ORIGINAL ARTICLE

The right tool for the job: what strategies do wild New Caledonian crows use?

Gavin R. Hunt · Robb B. Rutledge · Russell D. Gray

Abstract New Caledonian crows *Corvus moneduloides* (NC crows) display sophisticated tool manufacture in the wild, but the cognitive strategy underlying these skills is poorly understood. Here, we investigate what strategy two free-living NC crows used in response to a tool-length task. The crows manufactured tools to extract food from vertical holes of different depths. The first tools they made in visits were of a similar length regardless of the hole depth. The typical length was usually too short to extract food from the deep holes, which ruled out a strategy of immediate causal inference on the first attempt in a trial. When the first tool failed, the crows made second tools significantly longer than the unsuccessful first tools. There was no evidence that the crows made the lengths of first tools to directly match hole depth. We argue that NC crows may generally use a two-stage heuristic strategy to solve tool problems and that performance on the first attempt in a trial is not necessarily the 'gold standard' for assessing folk physics.

Keywords Cognition · Folk physics · New Caledonian crows · Tool manufacture and use

Introduction

The behaviour of tool-using animals suggests that they might have a rudimentary understanding of tool-related folk

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physics. Egyptian vultures *Neophron percnopterus* select stones of an appropriate size to throw at ostrich *Struthio camelus* eggs (Thouless et al. 1987). Woodpecker finches *Cactospiza pallida* can modify material in appropriate ways to make effective tools (Millikan and Bowman 1967; Tebbich and Bshary 2004). Vultures and finches seem to develop these abilities through trial-and-error learning. Captive cotton-top tamarins *Saguinus oedipus*, tufted capuchins *Cebus apella* and chimpanzees *Pan troglodytes* also develop sensitivity to functional aspects of tool tasks and can use this information to successfully complete them (Hauser 1997; Povinelli 2000; Hauser et al. 2002; Fujita et al. 2003; Evans and West-ergaard 2004). Povinelli (2000) takes a cautious approach and suggests that such problem solving probably involves associative rules developed by trial-and-error learning rather than sophisticated understanding of causal relations between objects. Chimpanzees have the most diverse tool use amongst nonhumans (McGrew 1992; Whiten et al. 1999). A heavy reliance on trial-and-error learning and signs of limited causal understanding have led researchers to suggest that this helps explain why chimpanzee populations have not evolved their tools incrementally over time (Nagel et al. 1993; Tomasello and Call 1997; Povinelli 2000).

If sophisticated tool manufacture requires a good understanding of the physical world, then New Caledonian crows *Corvus moneduloides* (NC crows hereafter) may have a good grasp of folk physics. NC Crows in the wild manufacture and use tools in ways more sophisticated than do other nonhumans (Hunt 1996, 2000a; Hunt and Gray 2002, 2003, 2004a,b). For example, they manufacture a range of hook tools using material-specific techniques (Hunt 1996; Hunt and Gray 2002). There is also evidence that their hooked-twig and stepped pandanus tool designs evolved through diversification and cumulative change (Hunt and Gray 2003, 2004a). Cumulative technological evolution is thought to

require a suite of complex cognitive abilities, especially accurate social learning (Tomasello 1999).

Experimental evidence is emerging that NC crows' manufacture skills in the wild could be based on a good understanding of what characteristics a tool should have to complete a specific task. A team led by Alex Kacelnik has published three papers investigating the behaviour of a male (Abel) and a female (Betty) NC crow when they selected or modified material for use as tools in different tasks. The main findings they reported are as follows: (i) the crows chose stick tools of an appropriate length for a task and significantly matched tool length to distance-to-food (Chappell and Kacelnik 2002), (ii) Betty chose stick tools of a suitable diameter to insert in different sized holes and both crows made tools of thicknesses that significantly 'tracked' the size of the holes in which they were used (Chappell and Kacelnik 2004), and (iii) Betty modified unfamiliar material without trial and error to solve a novel task; she bent straight sections of wire to extract a small bucket containing food from a vertical tube (Weir et al. 2002).

What cognitive strategies might animals use to solve a tool problem? They might use on-the-spot trial-and-error learning. This would produce random success or failure until the correct solution was found and not a consistently successful outcome. They could also use immediate causal inference (ICI), or insight, assessing the problem before attempting it and then solving it. Another possibility is that animals use a two-stage heuristic strategy. They initially tackle a tool problem using a behavioural routine developed by prior experience that works most of the time, with little attention to the specific tool characteristics that are required (we call this 'default behaviour'). If the default behaviour fails, it is then appropriately adapted to solve the problem. Heuristic strategies based on routines are common in human decision-making where deviation from a routine can be difficult even after it produces a detrimental outcome (Betsch et al. 2004). Two possible mechanisms could allow rapid problem solving after an animal's default behaviour fails. The first is a previously developed associative learning rule (PDALR) based on the outcome of the default behaviour. For example, if a tool fails make a longer one. Apparently sophisticated behaviour is often the product of simple mechanisms like decision rules based on associative learning (Povinelli 2000; Sterelny 2003). Alternatively, the problem may be solved by causal inference (we call this delayed causal inference, or DCI).

Is it possible to distinguish between a PDALR and DCI in two-stage heuristic problem solving? In a tool-length experiment, for example, a PDALR might see the length of the second tool closely related to the length of the first tool. A qualitative DCI (based on the perception that the hole is 'deep') might also produce the same outcome as a PDALR. In contrast, a quantitative DCI (e.g. a 15 cm tool is needed) requires accurate depth perception. A PDALR or qualitative DCI that made second tools longer than failed first tools by roughly a fixed amount (e.g. 3 cm) should give a significant positive correlation between the lengths of first and second tools. A quantitative DCI that made the lengths of second tools closely related to hole depth (e.g. matching) should produce little correlation between the lengths of first and second tools (i.e. a tool close to 15 cm is made regardless of the length of the first tool). Accurate depth perception necessary for quantitative DCI could be obtained by stereoscopic vision through binocular overlap of the left and right visual fields. Birds, including *Corvus*, that use visual guidance to forage with their bills probably have binocular vision (Martin and Katzir 1999a,b). It has been argued that binocular vision in most birds is not adaptive for stereoscopic vision (depth perception), but to allow each eye's field of vision to project into the contralateral visual field to control the position of the bill or feet during the dynamics of capturing prey (Martin and Katzir 1999a,b; Martin and Coetzee 2004). However, depth perception in animals, including birds, can also be determined by 'motion parallax' (Kral 2003). That is, the use of head movements to determine the relative degree to which objects move in the visual field; close objects move more than do distant ones. To date, there have been no studies investigating depth perception in any *Corvus* species (Graham Martin, personal communication).

In this paper, we investigate the cognitive strategy that wild NC crows use in a tool task to extract food. In certain situations, field experiments are superior to laboratory studies because they allow an animal to use its natural range of responses to a problem (Sterelny 2003). Our experiments allowed two free-living crows to manufacture tools from the range of different materials present in their local environments to extract food from vertical holes of different depths. We tested them in distinctly different habitats. At the Sarraméa study site, the crow made leaf-stem tools to extract larvae from an artificial feeding box. On Maré Island, the crow manufactured wide pandanus tools to extract meat from holes in a dead log.

Experiment 1

Methods

Study area and subject

On 25 October 2002, we established a feeding site for NC crows at Sarraméa (see Hunt 2000b for a description of the study area). The site was on a gentle, grassed slope where widely spaced bancoulier *Aleurites molucanna* trees grew. The short grass was covered with fallen bancoulier leaves of various sizes. We first set up a 20–30 cm thick

fallen bancoulier log on the ground in the centre of a small clearing. Along the top of the log we drilled vertical holes 6–7 cm deep and 2.6 cm in diameter in which we placed live Cerambycidae larvae *Agrianome fairmairei* for crows to extract. We obtained the larvae from dead wood close to the feeding site. Visiting crows usually required tools to extract the larvae from the holes.

From 26 October to 2 November, it appeared that only one NC crow returned each day to feed. On 3 November we temporarily marked this bird (called Fabric in Rutledge and Hunt 2004) with a small dot of white acrylic paint on its body feathers. We did this by standing cotton buds soaked in the paint close to a hole in the log. The marked crow returned each day until the end of the experiment on 9 December 2002, by which time the paint was noticeably faded but still clearly visible. The paint appeared to have no adverse effects on the crow. On several occasions another NC crow flew to the log when the marked crow was feeding there and displayed submissively to it, which suggested that the marked crow was an adult.

Experimental task and general procedure

We used an artificial feeding box made of clear perspex and wood (Fig. 1a). We did this instead of using holes drilled in wood for several reasons: (i) the feeder box controlled for hole location while allowing hole depth to be easily changed, (ii) we needed a large hole that securely contained larvae in a horizontal position, and (iii) we wished to investigate the technique that NC crows used to extract larvae from holes; the perspex front provided a clear view of the tool manipulation in the hole (results of this work are not presented here). We recessed the box into one side of the log so that the hole was vertical. A vertical hole meant that the food was always at the base of the hole, thus controlling for food position in relation to hole depth. We adjusted hole depth by lowering or raising the wooden base of the box.

NC crows at the site commonly use dried leaf stems on the ground as tools to extract larvae placed in holes (Hunt 2000b). We also required the marked crow to extract larvae with tools naturally available at the site, therefore we did not restrict its choice of tool material (see Introduction section). However, we restricted the area in which it would likely search for a tool to a 1 m wide semi-circle of leaf litter 1 m away from, and behind, the feeding box by removing other litter and potential tools up to several metres from the box. This facilitated retrieving tools that the crow dropped and allowed us to quantify available tools. At the conclusion of part 1 of the experiment (see below) the crow had removed many leaf stems (tools) from the 1 m wide arc of leaf litter. To provide a similar range of tool material for part 2 of the experiment, we added new leaves (stems with leaf blades

attached) to the litter with stems to match the lengths of those that the crow had removed to use as tools. At the end of the experiment we quantified all potential tool material (leaf stems and sticks) in the 1 m wide arc and measured their lengths.

On 27 October, we began to habituate the marked crow to the box and our presence and establish a morning feeding routine. The initial inside measurements of the hole were 6.5 cm $\times$ 6.5 cm $\times$ 13 cm. The crow could extract a larva placed in the bottom of the box without tools, but it was initially unwilling to put its head into the apparatus. By 4 November, it readily took larvae out of the box without the aid of tools, but also occasionally used tools. We usually provided food in the log and the box only in the early mornings so the crow would forage naturally for the remainder of the day. From 27 October to 4 November, we collected 43 tools that the crow used in holes in the log and the box to extract food during the habituation period (10.9 ± 0.63 cm, mean $\pm$ S.E.M., $n = 43$).

The experiment took place from 5 to 27 November. We aimed to conduct five successful trials each morning; each successful trial involved the extraction of one larva from the box. We continued to present the square hole on 5–6 November to establish the baseline behaviour for feeding out of the box. The experiment was conducted in two parts: in the first part we used live larvae and in the second part we used dead larvae. Most larvae were 4–7 cm long. We used dead and live larvae to check if extraction technique influenced the length of tools. NC crows must lever a dead larva out of a hole, but can 'fish' out a live larva by aggravating it so it clamps its strong mandibles onto the end of the tool (Hunt 2000b). Each part of the experiment involved alternating between a shallow (2 cm $\times$ 6.5 cm $\times$ 9 cm deep) and a deep condition (2 cm $\times$ 6.5 cm $\times$ 15 cm deep) as follows: shallow–deep–shallow–deep–shallow. Each condition was presented for 2 days, taking a total of 10 days to complete each part of the experiment. Once the crow had finished feeding it left the site. We then placed another larva in the box and waited for the crow to return. Because of disturbance from a school outing, we excluded trials carried out on 7 November. We filmed each trial from a hide positioned ca. 6 m downhill from the log. Except for one day, we began trials between 05:00 and 06:15.

For each trial we recorded (i) whether or not the crow looked into the box before getting a tool, (ii) the location it collected the tool from, (iii) the number of tools used, (iv) the characteristics of the tools (type of material, length), and (v) the order multiple tools were used. We measured the lengths of tools and potential tools in a straight line between the ends. Tools were measured to the nearest millimetre and potential tools in the 1 m strip of litter to the nearest centimetre.

Fig. 1 **a** The Sarraméa crow attempting to extract a live cerambycid larva from a 15 cm deep hole in the perspex box with a leaf-stem tool. **b** The Maré crow extracting meat from a shallow hole with a wide pandanus tool (16.9 cm long) that has a newly hooked-out piece of meat attached to the working end (indicated by *white arrow*)


Analysis

Statistical analyses related to single-subject data might lead to violations of assumptions in parametric tests, therefore we used non-parametric tests throughout. We used the Wilcoxon two-sample test to look for differences between the means of two independent samples. We used the Wilcoxon signed-ranks test when we tested between two related samples. We examined the difference between two distributions using the Kolmogorov–Smirnov test. We used general linear models (GLMs) to carry out regression (SAS version 9.0, SAS Institute Inc., Cary, NC). When testing for correlations between two variables, we used Spearman correlation coefficients. Where applicable, all the statistical tests were two-tailed.

Results

The marked crow always approached the log from the side opposite to where the box was recessed. Except for rare occasions, after arrival at the site it stood on the log and looked down into the box before obtaining a tool, or extracting the larva without a tool. For each of the 10 baseline trials, it only used its bill to extract larvae. All of the 204 tools it brought to the log for use in the box were found on the ground close to the log (>80% from the 1 m wide arc of leaf litter behind the log). Two of these tools were twigs and the rest were bancoulier petioles, or leaf stems. Our observations and bill marks on the stem tools showed that the crow commonly modified a leaf to make a tool by breaking off the leaf blade (marks identified on 115 of the 202 stem tools), as was described previously (Hunt 2000b). The crow usually broke off the blade close to its base (at least 158 of the 202 tools), and always did so before it returned to the log. The crow's efficient and consistent manufacture and use throughout the experiment suggested that it commonly used leaf stems as tools. It showed remarkable persistence in trying to extract a larva, indicated by the high success rate (100 out of the 107 trials that required tools). Of the 107 trials, 32 involved the use of more than one tool to extract the larva; 27 of the 32 trials involving multiple tools were for the deep hole (in 2 of these 27 trials we did not know the order that tools were used).

There was an obvious overall trend of longer tools as the experiment progressed (Fig. 2). A GLMs analysis with time and live versus dead larvae as predictors showed that time explained much more of the variation in tool lengths than did larvae status (time: $\chi^2_{1,200} = 3.46$, $P = 0.06$; larvae condition: $\chi^2_{1,200} = 0.05$, $P = 0.82$). For simplification, we
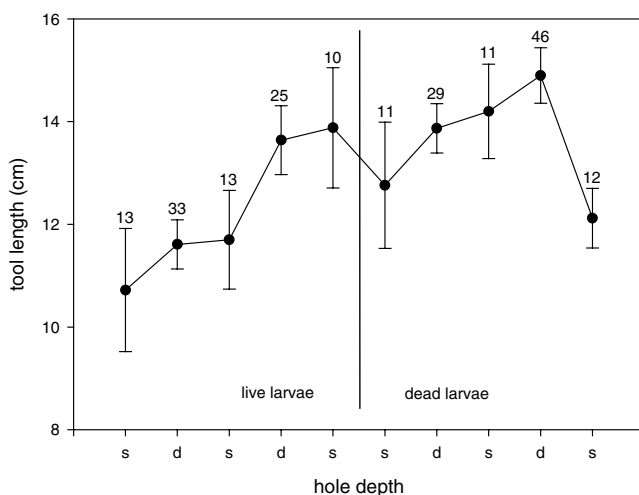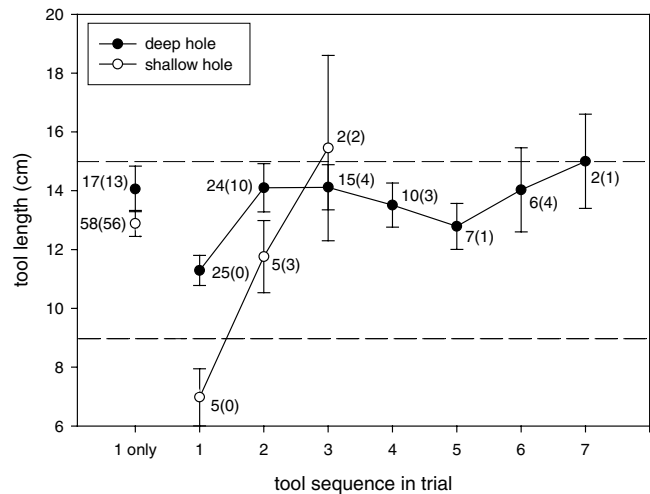
Fig. 3 Mean lengths of leaf-stem tools ($\pm$ S.E.M.) used by the Sarraméa crow to extract larvae from the perspex box. The first mean length ('1 only') is for tools when only one was used in a trial. The other mean lengths are for trials where more than one tool was used. The x-axis indicates the order in which tools were used. Sample sizes are given along with the number of tools that successfully extracted a larva (in brackets). *Dashed lines* indicate hole depth

combined data for dead and live larvae to examine what effect hole depth had on tool length. The lengths of all tools the crow used when extracting larvae from the shallow hole were shorter than that of all tools it used when extracting larvae from the deep hole ($z = 2.21$, $n = 203$, $P = 0.03$). However, there was no correlation between tool length and hole depth for the first tools that the crow used in a trial ($r_s = 0.00$, $n = 105$, $P = 1.0$). We examined the data in more detail to see how the increase in tool length came about. The crow's success rate at extracting larvae using the first tool in a trial was much greater for the shallow hole (56 of 63 trials) than it was for the deep hole (14 of 42 trials) (Fig. 3). This was probably because the mean length of the first tools it made for the shallow hole (12.4 ± 0.46 cm, $n = 63$) was the same as that of the first tools it made for the deep hole (12.4 ± 0.48 cm, $n = 42$). Although there was no significant difference between the lengths of second and all subsequent tools used in a trial (data combined) ($z = 0.47$, $n = 71$, $P = 0.64$), we examined the lengths of second tools separately because we were especially interested in the lengths of tools the crow made immediately after initial failure at extracting larvae. For deep holes, the second tools that the crow used in a trial were longer than the first tools (Wilcoxon signed-ranks test: $z = 2.97$, $n = 24$, $P = 0.0003$) (Fig. 3). The length of second tools was also longer than that of first tools in the shallow condition (Wilcoxon signed-ranks test $z = 2.09$, $n = 10$, $P = 0.04$) (Fig. 3). There was no significant difference in the lengths of second tools when compared between the deep and shallow conditions ($z = 1.24$, $n = 29$, $P = 0.21$). There was also no significant relationship between the lengths of

Fig. 2 Variation over time in the mean length of leaf-stem tools ($\pm$ S.E.M.) used by the Sarraméa crow (sample sizes above error bars). The legend for the x-axis gives the temporal sequence of the shallow ('s') and deep ('d') conditions

first and second tools used in the deep condition (GLMs analysis: $\chi^2_{1,21} = 1.23$, $P = 0.27$).

At the end of the experiment, we counted 937 complete leaf stems in the 1 m wide arc of litter behind the log but only 35 twigs (14.9 ± 1.3 cm long). The distribution of lengths of available stems was different from the distribution of the lengths of tools (Kolmogorov–Smirnov test: $z = 2.0$, $n = 56$, $P = 0.001$).

Experiment 2

Methods

Study area and subject

On 5 August 2003, we established a feeding site on Maré using similar techniques to those in Hunt and Gray (2004b). The site was in primary forest ca. 5 km inland of Wabao village in the south of the island. We observed and filmed a NC crow from a hide ca. 7 m from a feeding table. We placed two dead logs on the table and initially drilled eight vertical holes 2.6 cm in diameter and 6–7 cm deep (four in each log) and positioned a pandanus tree at the table. In the holes we placed small pieces of fresh meat which the crow extracted with tools. We replaced the pandanus tree at the table when around 40 tools had been made because by then space on its leaves was limited. We selected trees that had leaves of very similar length and width. From 5 to 13 August only two NC crows visited the feeding table regularly. The crows were a mated pair because we observed the male courtship feeding the female. We are confident that it was the same pair because of consistent individual behaviour. For example, both crows held tools only on the right sides of their heads (see Fig. 1b); previous work with 14 NC crows showed that individuals strongly preferred to hold tools on one side of their heads, but the side was just as likely to be the right side as the left one (Rutledge and Hunt 2004; Weir et al. 2004). In late September we fitted a coloured leg band on the male and verified that it and its partner were the pair that visited the table each day.

Experimental task and general procedure

During the habituation period we placed meat in the holes in the logs and at the bases of pandanus leaves. We placed meat in the leaves to initiate pandanus tool manufacture. The male only made tools to extract meat from the holes in the logs. The lengths of the tools that he used in the initial shallow condition during the habituation period were 15.2 ± 1.04 cm ($n = 26$). The first tools that we saw the female make were used to extract meat from the pandanus tree, and on 13 and 14 August we collected six of these

tools (mean length = 12.3 ± 0.70 cm). We continued to use multiple holes in the logs for the experiment rather than the feeder box that we used in experiment 1 because both the male and female crows were usually present at the site extracting meat. At that time on Maré, we did not have access to multiple feeder boxes. We did this to ensure that the female fed even when she arrived after the male, thus also reducing any effect on tool length that might be caused by competition for food between the partners (e.g. by making tools hurriedly to get meat first). We designed the experiment for the length of tools that the female made. We determined the depth of the holes in the deep condition (15 cm) based on the average length of tools that she used in the shallow condition. The 15 cm deep holes were inappropriate for the male because the tools he used in the shallow condition averaged more than 15 cm long, therefore we excluded his data.

We began the experiment on 14 August when the female was regularly manufacturing wide tools on the tree at the table to extract meat from the holes in the logs, and completed it on 3 September. Over this period we varied hole depth in a classical A–B–A design: shallow–deep–shallow. We provided a single piece of meat in each of the eight holes before the pair visited. Each visit was recorded as a trial, which we filmed from the hide. The pair usually visited several times per day. After a trial we collected any tools and removed their counterparts from the tree, and replaced the meat in the holes. Tools and counterparts were placed in 70% ethanol for shape preservation and later analysis. We continued the experiment daily, usually from dawn to dusk, because the low number of trials per day indicated that the pair spent a considerable amount of time foraging naturally. On 22 August we replaced the pandanus tree and deepened the eight holes. To ensure that the pair still obtained food with tools and did not abandon the site, we drilled the four holes in one log 12 cm deep and the four in the other log 15 cm. It was difficult for us to see the meat at the bottom of the deeper holes, especially in the early mornings when the pair often first visited. To make the meat more visible and increase the opportunity for the crow to assess the depth of holes, we painted the bottom of the holes with white acrylic paint. On 25 August we again changed the tree and drilled the four 12 cm holes to 15 cm deep as well and painted their bases white. On 28 August we repeated the shallow condition, turning the logs over and drilling 6–7 cm vertical holes in the new top surface.

For each trial we recorded (i) whether or not the female crow looked into a hole before getting a tool, (ii) the length of the tool (to nearest millimetre), (iii) the order in which tools were made, and (iv) whether the female lost or discarded a tool before manufacturing another one.

Analysis

We excluded data when the female made pandanus tools (i) on a tree away from the table to use in the logs and (ii) on leaves next to where we had removed counterparts. The latter tools were often shorter and wider than tools made on sections of undamaged leaf edge. The statistical analyses used here are explained in the Methods section of Experiment 1. For non-parametric ANOVA we used the Kruskal–Wallis test.

Results

We analysed 52 trials with the female crow over 15 days to extract meat from the shallow holes and 28 trials over 6 days to take meat out of the deep holes. She mostly flew to the feeding table and looked into the holes containing meat before moving into the pandanus tree and manufacturing a wide tool (64 of 71 trials in which we saw the female arrive). Her proficient manufacture and persistent use of pandanus tools rather than twigs (common at the site) showed that she was used to making wide tools (see video footage of her making a wide tool at http://language.psy.auckland.ac.nz/crows/video-clips.htm). She made 148 tools from the four trees at the table in 80 trials. The female often made a tool to replace the one that she lost on the ground under the table after she extracted meat ($n = 27$ with shallow holes; $n = 19$ with deep holes). She also obviously discarded tools after failure to extract meat, doing this more with deep holes ($n = 34$) than with shallow holes ($n = 4$). She sometimes successfully extracted meat with a tool before discarding it to make another one.

The way tool lengths varied over the course of the experiment suggested a classic adaptive response to the A–B–A experimental paradigm (Fig. 4). The tools the female made for use in the deep holes (13.8 ± 0.27 cm, $n = 79$) were longer than those made for use in the shallow holes (12.2 ± 0.27 cm, $n = 69$) ($z = 4.20$, $n = 148$, $P < 0.0001$). However, there was no correlation between tool length and hole depth for the first tool that the crow made in a trial ($r_s = 0.12$, $n = 80$, $P = 0.28$; when both 12 and 15 cm deep holes were presented we averaged the depth). As we did for experiment 1, we examined the data in more detail. The mean length of all the first tools made for shallow holes (11.9 ± 0.32 cm, $n = 52$) was very similar to that for all the first tools made for deep holes (12.4 ± 0.39 cm, $n = 28$) ($z = 1.07$, $n = 80$, $P = 0.28$). Because the first tool the female made in a trial was consistently around 12 cm in length regardless of hole depth, she often only needed to make one tool per trial with shallow holes (30 of 52 trials), but mostly used more than one tool on visits to deep holes (23 of 28 trials) (Fig. 5). Although the lengths of second tools did not differ from the lengths of third and subsequent tools in a trial (data combined) ($z = 0.64$, $n = 68$,
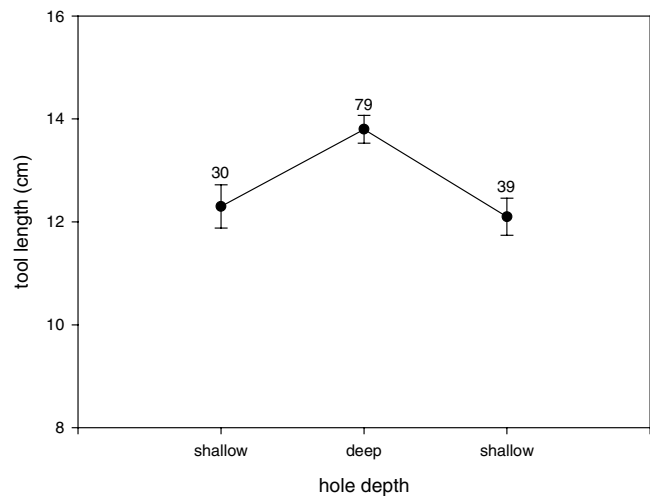

Fig. 4 Variation in the mean lengths of pandanus tools ($\pm$ S.E.M.) over time used by the Maré crow (sample sizes above error bars). The legend for the *x*-axis gives the temporal sequence of the shallow ('s') and deep ('d') conditions

$P = 0.52$), we again focused on the second tool that the female made in multi-tool trials. With deep holes, the second tools used in trials were longer than first tools (Wilcoxon signed-ranks test: $z = 3.60$, $n = 20$, $P < 0.0001$). When we only included second tools if they were replacements for discarded first tools, the result was still significant (Wilcoxon signed-ranks test: $z = 3.08$, $n = 14$, $P = 0.002$). Although the female usually made a second tool to use in shallow holes because she lost the first tool, the length of the second tools was longer than that of the first tools (Wilcoxon signed-ranks test $z = 2.25$, $n = 16$, $P = 0.02$) (Fig. 5). However, the length of the second tools used in shallow holes was significantly shorter than the length of the second tools made for deep holes ($z = 2.91$, $n = 37$, $P = 0.004$). There was no significant relationship between the lengths of first and second tools used in the deep condition (GLMs analysis: $\chi^2_{1,17} = 3.57$, $P = 0.06$).

The use of different trees was also unlikely to have influenced tool length because the lengths of the first tools made in a trial did not significantly vary between trees (Kruskal–Wallis test: $\chi^2_3 = 5.59$, $P = 0.13$).

General discussion

The crows that we tested appeared to be using a two-stage heuristic strategy to extract meat from holes of different depths. Both birds exhibited strikingly similar behaviour. The average length of the first tools the crows made in a trial was not closely related to hole depth. The second tools they made for use in deep holes were consistently longer than the usually unsuccessful first tools (see Fig. 6). The similarity of their behaviour is surprising given that the experiments differed substantially with regard to design, habitat, tool
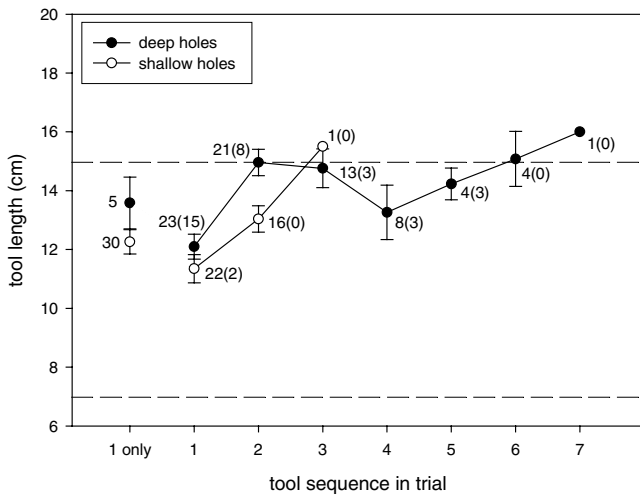
Fig. 5 Mean lengths of wide pandanus tools ($\pm$ S.E.M.) used by the Maré crow to extract meat from holes drilled in two dead logs. The first mean ('1 only') is for tools when only one was used in a trial. The other means are for tools when more than one was used. The *x*-axis gives the order in which tools were used. Sample sizes are given along with the number of tools classified as intentionally discarded in order to manufacture a new tool (in brackets). *Dashed lines* indicate hole depth (12 and 15 cm deep holes were presented at the beginning of the deep condition)

material, tool manufacture method, food extracted and extraction technique.

The lengths of the crows' first, or 'default', tools made in a trial were probably similar to the lengths of tools that they made when foraging naturally. It seems unlikely that the default tool length was established during the habituation period prior to the experiment. The lengths of the tools that the Maré crow first made on a visit were very similar to the lengths of wide-tool counterparts on pandanus leaves in
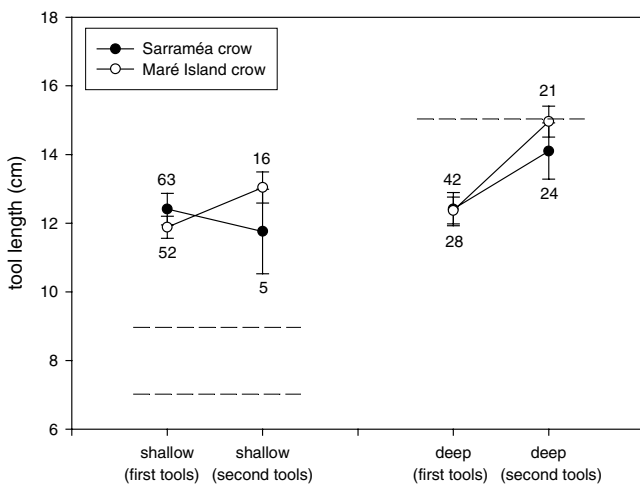
Fig. 6 The mean lengths of all first and second tools for each depth condition used by the Sarraméa and Maré crows. Respective samples sizes are given above the error bars. *Dashed lines* indicate hole depth; the *top line* for the shallow condition is the hole depth at Sarraméa and the *bottom line* the depth on Maré. Data are taken from Figs. 3 and 5

her foraging range (G. R. Hunt and R. D. Gray, unpublished data). Also, the lengths of the small number of tools that she made over the 2-day habituation period to extract meat from the pandanus tree were similar to the lengths of the first tools she used in the experimental trials. The Sarraméa crow used many more tools in shallow holes before the experiment began, but it probably also had experience with deeper holes when foraging naturally for most of the day after each morning's trials were completed.

What were the cognitive mechanisms underlying the two crows' strategy? The lengths of their first tools were not related to hole depth. The crows may have used default behaviour without assessing what length of tool was required or they were unable to make the assessment because of an inability for depth perception (see Introduction section). In either case, the lack of an association between the length of first tools and hole depth demonstrates that they did not immediately grasp the solution to the problem (ICI). The actual problem solving occurred when the crows made second and subsequent tools in a trial with deep holes. These second tools were on average longer than the first tools. This excludes on-the-spot trial-and-error learning because it would have produced random variation around the average length of first tools not consistently longer second tools. The crows could, therefore, have been using either a PDALR or DCI to finally solve the problem. To recall, in two-stage heuristic problem solving a PDALR or qualitative DCI should produce a significant positive correlation between the lengths of first and second tools, but quantitative DCI (e.g. matching hole depth) should produce little correlation. The relationship between the length of first and second tools in a trial for each crow was not significant. However, the probability values ($P = 0.06$ and $P = 0.27$) also did not support quantitative DCI. Further work is needed to identify what strategy the crows might have used to usually manufacture longer second tools.

The initial use of default behaviour by wild NC crows in our experiments appears to be inconsistent with Betty's behaviour in the wire bending experiment (Weir et al. 2002). Without training Betty bent 10 sections of straight wire (on 4 of the 10 occasions beyond 90° into hooks when the angle between the two ends of a wire is measured) to lever or hook out a small bucket containing food from a plastic tube. Significantly, however, in 9 of the 10 trials where she bent the wire Betty unsuccessfully *tried the straight wire in the tube before bending it*. Subsequent experiments have also shown that Betty generally initially used a tool before making any modifications to it despite prior experience with a task (Weir and Kacelnik 2006). Betty might have reasoned that an initial try with the straight wire was 'worth a go', but she failed to obtain food using the straight wire in the nine trials where she initially used the straight wire. Her persistence at doing this on the first attempt in a trial suggests that

she tackled the problem using default behaviour, and only adapted her behaviour after failing to obtain food. Although such two-stage heuristic problem solving rules out immediate insight, it would still allow resourceful individuals like Betty to solve tool problems rapidly and innovatively. More tests were required to determine whether the second stage of Betty's problem solving strategy was based on a sophisticated understanding of the causal relations of the task (Emery 2006). Follow-up tests by Weir and Kacelnik (2006) demonstrated that although Betty may have a better understanding of physical problems than do other nonhuman animals, the exact level of her understanding remains a mystery.

The default behaviour by the wild NC crows that we tested is inconsistent with the 'matching' and 'tracking' reported for Betty and Abel by Chappell and Kacelnik (2002, 2004). The matching and tracking is surprising given the lack of obvious ecological rationale for such behaviour in the wild. Free-living NC crows usually position the non-working ends of tools along one side of their heads, which means that they are held securely and their lengths would rarely match hole depth (Hunt 2000a; Rutledge and Hunt 2004). Betty and Abel also preferred to hold tools laterally (Chappell and Kacelnik 2002). We frequently observe wild crows adjusting the position that they hold a tool along its length in response to changing hole depth and/or dynamics of extracting food from a hole. By altering the holding position, a long tool can be used effectively in holes of various depths. This is appropriate behaviour because prey are generally cached under material making the depth of food in holes in the wild rarely evident (e.g. in the detritus-filled end of a broken branch), and it is not uncommon for NC crows to use the same tool at different search sites (Hunt 1996). A tool that can be used in a range of holes is more likely to be adaptive than one that is made or selected to match a specific hole depth. We have few data on the characteristics of holes in which crows search with tools, but the stick tools that we have collected in the wild are consistently around 2–4 mm wide near the working ends (Hunt 1996; Hunt and Gray 2002).

The two NC crows that we tested initially made or chose a tool without close attention to the tool characteristics required. This is generally consistent with studies testing other nonhuman species in tool tasks (e.g. Visalberghi and Limongelli 1996; Hauser 1997; Povinelli 2000). However, Tebbich and Bshary (2004) presented woodpecker finches with a tool-length experiment similar to that used by Chappell and Kacelnik (2002). Three of the five finches usually selected tools sufficiently long enough to obtain the food in the tube. The authors stated that '. . . some of the finches were able to assess the necessary length in advance.', possibly after '. . . a fast learning process.'. Establishing the reason for the difference between our findings in field experiments and those of Chappell and Kacelnik's (2002,

2004) and Tebbich and Bshary's (2004) with captive birds requires further investigation.

An individual's first response in a trial is commonly used as a 'gold standard' (Silva et al. 2005) for assessing folk physics (e.g. Povinelli 2000; Chappell and Kacelnik 2002, 2004; Tebbich and Bshary 2004). Our findings demonstrate that this assumption may be misleading. Such an approach in the current study would have prematurely ruled out any sophisticated cognitive assessment of the task. NC crows, like humans (Betsch et al. 2004), might often initially rely on default behavioural routines when faced with a problem, but then closely assess a task following an initial failure. Betty's successful wire bending after initial failure is also consistent with the usually expeditious way that the two crows we tested appropriately adapted their tool manufacture. This contrasts with the behaviour of nonhuman primates where consistent success in tool problems often requires considerable training (e.g. Povinelli 2000).

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