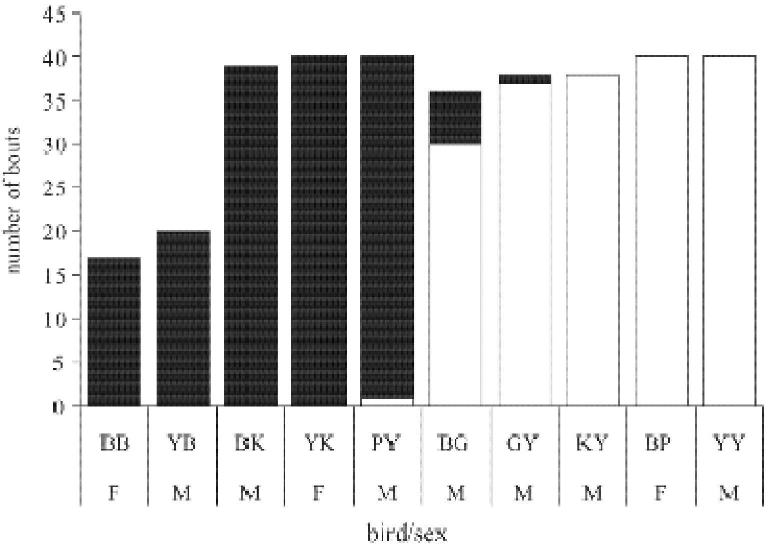

Figure 1. Laterality of tool use in NC crows. Filled bars represent 'right-lateral' tool use, and open bars represent 'left-lateral' tool use. Bird identification and sex are shown on the *x*-axis, and the number of bouts of lateralized tool use is shown on the *y*-axis.

(2004) provided the first report of direct observations of a crow making and using pandanus tools. Strikingly, they found that this single individual made tools from both the left and the right edges of pandanus leaves, with a preference (74%, if results from clockwise- and anticlockwise-spiralling trees are combined) for the left edge. This contrasts with the exclusive left-lateralized *use* of pandanus tools by the same individual, and the observations here of exclusive lateralization in nearly all individuals. If future studies confirm that other wild NC crows make tools from both the left and the right edges of pandanus leaves, this would strongly suggest that tool use and manufacture have different neural bases: the first demonstration (to our knowledge) of such a difference in any organism.

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Visit www.journals.royalsoc.ac.uk and navigate to this article through *Biology Letters* to see the accompanying electronic appendix.

Chapter 6

Tool manufacture by naive juvenile crows

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Tool manufacture by naive juvenile crows

The use of twigs by these birds to coax out hidden food seems to be an instinctive skill.

New Caledonian crows (*Corvus moneduloides*) are the most prolific avian tool-users[1,2]. Regional variation in the shape of their tools may be the result of cumulative cultural evolution[3] — a phenomenon considered to be a hallmark of human culture[4]. Here we show that hand-raised juvenile New Caledonian crows spontaneously manufacture and use tools, without any contact with adults of their species or any prior demonstration by humans. Our finding is a crucial step towards producing informed models of cultural transmission in this species, and in animals in general.

Figure 1 Tool use by a naive New Caledonian crow. **a,** A hand-raised juvenile uses a twig to retrieve meat from an artificial crevice. This individual has never witnessed tool use by a conspecific or by its human foster parents. **b,** Close-up of a tool made from a *Pandanus* leaf (provided by the Royal Botanic Gardens, Kew, London) by the same bird (see movie in supplementary information); scale bar, 1 cm. This work was carried out in accordance with the University of Oxford's procedures for local ethical review.

H. TOFT

Using four juveniles (three males, one female) bred in our captive colony in 2004, we tested whether New Caledonian crows have inherited characteristics that support tool-making and use. We hand-raised chicks in artificial nests and subsequently transferred them to enriched aviaries that contained twigs of assorted shapes and sizes, and food items hidden in holes and crevices. None of the subjects was ever allowed to observe an adult crow. Two of them, a male and a female, were housed together and were given regular demonstrations by their human foster parents of how to use twig tools to retrieve food. The other two were housed individually and never witnessed tool use; one of them, named Corbeau, never saw objects being handled that he could have used as a tool.

All four crows developed the ability to use twig tools (Fig. 1a). (For movies showing the events described here, see supplementary information.) Although the tutored crows paid close attention to demonstrations, we observed no qualitative difference between them and the untutored birds in their tool-oriented behaviour. We first observed successful food retrieval from a crevice by the tutored birds when they were 68 and 72 days old, and by the untutored birds at 63 and 79 days old. All juveniles continue to use twig tools to probe holes or crevices whenever the opportunity is provided.

We also tested the juveniles' response to leaves from trees of the genus *Pandanus*, similar to those from which wild individuals make tools that vary regionally in shape and complexity[3]. We mounted the leaves on wooden frames so that the birds could access them roughly as they would in the wild. On the first day that he was presented with *Pandanus*, Corbeau (then aged 99 days) produced a straight tool, 13 centimetres long, from one side of the leaf by using a swift 'cut–tear–cut' action. Immediately after producing the tool (Fig. 1b), Corbeau carried it to a crevice where food was often hidden and used it as a probe, a sequence that he has since repeated several times, successfully retrieving food.

All four crows attacked the leaves, cutting and tearing them into a variety of different shapes: only some of these would have been suitable as tools and none resembled the distinct 'stepped-cut' *Pandanus* tools fashioned by adults in the wild[3]. So far, we have observed only Corbeau using leaf pieces to retrieve food.

These results show that the ability of this species to manufacture and use tools is at least partly inherited and not dependent on social input. Spontaneous tool use has been recorded in a range of primate species[5,6] and in the woodpecker finch (*Cactospiza pallida*)[7], the only other bird known to use stick tools regularly in the wild. However, to our knowledge, ours is the first demonstration of spontaneous tool manufacture in a naive juvenile vertebrate — previous descriptions of manufacture concern groups of primates containing adults with prior experience of tool use[8,9].

In the light of our findings, it is possible that the high level of skill observed in wild adult crows is not socially acquired. Social input, however, may be important in transmitting specific techniques[10] and tool shapes[3]. This idea is supported by the close attention our juveniles paid to demonstrations of tool use by their human foster parents.

The fact that an inherited predisposition can account for a complex behaviour such as tool manufacture highlights the need for controlled investigation into behavioural ontogeny in other species that seemingly show culturally transmitted behaviour. The New Caledonian crow could be a valuable model for investigating interactions between inherited traits and individual[11] and social[3] learning during the development of tool technology — an issue central to the understanding of the emergence of human culture.

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Chapter 7

Concluding remarks

My aim at the start of my DPhil was to try to find out more about the biology of tool use and manufacture in New Caledonian crows. Specifically, I was interested in the extent to which their highly unusual behaviour in the wild was based on an understanding of tools and physical forces, and whether they had a genetic propensity to use and make tools, or instead relied exclusively on social learning.

In the work I have described I think we have made some progress towards answering these questions, although there is still a huge amount we do not yet know. In this chapter, I will briefly review the major findings of the thesis, discuss their implications, and outline possible future directions for the field in general and work with New Caledonian crows specifically.

7.1 SUMMARY OF THE MAIN FINDINGS

The first issue to tackle was the question of what we actually mean by ‘understanding’ in the context of tools, since this is the linchpin upon which much of the rest of the thesis depends. I attempted to explain what *I* mean by understanding in Chapter 1, but my main conclusion was that we still lack clear definitions and ways of discriminating between it and other processes. Intuitively, we seem to know what we mean by ‘understanding’ – namely, mental representation of a problem and the ability to work out a solution without requiring trial-and-error – but how, in a non-linguistic species, to tell the difference between behaviour based on this process rather than (for example) generalisation from previous experience is still hotly debated. I also reviewed the existing experiments into ‘folk physics’ in non-human animals, primarily birds and primates, which have produced somewhat surprising results: there is little convincing evidence for understanding and mental representation (in terms of physical causality) in any non-humans. Furthermore, there is also no clear dividing line between the performance of non-human primates and other animals, contrary (perhaps) to our naïve expectations. In many ways this field is still in its infancy, in terms of systematic long-running programmes with a range of species.

Observations of tool use in wild animals have often been linked with claims for cognitive abilities, so I examined these claims in detail in Chapter 2. By explicitly considering the processes by which behaviour can be produced, I argued that no single attribute of tool use or manufacture in the wild can implicate the involvement of cognitive processes beyond genetic canalization and simple associative learning. However, I proposed that by thinking about four characteristics of tool-oriented behaviour in combination, it might be possible to identify species where cognition was likely to be more important. Application of this framework revealed that New Caledonian crows rank alongside chimpanzees, orangutans, and capuchins in the sophistication of their natural technology, suggesting that they might be suitable candidates for investigation into their cognitive abilities.

I examined the cognitive basis of New Caledonian crows' tool use in several experiments reported in Chapters 3 and 4 (see also Appendix 2). These focussed on one subject, Betty, and conclusively demonstrated that her tool use was not stereotyped and inflexible, since she spontaneously and repeatedly modified the shape of unnatural materials to make appropriate tools. It was less, clear, though, whether her behaviour reflected a true and full understanding of how tools work, or if it resulted from a combination of generalisation and very quick learning; the latter is the conclusion that parsimony dictates we must draw. Part of our difficulty in distinguishing between the two possibilities is because at present the whole issue of understanding is poorly defined, and on the rare occasions that clear hypotheses are proposed they are usually formulated in absolute terms – either the subjects fully understand the problem, or are incapable of any understanding or reasoning at all. In Chapter 4 I proposed that we should move beyond such simplistic analyses, and try to explicitly model 'degrees of understanding' by using learning algorithms developed in the field of artificial intelligence that take prior knowledge into account to different extents.

Following Hunt and colleagues' finding that New Caledonian crows had a population-wide bias towards using the left side of their bill to *make* pandanus tools (Hunt, 2000; Hunt et al., 2001; Hunt & Gray, 2004), in Chapter 5 I examined whether captive crows show a lateral bias in their *use* of tools. I found that 10 individual crows were almost exclusively lateralised, a result consistent with Rutledge and Hunt's (2004) observations in four wild New Caledonian crows, and studies showing that apes have strong individual lateralisation for tasks requiring manual dexterity (tool use and complex food processing; e.g. Boesch, 1991; McGrew & Marchant, 1992; McGrew et al., 1999; Sugiyama et al., 1993). However, across the 14 subjects (pooled from the two studies), left and right preferences were exactly equal, so it seems unlikely that there is a strong population-wide bias. If further research shows that there is true a difference in laterality between tool use and manufacture, this might imply that different regions of the brain are involved, which is potentially of great interest. It is unclear at present whether these lateral preferences specifically evolved in the context of cognitive abilities involved in tool use and manufacture (an argument some put forward to account for the evolution of right-handedness in humans; e.g. Corballis, 2003), or are a reflection of the apparently ancient lateralisation found in most vertebrates (reviewed in Rogers, 2002), and similar to the foot-use preferences found in Japanese jungle crows (*Corvus macrorhynchos*; Izawa et al., 2005).

The last chapter (6) dealt with the question of development: do New Caledonian crows have a specific genetic propensity to use and make tools, do the behaviours emerge purely from a combination of object manipulation followed by reinforcement from food retrieval, or are they dependent on observing the behaviour of others? In an experiment carried out in collaboration with Ben Kenward and other colleagues, two hand-raised crows were exposed to regular demonstrations of tool use by their human foster parents (using a stick to get food out of holes and wooden crevices) from just after they started leaving their artificial nests, and whereas two were kept completely naïve. All four developed tool use at roughly the same age, and one even made crude pandanus tools; clearly, observing tool use is not essential for the development of this behaviour. Detailed analysis of the development of object manipulation in these juveniles (Appendix 6) showed that all four crows had a strong predisposition to insert twigs into holes, and before they reached this stage they displayed several stereotyped ‘precursor’ behaviours, such as rubbing twigs against perches in an action resembling functional probing. These observations suggest that New Caledonian crows do have a specific genetic propensity to use tools, an inference supported by comparative studies on the development of food-caching in ravens, which show related but distinct stereotyped actions (Bugnyar et al., in prep; Kenward et al., in prep). However, the New Caledonian crows that received demonstrations of tool use did carry and insert tools almost twice as frequently from a few weeks after fledging as those that were naïve, whereas non-tool-related behaviours (such as locomotion, and carrying and inserting non-twig items) did not differ; moreover, the crows were also strongly attracted to objects that humans had just been interacting with (Appendix 6). Together with the fact that none of our juveniles developed the sophisticated tool manufacture seen in wild crows, we therefore cannot exclude the possibility that social influence is important for the development of tool use and manufacture in the wild. This possibility is enhanced by the observed regional variation in the shape of the crows’ pandanus tools (Hunt, 2000; Hunt & Gray, 2003), which has no known ecological correlates.

There are several other potentially important issues that we could also not investigate, such as the role of food retrieval in the development of tool use (do the precursor behaviours require reinforcement to become functional?), and the relationship between the development of tool use and the development of cognitive abilities (does functional tool use only emerge after appropriate cognitive abilities have developed, or do they develop independently?).

7.2 IMPLICATIONS

I believe that there are three broad implications from the discoveries about Betty's cognitive abilities. The first regards the millennia-old debate about the relationship between language (or 'symbolic thought') and reasoning (reviewed in Radick, 2000). It is still commonly argued that non-human animals are incapable of using mechanisms other than associative learning to make causal inferences (e.g. Dickinson, 2001; Dickinson & Shanks, 1995; Rescorla, 1988), whereas humans use some form of inductive or explanation-based reasoning as well (e.g. Evans, 2003; although note that Dickinson argues that associative learning is the basis of human causal learning as well; Reboul, 2005), and this is reliant on language (e.g. Fodor, 1976). I do not think that I have conclusively demonstrated that New Caledonian crows go beyond associative mechanisms, but I have perhaps provided suggestive evidence for this possibility, because it would be fairly surprising (although not impossible) if Betty's remarkable speed of learning and generalisation could arise through such mechanisms, when other animals (with presumably similar associative learning abilities) do not perform as well. If confirmed by future research, this would either require a rethinking of the argument that non-associative reasoning requires language or symbolic thinking, or imply that New Caledonian crows have these abilities.

The second implication concerns the evolution of this kind of cognition. Although Betty failed to perform perfectly in the experiments described above, it is notable that she was at least as proficient as, if not better than, chimpanzees tested in analogous paradigms, which is remarkable considering the traditional assumptions about the relative intelligence of birds and mammals (e.g. Eddy et al., 1993), let alone birds and great apes. This is consistent, however, with recent findings that other corvids perform similarly to primates in other cognitive domains (reviewed by Emery & Clayton, 2004a, 2004b): for example, social cognition (Bednekoff & Balda, 1996; Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2004; Bugnyar et al., 2004; Emery & Clayton, 2001; Heinrich & Pepper, 1998; Prior & Güntürkün, 2005), episodic-like memory (Clayton & Dickinson, 1998, 1999; Clayton et al., 2001a; Clayton et al., 2001b, 2003), transitive inference (Lazareva et al., 2001; Paz-y-Miño C et al., 2004), and numerical abilities (Smirnova et al., 2000) (not to mention the extraordinary numerical, conceptual, and linguistic abilities demonstrated in African grey parrots (*Psittacus erithacus*); Pepperberg, 1999; Pepperberg, in press; Pepperberg & Gordon, 2005). If, as these results seem to suggest, the cognitive abilities of corvids (and, perhaps, psittacids) truly do rival those of non-human primates, this raises many interesting questions about the selective pressures that promoted the evolution of these abilities, the extent to which each cognitive domain depends on the others, and whether there were any pre-adaptations in the ancestral species that made the evolution of this kind of cognition more likely. Indeed, it has been suggested that this apparent convergent evolution of cognitive abilities in corvids and primates is the result of selection to solve many of the same socioecological challenges, such as foraging on perishable scattered or embedded food, and coping with the consequences of living in long-lasting, relatively stable social groups (e.g. Emery & Clayton, 2004b).

The third issue is the neural architecture underlying tool use in New Caledonian crows, and corvid (and psittacid) cognitive abilities more generally. In this context it is interesting to note that it has recently been recognised that many avian brain areas originally thought to be striatal in origin (and therefore historically assumed to control ‘instinctive’ behaviours; reviewed in Jarvis et al., 2005) are actually homologous to mammalian pallial regions, including the neocortex (thought to be responsible for ‘planned’ and ‘intelligent’ behaviour), and occupy roughly the same proportion of the total brain volume (Jarvis et al., 2005; Reiner et al., 2004). Particularly relevant are observations that the newly-recognised avian homologues of the mammalian cortex (the old ‘hyperstriatum’ and ‘neostriatum’, now known as hyper- / meso-pallium, and nidopallium respectively) are enlarged to relatively the same extent in parrots and corvids compared to other birds (specifically, compared to Galliformes), and in primates compared to other mammals (specifically, Insectivores) (Rehkämper et al., 1991; see Emery & Clayton, 2004a and Lefebvre et al., 2004 for similar results). Further work is obviously necessary to identify the specific brain areas involved in New Caledonian crows' tool-oriented behaviour, and the recognition of homologies between avian and mammalian brains makes this a particularly interesting question – are similar brain regions involved in avian and primate tool use? If similar brain regions are involved, how does the distinct neural architecture of avian brains (avian pallium lacking the laminar structure of mammalian neocortex; Karten, 1991) support similar cognitive processing (Emery & Clayton, 2004a)? It has been suggested (e.g. Emery & Clayton, 2005; Reiner et al., 2005) that despite the substantial difference in the superficial appearance of avian and mammalian brains, the underlying pattern of connectivity is similar, so it would be particularly interesting to investigate whether tool use in New Caledonian crows and primates involves brain areas with similar connectivity.

7.3 FUTURE DIRECTIONS

There are two particular issues raised in the preceding chapters that I believe are important to consider in future work. The first is, as Sara Shettleworth pointed out over a decade ago (Shettleworth, 1993), that most 'comparative cognition' experiments (including those reported in this thesis) still lack true 'comparisons'. Not only do we often fail to test multiple species on similar and comparable tasks, but we frequently judge the performance of our single subject species against a hypothetical 'perfect' performance that we assume we would show. Silva and colleagues (2005) elegantly illustrated the dangers of formulating hypotheses based on how we *believe* humans would perform without explicitly testing this assumption: we may not always perform in what is the most rational, logical, manner (as economists and cognitive psychologists have known for years; e.g. Kahneman, 2000). We therefore have to be very careful about concluding that non-human animals do not understand problems based on negative results from just one species. Even when similar experiments are carried out with several species, only rarely are they truly comparable (the trap-tube task is almost the only one to date, and that has many flaws; Machado & Silva, 2003; Silva et al., 2005), and even when they are, many factors (e.g. motivational, ethological, morphological) other than cognition could be responsible for performance differences (e.g. Macphail, 1985; Shettleworth, 1998).

I also think that we need to move beyond the approach of simply asking whether animals pass or fail tasks, and make more use of problems designed so that during the acquisition phase, both a causally-relevant and causally-irrelevant cue predict success.

Transfer tests could then be carried out in which the two cues conflict, thereby revealing subjects' propensity to learn about causally-relevant factors (e.g. Bates et al., 1980; Brown, 1990; Cummins-Sebree & Fragaszy, 2005; Fujita et al., 2003; Hauser, 1997; Hauser et al., 1999; Schlesinger & Langer, 1999; van Leeuwen et al., 1994). Recent experiments by Clayton and Emery's group also illustrate this paradigm: in one modified version of the trap-tube task, one rook (*Corvus frugilegus*) did learn about the causally-relevant feature (the trap) (Seed et al., in press), whereas in another version of the task neither rooks (Helme et al., in press) nor bonobos (*Pan paniscus*; Helme, pers. comm.) learned the causally-relevant features, and instead used cues such as which end of the tool protruded more (rooks), or the location of the food (bonobos), to determine which end of the tool to pull. These experiments are conceptually similar to the tests of concept formation in pigeons and corvids carried out by Wilson and colleagues (1985), which showed that despite similarities in acquisition on matching-to-sample tasks, when the rules were reversed corvids but not pigeons showed reduced performance, suggesting that they had learned concepts rather than a set of specific associations. These kinds of experiments have the advantage over traditional tests that it might be possible to compare different species' propensities to learn causally-relevant features in a quantitative manner, overcoming the 'all-or-none' problem just mentioned.

There remain many unanswered questions from the research I have described. In particular, how general are the abilities that Betty displayed – will other crows show the same capacities? Although we have had up to 20 other New Caledonian crows for the past 3 years, all but 4 were wild caught, and have taken a long time to habituate to captivity. Furthermore, many subjects were reluctant to push through the bob-wires to access the testing room, which made experiments with them very difficult and time-consuming. We have now moved to a pair-housed system where each pair has its own testing chamber, and hope that this will allow us to expand the research onto many more subjects.

If other crows do display similar behaviour to Betty, we can examine issues such as what the preconditions are – do they have to use wire hooks beforehand, or will experience with wire in a non-experimental context be sufficient? Would emergence of the behaviour be facilitated by watching others? How will the crows perform on other kinds of tool use problems – are they generally proficient, or is there big variation between individuals and tasks? Finally, how do New Caledonian crows' abilities in domains not involving tool use compare to other corvids, other birds, and other animals (particularly primates)? These are all empirical questions, and work is currently underway to address them.

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Appendix 1

Morphology and sexual dimorphism of the New Caledonian Crow *Corvus moneduloides*, with notes on its behaviour and ecology

Kenward, B. Rutz, C., Weir, A. A. S., Chappell, J. & Kacelnik, A. (2004). *Ibis* **146:** 652-660. DOI 10.1111/j.1474-919x.2004.00299.x.

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Morphology and sexual dimorphism of the New Caledonian Crow *Corvus moneduloides*, with notes on its behaviour and ecology

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New Caledonian Crows *Corvus moneduloides* are known to be extraordinary tool makers and users, but little is known of other aspects of their biology. Here, we report recent field observations of their behaviour and ecology, along with measurements of 19 morphological traits and two flight performance parameters taken from 22 captured Crows. These measurements showed that the Crows were sexually dimorphic in size (the males were larger) but not in shape. We also found that the crows lived in mixed-sex groups, and we observed juvenile-type begging behaviour and feeding by regurgitation, which supports the hypothesis that these may be family groups.

The New Caledonian Crow *Corvus moneduloides* is endemic to the semitropical Grande Terre island of New Caledonia in the South Pacific. This species has recently become a focus of interest because of its complex tool-oriented behaviour, which includes species-wide manufacture of a diverse range of tool types (Hunt & Gray 2002), laterality in tool manufacture (Hunt 2000a, Hunt *et al.* 2001) and use (Rutledge & Hunt 2004, Weir *et al.* in press), hook manufacture from natural substances and from novel material (Hunt 1996, Weir *et al.* 2002, Hunt & Gray 2003a), flexibility of tool selection (Chappell & Kacelnik 2002) and shaping of material to a rule system (Hunt 2000a, Hunt & Gray 2003b). There is also strong indirect evidence for cumulative change in tool design, mediated by social transmission (Hunt & Gray 2003c). Although some of these behaviours are rare or unknown in non-human animals, very little is known of other aspects of the Crows' biology. In this context there is a great need to learn more, and the possible existence of socially transmitted cumulative technology means that a better understanding of their social dynamics is essential.

The main thrust of our research programme is to study cognitive aspects of the Crows' tool use. To this end, in 2002 we spent 6 weeks observing Crows in New Caledonia with the main intention of trapping a sample for captive study. This gave us an opportunity to make our own observations of their wild behaviour, and also to learn more about the composition of their social groups, because we were able to determine the sex of the captured individuals *post facto* and to observe their interactions over a long period at close quarters in captivity. The second opportunity presented to us by captive birds is the ability to make detailed morphological measurements, which enable both the identification of any sexual dimorphism and also comparisons with other species.

We begin by summarizing current ecological and morphological knowledge, and then present the methods and results of our observations, captures and morphological measurements.

CURRENT KNOWLEDGE OF NEW CALEDONIAN CROW ECOLOGY AND MORPHOLOGY

The New Caledonian Crow's diet includes insects and their larvae, snails, nuts, fruit, seeds, flowers, and other birds' eggs (Layard & Layard 1882, Hannecart & Letocart 1980). Their tool use seems exclusively directed at obtaining insects and other invertebrates, and their techniques can be divided into two classes: those for obtaining large cerambycid larvae, which bore deep into wood, and those for obtaining small invertebrates from under bark and in other crevices (Hunt & Gray 2002). The proportion of their diet

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typically made up of invertebrates obtained by tool use is unknown. Many corvids engage in other behaviours, which may be cognitively complex, such as food caching and the breaking of snails or nuts by dropping, and both these behaviours have been documented in the New Caledonian Crow (Hunt 2000b, Hunt *et al.* 2002).

New Caledonian Crows are common throughout the range of forest types found on Grande Terre (Hunt 2000a, personal observations by B.K., A.W. and C. Burn (field assistant)) and are also found in the Niaouli savannah (Hannecart & Letocart 1980) and in agricultural areas (Vuilleumier & Gochfeld 1976, our pers. obs.). The Crows usually occur in groups ranging in size from pairs up to 30 birds, though most often the groups are small, and it has been suggested that the larger groups are temporary conglomerations of multiple small groups (Hunt 2000b). It has also been assumed that these are family groups; certainly, nutritionally independent juveniles have been seen closely associating with adults (Hunt 2000b). There is some evidence that group size varies across areas (Hunt 2000a). The literature does not agree precisely on nesting period, although the most authoritative source (Hannecart & Letocart 1980) gives it as October–January, and states that clutch size is one or two.

Their appearance is that of a 'typical' crow (*sensu* Goodwin & Gillmor 1986), except for the unusually shaped bill, particularly the maxilla, which has almost no downwards curve. Although the weights of 22 dead crows have been reported (mean 275.4 g (n = 22), males 289.3 g (n = 7), females 275.4 g (n = 13)), no statistics were calculated in the above study to examine the significance of the apparent sexual dimorphism in weight (Ross 1988).

METHODS

Field observations and capture

During July and August 2002, we observed and caught Crows from three trap sites in the west of New Caledonia. Two sites were approximately 1 km apart in the Ouatchoué river valley near Boulouparis (21°53.200′S, 165°59.076′E, elevation 20 m; and 21°52.646′S, 165°59.513′E, elevation 20 m) and the third was approximately 40 km away in the Moindou river valley near Tendéa (21°38.054′S, 165°43.830′E, elevation 240 m). The two areas had different habitats: the Boulouparis sites were in low-lying farmland with more open areas, and the Tendéa site was less cultivated, with more forest and a different composition of tree species owing to the altitudinal difference. We baited each area with meat and carried out observations for several days until groups of Crows were feeding there regularly. We used a whoosh net (supplied by P. Reid, pete@whoosh.fslife.co.uk), which enabled us to catch groups of co-feeding Crows. The net was only released if we were as certain as we could be that any juveniles accompanying the group were inside the catching area, to minimize the possibility of separating them from their parents.

The captured Crows were housed in aviaries at Park Forestier, Nouméa, New Caledonia. Blood samples were taken for sex determination by genetic analysis (see Appendix 1), before the birds were shipped by air to the UK.

Morphology

Subjects

In total, 21 of the captured Crows (13 males and eight females) were sent to Oxford, UK, where they joined one female Crow caught previously in March 2001 on the coast at Yaté (approximately 22°11′S, 166°57′E, at sea-level), making our sample 22 birds. At the time of measurement, the Crows were housed in two groups, one of ten and one of 12 individuals, each with indoor and outdoor accommodation. Each group consisted of Crows from only one area (except for the single female from Yaté, which was housed with the Tendéa birds).

Measurements

On 6 May 2003 the birds in one group were caught and measured, with the remaining group measured on 9 May. During each session, three birds from the other group (the first three birds that we could catch) were also measured as replicates, to estimate our measurement error. The Crows were deprived of food but not water 15 h before measurement to reduce weight variation due to gut contents (they are usually fed *ad libitum*). Of the 22 Crows, 16 had also been weighed on the day of capture in the wild.

We are not aware of a method to determine the age of these Crows, but if the latest nesting is January they are all likely to have been at least 16 months old at the time of measurement. We measured 17 variables from each of the 22 Crows, and took wing profiles from 13. The wing profiles were used to calculate morphological flight parameters (total wing area, wing span, aspect ratio and wing loading), giving a total of 21 variables. For details of the measurements, see Table 2 and Appendix 2.

Statistical analyses

To analyse variation between the sexes it was first necessary to test that capture site was not responsible for variation, because the proportion of males from Tendéa was higher than that from Boulouparis. For three response variables (weight, tarsus length and head width), we calculated a general linear model (GLM) with sex and site as fixed factors (e.g. Grafen & Hails 2002) (all statistical calculations were performed with SPSS v. 11.5.0, from SPSS Inc). Because of the close proximity of the two sites at Boulouparis, we considered them to be one site for this analysis, and we excluded the single Crow caught at Yaté; there were thus two sites analysed. It is standard for sex to be a fixed factor in a GLM. Because site is included as a fixed factor it is not valid to make general conclusions from this model regarding Crows caught from other sites. Unfortunately, we could not include site as a random factor in a general linear mixed model (GLMM) because, with only two female Crows from Tendéa, our power would have been too low to draw any conclusions.

To quantify any sexual dimorphism present, we calculated a mean for each sex for each of the morphological variables, and applied *t*-tests to check for significant differences. Because we were testing 21 variables, we applied a Bonferroni correction for multiple *P*-values (e.g. Sokal & Rohlf 1995) to obtain a threshold of statistical significance of 0.002. We were also interested in whether there might be sexual dimorphism in shape as well as size. To examine this, we calculated ratios between each pair of the following variables, which we considered to be most biologically meaningful: bill depth at base, gonys length, head width, head length excluding bill and tarsus length. We then applied *t*-tests on the ten ratios obtained for each individual to check for significant sex differences. Bonferroni correction gave a threshold of statistical significance of 0.005 for these tests.

We also used discriminant function analysis (DFA) to obtain a mathematical function that would allow us to predict the sex of a bird (e.g. Renner *et al.* 1998). We only included variables for which we had obtained a valid measurement for every bird, to maximize our data set. We used a forward stepwise method in which each variable is introduced into the function, in order of maximum discriminatory power (measured by the overall Wilks' lambda), until there is no variable left with an *F*-value at least as significant as 0.05. We also required a function that was not dependent on weight (which is more prone to vary due to factors such as season or condition), so we also performed a DFA excluding weight.

Discriminant functions are most reliable when they can be verified by testing with data that were not used to generate the functions. However, our limited sample size meant that we needed to use all available data, so we performed a jack-knife analysis (Sokal & Rohlf 1995). To test for normality, each variable distribution (including the calculated ratios) was compared, using a Kolmogorov–Smirnov test, with a normal distribution generated mathematically with the same parameters (Sokal & Rohlf 1995). Because our GLMs and *t*-tests compared the effects of sex and site, we performed separate tests for normality with the variable distributions divided by those factors. These tests indicated that none of the distributions deviated significantly from normality. The data also satisfied the other assumptions necessary for DFA: there was no significant difference between the covariance matrices for the sexes (Box's $M = 25.3$, $P = 0.27$), and within-sex correlation coefficients were low (maximum 0.505), showing that there was little co-linearity.

RESULTS

Observation in the field and capture

At Tendéa we had an excellent vantage point from which we could see for hundreds of metres both across and up and down the valley. The Crows often flew above the canopy across the valley, allowing us to see that there were often several separate groups in an area of roughly 1 km^2. The groups appeared to some extent fluid, with individuals joining or leaving groups and flying off in different directions. In both areas we saw solitary birds, but groups were more usual. These varied in size from pairs up to eight, with median and mode both of three, and mean of 3.8 (se = ± 0.18, $n = 100$). However, these statistics should be regarded with caution, because: (a) group fluidity and dense vegetation hindered counting, (b) we did not record group size every time we saw Crows and (c) most of the counts were made at the three trap sites so individuals and groups will have been counted more than once.

When there were temporary large groups of Crows, they were often much noisier than usual, producing a very loud high pitched *wak-wak* vocalization (Goodwin & Gillmor 1986). (Given the acoustic properties of this call and the fact that it is most commonly made when birds are out of visual contact with one another, we believe it may generally serve as a contact call.) Carrion seemed to be a regular component of the Crows' diet as there are many pig and deer carcasses in the forest. For this reason our extra provision of food was probably not creating artificially high concentrations of Crows, and we saw similar concentrations of Crows at sites that we had not baited.

We observed some individuals begging, with a characteristic vocalization, wing-holding and gaping, and they were occasionally fed by regurgitation. Bouts of begging behaviour were occasionally prolonged and insistent. In these instances the target of the begging was often forced to move away and was tenaciously followed from perch to perch. We know that some of the Crows showing begging behaviour were nutritionally independent, as we observed them feeding themselves from our bait. However, if nesting occurs until January (Hannecart & Letocart 1980), these begging Crows were at least 7 months old when we made our latest observation of begging behaviour (21 August).

We recorded a number of aggressive interactions between Crows, all of which occurred around the bait. These interactions were rarely serious and usually seemed to be dominance interactions within a group, in which an individual was forcibly displaced from its feeding position, rather than territorial interactions. Sometimes solitary individuals waited in trees above the bait until a feeding group had left, and then fed themselves. These individuals were much more vigilant than Crows in groups. Mobbing of raptors (some identified as Whistling Kites *Haliastur sphenurus*) was also common: raptors were frequently attracted to our bait, but the Crows invariably displaced them from the meat. Some of the largest group sizes we saw occurred when the Crows were defending carrion from raptors, and it seemed likely that different groups were coming together to mob. There was much *wak–wak* vocalization during these periods.

Table 1 shows the results of trapping and sexing. The group sizes shown are not representative of the average group size we observed, as we were more likely to fire the net when there were larger groups. In total we caught 26 Crows in eight groups, comprising 15 males and 11 females. This is not a significant deviation from a 50 : 50 ratio ($\chi^2_1 = 0.727$, $P = 0.394$). Every group captured was mixed-sex, although there were two captures of solitary birds.

Table 1. Date of capture, site and sex composition of trapped groups of New Caledonian Crows.

Date	Site	No. captured[a]	*N* males	*N* females
28/7/02	Bouloupari 1	1 (3) [3]	1	0
29/7/02	Bouloupari 1	4 (0) [2]	3	1
29/7/02	Bouloupari 1	4 (1) [2]	1	3
1/8/02	Bouloupari 2	5 (0) [3]	2	3
1/8/02	Bouloupari 2	2 (1) [0]	1	1
1/8/02	Bouloupari 2	1 (0) [0]	0	1
22/8/02	Tendéa	4 (0) [0]	3	1
30/8/02	Tendéa	5 (1) [0]	4	1

[a] Numbers in parentheses indicate Crows that were feeding on the bait but escaped the net. Numbers in square brackets indicate Crows that were seen in nearby trees and might have been members of the group that was caught.

Morphology

Error and validity of measurements

Some of the Crows had damaged plumage at the time of measurement. Three had broken primary remiges, and three had broken central rectrices. Wing and tail measurements from these birds were therefore excluded from the analysis. As noted earlier, we were unable to age birds, so differences in plumage stages could be a source of error. Some individuals had moulted in captivity, but all of the longest primary remiges and central retrices were fully regrown. Although it is normal in wild birds for the tip of the maxilla to project slightly over that of the mandible, in 11 birds the maxilla projected more than 1.5 mm, which we considered to be an excessive overgrowth due to captive housing. For these birds we therefore excluded the following maxilla measurements: culmen length, culmen length to nostril and head length. Head length excluding bill was still valid for those birds despite being calculated from head length including bill, because the culmen length had been subtracted.

Our measurement error, determined by comparison between the measurements for the six birds that were measured twice, was in general very low (Table 2). For all measurements made with callipers, the greatest error was 1.8 mm (for a tarsus length measurement), and the greatest mean error was 0.8 mm (again for tarsus length), which is 1.5% of the mean variable value. Maximum error for the body girth measurements, which we had suspected might be inaccurate, was 7 mm, which is 2.5% of the mean variable value.

The Crows gained weight significantly during their period in captivity (paired samples *t*-test, $n = 16$, $t_{15} = 5.829$, $P < 0.001$). During the 9–10 months from capture, their weight increase averaged 32 g and there was no sex difference in weight gain (*t*-test, *n* males = 9, *n* females = 7, $t_{14} = -1.274$, $P = 0.224$). However, the procedure for weighing the birds in

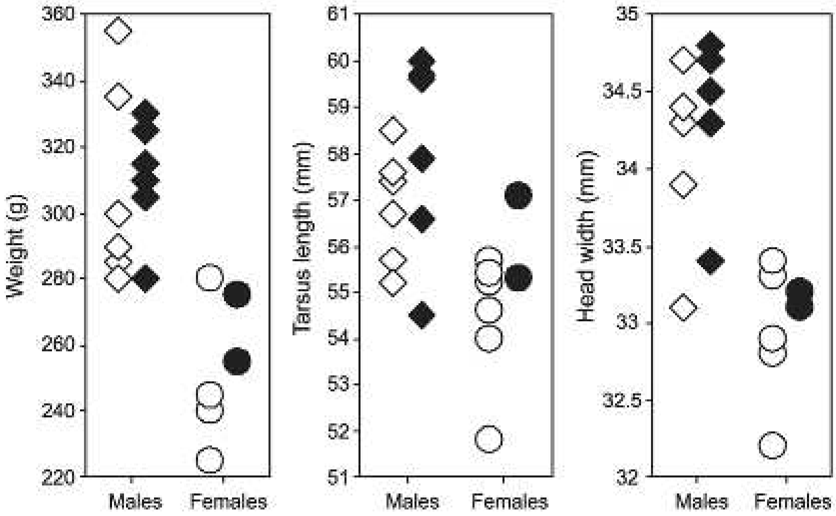

Figure 1. Morphometrics of New Caledonian Crows by sex. Filled symbols represent birds from Tendéa, empty symbols those from Boulouparis.

the field was different and possibly more subject to error. The weight gain in captivity could have been due to increased food provisioning or to juvenile growth, but because the proportional gain in weight was not correlated with weight at capture, the first explanation seems more likely (linear regression, n = 16, F_{15} = 3.609, ns). The fact that weight changed in captivity raises the possibility that other measurements could also have changed. This cannot be ruled out, as weight was the only measurement taken at the time of capture, but measurements that depend mainly on skeletal size (such as tarsus length) are unlikely to have changed in adult birds over the course of 8 months.

Effects of site and sex

In all the variables for which we calculated GLMs (weight, tarsus length and head width), sex explained a significant amount of variation, but neither site nor the interaction between site and sex explained any significant variation (Fig. 1) (weight: by sex $F_{1,17}$ = 25.149, $P < 0.001$, by site $F_{1,17}$ = 1.157, P = 0.297, by interaction $F_{1,17}$ = 0.605, P = 0.447; tarsus length: by sex $F_{1,17}$ = 7.686, P = 0.013, by site $F_{1,17}$ = 3.907, P = 0.065, by interaction $F_{1,17}$ = 0.028, P = 0.870; head width: by sex $F_{1,17}$ = 26.084, $P < 0.001$, by site $F_{1,17}$ = 1.229, P = 0.283, by interaction $F_{1,17}$ = 0.099, P = 0.757). The t-tests that test for sexual dimorphism are therefore valid despite the difference in proportions of the sexes from the different sites.

Quantifying sexual dimorphism

For all the size variables measured, the means for males were greater than those for females, significantly so for ten of 19 variables (Table 2). A lack of power and conservatism of the Bonferroni correction probably accounted for the non-significance of the differences in the remaining variables. The absolute differences were not great – the linear measurements for the males were on average 6.4% longer, and the males were 24% heavier. The differences were, however, quite reliable – only one female was as heavy as the lightest male (Fig. 1). The dimorphism was unlikely to have been a result of captivity conditions, because the males were also significantly heavier on the day of capture (independent samples t-test, n = 16, t_{14} = –3.383, $P < 0.01$). The sexes did not differ significantly in any of the ratios calculated, indicating that the dimorphism is primarily in size rather than in shape. Neither did the sexes differ in flight morphology variables, although as we only had four wing profiles for females, the power of this comparison was low.

The variables entered into the first DFA were gonys length, bill depth at base, beak height at nostrils, beak width at base, bill width at nostrils, head width, head length excluding bill, tarsus length, body girth and weight. The resulting discriminant function was:

$$D = 0.378 * \text{tarsus length} + 1.198 * \text{head width} + 1.888 * \text{bill depth at nostrils} - 1.479 * \text{bill width at nostrils} + 0.043 * \text{weight} - 87.073.$$

D is greater than zero for males and less than zero for females. This function correctly classified all 22 individuals. The jack-knife analysis produced functions that in every case correctly classified the individual omitted. The discriminant function obtained when weight was removed from the analysis was:

Table 2. Morphometrics of New Caledonian Crows trapped in 2002. Error estimates are based on six replicate measurements. All measurements were made using standard methods or as explained in the table footnotes.

	All		Female		Male		Sex comparison *t*-test			Error		
Variable	*n*	Mean (±sd)	*n*	Mean (±sd)	*n*	Mean (±sd)	*t*	*df*	*P*	Mean	Max.	Mean as % of mean variable value
Culmen length[ai] (mm)	11	45.0 ± 2.7	4	42.2 ± 1.3	7	46.6 ± 1.6	−4.686	9	0.001*	0.3	0.9	0.6
Culmen length to nostril[bi] (mm)	11	30.2 ± 1.7	4	28.5 ± 0.4	7	31.2 ± 1.3	−4.064	9	0.003	0.3	0.7	0.9
Gonys length[ci] (mm)	22	26.5 ± 1.4	9	25.5 ± 0.6	13	27.2 ± 1.3	−3.526	20	0.002*	0.3	0.6	1.1
Bill depth at base[ci] (mm)	22	20.9 ± 1.1	9	20.0 ± 0.6	13	21.4 ± 1.0	−3.743	20	0.001*	0.6	1.3	2.9
Bill depth at nostrils[ci] (mm)	22	18.3 ± 1.0	9	17.4 ± 0.4	13	18.9 ± 0.8	−5.093	20	< 0.001*	0.5	1.4	2.5
Bill width at base[ci] (mm)	22	20.9 ± 1.1	9	19.3 ± 0.8	13	19.9 ± 0.6	−1.825	20	0.083	0.3	0.5	1.4
Bill width at nostrils[ci] (mm)	22	18.3 ± 1.0	9	14.2 ± 0.9	13	14.7 ± 0.6	−1.445	20	0.164	0.5	1.2	3.7
Head width[ci] (mm)	22	33.7 ± 0.8	9	32.9 ± 0.4	13	34.2 ± 0.5	−6.325	20	< 0.001*	0.4	1.2	1.1
Head length including bill[di] (mm)	11	83.5 ± 2.8	4	80.1 ± 0.4	7	85.4 ± 1.1	−9.202	9	< 0.001*	0.2	0.5	0.2
Head length excluding bill[e] (mm)	22	38.4 ± 1.3	9	37.8 ± 1.1	13	38.8 ± 1.2	−1.832	20	0.082	0.6	1.4	1.5
Tarsus length[f] (mm)	22	56.5 ± 2.2	9	54.9 ± 1.4	13	57.6 ± 1.9	−3.648	20	0.002*	0.8	1.8	1.5
Tarsus height[ij] (mm)	22	6.5 ± 0.4	9	6.2 ± 0.4	13	6.7 ± 0.3	−3.402	20	0.003	0.2	0.5	2.6
Tarsus width[ik] (mm)	22	5.0 ± 0.4	9	4.8 ± 0.3	13	5.1 ± 0.4	−1.749	20	0.096	0.4	0.8	8.7
Body girth[cl] (cm)	22	18.8 ± 1.1	9	17.8 ± 0.7	13	19.5 ± 0.7	−5.257	20	< 0.001*	0.5	0.7	2.5
Weight[m] (g)	22	284.8 ± 36.4	9	249.4 ± 17.8	13	309.2 ± 22.8	−6.586	20	< 0.001*	6.7	15	2.3
Wing length[gn] (cm)	19	26.4 ± 1.1	6	25.2 ± 0.5	13	26.9 ± 0.8	−4.481	17	< 0.001*	0.1	0.2	0.2
Tail length[hn] (cm)	19	16.8 ± 0.9	8	16.1 ± 0.6	11	17.3 ± 0.7	−3.751	17	0.002	0.1	0.2	0.7
Total wing area[o] (cm^2)	13	1056.7 ± 111.8	4	950.7 ± 116.3	9	1103.8 ± 74.5	−2.898	11	0.015	–	–	–
Wing span[o] (cm)	13	71.4 ± 5.3	4	66.8 ± 6.3	9	73.4 ± 3.4	−2.476	11	0.031	–	–	–
Aspect ratio[o]	13	4.83 ± 0.30	4	4.71 ± 0.36	9	4.89 ± 0.27	−1.033	11	0.324	–	–	–
Wing loading[o] (g/cm^2)	13	0.275 ± 0.031	4	0.257 ± 0.032	9	0.283 ± 0.028	−1.502	11	0.161	–	–	–

[a] Length of exposed culmen as in Baldwin *et al.* (1931), except we define the base of the culmen as where it meets the skin rather than the feathers because this measurement seems more repeatable.

[b] Position of nostril in maxilla from tip of bill as in Baldwin *et al.* (1931).

[c] As in Baldwin *et al.* (1931).

[d] Measured from the tip of the bill to the most posterior part of the head.

[e] Calculated by subtracting length of culmen from length of head including bill.

[f] With foot bent, the distance from the intertarsal joint to the last undivided leg scute.

[g] Maximum wing length when fully flattened and stretched.

[h] Length of fully flattened and stretched central rectrices, measured underneath.

[i] Measured with digital callipers to the nearest 0.1 mm.

[j] Major diameter close to foot.

[k] Minor diameter close to foot.

[l] Measured with a tailor's tape measure to the nearest 1 mm.

[m] Measured with a spring balance to the nearest 5 g.

[n] Measured with a ruler to the nearest 1 mm.

[o] Calculated as in Appendix 2.

* Significant difference between sexes of $P = 0.002$.

$D = 1.862 * \text{head width} + 1.168 * \text{bill depth at nostrils} - 84.134.$

This function also classified all 22 individuals correctly. However, the jack-knife analysis without weight misclassified two males as females, giving a 90.9% success rate.

DISCUSSION

Sexual size dimorphism

Many hypotheses have been proposed to explain sexual size dimorphism in birds (e.g. Blondel *et al.* 2002). Our knowledge of New Caledonian Crow ecology does not allow us to rule many of them out. One explanation that does seem unlikely is niche differentiation to reduce intrasexual competition (e.g. Shaffer *et al.* 2001), because we know that the Crows forage in mixed-sex groups (we caught Crows in mixed-sex groups while they were foraging). In captivity at least, observations indicate that both sexes are similarly prepared to use tools to obtain wood-boring insects, which are otherwise difficult to obtain, although we do not yet know whether the sexes differ in the size or kind of tools they make and use, or in the sort of prey they seek. We have reported here that we found no shape dimorphism in New Caledonian Crows. Had we found such a difference, it might have been an indicator of niche differentiation resulting from the different selection pressures on individuals experiencing different environments. For example, Wandering Albatrosses *Diomedea exulans* sexes may differ in flight morphology because they forage in different ocean areas (Shaffer *et al.* 2001).

Other proposed hypotheses relate to sexual selection (e.g. Andersson 1994). One suggests that strong intermale competition for females promotes an increase in body size in males. This hypothesis predicts that in species or populations with greater male–male competition, sexual size dimorphism will be greater. Another hypothesis suggests that the necessity for territorial defence may promote sexual size dimorphism, especially if there is a division of roles within the pair. We know too little about the reproductive behaviour of the Crows to comment on the applicability of these hypotheses.

The DFA distinguished effectively between the sexes. Genetic analysis, although certainly more reliable, is time consuming and expensive, so our functions could have applicability in the field. However, it should be noted that body size can vary within a species between different populations, and we have generated the functions using data from only two sites. We were able to use a GLM to confirm that the dimorphism we discovered was not due to variation between sites. However, because of our small sample size we were not able to use a more powerful GLMM, which would allow us to generalize our results to other areas. In addition, because our Crows gained weight in captivity, we would not advocate using our functions to sex Crows from other areas – although it is likely that the larger of a breeding pair would be the male.

Weight gain in captivity could be due to increased availability of food, and/or to the possibility that we caught juveniles that were not then fully grown. Ross's (1988) wild birds were 10 g lighter than ours in captivity, which supports the hypothesis that the birds gained weight, but does not indicate the magnitude of the effect.

Flight morphology

Rayner (1988) has plotted regression lines of flight morphology parameters for a very large number of bird species. Including our results as points on his figures 12 and 13 reveals that in relation to body mass, the wings of New Caledonian Crows are of average length but with larger area than expected, meaning they have low wing loading. The low wing loading is explained by the wings being broader rather than longer. This is appropriate for a woodland bird that routinely navigates its way past branches and other obstacles. There is no evidence that the sexes differ in flight performance. It would be difficult to draw further conclusions from these parameters without the opportunity to compare these data with other corvids. Unfortunately, to our knowledge not enough relevant data on corvids are available for comparison.

Sociality and other ecological conclusions

Our results strengthen the view that social groups are in fact family groups. Certain individuals were fed by others, and all the groups we caught were mixed-sex. It is interesting to note that the normal clutch size of one or two eggs plus two parents would produce the very commonly seen group sizes of three or four. One of our male Crows in captivity has continued to feed two of the others with which it was caught, and we have also observed another bird being fed (but were unable to identify the individuals involved). This provides further evidence that families stay together in the wild. However, we have not yet performed any genetic analyses for relatedness, which should be conclusive.

We observed no physical aggression in the wild except for dominance interactions around food, despite often seeing several groups in the same area. However, when large numbers of Crows were together in close proximity they were often extremely noisy. On the basis of our observations, it therefore seems unlikely that the Crows defend any territorial boundaries with physical aggression, but that vocalizations may serve to enforce territories.

Although we know much of what makes up the Crows' diet, we have very little idea of the proportions of different components. It is noteworthy that carrion, which seems to be a major component of their diet, must be a recent addition, because the only large mammals on the island (pigs and deer) are introduced, and there are no large native mammals. The evolution of tool use in New Caledonian Crows could be related to this absence of native mammals: tool use allows the Crows to obtain protein-rich foods that are otherwise unavailable. Also absent from the native fauna are woodpeckers – whose wood-probing niche the Crows may partially occupy – although Horned Parakeets *Eunymphicus cornutus* might also compete in this niche (Orenstein 1972). We also speculate that the peculiar bill shape of the Crows may be related to their tool use. The straightness of the maxilla probably makes tool use easier, so a pre-existing straight bill may have promoted the emergence of tool use. Alternatively, the pre-existence of tool use may have been an evolutionary pressure on bill shape.

As this contribution testifies, virtually nothing is known about the ecology of the New Caledonian Crow and very little about its behaviour. Until now, in spite of the growing attention that this species has received because of its tool-oriented behaviour, even basic morphometric information was missing. We have summarized available information regarding their field biology, listed all the relevant literature and provided a set of basic measurements that we hope will serve as reference and orientation for further field studies.

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APPENDIX 1

Details of sexing by genetic analysis

The DNA was extracted using a chelex extraction technique (Walsh *et al.* 1991). Sex was determined by PCR amplification of the *CHD1-W* and *CHD1-Z* genes using P2 and P8 primers (Griffiths *et al.* 1998). Products were separated by electrophoresis through 4% polyacrylamide gels and visualized using silver staining (Bassam *et al.* 1991). Sex was determined by the presence/absence of the *CHD1-W* band: both sexes have the *CHD1-Z* band but only males have the *CHD1-W* band.

APPENDIX 2

Details of measurement methodology

See Table 2 for details of how most measurements were made. Wing profiles were obtained by holding the Crow against the side of a table, stretching one wing across a cardboard sheet on the table, spraying a mist of water on to the sheet and then sketching around the silhouette created (e.g. Shaffer *et al.* 2001). The profiles were scanned into a computer, and the wing length, root chord and area were measured using image analysis software (ImageJ 1.29x, by W. Rasband, National Institutes of Health, USA; http://rsb.info.nih.gov/ij). Total wing area (S) was calculated by doubling the single wing area, and adding the interwing area (estimated as the root chord * body girth/π). Wing span (b) was calculated by doubling the wing length and adding the body girth/π. Aspect ratio (A) and wing loading (W) were then calculated ($A = b^2/S$, $W = N/S$, where N is weight) (Pennycuick 1989).

All measurements were taken from the birds' right-hand sides. All measurements were taken by C.R., except weight, which was taken by B.K. C.R. and B.K. were blind to the sexes of birds at the time of measurement, except for two females that had been the subjects of previous behavioural experiments.

Appendix 2

Shaping of Hooks in New Caledonian Crows

Weir, A.A.S. Chappell, J., and Kacelnik, A. (2002). *Science* **297:** 981. DOI 10.1126/science.1073433.

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ECOLOGY AND BEHAVIOR

Shaping of Hooks in New Caledonian Crows

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Many animals use tools, but their understanding of physical forces or causal relations is unclear (*1*, *2*). Primates are considered the most versatile and complex tool users, but observations of New Caledonian crows (*Corvus moneduloides*) (*3*–*5*) raise the possibility that these birds may rival nonhuman primates in tool-related cognitive capabilities.

We report here an experiment inspired by the observation that a captive female spontaneously bent a piece of straight wire into a hook and successfully used it to lift a bucket containing food from a vertical pipe (Fig. 1A). This occurred on the fifth trial of an experiment in which the crows had to choose between a hooked and a straight wire and only after the hooked wire had been removed by the other subject (a male). The animals had prior experience with the apparatus, but their only previous experience with pliant material was 1 hour of free manipulation with flexible pipe-cleaners a year before this experiment, and they were not familiar with wire (*6*).

To investigate the importance of this observation, we conducted several new trials in which we placed a single straight piece of garden wire (0.8 mm in diameter, 90 mm long) on top of the tube and did not intervene until either of the birds obtained the food (a valid trial) or dropped the wire irretrievably into the tube (an invalid trial).

Out of 10 valid trials (interspersed with seven invalid ones), the female bent the wire and used it to retrieve the food nine times, and the male retrieved the food once with the straight wire (*7*). To bend the wire, she first wedged one end of it in sticky tape (available around the bottom of the tube and the side of the plastic tray containing the apparatus) or held it in her feet at a location 3 m from the food, where there was no tape. She then pulled the other end orthogonally with her beak (see Movie S1), resulting in a bend with an angle of 74 ± 30° (mean ± SE) (see Fig. 1B for individual tool shapes). She started to bend the wire 35 ± 8 s after the start of each trial and used the resulting hook 6 ± 2 s later. In all cases but one, she tried with the straight wire (for 15 ± 4 s) before starting to make the hook. In all valid trials, the birds retrieved the food within 2 min.

Thus, at least one of our birds is capable of novel tool modification for a specific task. In the wild, New Caledonian crows make at least two sorts of hook tools using distinct techniques (*3*, *4*), but the method used by our female crow is different from those previously reported and would be unlikely to be effective with natural materials. She had little exposure to and no prior training with pliant material, and we have never observed her to perform similar actions with either pliant or nonpliant objects. The behavior probably has a developmental history that includes experience with objects in their environment (just as infant humans learn about everyday physics from their manipulative experience), but she had no model to imitate and, to our knowledge, no opportunity for hook-making to emerge by chance shaping or reinforcement of randomly generated behavior. She had seen and used supplied wire hooks before but had not seen the process of bending.

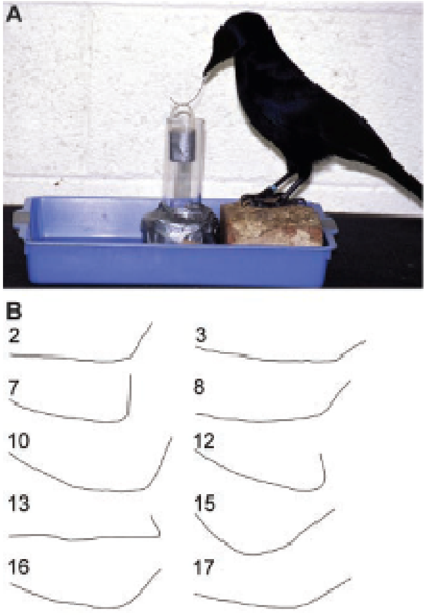

Fig. 1. Bending wire into hooks by a captive New Caledonian crow. **(A)** The female New Caledonian crow extracting the bucket containing meat using a piece of wire she had just bent. This is a photo taken after the experiment was completed, but the hook and posture depicted are typical of experimental trials. **(B)** Outline tracings of all the bent wires, with the end inserted into the tube facing right. Numbers refer to trial number. The wire bent in trial 8 was not successfully used to retrieve the bucket (it was dropped into the tube). Because of experimenter error, the wire in trial 10 was 2 cm longer than the wire in the other trials. Scale bar, 5 cm.

Purposeful modification of objects by animals for use as tools, without extensive prior experience, is almost unknown. In experiments by Povinelli [experiments 24 to 26 in (*2*)], chimpanzees (*Pan troglodytes*) repeatedly failed to unbend piping and insert it through a hole to obtain an apple, unless they received explicit coaching. Further experiments [exp. 27 in (*2*)] (*8*) have shown a similar lack of deliberate, specific tool modification in primates. There are, however, numerous suggestive field observations (*9*) and one report of a male capuchin monkey (*Cebus apella*) unbending a piece of wire to obtain honey (*10*).

Our finding, in a species so distantly related to humans and lacking symbolic language, raises numerous questions about the kinds of understanding of "folk physics" and causality available to nonhumans, the conditions for these abilities to evolve, and their associated neural adaptations. Comparisons between New Caledonian crows and their relatives, as well as between other cognitively exceptional birds and their relatives (*11*), offer a unique natural experiment to examine hypotheses about the ecological and neural preconditions for complex cognition to evolve. It is not yet known if New Caledonian crows are also exceptional in cognitively demanding tasks not involving tools.

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6. The female subject was wild-caught as a juvenile in March 2000 and has been in our laboratory ever since. The male subject was in a zoo in New Caledonia for over 10 years until he was moved to our laboratory, also in March 2000 (it is not known when or how he was caught). See (*5*) for further details of subjects, history, and housing conditions.
7. The male rarely attempted this task and never bent the wire. He observed the female bending the wire and stole the food from her in three trials. The birds are tested together because they are highly social and, when separated, are less motivated to participate in experiments.
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Supporting Online Material
www.sciencemag.org/cgi/content/full/297/5583/981/DC1
Movie S1

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Appendix 3

Trial descriptions for Chapter 3

Table 1: Trial-by-trial description of Experiment 2, Chapter 3. Note that latencies do not include time spent away from the apparatus table (so if, for example, Betty only arrives at the table 30 seconds into a trial, her actions will then be timed from when she arrived at the table).

Trial	Success?	Trial duration (mm:ss)	Modified tool?	Modified before use?	Description
1	n	00:07	n	n	Betty probed once (for 5s) with the unmodified wire and then dropped it irretrievably into the tube.
2	y	01:15	y	n	Betty probed twice (for 17s) with the unmodified wire (she was displaced by Abel between the two probes for 26s). After 27s, she poked the wire into the Gaffa tape at the base of the tube and pulled it around the tube, bending it 62°. She probed once (for 8s) with the modified tool (modified end), before being displaced by Abel. She took the tool with her and probed in the end of a perch with it, but Abel again displaced her, and she left the tool at the end of the perch. Abel retrieved the tool, and probed in the apparatus once (for 9s) with the modified end, retrieving the bucket.
3	y	01:52	y	n	Betty probed 6 times (for 41s) with the unmodified tool, interspersed by three pokes (for 8s) at the Gaffa tape at the base of the tube. After 1min 18s she poked the wire into the tape at the base of the tube and pulled it around the tube, bending it 39°. She then probed twice more (for 15s; she was displaced by Abel for 9s between the two probes) with the modified end of the tool, retrieving the bucket.
4	n	00:09	n	N/A	Betty probed twice (for 5s) with the unmodified wire and then dropped it irretrievably into the tube.
5	n	02:17	n	N/A	Abel probed 11 times (for 1min 2s) with the unmodified wire (interspersed with 3 pokes (for 8s) at the Gaffa tape at the base of the tube), and then dropped it irretrievably into the tube.

6	n	01:34	n	N/A	Betty probed twice (for 9s) with the unmodified wire (interspersed with one poke (for 1s) at the Gaffa tape at the base of the tube). After 22s she poked the wire into the tape at the base of the tube again and pulled the proximal end partially around the tube, but the wire only bent very slightly (less than 10°). She then probed 3 times (for 53s), twice being displaced by Abel (but keeping the tool), before dropping the wire irretrievably into the tube.
7	y	00:43	y	n	Betty probed once (for 17s) with the unmodified wire, following a 5s displacement by Abel. After 26s, she poked the wire into the tape at the base of the tube and pulled it around the tube, bending it 99°. She then probed once (for 7s) with the modified end of the wire, retrieving the bucket.
8	n	01:46	y	n	Abel probed 3 times (for 10s) with the unmodified wire, which he then dropped onto the table. Betty then poked with the wire behind a brick (for 4s) and at the tape at the base of the tube (for 1s), before probing twice (for 12s) into the tube with the unmodified wire (interspersed with two pokes at the tape at the base of the tube, for 9s). After 1min 23s, Betty poked the wire into the tape at the side of the tray, and pulled the proximal end, resulting in a bend of 48°. She then probed once (for 4s) with the modified end of the wire, but dropped it irretrievably into the tube.
9	y	00:11	n	N/A	Abel probed once (for 9s) with the unmodified wire, retrieving the bucket. (It appeared that he managed to wedge the end of the wire between the bucket and the tape holding its handle on.)
10	y	00:37	y	n	Betty probed once (for 10s) with the unmodified wire. After 18s, she poked the wire into the tape at the base of the tube and pulled it around the tube, bending it 92° (made up of two bends, one of 22° and the other of 70°). She then probed once (for 10s) with the modified end of the wire, retrieving the bucket.
11	n	01:23	n	N/A	Abel probed 4 times (for 45s) with the unmodified wire (interspersed with 2 pokes (for 4s) at the tape at the base of the tube), and then dropped it irretrievably into the tube.

12	y	01:03	y	n	Betty probed once (for 2s) with the unmodified wire. After 15s, she poked the wire into the tape at the side of the tray and pulled the proximal end, bending it 117°. She then probed once (for 4s) with the modified end of the wire, retrieving the bucket.
13	y	00:43	y	y	Betty picked up the wire and carried it to a perch elsewhere in the room. After 11s, she appeared (the camera view was partially obscured) to hold the wire in her feet along the perch and bend one end of it with her beak to an angle of 113°. She immediately flew back to the table with the apparatus, and probed once (for 3s) with the modified end of the wire, retrieving the bucket.
14	y	01:42	y	n	Betty probed 4 times (for 20s) with the unmodified wire, interspersed with 2 pokes at the tape at the base of the tube (for 8s) and 1 poke at the wire at the side of the tray (for 1s). After 54s, she poked the wire into the tape at the side of the tray and pulled the proximal end with her beak, bending it 74°. She then probed once (for 29s) with the modified end, retrieving the bucket.
15	n	00:11	n	N/A	Betty probed once (for 6s) with the unmodified wire and then dropped it irretrievably into the tube.
16	y	00:48	y	n	Betty poked the unmodified wire at the tape at the base of the tube (for 2s), and then probed once (for 7s) into the tube. After 26s, she poked the wire into the tape at the base of the tube and pulled it around the tube, bending it 55°. She then probed once (for 6s) with the modified end, retrieving the bucket.
17	y	00:26	y	n	Betty probed once (for 5s) with the unmodified wire, and was then displaced by Abel for 11s. After 26s, she poked the wire into the tape at the side of the tray and pulled the proximal end, bending it 40°. She then carried the wire to a perch elsewhere in the aviary, and returned after 12s. She probed once (for 3s) with the modified end, retrieving the bucket.

Appendix 4

Trial descriptions for Chapter 4

Table 2: Trial-by-trial description of Betty's behaviour in Experiment 1, Chapter 4.

Trial	Success?	Trial duration (mm:ss)	Modified tool?	Modified before use?	Description
1	x	09:00	NA	NA	Used her own tool (feather shaft).
2	n	01:00	n	NA	Probed for 2 seconds with unmodified tool, which was then dropped irretrievably into tube. Trial aborted.
3	y	06:36	y	n	Probed 9 times with the straight tool (for 2min 36s). 3min 31s after the start of the trial, slightly modified the tool by poking against base of tube, and probed with this 8 times (for 1min 53s), almost raising bucket on several occasions. After 6min 15s, poked the tool into Gaffa tape (bottom of tube) and twisted proximal end into L-shape. Turned the tool around, and used L-shape to retrieve bucket.
4	y	03:19	y	n	Probed twice (for 16 seconds total) with the unmodified tool. After 27s, modified tool slightly by poking into Gaffa tape (bottom of tube) and twisting proximal end to form a 45° bend. Probed 3 times with unmodified end (for 27s), then turned around and probed 7 times with modified end (for 1min 35s), interspersed with poking tool at Gaffa tape (but no apparent additional modification). Almost raised bucket twice before final success.
5	y	01:46	n	NA	Probed 6 times (for 1min 24s) with the unmodified tool, and eventually managed to wedge the tool into the sticky tape holding the bucket's handle on and thus successfully withdraw the bucket.
6	n	01:28	y	n	Probed 5 times (for 46s) with unmodified tool, interspersed with poking at Gaffa tape at base of tube. After 1min 13s, wedged proximal end into Gaffa tape and twisted distal end into a 360° helix. Probed once for 9s with unmodified end, then dropped (seemingly accidentally) irretrievably into tube.

7	y	01:14	y	n	Probed twice with unmodified tool (for 8s). After 14s, modified tool slightly (~30° bend in middle) by poking end onto Gaffa tape. Probed twice (for 8s) with the slightly modified tool. After 36s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end into a slight helix, with a bend of around 50°. Probed once (for 21s) with the unmodified end, then turned tool around and probed once (for 4s) with the modified end, retrieving the bucket.
8	y	00:49	y	n	Probed twice with the unmodified tool (for 15s). After 25s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end around beak to form two bends, one of 90° and one of ~60° back in the other direction. Turned around *before* using, and probed once (for 8s) with the modified end, retrieving the bucket.
9	n	00:37	y	n	Probed once (for 6s) with unmodified tool. After 10s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end around 90° (in 2 bends), yielding an L-shaped tool with the bend roughly in the middle. Probed once for 11s with unmodified end, then turned around and probed once (for 3s) with modified end, then dropped (seemingly accidentally) irretrievably into tube. Tool seemed too short after the bend to reach the bucket's handle.
10	y	01:02	y	n	Arrived with her own stick tool, but immediately dropped it into the tube. Probed twice (for 10s) with unmodified tool. After 29s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end several times into a large hook-like shape. Probed once (for 13s) with the unmodified end, then turned around and probed once (for 7s) with the modified end, retrieving the bucket.
11	y	00:24	y	n	Probed once (for 2s) with unmodified tool. After 9s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end once to form a large 90° L-shape. Immediately turned around (without probing), and probed once (for 3s) with the modified end, retrieving the bucket.

12	y	00:18	y	n	Probed once (for 2s) with unmodified tool. After 7s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end once to form a small 90° L-shape. Immediately turned around (without probing), and probed once (for 5s) with the modified end, retrieving the bucket.
13	y	01:23	y	n	(N.B. 3 days later.) Probed 3 times (for 19s) with unmodified tool. After 1min 15s (there were times when she was not manipulating the tool), wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end once to form a small V-shape. Immediately turned around (without probing), and probed once (for 2s) with the modified end, retrieving the bucket.
14	n	01:46	y	n	Probed twice (for 3s) with unmodified tool, interspersed by poking Gaffa tape. After 37s (she flew elsewhere in the room for a while), wedged distal end in Gaffa tape (bottom of tube) and twisted proximal slightly (~15° angle). Turned around and probed twice (for 9s) with the modified end. Again wedged distal end in Gaffa tape and twisted a little more (in the middle of the tool, ~30° angle). Probed twice (for 13s) with the same end as previously, then turned around and probed once (for 4s) with the other end, before dropping wire into tube.
15	y	00:24	y	n	(N.B. 2 days later.) Probed once (for 5s) with the unmodified tool. After 11s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end into ~150° V-shape using beak. Immediately turned around (without probing), and probed once (for 5s) with the modified end, retrieving the bucket.
16	y	00:38	y	n	Probed once (for 3s) with unmodified tool. After 17s, wedged distal end in Gaffa tape (bottom of tube) and twisted proximal end twice (~180°) into spiral. Probed once with unmodified end (for 1s), then turned around and probed once with modified end (for 3s), retrieving the bucket.

17	y	00:28	y	n	Probed once (for 2s) with unmodified tool. After 15s, wedged distal end in Gaffa tape (bottom of tube), and *bent* (not twisted) proximal end into V-shaped hook (~120° bend). Immediately turned around, and probed once (for 3s) with modified end, retrieving the bucket.
18	y	00:24	y	n	Probed once (for 5s) with the unmodified tool. After 12s, wedged distal end in Gaffa tape (bottom of tube), and bent proximal end into V-shaped hook (~120° bend). Immediately turned around, and probed once (for 4s) with modified end, retrieving the bucket.
19	y	00:43	y	n	Probed once (for 2s) with the unmodified tool. After 21s, wedged distal end in Gaffa tape (bottom of tube), and bent proximal end 3 times into triangular shape (1 bend of ~20° degrees backwards, then 2 bends forwards by ~120°; she initially bent it just once into a V-shape, but the other bends happened as she appeared to be trying to remove the tool from the Gaffa tape). Immediately turned around, and probed once (for 5s) with modified end without retrieving the bucket. Put the tool down again and turned it around the shaft (i.e. still holding the same end, but rotating around the shaft 180°), probed again with the modified end (for 2s), retrieving the bucket.
20	n	01:47	y	n	Probed once (for 3s) with the unmodified tool. After 10s, wedged the distal end in Gaffa tape (bottom of tube), and twisted proximal end into a spiral. Immediately turned around, and probed 5 times (for 32s) with the modified end of the tool, interspersed by putting it down and picking it up again having readjusted grip. After 1min 47s, dropped tool irretrievably into well. Left the testing room, but returned with her own twig tool before the experimenter had removed the apparatus, and used this to retrieve the bucket (and aluminium tool).
21	y	00:44	y	y	After 17s, wedged distal end in Gaffa tape (bottom of tube), and bent proximal end twice to form a rough hook shape. Immediately turned around, and probed once (for 12s) with modified end, retrieving the bucket.

22	x	01:36	y	y	After 13s, wedged distal end in Gaffa tape (bottom of tube), and bent middle (but slightly nearer beak) of the tool ~80°. Turned around immediately, and probed three times (for 19s) with modified end, partially raising the bucket once, but the bend was too near the middle for complete success. After 2min 50, probed behind the brick with the tool and dropped it there (out of reach). Left the testing room and returned with her own twig, which she used to probe behind the brick and retrieve a waxworm (missed by the experimenter when preparing the apparatus). Then used the twig to probe 4 times for the bucket, eventually retrieving it. Note that between probes, she wedged the end of the twig in the Gaffa tape (bottom of tube) 3 times, and performed similar actions to it that she uses with the aluminium tool.
23	y	00:21	y	y	After 14s, wedged distal end into Gaffa tape (bottom of tube) and bent proximal end into ~90° degree small hook. Turned around immediately, and probed once (for 7s) with modified end, retrieving the bucket.
24	y	01:06	y	n	(2 days later). Probed 3 times (for 6s) with unmodified ends (these were classed as probes because she inserted the tool into the tube, but she only contacted the handle of the bucket on one of them). After 52s, poked distal end against Gaffa tape (bottom of tube), and caused the tool to bend very slightly (~5°) at the proximal end. Immediately turned around, and probed once (for 5s) with the slightly modified end, retrieving the bucket.
25	y	00:36	y	n	Probed twice (for 3s) with unmodified end (did not contact bucket handle). After 11s, wedged distal end in hole in wooden block and bent the proximal end by ~45°. Immediately turned around, and probed once (for 6s) with the modified end, retrieving the bucket.
26	x	00:04	NA	NA	Arrived with her own tool, and used successfully.

27	y	01:44	y	n	(18 days later) Probed 7 times (for 44s) with unmodified tool, turning it around 3 times in between probes. After 1min 33s, wedged distal end in Gaffa tape (bottom of tube) and bent proximal end 180° to form a neat hook. Immediately turned around and probed once (for 1s) with the modified end, retrieving the bucket.
28	y	00:32	y	n	Probed twice (for 6s) with unmodified tool. After 20s, wedged distal end in Gaffa tape (bottom of tube) and bent proximal end ~110° to form a hook. Immediately turned around and probed once (for 6s) with the modified end, retrieving the bucket.
29	y	02:01	y	n	Probed once (for 1s, did not contact bucket handle) with unmodified tool. After 6s, poked distal end of tool against Gaffa tape (bottom of tube), and bent proximal end very slightly (~5°). Immediately turned around, and probed once (for 3s) with slightly modified end. After 33s, again poked distal end against Gaffa tape (bottom of tube) and bent *distal* end a further 5° or so. Did *not* turn around, and probed 3 times (for 51s) with slightly modified end, almost raising the bucket 3 times. After 1min 47s, poked distal end against Gaffa tape (bottom of tube) and bent proximal end ~150° into large hook. Immediately turned around and probed once (for 6s) with modified end, retrieving the bucket.
30	y	00:18	y	n	Probed once (for 3s) with unmodified tool. After 6s, poked distal end of tool against Gaffa tape (bottom of tube), and bent the proximal end into ~80° hook. Immediately turned around and probed once (for 3s) with modified end, retrieving the bucket.
31	y	00:31	y	n	Probed once (for 1s, did not contact bucket) with unmodified tool. After 14s, poked distal end against Gaffa tape (bottom of tube), and bent the proximal end into ~150□ hook. Immediately turned around and probed twice (for 10s) with modified end, adjusting her grip in between probes, retrieving the bucket.
32	y	00:13	y	y	(167 days later) After 4s, poked distal end against Gaffa tape (bottom of tube), and bent the proximal end into ~150° hook. Immediately turned around and probed once (for 5s) with modified end, retrieving the bucket.

33	y	00:11	y	y	After 2s, poked distal end against Gaffa tape (bottom of tube), and bent the proximal end into ~150° hook. Immediately turned around and probed once (for 3s) with modified end, retrieving the bucket.
34	n	00:42	y	y	Picked up the tool and immediately left the testing room. Returned 5 minutes later with the tool (still unmodified), and poked the distal end against the Gaffa tape (bottom of tube), and bent the proximal end very slightly (~5 °) with her beak. Immediately turned around, looked into the tube but did not probe, and again poked the distal (now slightly modified end) against the Gaffa tape (bottom of tube) and slightly bent the proximal end (again, by ~5°). Turned around again, but in the process dropped the tool irretrievably behind the brick.

Table 3: Trial-by-trial description of Betty's behaviour in Experiment 2, Chapter 4.

Trial	Success?	Trial duration (mm:ss)	Modified tool?	Modified before use?	Description
1	x	00:22	NA	NA	Pecked hard at the opening to the apparatus, causing the bucket to jump out of the vertical arm!
2	y	00:32	y	y	Had some difficulty picking up the tool, dropping it several times. After 14s, picked up the tool by squeezing together one of the hooked ends with her beak, thereby flattening that end of it. After 18s, probed (for 14s) into the vertical arm of the apparatus with the unmodified (hooked) end of the tool, and successfully retrieved the food.
3	y	00:35	y	y	Again had difficulty picking up the tool, dropping it several times. After 14s, picked up the tool by squeezing together one of the hooked ends with her beak, thereby flattening that end of it. After 18s, probed (for 4s) into the horizontal arm of the apparatus with the unmodified (hooked) end. After 29s, turned the tool around (when picking it up the other way around, squeezed together the other hooked end as well) and poked it through the hole in the horizontal arm, successfully retrieving the bucket.

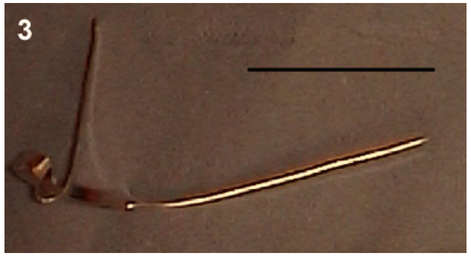
Table 4: Trial-by-trial description of Betty's behaviour in Experiment 3, Chapter 4.

Trial	**Success?**	**Trial duration (mm:ss)**	**Modified tool?**	**Modified before use?**	**Description**
1	y	00:35	y	y	Had difficulty initially picking up the tool. After 8s, picked up the tool by opening her beak wide and squeezing together the ends, making a straight tool. Probed 3 times (for 21s) with the modified tool, just managing to reach and retrieve the food.
2	n	03:56	n	NA	Probed 11 times (for 1min 26s) with the unmodified tool, turning it around 4 times, but never made any obvious attempt to modify it. Did not retrieve bucket, and after 3min 56s left the testing room with the tool.
3	y	06:20	y	n	Probed 5 times (for 16s) with the unmodified tool (did not turn it around). After 4min 14s (she had spent a lot of time not interacting with the apparatus), she returned, probed once (for 2s), and then, while holding the end of the tool in the tube, lifted her head and beak, thereby bending the proximal end of the tool backwards (~40°) using the lip of the tube as a fulcrum. Immediately carried on probing with the partially-unbent tool, eventually retrieving the food after 7 more probing bouts (lasting 1min 31s in total; 4 were with the unmodified end, and 3 with the modified end).
4	y	03:31	y	n	Probed 8 times (for 43s) with the unmodified tool (did not turn it around). Spent several minutes not interacting with the apparatus, and after 3min 23s unbent the tool slightly using a very similar action to that in trial 3 (resulting in a backwards bend of ~25°), using the lip of the tube as a fulcrum. Immediately carried on probing with the unmodified end of the partially-unbent tool, retrieving the food after 2 more probing bouts (lasting 6s in total, both with the unmodified end).

Appendix 5

Final tool shapes in Experiment 1, Chapter 4

Appendix 5: *Final tool shapes in Experiment 1, Chapter 4*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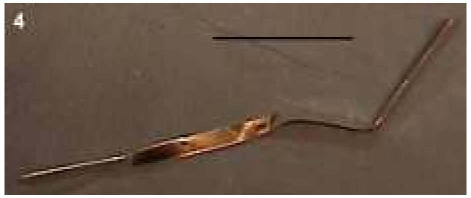
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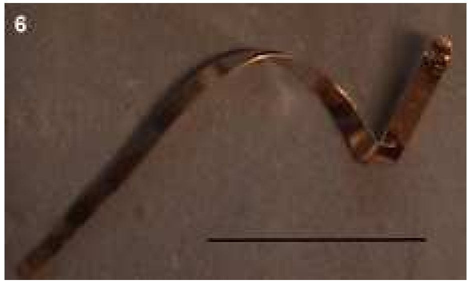
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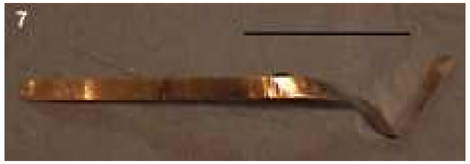
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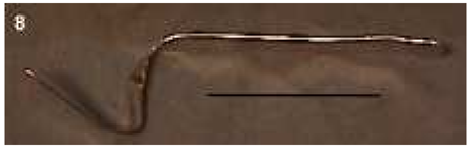
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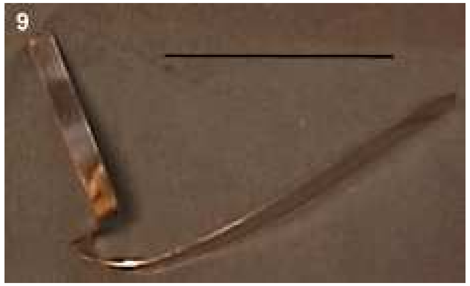
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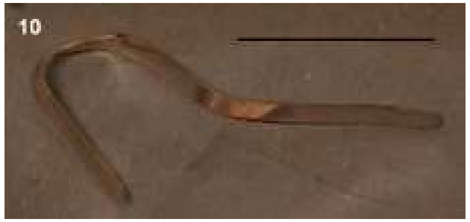
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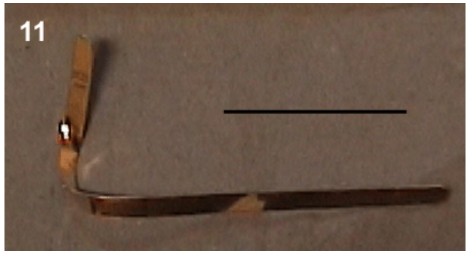
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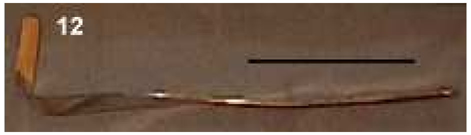
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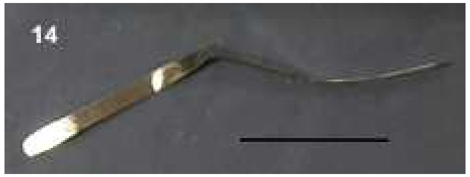
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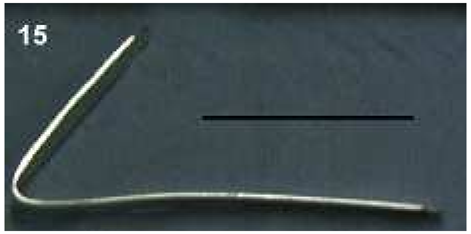
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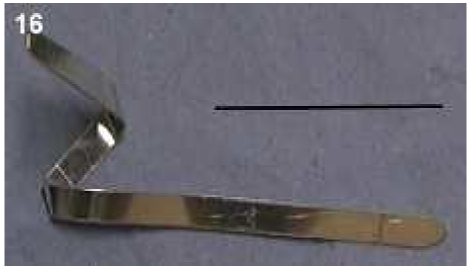
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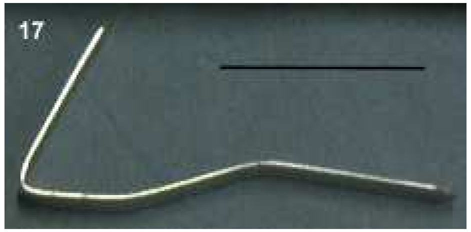
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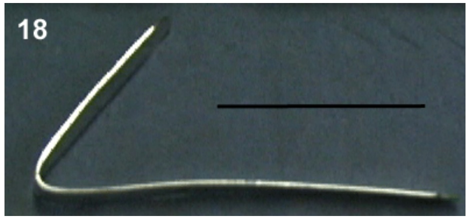
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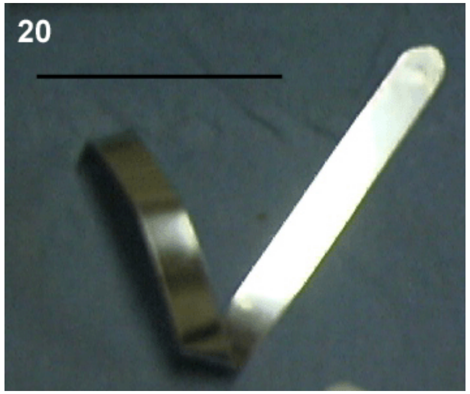
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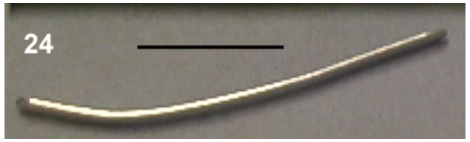
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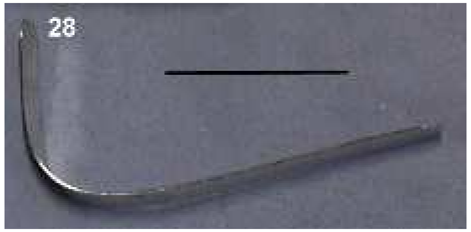
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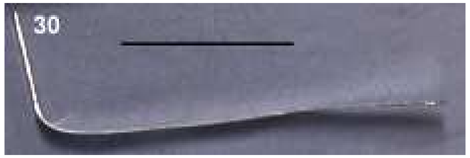
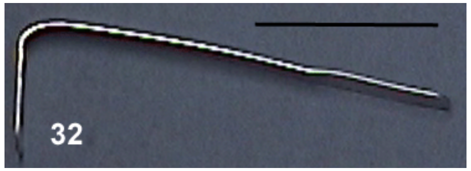
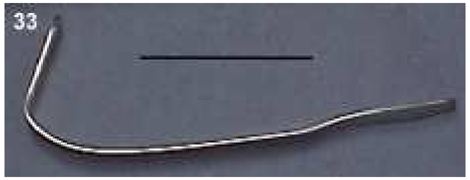
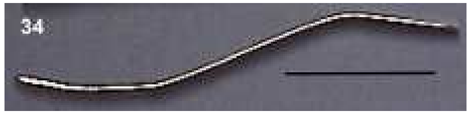
Appendix 5: *Final tool shapes in Experiment 1, Chapter 4*









In each photo, the number refers to the trial on which the tool was made, and the scale bar represents 3 cm.

Appendix 6

Development of tool use in New Caledonian crows: inherited action patterns and social influences

Kenward, B., Rutz, C., Weir, A. A. S., & Kacelnik, A. (in press). *Animal Behaviour.*

A6.1 Abstract

New Caledonian crows (*Corvus moneduloides*) are the most advanced avian tool makers and tool users. We previously reported that captive-bred isolated New Caledonian crows spontaneously use twig tools and cut tools out of *Pandanus* spp. tree leaves (an activity possibly under cultural influence in the wild). However, what exactly is inherited and how it interacts with individual and social experience remained unknown. To examine the interaction between inherited traits, individual learning, and social transmission, we observed in detail the ontogeny of twig tool use in hand-reared juveniles. Successful food retrieval was preceded by stereotyped object manipulation action patterns that resemble components of the mature behaviour, demonstrating that tool-oriented behaviours in this species are an evolved specialisation. However, there was also an effect of social learning: juveniles which had received demonstrations of twig tool use by their human foster parent showed higher levels of handling and insertion of twigs than their naïve counterparts; and a choice experiment showed that they preferred to handle objects which they had seen being manipulated by their human foster parent. Our observations are consistent with the view that individual learning, cultural transmission, and creative problem solving all play roles in the acquisition of the tool-oriented behaviours in the wild, but demonstrate a greater role for inherited species typical action patterns than was heretofore recognised.

A6.2 Introduction

New Caledonian crows (*Corvus moneduloides*, hereafter 'NC crows') are renowned for their complex tool-oriented behaviour (hereafter 'TOB'), which involves both tool use and manufacture. In comparison with most other tool-using animals (see Beck 1980; Kacelnik et al. in press), this species stands out with regard to: the frequency of their TOB and the diversity and complexity of tool shapes routinely used in the wild (Hunt 1996; Hunt 2000; Hunt & Gray 2002; Hunt & Gray 2004a; Hunt & Gray 2004b); their ability to select tools appropriate for a given task (Chappell & Kacelnik 2002; Chappell & Kacelnik 2004); and their capacity to create novel tools according to need (Weir et al. 2002). Furthermore, circumstantial evidence in the form of regional variation suggests cultural transmission may be involved in tool manufacture (Hunt & Gray 2003). This suite of attributes makes the species particularly interesting as a research model for studying the acquisition of TOB, but till now a detailed study of the process has been lacking. Some of the theoretical questions are similar to, and also relevant to, problems posed by acquisition of TOB in all other species, including humans.

The emergence of tool use in the human child involves a complex interplay between inherited, individually learnt, and social factors. It therefore presents a challenge to experimental studies, not least because many developmental experiments, such as long term manipulation of the social or physical environment, cannot be performed. Birds, however, are particularly suitable for this type of study, both because of the possibility of experimentation and because their rapid development makes practical experiments which would be much more time consuming to conduct in primates. With care, insights gained from such studies may allow parallels to be drawn that could promote understanding of general principles of behavioural development, including the evolution and individual development of TOB in our own species.

We hand-raised four captive-bred NC crow chicks under controlled laboratory conditions to investigate the role of both social and non-social factors in the ontogeny of TOB in this species. Two crows received regular demonstrations by their human foster parent of how to use twig tools for retrieving food, whereas the other two birds never saw tool use. We have reported elsewhere (Kenward et al. 2005) that all four juveniles spontaneously began to use twig tools to obtain otherwise inaccessible food at similar ages, and that one untutored subject promptly manufactured functional tools when exposed to pandanus (*Pandanus* spp.) leaves. The remaining birds showed interest in the leaves but within the short time during which we had fresh leaves available were not observed to use them to make tools. These findings demonstrated conclusively that the species possesses an inherited predisposition for using and manufacturing tools. In this paper, we present detailed ethological data and further analyse the development of TOB in these individuals, in order to examine how inheritance and experience interact during development and to examine the influence of social inputs. To achieve these goals, we: (i) describe in detail the development of TOB so as to determine more precisely what is inherited; and (ii) investigate whether demonstrations of tool use by human foster parents have a measurable effect on the ontogeny of TOB.

Tool use does not necessarily require a high level of cognition (e.g. Hansell 2000). For example, there is no reason to believe that the sensorimotor integration required for, say, carrying eggs to safety on a leaf by a fish (Timms & Keenleyside 1975) is any more cognitively demanding than the foraging and courtship behaviours which allowed the fish to produce the eggs. However, TOB may be particularly revealing about processes of physical cognition, because it involves creating relationships between two or more external objects in a manner which is easily observable (and amenable to experimental manipulation). Our finding of an inherited predisposition for TOB in NC crows (Kenward et al. 2005) raises the questions of exactly what is inherited.

Many hypotheses are conceivable, varying in how the canalization (*sensu* Waddington 1957) is achieved (and therefore also how robust it is). Rigid developmental programs for sets of motor patterns could be under tight genetic control, with little variation in adult behaviour being explained by the subject's experience. Other hypotheses, however, allow for varying degrees of learning. Animals could inherit a general tendency to explore objects in a manipulatory fashion, leading to the acquisition of various modalities of tool use by reinforcement of random or exploratory object-manipulation acts. Alternatively, each juvenile NC crow could be equipped with cognitive mechanisms which allow it to learn physical laws by observing object interactions, and then plan goal-directed TOB exploiting these laws (a process customarily identified as 'insight', see Thorpe 1963). The concept itself is problematic, and even ignoring the conceptual difficulties, evidence of insight in non-human animals is rare and controversial. We use the term, however, for its heuristic value and because it can be separated from other extreme alternatives by specific predictions about the acquisition of behaviour.

Each of these hypotheses predicts different observable patterns of behaviour development. Insight would result in sudden marked changes in behaviour, with immediate drop-off of inefficient behaviours following the moment when the bird mentally solves each problem. If motor patterns are under tight genetic control, then one might expect to see incomplete actions emerging prior to the directly functional versions (similar to the rehearsal of flight movements by chicks before fledging), and less individual variation would be observed than under the hypotheses involving looser canalization. If TOB emerges because of a general manipulatory tendency coupled with learning, the predictions depend upon the type of learning. If operant conditioning was responsible, specific tool-related acts would begin to dominate the repertoire of object oriented behaviour only after they had been associated with food rewards. However, an alternative form of learning, perception-action development (e.g. Gibson & Pick 2000), does not require food reinforcement. If discovery itself is reinforcing, then this account would also explain the motivation to explore. This hypothesis predicts that individuals would persistently perform actions which enable them to learn more about the affordances of objects and the environment.

These hypotheses are not necessarily mutually exclusive – different processes may be involved at different developmental stages and besides, different levels of cognition could accompany the performance of externally similar actions. For example, it is unlikely that insight precedes or causes the early stages of the acquisition of tool use in children (Lockman 2000), but it is obviously available to older individuals. Moreover, an individual is unlikely to experience insight regarding tool use unless it possesses tendencies which already caused it to experience the manipulation of objects, so a sudden transition might not be present in overt behaviour even if it does occur in underlying cognitive processes.

Distinguishing between inherited motor patterns and a general manipulatory tendency is also problematic. Inherited motor patterns may be accompanied by learning – even a spider building its web according to a rigid set of inherited motor patterns is able to use experience to modify its web so as to take maximum advantage of the available prey (Heiling & Herberstein 1999). Conversely, lack of observable evidence for inherited motor patterns does not rule them out. For these reasons, our goal is not to categorise TOB in NC crows as being the result of one particular process (for instance, deciding whether TOB is cultural or not) but to determine as precisely as possible how the complex behaviour of adult NC crows emerges from the interaction of heritable trends and specific individual and social learning processes (see Bateson 1978; Bateson 1991 for discussions of this general approach to understanding development of behaviour).

In the only other study of the ontogeny of twig tool use in birds, the presence or absence of adult demonstrators made no significant difference to the time it took juvenile woodpecker finches (*Cactospiza pallida*) to start using tools successfully (Tebbich et al. 2001). Two other TOBs have been observed to develop in isolated birds – egg breaking with stones by Egyptian vultures (*Neophron percnopterus*) (Thouless et al. 1989), and the use of pieces of plant material to wedge nuts while opening them by hyacinth macaws (*Anodorhynchus hyacinthinus*) (Borsari & Ottoni 2005) – thus proving that social input was not necessary. For wild NC crows, however, there is circumstantial evidence suggesting that birds acquire at least certain tool manufacture skills by social learning: crows cut tools from the edges of the rigid, thorny leaves of pandanus trees, with tool shapes varying regionally in shape and complexity in a manner consistent with cultural transmission (Hunt & Gray 2003). The possibility that aspects of TOB are culturally sustained would be strengthened if we could show that social influence indeed plays a role in NC crow development of TOB. If social factors are important, one should expect not only long term regional differences in the shape of tools produced by adults but also short term influences on manipulatory behaviour according to the exposure to tutors. We therefore also conducted an experiment with our tutored birds to investigate if NC crows match object choice to that of a human demonstrator.

In summary, although we do not see TOB as necessarily demanding in cognitive terms, we see it as a revealing behaviour that allows for a general understanding of animal physical cognition and in particular its development. For this reason, as far as possible we place the developmental observations of TOB in the general framework of behavioural development in birds.

A6.3 Methods

A6.3.1 Subjects and Housing

The subjects were four laboratory-born, hand-reared NC crows. They comprised two male siblings named 'Oiseau' and 'Corbeau', a male named 'Nalik' and a female named 'Uék' (all words meaning crow or bird in languages spoken in New Caledonia). All were offspring of members of our colony, and one (Uék) was the daughter of an individual (Betty) who has participated in all previous studies with captive NC crows in our laboratory. This was the first successful breeding of NC crows in captivity, and we used all available subjects. Uék was incubated by her parents and removed from the nest at 1 day old. The other subjects came from eggs that were removed from the nests shortly after being laid and artificially incubated. The chicks were hand-raised in artificial nests, initially in brooders and then in small pens mounted at table level in indoor aviaries. Pens were left open during the day, allowing the chicks to leave them at fledging. As nestlings, the birds showed a gradually increasing tendency to locomote inside and then outside the nest, so there was no sharp fledging point. At 25-26 days old, however, all four birds began to leave the nest and climb around the perches – a behaviour known as branching. We took branching, rather than fledging, as the starting point for recording behaviour, because it was at this stage that they began to locomote and manipulate objects.

Each aviary measured 3.3 by 3.9 by 2.5 m high, was on a natural daylight cycle, contained natural wooden perches and a woodchip substrate, and was enriched with at least 30 twigs of assorted shapes and sizes, live vegetation, ropes, toys and mineral blocks (some suspended from perches and some unattached). Holes, drilled into perches and into logs on the floor, were regularly provisioned with chopped meat and mealworms, most of which were accessible only through tool use.

Additional holes and crevices were used for tool use demonstration (see below), though they were also regularly replenished with food outside of experimental sessions. Five wooden blocks, with holes drilled horizontally 2 cm wide and 7 cm deep, were mounted onto perches, each in a different position in the aviary (the block holes; Figure 1a). Five crevices, of length 7 to 11 cm, depth 2 to 6 cm, and width 4 to 18 mm, were made with pairs of parallel wooden plates, and mounted on a wooden platform fixed to the wall (the crevice platform; Figure 1b). Crevice platforms were not installed in the aviaries until mid-way through the observation period (see below).

Growing nestlings were hand-fed chopped neonate rats (supplied frozen by Livefoods Direct®) with vitamin supplements; the amounts of this food type provided through active feeding were reduced gradually as the birds weaned. Post-fledging, the subjects had ad libitum access to the food mixture that we use to feed adult crows in our captive colony (soaked Go-Cat® cat biscuits, Orlux Universal® and Orlux Granules® insect and fruit mixes, peanuts, and mealworms). However, the most preferred food, meat, was only available during hand-feeding, by tool use, and during experimental and observation sessions (see below). Drinking and bathing water were permanently available. Each bird also had a cage (90 by 60 by 80 cm high) inside the home aviary, into which it was placed

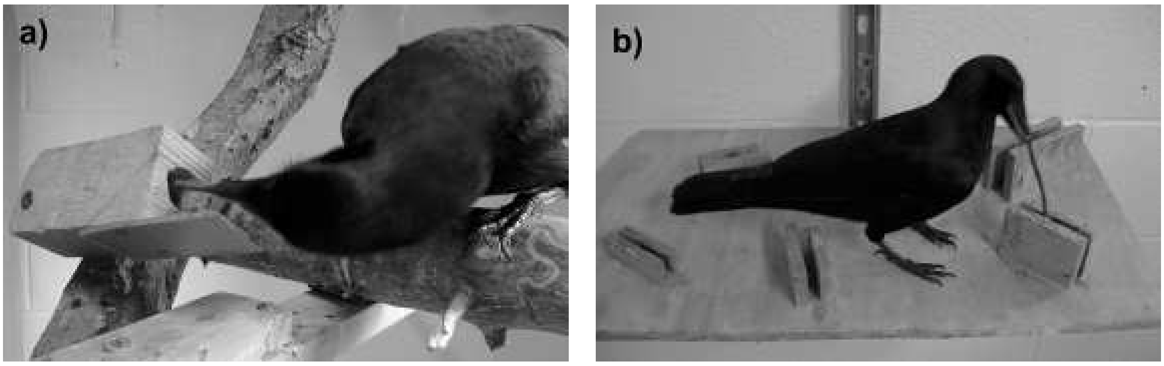


Figure 1: Photographs of **(a)** a block hole and **(b)** a crevice platform, both with a twig being inserted by Uék. For dimensions see text.

at night and also sometimes during experimental sessions (see below).

To determine the effects of demonstration of tool use by human foster parents while allowing them to experience social contact with a conspecific, we tried to keep the birds as two pairs, – the tutored group (Uék and Nalik), and the untutored group (Oiseau and Corbeau) – each in its own aviary. However, midway through the experiment, 33 and 34 days post-branching, Oiseau and Corbeau started to show a level of mutual aggression that potentially threatened their welfare, and they were therefore separated before they had a chance to injure one another. Thereafter one of them (rotated during the study) was housed in a separate covered outdoor aviary, of similar size as the other aviaries, and provisioned and enriched in the same way as described above.

A6.3.2 Ethical Note

Although no individuals were originally intended to be housed alone, due to the split of the untutored group, this became inevitable. However, because the individuals were hand-raised, they had frequent human social contact, not only during experimental sessions but also during additional informal ‘play’ sessions.

A6.3.3 Treatment and Observation Procedure

We first observed informally what type of behaviours the juveniles exhibited. On the basis of these preliminary observations, we defined behaviours for subsequent use in formal ethogram recording. Uék was the oldest, and she was therefore observed for this purpose until she was 21 days post-branching (at which time Nalik was 7, Corbeau 1, and Oiseau 0 days post-branching), when regular formal experimental observation sessions began. As the ethogram forms an integral and original part of this study, we report detailed descriptions and definitions of behaviours in the Results section.

There were three types of session: ‘observation’ sessions, which were for all birds, and two experimental session types – ‘teaching’ sessions, only for the tutored group, and ‘control’ sessions, for both groups. Before an observation session started the target individual and the co-housed bird were both placed in their cages, which were then covered so that the birds were unable to observe the experimenter (always BK) manipulate objects in the aviary. Food was removed from the aviaries, and meat was replenished in each of the five block holes. To give the subject easy access to suitable tools, ten twigs were taken from the floor and five each placed on two small perch-mounted platforms. The target bird was then released from its cage (the other bird remained within its covered cage throughout the session), and the experimenter sat on a chair in the aviary and observed the bird for 30 minutes, using a custom-written event recorder on a standard laptop. During 10% of the sessions a second experimenter was present, to make simultaneous video recordings for documentation purposes. Behaviour oriented towards the experimenters was infrequent in comparison to other behaviour types until the later stages of observation (see below), and was discouraged whenever it occurred by gently displacing the bird away from the experimenter.

Teaching sessions were as observation sessions, except for the addition of demonstrations by the human experimenter. There were five demonstrations during each teaching session, at the start and at 6 minute intervals thereafter. For each demonstration the experimenter got up from his chair, picked up a twig from the floor, used it to retrieve a piece of meat from one of the block holes, and left the meat for the bird to eat (the twig was also left in the hole; see supplementary movie clip 1 in Kenward et al. 2005[11]). When the birds ranged between 25 and 49 days post-branching, two modifications were made to this protocol: firstly, on two randomly selected demonstrations per session, the food was withheld in order to encourage the birds to obtain food for themselves, similarly to what has been reported in birds of other species feeding nestlings (Davies 1976); and secondly, two random demonstrations per session took place at a crevice on the crevice platform instead of at a block hole. The decision to include crevices was based on the observation that early tool manipulations were rather clumsy. To increase the chance of emergent TOB resulting in food rewards we therefore presented a food retrieval task which was still naturalistic but easier than the block holes because they required a less delicate manipulation of the tool.

Control sessions were as teaching sessions except that, instead of retrieving meat from the hole with a twig, a new piece of meat was placed next to the hole at the appropriate times. To control for the amount of local enhancement at the meat delivery sites across session types, the time taken to produce meat was the same in teaching and control sessions. Subjects in the untutored group were never exposed to tool use for food retrieval, or handling of twigs or twig-like objects (such as pens); due to experimenter

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[11] This is provided as Supplementary Movie 6-1 with this thesis.

error, however, Oiseau was exposed to twigs being picked up and placed on the platforms on four brief occasions between 33 and 37 days post-branching, but, like Corbeau, never witnessed tool use.

NC crows in the field continue to receive parental feeding for many months after fledging (Kenward et al. 2004), and we therefore continued to offer food to the subjects by hand at 1.5 hour intervals throughout the observation period. Feedings were staggered so that roughly half the sessions took place immediately after feeding, with the other half taking place approximately 45 minutes afterwards.

The criterion for termination of the formal observation and demonstration period was when the bird had reached the stage of successful tool use, defined here as the successful retrieval of food from either a hole or a crevice. In 3 birds, however, human-oriented behaviours increased to such a level that data recording was terminated prematurely to avoid biased data. In these cases, informal observation from outside the aviary and remote video recording were continued solely for the purpose of confirming successful tool use. Formal observation and demonstration lasted until 51 days post-branching for Uék, 38 for Nalik, 43 for Corbeau, and 44 for Oiseau.

Sessions took place between 07h30 and 19h30, were blocked pseudo-randomly so that different types occurred at all times throughout the day, and the different types were spread evenly throughout the period. Prior to 8 days post-branching, however, there were only observation sessions (i.e. neither teaching nor control sessions), because the birds were not yet mobile enough to follow and observe the demonstrator. Due to logistic constraints, it was impossible to employ a fully balanced design over the entire observation period (most noticeably, no data exists for Nalik in week 7), but the mean numbers of sessions per day were similar for the tutored and untutored group (tutored group: 0.5 observation sessions / day, 1.2 teaching sessions / day, and 0.3 control sessions / day; untutored group: 0.6 observation sessions / day, and 1.1 control sessions / day).

We also tested the crows' response to leaves from trees of the genus *Pandanus*, similar to those from which wild individuals make tools that vary regionally in shape and complexity; we do not give details here because these experiments have been presented elsewhere (Kenward et al. 2005).

A6.3.4 Statistical Analysis

As measures of the birds' behaviour, we calculated the proportion of time spent performing certain acts in each observation session. For parametric statistical analyses, we used arcsine square root-transformation of response variables to normalise errors (Zar 1999). We employed general linear models (GLM), using sequential sums of squares (Grafen & Hails 2002). We checked model fit by inspecting diagnostic scatter plots, using standardised residuals (Grafen & Hails 2002). All models were implemented in Minitab 14.1. 'Treatment group' was included as a factor in some of our GLMs. Because of the limited sample size, results of those analyses cannot be generalised beyond the four subjects investigated, and we consider the robustness of this aspect of our study in the Discussion.

Analyses of proportional data, as carried out in this study, may suffer from the 'unit sum constraint': as the proportion of one behaviour increases, the proportions of other behaviours are bound to decrease. Our analyses, however, were unlikely to be affected by this problem, as the behaviours of interest were performed infrequently and proportions were therefore comparatively small (see Results, especially Figure 6). It is worth reporting that we also modelled our data with continuous time Markov chains, which overcome problems of non-independence inherent in proportional data (Haccou & Meelis 1992); all analyses, however, yielded similar results to with the proportional data, and we therefore present proportion results only, because of their more intuitive interpretation.

A6.3.5 Matching of Object Choice

To further examine the importance of social input, we conducted an experiment into object choice with the two tutored subjects, when they were between three and four months post-branching (two months after formal observation and demonstration ended). We used thirty-two novel objects, mainly small toys and household items, that were small enough for an NC crow to carry. We assigned objects into 16 pairs so that each object in a pair would be of roughly similar attractiveness; we based this matching on criteria such as size and shininess.

A random object from each pair was assigned as the target object for Uék, and the other object for Nalik. Each object pair was then tested with each bird over 32 trials as follows: both birds were placed in their cages, which were covered with an opaque material, and then the objects were placed 40 cm apart on a table in the aviary, and also covered with an opaque material. The location of the target object was pseudo-randomised so that it could not occur on the same side for more than two trials in a row for one individual, and so that the target object was on each side eight times for each bird. The subject was then released from its cage, and a minute later the experimenter removed the object's cover and began the session, which consisted of a one minute demonstration period and a subsequent three minute period with no demonstration, followed by an additional demonstration and a non-demonstration period (so the sequence was Demo 1; Non-demo 1; Demo 2; Non-demo 2).

During the demonstration periods, the experimenter manipulated the target object by lifting it from the table and slowly rotating it in one hand, replacing it at the end. During the non-demonstration periods, the experimenter sat still on a chair. The bird had free access to both objects at all times – the experimenter allowed touching of the target object during demonstration but did not allow it to be carried away. If the objects had been moved by the bird in the first half of the session they were replaced in position before the second manipulation period, using a cover over the non-target object to prevent the subject seeing it manipulated. The sessions were video recorded and subsequently scored to determine, for each period, which object was manipulated most often, and for which object a bout of manipulation began first.

A6.4 Results

A6.4.1 General Pattern of Development and Ethogram Definitions

All four birds followed a qualitatively similar developmental pattern. We therefore begin by describing this common pattern, and providing definitions to be used in the ethogram (Table 1). We define three classes of object manipulation, namely: four kinds of 'touching' (including 'carrying'); four kinds of 'precursor actions', so named because they resemble aspects of mature tool use but are not directly functional in terms of allowing access to food; and actions of 'insertion', which we treat as directly functional because they can result in successful food extraction, and/or possibly food caching. Precursor actions were first observed in the second week post-branching, and reached a maximum level in week 4, at the same time that the first insertion actions occurred; the frequency of precursor actions remained roughly constant thereafter, whereas insertions increased steadily over the remaining observation period (Figure 2). Of the four precursor behaviours, the most common were ‘rubbing’ and ‘proto-probing’ (Table 1, Figure 3, Supplementary Movies A6-1 and 2, respectively). Proto-probing was a particularly striking behaviour in which the birds held twigs in their beaks and moved them back and forth, in a similar manner to how they probe holes and crevices, except that the twig was not inserted in any hole or crevice.

‘Touching’ starts while locomotion is only just beginning to develop, and ‘carrying’ develops in step with locomotion (Figure 4). The objects manipulated changed as the birds developed (Figure 5). As for caching, we observed that food was often inserted into holes and left there. The crows usually, but not always, retrieved the food immediately. This behaviour appears to be proto-caching, but unfortunately we were unable to collect data on whether individuals specifically retrieved food they had hidden.

Table 1: Ethogram definitions of object oriented behaviours in juvenile NC crows

Behaviour category	**Behaviour**	**Description**
Touching	Grasping	Contacting an object by placing the beak parts on either side
	Nibbling	Grasping but with open and close or back and forth movements of the beak
	Pecking	Self-explanatory
	Carrying	Grasping an object so it is no longer attached to or supported by a substrate
The following behaviours are all possible only during carrying:		
Precursor action	Rubbing	Rubbing any object against any substrate with at least two (and usually more) back and forth movements (excluding proto-probing, wrong-angle probing, and insertion [below]) (Supplementary video 1)
	Proto-probing	Holding a twig in a manner appropriate for probing a hole or crevice, touching it against a substrate which is not a hole or crevice (for example, the side of a perch), and moving it back and forth against the substrate (Supplementary video 2)
	Poking	Holding a twig and jabbing the end against any flat substrate
	Wrong-angle-probing	Holding a twig and performing motions which could result in an insertion, because the behaviour is directed towards a hole or crevice, but do not because the twig is held at the wrong angle – emerging either sideways or backwards out of the beak
Directly functional action	Inserting	Inserting any object into a hole or crevice. Sometimes this behaviour also includes back and forth head motions which we call ‘probing’, but in practice it is difficult to distinguish between probing and non-probing insertion, so probes were not recorded separately from other insertions

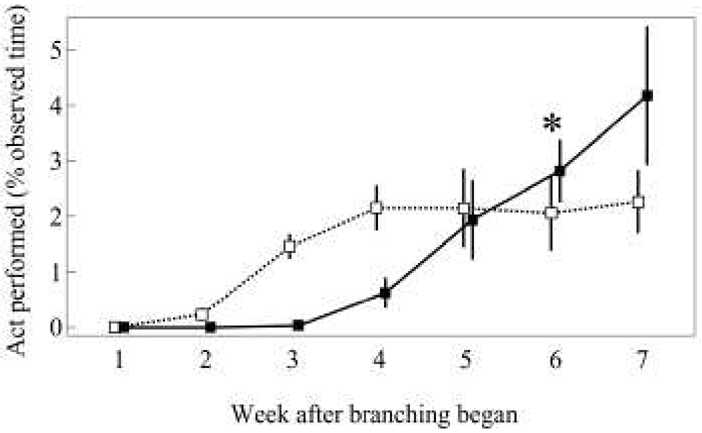


Figure 2: Development of precursor actions (□) and insertion (■) in four juvenile NC crows. The asterisk indicates the week when successful food retrieval was first observed. Note that, in order to show general development, tutored and untutored birds are pooled (see Figure 6 for differences between the groups). Error bars indicate standard error. Data points in each week are slightly offset to avoid overlap.

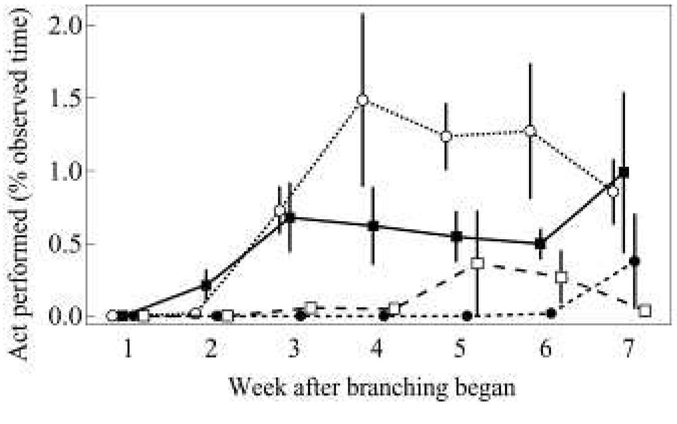


Figure 3: Types of precursor action shown by four juvenile NC crows, showing rubbing (○), proto-probing (■), poking (●), and wrong-angle-probing (□). Data pooled as in Figure 2. Error bars indicate standard error. Data points in each week are slightly offset to avoid overlap.

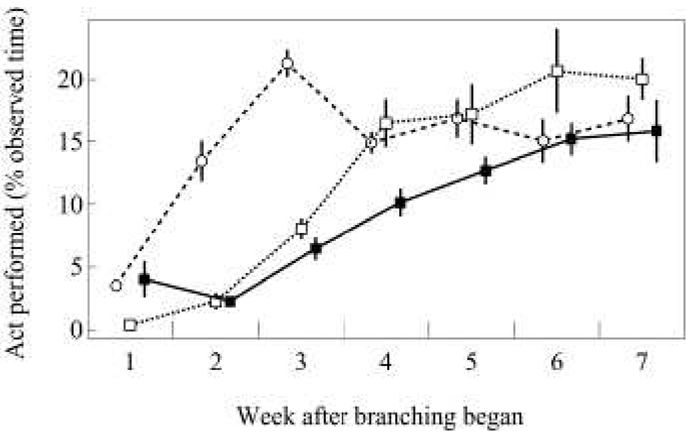


Figure 4: General pattern of development in four juvenile NC crows, showing locomotion (■), object touching excluding carrying (○), and object carrying (□). Error bars indicate standard error. Data points in each week are slightly offset to avoid overlap.

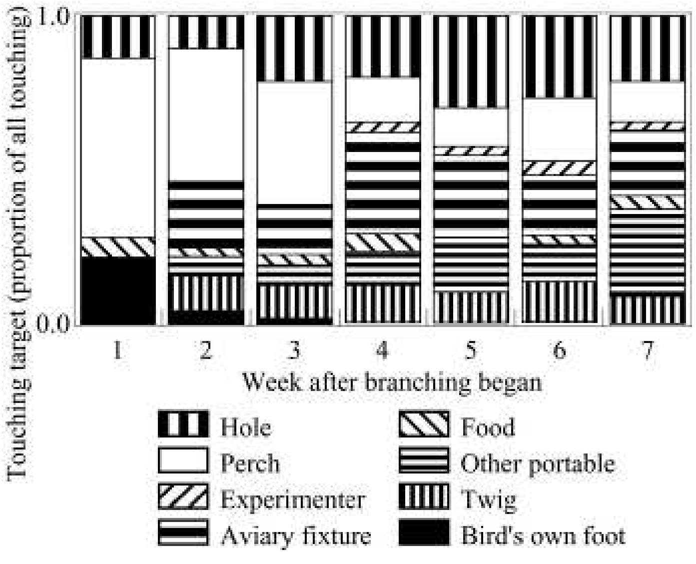


Figure 5: Object categories touched by four juvenile NC crows. Categories are self-explanatory or defined as follows. Hole: the lip or cavity of any natural or artificial holes and crevices in the aviary. Perch: Any wooden part of the aviary fixtures. Aviary fixture: Any part of the aviary not covered by other categories. Other portable: any non-food non-twig item which the bird could carry (e.g. toys).

A6.4.2 Comparison of Treatment Groups

First we examined whether the behaviour of the two subjects in the tutored group differed significantly between teaching, observation, and control sessions. Taking only the data for Nalik and Uék, we formulated GLMs, entering in the following order these predictor terms: 'age' (in days since branching began) as a covariate, 'individual', and 'session type' as fixed factors, and the four possible interactions terms. Of seven response variables, session type and its interactions were not significant predictors for the following six: locomotion, twig carrying, non-food non-twig item carrying (e.g. toys or wood chips), food inserting, non-food non-twig item inserting, or twig inserting. The only variable which session type significantly affected was food carrying ($F_{1,114} = 10.18$, $P < 0.001$), with birds showing a higher proportion of this behaviour in teaching and control sessions compared to observation sessions; this is somewhat trivial, as food was not provisioned in observation sessions (see Methods).

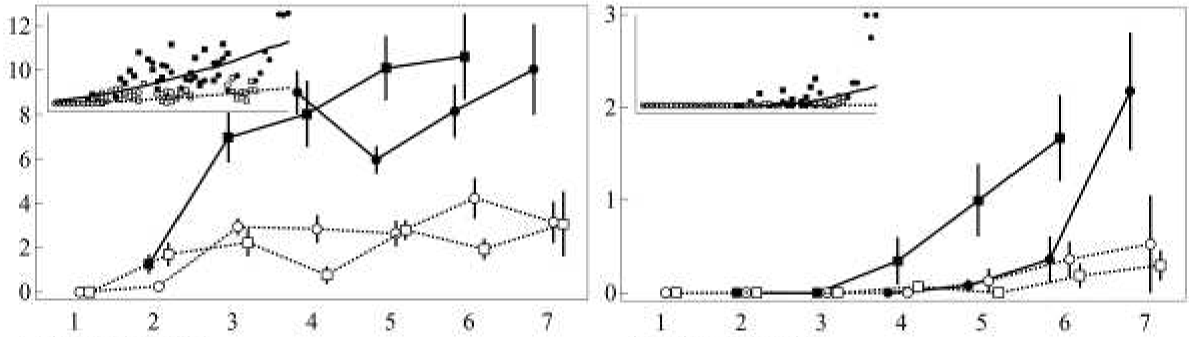
For the six variables statistically unaffected by session type, we pooled data from the different sessions to compare behaviour between treatment groups. To examine the effect of social experience we fitted GLMs, entering in the following order these predictor terms: 'age' as a covariate, 'individual' nested within 'treatment group' and 'treatment group' as fixed factors, and the interactions between 'age' and 'individual', and between 'age' and 'treatment group' (Table 2).

As might be expected, the frequency of all analysed behaviours increased with age (Figure 6). More important, however, is that we found significant positive effects of tutoring on the proportions of twig carrying (Figure 6a) and twig inserting (Figure 6b). For twig carrying, and all types of inserting, there were significant interactions between treatment group and age, indicating that the tutored group had a faster rate of increase in the frequency of those activities (Figure 6a,b,d,e). For locomotion and non-food non-twig item carrying, we found individual differences but no significant differences between treatment groups (Figure 6c,f).

Table 2: Effects of age, treatment group, and individual difference on behaviours in juvenile NC crows.

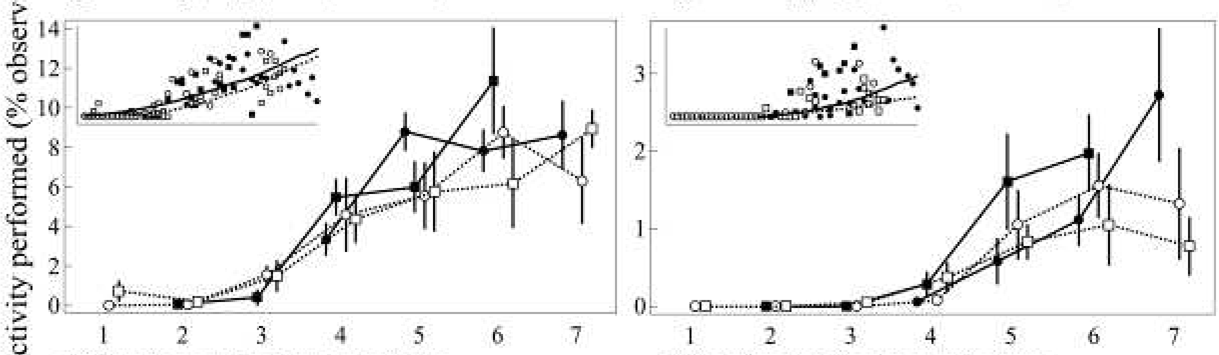
	Age		Individual		Treatment group		Age * Individual		Age * Treatment Group	
Response variable	$F_{1,264}$	P	$F_{2,264}$	P	$F_{1,264}$	P	$F_{2,264}$	P	$F_{1,264}$	P
Carrying twigs	202.27	< **0.001**	1.41	NS	115.11	< **0.001**	3.67	**0.027**	8.88	**0.003**
Inserting twigs	149.01	< **0.001**	0.22	NS	9.20	**0.003**	14.45	< **0.001**	99.82	< **0.001**
Carrying non-food non-twig items	283.19	< **0.001**	0.14	NS	0.30	NS	17.94	< **0.001**	0.97	NS
Inserting non-food non-twig items	155.84	< **0.001**	1.58	NS	0.00	NS	1.19	NS	9.24	**0.003**
Inserting food	124.63	< **0.001**	1.16	NS	0.41	NS	1.42	NS	10.00	**0.002**
Locomotion	352.13	< **0.001**	6.19	**0.002**	0.01	NS	11.75	< **0.001**	1.09	NS

Significant *P* values shown in bold. See methods section for GLM details and Figure 6 for visualisation.



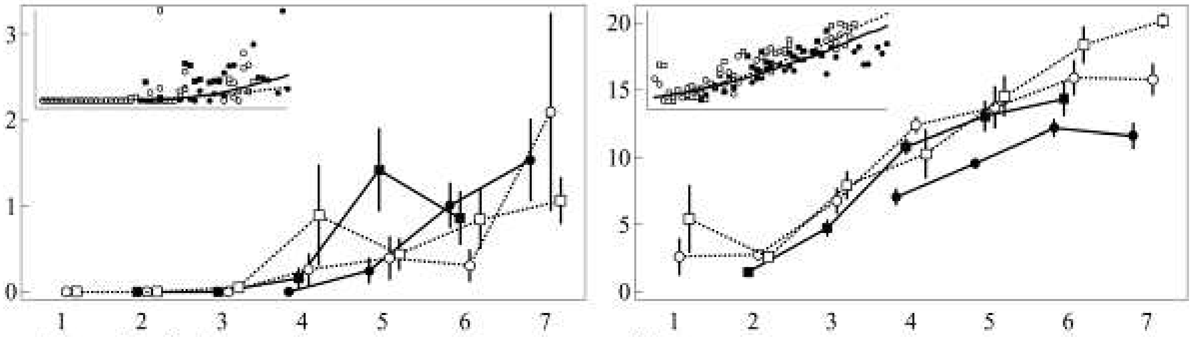
a) Carrying twigs.
Age ($F_{1,264}=202.27$, $P<0.001$),
Group ($F_{1,264}=115.11$, $P<0.001$),
Age * Individual ($F_{2,264}=3.67$, $P=0.027$),
Age * Group ($F_{1,264}=8.88$, $P=0.003$).

b) Inserting twigs.
Age ($F_{1,264}=149.01$, $P<0.001$),
Group ($F_{1,264}=9.20$, $P=0.003$),
Age * Individual ($F_{2,264}=14.45$, $P<0.001$),
Age * Group ($F_{1,264}=99.82$, $P<0.001$).



c) Carrying non-food non-twig items.
Age ($F_{1,264}=283.19$, $P<0.001$),
Age * Individual ($F_{2,264}=17.94$, $P<0.001$).

d) Inserting non-food non-twig items.
Age ($F_{1,264}=155.84$, $P<0.001$),
Age * Group ($F_{1,264}=9.24$, $P=0.003$).



e) Inserting food.
Age ($F_{1,264}=124.63$, $P<0.001$),
Age * Group ($F_{1,264}=10$, $P=0.002$).

f) Locomotion.
Age ($F_{1,264}=352.13$, $P<0.001$),
Individual ($F_{2,264}=6.19$, $P=0.002$),
Age * Individual ($F_{2,264}=11.75$, $P<0.001$).

Week after branching began

Figure 6: Comparison of development in four juvenile tutored and untutored NC crows. Tutored group (solid lines): Uék (●) and Nalik (■); Untutored group (dashed lines): Oiseau (○) and Corbeau (□). Inset panels show the raw data and model fit for the two groups. Error bars indicate standard error. Panel legends show significant predictors for each dependent variable. For details of statistical model, see text and Table 2.

A6.4.3 Matching of Object Choice

Both birds were eager to manipulate the objects, during both the demonstration and non-demonstration periods – in only two trials out of 32 did a bird not manipulate both objects at least once. Nalik performed a mean ± SE of 11.4 ± 1.1 bouts of touching per trial with mean length of 10.1 ± 0.8 s, and a mean of 5.0 ± 0.9 carrying bouts with mean length of 8.6 ± 1.5 s – corresponding figures for Uék were, respectively, 11.2 ± 0.7 bouts and 10.7 ± 0.8 s; and 8.6 ± 0.9 bouts and 7.7 ± 0.7 s. On six occasions a bird picked up one object and poked the other object with it.

The birds demonstrated a clear preference for the target object (Figure 7), both in terms of which object they manipulated first, and which object they manipulated most often. There was a trend for this effect to increase in the second half of the trial, so that the target object was not manipulated significantly more often until the demonstration 2 period.

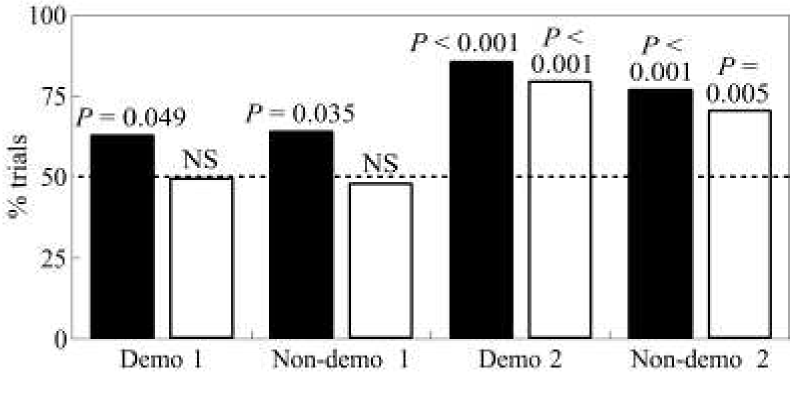


Figure 7: Juvenile NC crow object preference after witnessing human foster parent manipulating one of a pair of novel objects. The categories are the phases within a trial, in sequence (see method section for details). Bars indicate how often the subject manipulated demonstration target first (■), and most often (□). Dashed line indicates results expected under the null hypothesis of no effect of demonstration. $N = 32$ (16 trials each for Uék and Nalik, pooled). P values are calculated against the chance binomial distribution.

A6.5 Discussion

A6.5.1 General Pattern of Development

In all detailed studies of the ontogeny of avian object oriented behaviour of which we are aware, similar patterns of development have been observed: precursor behaviours (with no direct function) appear first, with directly functional behaviours emerging in the course of gradual improvement. The following are some examples. In song thrushes (*Turdus philomelos*), snail-smashing on anvils is preceded by the attempted smashing of non-snail objects, and also by flicking movements in which the object does not connect with the anvil (Henty 1986). In laughing gulls (*Larus atricilla*), the pecking response at the parent's bill which elicits parental feeding is initially sometimes directed at inappropriate objects, and improves in accuracy over time (Hailman 1967). Even in precocial species, such as the greater rhea (*Rhea americana*), feeding motor patterns are initially displayed when there is no relevant stimulus (Beaver 1978). Caching Parids begin by inserting food items into crevices without actually letting go and leaving them in place (Clayton 1992; Haftorn 1992). In the development of tool use in woodpecker finches (*Cactospiza pallida*), juveniles pass through a number of tool-oriented developmental stages before successfully using tools, such as 'uncoordinated manipulations' and 'exaggerated, playful movements' while holding twigs (Tebbich et al. 2001).

Nest building is particularly relevant to our study because it also involves twig handling. Its ontogeny, however, has hardly been studied, with a notable exception provided by Collias and Collias (1964; 1973; 1984) who report that village weaverbirds (*Textor cucullatus*) begin manipulating nest materials within weeks of fledging and continue to do so until they build their first nest. Kortland (1955) describes how cormorant chicks (*Phalacrocorax carbo*), still in the nest, perform a quivering movement with the head while holding a twig, a movement they later combine with a jab which incorporates the twig into the nest. Many non-object oriented avian behaviours also develop in a similar manner, such as dust-bathing (Larsen et al. 2000) and social display (Groothuis 1993).

In addition to the presence of precursors, the TOB we observed in NC crows has other things in common with all these avian behaviours. Although developmental field work is missing, the fact that all four individuals developed tool use in a qualitatively similar manner implies that the TOBs we observed in these juveniles are species-typical and include stereotyped action patterns such as proto-probing which develop in a predictable manner without the need of being shaped by successful food extractions. Similarly to other cases of an apparently missing role for food reinforcement, such as song learning or imprinting, experience may still have a role in shaping the functional behaviour, because the sensory feedback from rubbing twigs against any substrate may serve to hone the motor control to be used later on in food extractions.

The involvement of stereotyped, inherited action patterns would once have earned TOB the description of ‘innate’. Due to many problems with the term, however, including that it discourages investigation of development without actually explaining it (Lehrman 1953; but see Lorenz 1965; Berridge 1994; Marler 2004), and that it has been variously defined as implying a number of different characteristics which have not in fact been shown to reliably co-occur (Mameli & Bateson, in press), the term has been almost abandoned. We prefer to avoid the label, partly for these reasons, but also because of its common but unwarranted association with non-intelligent behaviour. It has often been assumed that there is a trade off between the degree of inheritance of patterns of behaviour and their cognitive sophistication: behaviour seen to be largely innate (or instinctive) is in these cases assumed to be less likely to be accompanied by complex cognition. In fact, a rich hereditary endowment (such as the human predisposition for language acquisition, the inclination to social nesting in parrots or the use of tools in NC crows) may be the platform that allows and enhances sophisticated cognitive development (see Gibson 1990). In the case of TOB, we have found that NC crows do have an inherited developmental program that includes well defined motor schemes, some of which emerge before their integration in directly functional TOB. This does not exclude the intervention of flexible cognitive processes in the acquisition and/or deployment of the behaviour.

It has been argued (Hansell 2000) that because nest building rivals NC crows’ TOB with respect to diversity of materials used and complexity of their combination, TOB may not be cognitively more complex, and may be under tight genetic control, as nest building seems to be. As we have argued, however, the presence of inherited action patterns does not exclude advanced cognition, and indeed from this perspective nest building may have been underestimated in its cognitive sophistication, rather than TOB being overrated.

The inherited component we observed in the development of TOB opens the possibility that regional differences in tool manufacturing, especially those shown for tools made with pandanus leaves (Hunt & Gray 2003) could be due to genetic differences. This possibility requires some attention before conclusions about cultural transmission are accepted, especially given that it is known that complex sequences of action patterns can be inherited (e.g. Colonnese et al. 1996), and the recent discovery that spatial genetic variation can be maintained over surprisingly small scales (Garant et al. 2005).

We have suggested that a possible function of the precursor behaviours is to hone the functional TOB. However, behaviour performed by juveniles which resembles that of adults without achieving the same ends need not be causally related to the emergence of adult behaviour, but instead may be expressed as a consequence of maturation of the organism's nervous system (Harrison 1904; Haverkamp & Oppenheim 1986). Amongst the previously mentioned avian behaviours, there are several examples where denying juveniles the chance to perform precursor behaviour does not prevent them from later performing the directly functional behaviour. This is true for nest-building (Collias & Collias 1973); feeding in chicks (Cruze 1935; Hailman 1967); caching in Parids (Clayton 1994); and snail-breaking by thrushes (Henty 1986). Similarly, one of our subjects made functional tools on the first day of being exposed to pandanus leaves (Kenward et al. 2005). Experimental manipulation can even cause precursor behaviours to be replaced earlier by the directly functional behaviour – gull chicks, which perform precursor versions of aggressive social displays, can be caused by testosterone administration to perform the full display (Groothuis 1989; Baerends 1990). The "precursor" label is thus just descriptive, and the function of such behavioural patterns must be seen as a topic to investigate, rather than assuming that they serve to prepare the adult's version of the behaviour.

It is likely, however, that the precursor behaviours do serve some function. Hogan (1994; 2001) has argued that in the development of behaviour "systems" ranging from hunger and feeding to social displays, some general principles apply. In his view, motor, perceptual, and central control mechanisms pertaining to different systems often initially develop independently, but later become integrated. For example, motor components of dustbathing in fowl are at first performed in the absence of any eliciting stimuli, and only later become connected to the perceptual and control mechanisms (Kruijt 1964). NC crow TOB can fit this idea. The motor mechanisms which will later result in hole-probing are initially performed in the absence of the stimulus provided by holes, resulting in proto-probing. Later, the same motor mechanisms become integrated with perceptual and control mechanisms which allow the behaviours to be performed at the appropriate times.

In junglefowl chicks (*Gallus gallus spadeus*) hunger and pecking are under independent control immediately after hatching, and chicks must learn that pecking leads to ingestion before the systems can function together (Hogan 1984). The initial function (or at least the consequence) of pecking is thus not primarily to allow the chick to feed, but rather to allow learning about the consequences of pecking. Similarly, the function of the NC crow precursor behaviours might be to learn about the consequences of object manipulation. Clearly, they cannot learn how to extract food from proto-probing. But, just as the junglefowl chicks need to learn about ingestion before they can learn what to eat, the crows may need to learn fundamentals such as that inserting into a solid object is only possible at a concavity.

This form of tool use acquisition, in which the affordances of objects and surfaces are learned by trial and error manipulation beginning at an early stage of development, has also been described as perception-action development, and has been argued to be of fundamental importance in the acquisition of tool-oriented skills in children and other primates (Gibson & Pick 2000; Lockman 2000). Although couched in different language, this interpretation is consistent with classic explanations for behaviour development – for example the way in which begging gull chicks are born with a tendency to peck at objects resembling their parent’s beak, but subsequently learn more about the relevant stimuli and the results of their own actions (Hailman 1967).

Confirming the importance of perception-action routines for NC crows requires additional experiments, but the idea provides a good framework to think about, for example, the emergence of insertion out of proto-probing. Note that this account assumes some form of internal reinforcement for inserting objects, which would itself need to be inherited, because the subjects performed many insertions over a period of several weeks before they resulted in food rewards. Object insertion could be inherently rewarding, and/or the learning of affordances enabled by the act could be rewarding. The latter possibility is emphasised by traditional accounts of perception-action learning, but the fact that the crows persisted in performing actions without food reward long after they had probably learned their consequences means the former is also a likely factor. A similar process could also explain the occurrence of precursor action patterns – it may be that what are inherited are not developmental programs for motor patterns, but rather for tendencies to find certain actions rewarding.

Perception-action learning may also be important in the acquisition of more sophisticated forms of goal-directed control, for example learning the relationship between holes of certain depths and diameters and twigs of appropriate dimensions, which leads to the known ability of adults to select and modify tools for specific circumstances (Chappell & Kacelnik 2002; Weir et al. 2002; Chappell & Kacelnik 2004). Indeed, it is reasonable to speculate that natural selection may act on variance for what constitutes reinforcement, and that minor mutations in this may lead to the emergence, by the normal, pre-existing processes of learning by reinforcement, of vastly different adult behaviour. The process of discovering internally reinforced actions by exploring possible behaviours would manifest as play.

Much of the crows' object-oriented behaviour can be described as play, which is frequently observed in birds (Ficken 1977; Ortega & Bekoff 1987; Diamond & Bond 2003). Burghardt (2005) defines play as "repeated, incompletely functional behaviour differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily when the animal is in a relaxed or low-stress setting". In our subjects, precursor behaviours continued after directly functional behaviour had been developed; indeed, our wild-caught adults also frequently show apparently functionless behaviour, such as inserting stones into holes in logs and repeatedly breaking pieces of wood. As a prolonged development period, including much play, is thought to be an adaptation that allows animals to develop a variety of skills (e.g. Burghardt 2005), the play observed in NC crows could enable them to learn the wide range of TOBs displayed by the species in natural circumstances. Our subjects sometimes engaged in playful behaviours which did not fit easily into our ethogram categories and consequently were not recorded formally in detail: for example, Oiseau sometimes spent time holding one end of a long cardboard tube whilst running on the ground pushing the tube along in front. These observations supports the hypothesis that behaviour which allows the learning of object affordances is inherently rewarding.

A6.5.2 Caching

Our observations of food being frequently inserted and left in holes supports the hypothesis that NC crows are a caching species, although we did not record whether the birds retrieved food after a long enough period for this to be conclusive. Inserting and quickly retrieving food is a precursor to caching in titmice (*Parus* spp.) (Clayton 1992; Haftorn 1992). Given the existence of anecdotal reports of caching in the wild (Hunt 2000; our pers. obs.), and the facts that almost all corvids cache (Goodwin 1986) and the common ancestors of both the Corvidae family and the *Corvus* genus were almost certainly cachers (unpublished data S. R. de Kort & N. S. Clayton), it is very likely that NC crows do cache food. Caching and tool use are physically similar in that they both involve inserting objects into concavities. Since different motor patterns can develop from the same precursor by differentiation (Berridge 1994), it is possible that caching and TOB might be ontogenetically and/or phylogenetically related – a hypothesis explored elsewhere (unpublished data B. Kenward, C. Schlögl, A. A. S. Weir, C. Rutz, T. Bugnyar & A. Kacelnik).

A6.5.3 Ontogeny of Tool Use in Other Species

With the notable exceptions of the woodpecker finch (Tebbich et al. 2001) and the Egyptian vulture (Thouless et al., 1989), previous detailed studies of TOB ontogeny have focussed on primates (e.g. Beck 1978) – although Borsari & Ottoni (2005) also describe an avian TOB thought to result from inherited action patterns. The development of manipulatory behaviour has often been investigated from the perspective of cognitive development, by testing sensitivity to functional aspects of objects (e.g. Hauser et al. 2002; Spaulding & Hauser 2005), or by using conceptual tools such as neo-Piagetian theory (e.g. Potì & Spinozzi 1994). A similar approach is beyond the scope of this study (we have not yet completed an analysis of Piagetian stages in NC crows).

Longitudinal ethological studies of object manipulation ontogeny in primates show that a long period of object exploration and learning, during which object oriented behaviours become progressively more complex, precedes successful tool use (Fragaszy & Adams-Curtis 1997; Inoue-Nakamura & Matsuzawa 1997; Biro et al. 2003; Lonsdorf 2005; Lonsdorf 2006). It is also known that juveniles from many primate species have a predisposition to perform certain manipulatory action patterns, such as insertion – e.g.

chimpanzees, *Pan troglodytes* (Schiller 1952; Hayashi & Matsuzawa 2003); capuchins, *Cebus apella* (Parker & Potì 1990; Fragaszy & Adams-Curtis 1997); and baboons, *Papio cynocephalus anubis* (Westergaard 1992) – although for many of these studies social influence cannot be ruled out. Fragaszy and Adams-Curtis (1991), and Parker and Potì (1990), both interpreting their observations of the ontogeny of manipulatory behaviour in capuchin monkeys, concluded that tool use probably develops due to learnt associations between motor patterns (aspects of which are inherited) and their consequences. Fragaszy and Adam-Curtis (1991) point out that the fact that inefficient behaviours are only gradually reduced is more consistent with a behaviourist explanation than with neo-Piagetian processes such as assimilation and accommodation, and the same logic applies to our observation of the continuation of precursor behaviours after directly functional behaviour was established. Our account of NC crow TOB ontogeny in terms of inherited predispositions and the learning of object affordances through exploration that is not externally reinforced therefore corresponds well to accounts of the development of tool use in primates, including humans (Gibson & Pick 2000; Lockman 2000).

Among the most complicated TOBs described in non-human animals is nut-cracking as performed by chimpanzees (Inoue-Nakamura & Matsuzawa 1997; Boesch & Boesch-Achermann 2000; Biro et al. 2003; Hayashi et al. 2005) and capuchins (Fragaszy et al. 2004). Juvenile chimpanzees acquire the skill at about 3.5 years of age, after extensive object exploration since infancy. With respect to manipulation of stones alone, Inoue-Nakamura and Matsuzawa (1997) recorded 21 different fundamental actions – more than twice as many categories of object manipulation as we recorded. This is partly due to unavoidable arbitrariness in categorizing behaviour, but it may also reflect real complexity and be due to the fact that primates are equipped with four five-digit manipulatory appendages, plus a mouth, whereas NC crows make do with a beak and two feet which are less dextrous than chimpanzee hands. Skills like nut-cracking with stones, which involve the positioning of three objects, may be impossible for crows mainly because of differences in anatomy, not cognition (though crows have their own solution to this problem: Hunt et al. 2002). For both twig tool use in NC crows and nut cracking in chimpanzees, although suggestive evidence exists, there is no conclusive proof that the agents have knowledge of the physical forces involved – the behaviours are best accounted for by a combination of inherited predispositions and learnt knowledge of object affordances.

A6.5.4 Social Influence

As mentioned already, wild NC crows show some forms of TOB which are more complex than ‘simple’ twig tool use, including manufacture of step-cut pandanus leaf tools (Hunt & Gray 2003) and hooked twig tools (Hunt & Gray 2004a). Furthermore, wild-caught NC crows investigated under controlled conditions in the lab show tool-related skills (Chappell & Kacelnik 2002; Weir et al. 2002; Chappell & Kacelnik 2004) which clearly exceed those observed so far in our hand-raised juveniles. We know that crows can make the simple pandanus tools without the opportunity for observation (Kenward et al. 2005), and it is still possible that given a longer period the juveniles would, by themselves, develop these advanced forms of tool-making. However, the possibility remains that social learning plays a role in the acquisition of more advanced TOB behaviours – specific techniques and tool shapes may be socially transmitted. In the following paragraphs, we critically discuss this possibility.

The results of our object choice experiment show that there is a clear effect of social influence by human foster parents on object manipulation in NC crows – an effect which could be described as either stimulus or local enhancement depending upon whose definitions are used (Galef 1988; Heyes 1994). The preference is robust to the extent that it is displayed not only during demonstrations but also when the demonstrator is no longer interacting with the objects. Preferential attention to objects or sites attended to by tutors could provide a mechanism for wild juvenile NC crows to learn socially which objects are relevant for tool use. It is worth noting, however, that if social transfer is responsible for regional differences in pandanus tool manufacture (Hunt & Gray 2003), it would require a mechanism such as imitation or emulation, which have been demonstrated experimentally in other (non-tool using) bird species (Zentall 2004) but have not yet been explored in this species.

The two tutored birds carried and inserted twigs more frequently than the untutored pair. This effect was found in all sessions, not only in those in which demonstration took place, indicating a lasting after-effect of demonstrations. They also increased twig-related behaviours, as well as insertions of other objects, at a faster rate than the untutored birds. While there are several caveats in the interpretation of these results (two of the subjects were siblings, and the sample was small, meaning that chance genetic or experiential individual differences cannot be ruled out), several lines of evidence suggest that their increased twig carrying and inserting was a result of the tutoring.

Firstly, our social enhancement experiment demonstrated that social influence does affect object choice. Secondly, differences between the tutored and untutored crows appeared in the parameters expected to differ if social learning takes place, but not in other parameters used to measure general development – locomotion and non-food non-twig item carrying. Thirdly, the effects we found were very marked – after two weeks post-branching, both tutored birds carried twigs more than twice as often as either of the untutored birds.

Juvenile NC crows in the wild observe their parents using tools and subsequently use the same tools (Hunt 2000), as do juvenile chimpanzees (e.g. Lonsdorf 2006), but it is unknown how this affects the crows' acquisition of TOB. The only other study investigating the ontogeny of twig-tool use in birds found no effect of social influence (Tebbich et al. 2001). However, social influence on tool use and object choice has been described for a number of primate species (e.g. Fragaszy & Visalberghi 2004; McGrew 2004).

A6.5.5 Concluding Remarks

In spite of its uniqueness and complexity, the development of TOB in NC crows has many features in common with the development of other avian behaviours, particularly in evidencing a complex interplay between a rich hereditary endowment, individual learning, and socially-transmitted knowledge. While much remains to be investigated, our observations allow for the elimination of several putative mechanisms of acquisition. In particular, we can exclude the extreme possibilities that TOB is entirely dependent on social inputs (i.e. sustained exclusively by cultural transmission and thus not reflecting a dedicated evolved adaptation), or that it has a purely individual, insight-based origin. Although we do not know yet how important TOB is in the economy of resource acquisition in the wild, it is also unlikely that tools are just a luxury: if they were, we would not see inherited action patterns that must have evolved through selection and are crucial in sustaining TOB in adult crows (see Tebbich et al. 2002 for an investigation of this issue in the woodpecker finch). In terms of cognition, and given NC crows' ability to find creative solutions to novel problems involving tools, it remains a priority to establish if TOB, or the circumstances that led to its evolution, have fostered specially advanced abilities for thoughtful inference.

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