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Selection of tool diameter by New Caledonian crows *Corvus moneduloides*

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Abstract One important element of complex and flexible tool use, particularly where tool manufacture is involved, is the ability to select or manufacture appropriate tools anticipating the needs of any given task – an ability that has been rarely tested in non-primates. We examine aspects of this ability in New Caledonian crows – a species known to be extraordinary tool users and manufacturers. In a 2002 study, Chappell and Kacelnik showed that these crows were able to select a tool of the appropriate length for a task among a set of different lengths, and in 2002, Weir, Chappell and Kacelnik showed that New Caledonian crows were able to shape unfamiliar materials to create a usable tool for a specific task. Here we examine their handling of tool diameter. In experiment 1, we show that when facing three loose sticks that were usable as tools, they preferred the thinnest one. When the three sticks were presented so that one was loose and the other two in a bundle, they only disassembled the bundle when their preferred tool was tied. In experiment 2, we show that they manufacture, and modify during use, a tool of a suitable diameter from a tree branch, according to the diameter of the hole through which the tool will have to be inserted. These results add to the developing picture of New Caledonian crows as sophisticated tool users and manufacturers, having an advanced level of folk physics.

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Keywords New Caledonian crow · Tool manufacture · Diameter · Folk physics

Introduction

New Caledonian crows show extraordinary tool behaviour in the wild (Hunt 1996, 2000a; 2000b; Hunt and Gray 2002), using and manufacturing several types of tools, and displaying diversification in tool designs between different geographical areas (Hunt and Gray 2003). The variety of tools made suggests that the tools may serve different functions, and in turn, that the crows might make and/or select instruments appropriate for each task. Selectivity implies that the tool agent has some foresight of the task ahead, and searches for or makes a tool according to the expected needs. This is compatible with an advanced level of cognitive ability (Parker and Gibson 1977; Tomasello and Call 1997). Furthermore, a recent study suggested that the (largely semantic) classification of tool-using birds into “true” tool users and “marginal” tool users correlates with an enlargement of the neo- and hyperstriatum ventrale (Lefebvre et al. 2002), indicating that the level of sophistication of tool using may reflect deep biological features of each species.

We have previously shown (Chappell and Kacelnik 2002) that two captive crows (a male and a female) are able to select an appropriate length of stick for a particular task from a range provided. Other physical attributes of tools, such as diameter, must also be important determinants of their suitability for a task. Here, we test the ability of the crows to take into account the appropriate diameter of a tool in anticipation of the task. We report on two experiments in this paper. In experiment 1, we provided pre-made tools of differing diameters and food in a tube accessible through a hole. We then recorded the choice of stick as a function of the diameter of the hole presented. To examine whether the crow showed active searching for a given tool, we used a task that required inserting a stick through a hole of variable diameter, and varied the availability of three tools. The three tools were used to present a choice between a readily available tool and two others that were tied in a bundle. The readily available tool could be too thick to be used, just thin enough to serve, or thin enough to serve in all conditions, while the

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bundle contained the remaining two tools. We considered three levels of sophistication (listed in increasing order): first, the bird might always pick the loose stick first, regardless of the needs of the task (the diameter of the hole). Second, it might always pick the thinnest stick (which is suitable in all conditions). Third, it might pick the loose stick only if it is usable with the current diameter of hole, and pick a suitable stick from the bundle if it is not. The second strategy implies engaging in unnecessary search in some of the trials but avoiding the risk of failure.

In experiment 2 we used the same apparatus, but instead of supplying sticks, we provided large bushy branches, so that the crows had to manufacture their own tools by removal of parts (“subtraction”: see Beck 1980). This allowed us to investigate whether they manufacture tools of dimensions that correspond to the needs of each task. Although New Caledonian crows frequently make tools by subtracting parts from branches, this may be the outcome of an inflexible program – in which a substrate that has removable parts is stripped until a smooth stick remains – rather than a creative and flexible response to a particular task.

Experiment 1: choice between supplied tools

Methods

Subject

The subject was a captive female New Caledonian crow held at the University of Oxford Field Station (see Chappell and Kacelnik 2002, for full details of subject’s history and housing conditions). Although we had a pair of crows at the time, the male would not participate when separated from the female, so only the female was tested in this experiment. Both crows were housed free-flying in a room (4.29 m×2.94 m×3.0 m high), with access to an outdoor aviary (2 m×4 m×2.5 m high) during the day. The subjects had participated in a number of experiments testing various aspects of tool use, including an experiment studying length selection (Chappell and Kacelnik 2002), but none had involved selecting different diameters of tool. During test sessions, the male was excluded from the room in the outdoor aviary, while the female was left alone in the room. The room was maintained on a 12L:12D lighting schedule.

Apparatus

The apparatus consisted of semi-transparent tubing made out of 5-cm-diameter Rotastack components made for pet rodent housing (see Fig. 1). The tubing was mounted as an inverted “L” shape using a standard clamp stand so that the long limb of the tube was horizontal, while the base of the L pointed downwards. The horizontal limb was closed with one of three interchangeable end caps, each of which was pierced with a different diameter hole: 4 mm, 7 mm or

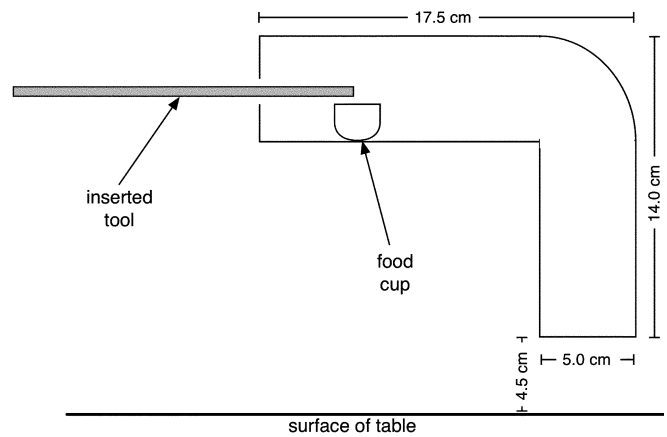


Fig. 1 Diagram of the apparatus used in experiments 1 and 2. Position of clamp stand not shown for clarity

9 mm. Food (a piece of pig’s heart 0.5 ± 0.1 g) was placed in a small plastic cup inside the horizontal part of the tube, so that a tool inserted through the hole in the end cap could push the cup until it dropped through the vertical limb, where it would be accessible to the subject. This arrangement prevented the crow from inserting tools from the open end of the tube, circumventing the constraint on the diameter of the tool required. Three straight wooden rods 24 cm long, with diameters of 3 mm, 6 mm and 8 mm (hereafter referred to as thin, medium and thick rods respectively) were supplied. Thus, the thin rod fitted all of the end caps, the medium rod only the 7 mm or 9 mm end caps, and the thick rod only the 9 mm end cap.

Training

Training consisted of four trials. In the first, the subject was presented with the apparatus without the end cap inserted and provided with a rod of a different length and diameter from those to be used in the experiment (a natural piece of oak, maximum diameter 5 mm, length 30 cm). Within 10 s it had pushed the cup so that it fell out of the vertical tube. In the remaining three trials, the same apparatus was presented once with each of the end caps and the thickest usable rod for each hole (thus there was no choice of tools involved). The order of presentation was thin rod with 4 mm hole, medium rod with 7 mm hole, and thick rod with 9 mm hole. Each of the four trials continued until the subject had successfully used the tool to push the cup containing the food out of the end of the tube. The latencies to achieve this were 163 s, 672 s and 195 s for the thin, medium and thick rods respectively. Thus, although accumulated practice would favour the shortest latency in the final training trial with the biggest hole and thickest rod, the bird was fastest with the thinnest.

Testing

During testing there were two types of trials. In the first type (“none-loose trial”), three tools were tied into a bundle with a strip of newspaper (3 cm wide) that was secured with a small piece of adhesive tape. In the other type of trial (“one-loose trial”), one of the rods was loose and the other two bundled together in the same way. In none-loose trials, the bundle of three rods was placed on the table, perpendicular to the apparatus, pointing at the midpoint of the horizontal tube. In one-loose trials, the single tool and the bundle of two rods were again placed perpendicular to the apparatus, equally spaced about the midpoint. The loose tool was pseudo-randomly placed on the left on half of the trials. Of a total of 24 trials, half were none-loose trials and half were one-loose trials. Within each type of trial, each diameter of end cap was presented on one third of trial occasions, giving a total of eight trials with each diameter of hole, of which four were none-loose, and four were one-loose trials, all randomly intermixed. The number of trials was kept to a minimum to avoid as much as possible training by reinforcement, as our main purpose was to examine the birds’ ability to anticipate the needs of novel tasks.

In the one-loose trials, the thickest rod that was just usable considering the diameter of the end cap was loose and tied in the bundle equally often (two trials of each). The food and end caps were placed in the apparatus outside the experimental room, and then the experimenter took the apparatus into the room and left. We recorded the total latency as the interval between the start of the trial and successfully removing the food, and handling time as the time from first touching any rod to successfully removing the food. The choice of rod was recorded as the first that touched the end cap of the apparatus.

Post-testing

The results of the testing phase revealed an apparent bias towards the thin rod (see following discussion). We therefore tested the subject on an additional 24 trials with the same apparatus to determine which rod the crow would choose when there were no constraints on tool diameter. The apparatus was the same, but the end cap was removed completely, so any of the three rod diameters would have allowed the bird to get the food. All three rods were freely available in each trial (i.e. not tied into a bundle).

Results

From the very first presentation of the bundled rods, the subject immediately took the bundle to a nearby perch and tore off the paper to remove one of the tools and discard the other two. Thus, she did not require training to be able to dismantle the bundle. In every trial, the subject successfully removed the food within 7 min. In the one-loose trials, she chose the thin rod in ten trials, the medium rod in one trial, the thick rod in no trials and the whole bundle

in one trial. In the none-loose trials, she chose the thin rod in 11 trials, the medium rod in no trials, the thick rod in no trials and the whole bundle in one trial. The picture is consistent over both types of trial: the crow had a strong preference for the thinnest rod, and used it almost exclusively. On two trials, the subject lifted the entire bundle and touched the end of the apparatus with it before attempting to dismantle it. However, the statistics were performed assuming that the crow had only three possible courses of action: choose the thin, medium or thick rod. This results in a more conservative estimate of the random probability of choosing any of the tools. Using a binomial test, the probability of obtaining the observed choices of thin tools was significantly different from random (binomial test: $n=24$, $P=0.333$, $P<0.0001$).

In the post-testing phase, when all three rods were untied, the subject chose the thin rod on all 24 of the trials. Thus, the bias towards choosing the thinnest rod in the testing phase appears to persist when there are no constraints on the diameter of the tool required. This preference might be because the thin rod is appropriate for all hole diameters presented or for ergonomic reasons. The rods were all the same length, so increasing the diameter also increased the weight. The increased diameter may also make the tool less comfortable to hold in the beak.

The cost of dismantling the bundle when the thinnest tool is tied and a thicker but still usable one is loose depends on the relative costs of using a heavier, less preferred tool, and having to dismantle the bundle, which might entail a time cost. We tested the latter hypothesis by comparing the handling time in trials where the bundle was dismantled, and those where the single rod was used. Although we cannot perform statistical tests on the data (each category has a different sample size), there are clear differences between the time taken to obtain the food after selecting a rod when the bundle was dismantled compared to when a single rod was used, so it does appear that dismantling the bundle unnecessarily is inefficient (see Fig. 2). Some of this difference in handling time probably arises from the crow’s habit of taking the bundle to a nearby perch to dismantle it, but using the loose rods immediately (particularly if the loose rod was the thin one).

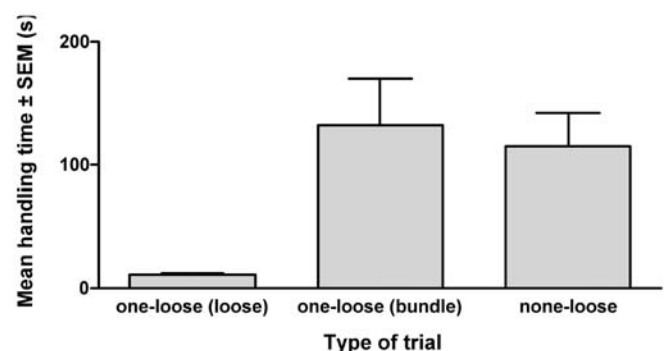


Fig. 2 Experiment 1: mean handling time \pm SEM as a function of whether the chosen tool was the loose tool in a one-loose trial, in the bundle in a one-loose trial, or in the bundle in a none-loose trial

Table 1 Experiment 1: action performed in the one-loose trials relative to the location of the thin rod (excluding trial in which whole bundle was touched to the end of the tube)

Action in one-loose trials	Thin rod is:	
	Loose	In bundle
Dismantled	0	7
Not dismantled	3	1

The post-testing data show that the crow strongly prefers the thin tool, and the handling time data during testing show that there is a time cost to dismantling the bundle. We can therefore analyse its decisions of whether or not to tackle the bundle, accepting the bird's preference for the thinnest rod as a given. In this case, in none-loose trials it should dismantle the bundle and choose the thin tool. In one-loose trials, it should choose the loose tool if that is the thin tool, and dismantle the bundle to obtain the thin tool if this is tied in the bundle. A Fisher's exact test was performed on the data from the one-loose trials to determine whether the bird actively sought the thin rod; namely, whether there was a significant association between dismantling the bundle versus using the loose tool and the location of the thin tool. (The trial in which the entire bundle was touched to the end of the tube was excluded.) There was a significant association (Fisher's exact test, $P=0.024$, $df=1$, see Table 1) between the crow's dismantling strategy and the location of the thin tool, suggesting that the female was dismantling the bundle only when required to obtain its preferred (thinnest) rod.

Experiment 2: crow-made tools

Methods

Subjects

In experiment 1 we found that the male would not participate in the experiment if he was separated from the female, and we therefore only used the female subject. In experiment 2 this was accepted as an unavoidable difficulty and both subjects were tested together. Although this compromises the independence of the observations, we chose this approach because our accumulated experience showed that the crows are highly social and they tend to have shorter latencies to approach the apparatus, spend less time performing unrelated behaviours (using tools in other parts of the room) and vocalise less when they are not separated for testing. Testing the subjects together appeared to only affect their latency to perform a task, not how they approached the task.

Apparatus

The apparatus was identical to that used in experiment 1. However, instead of providing sticks to use as tools, a

fresh, bushy branch of oak (*Quercus robur*) in leaf (approximately 1 m long) was placed in the room in each trial (see Electronic Supplementary Material, S1). Each branch had many twig diameters that included and exceeded the range of diameters of the holes in the end caps. Thus there was potential raw material to manufacture tools much narrower than the smallest hole in the end cap, and also material which would exceed the diameter of the widest hole in the end cap.

Testing

There was no training. The cup containing food (quantities as in experiment 1) was placed in the pipe outside the room, and then the whole assembly placed on a table in the room. Behaviour close to the pipe was recorded on digital video tape, and any tools made and touched to the end of the pipe were collected after each trial and measured with callipers to determine their maximum diameter to an accuracy of ± 0.1 mm. Since the diameter of the tool was only constrained for the first 9 cm from the tip (the minimum length required to push the food cup into the vertical section of pipe) we noted the orientation of the tool in use, and measured the maximum diameter of only the distal 9 cm of the tool. We also noted any modifications made to the tools after they had first been touched to the end of the pipe. It was not, of course, possible to measure the pre-modification diameter of these tools accurately. The interval from the start of the trial to obtaining the food (latency) was recorded. A trial continued until either of the crows obtained the food, or until 30 min had elapsed. One trial (hole diameter=4 mm) was terminated after 30 min, but in all others the crows got the food within 20 min. We performed one or two sessions of three trials on each day, with each of the diameters of end cap presented once per session in a random order. In total, 30 trials were performed; 10 with each hole diameter. Neither of the subjects were restrained, so both were free to participate in any trial.

Results

Both crows participated in manufacturing and using tools, completing equivalent numbers of trials (see Table 2), and were almost equally successful in obtaining the food. The male obtained the food in all 13 trials in which he participated, and the female in 16 of 17 trials in which she participated, so there were 29 of 30 trials in which food was obtained. In each trial, the crows approached the tube and looked at it, either from the nearest perch (approximately 0.5 m away from the tube), or they landed on the table next to the tube. On some occasions, they also pecked at the hole in the end cap. We are therefore reasonably confident that they had an opportunity to assess the size of the hole before making a tool. They then flew to the branch, snipped the leaves off large areas of twigs, and then finally removed a twig. Therefore, the leaves were unlikely

Table 2 Experiment 2: participation in trials by both subjects, with numbers of tools of different types made. “Un-modified”=tool used without modification to its form after its first use in the tube; “modified”=tool modified after first use in the tube; “discarded”=tool made, used in the tube unsuccessfully, and then discarded; “aborted trial”=neither bird succeeded in obtaining the food within 30 min

Hole size	Number of tools of type specified made by:			
	Type of tool	Male	Female	Total
4 mm	Un-modified	3	5	8
	Modified	0	1	1
	Discarded	0	2	2
	Aborted trial	0	1	1
7 mm	Un-modified	5	4	9
	Modified	0	1	1
	Discarded	1	1	2
	Aborted trial	0	0	0
9 mm	Un-modified	5	5	10
	Modified	0	0	0
	Discarded	0	2	2
	Aborted trial	0	0	0
Total		13/15 Trials un-modified	14/15 Trials un-modified	

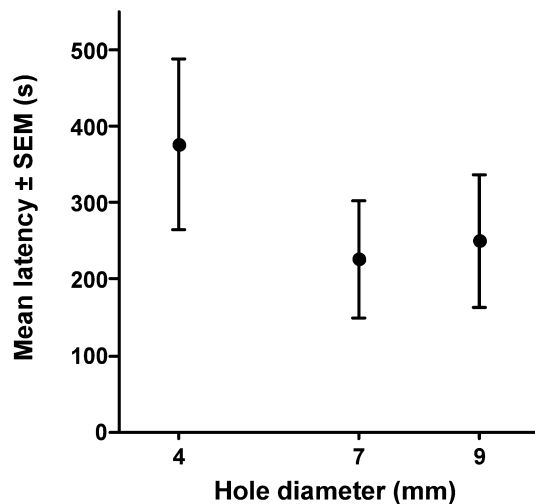


Fig. 3 Experiment 2: mean latency \pm SEM to obtain the food in seconds with each diameter of hole

to have been obscuring the diameters of the twigs from view. In only two trials did one of the crows (the female in both cases) modify a tool after she had attempted to insert it, by removing projections that prevented insertion of the tool in the hole (see Electronic Supplementary Material, S2 and S3 for a video clip of trial 1, in which the tool is modified by the female). Thus, 27 of 30 tools successfully used to obtain the food were defined in their dimensions before the bird first tried to use them. In six trials a tool was made and discarded and another was then made, yielding a total of 35 tools to analyse (See Table 2). Figure 3 shows the mean latency (excluding the trial that was terminated after 30 min) to obtain the food. The latencies were trans-

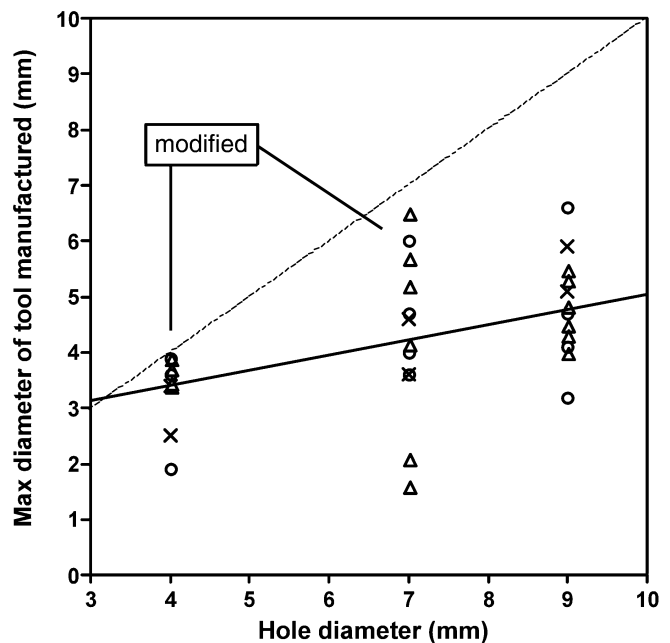


Fig. 4 Experiment 2: maximum diameter of the tool manufactured (distal 9 cm only) plotted against the diameter of the hole. *Open triangles* and *open circles* are tools used by the male and female respectively to obtain food successfully, *crosses* are discarded tools. The only two tools to be modified after the first attempt to insert them in the hole are indicated by the *labelled arrows*. The *dashed line* is the line where tool diameter would match hole diameter, and the *solid line* is the fitted linear regression

formed by taking logs to normalise the data (Kolmogorov–Smirnov test for normality post-transformation=0.148, $P>0.1$, $n=29$). There was no significant correlation between the diameter of the hole and the time required to obtain the food (Pearson correlation coefficient $r=-0.235$, $P=0.219$, $n=29$).

Figure 4 shows the maximum diameter of the crows’ manufactured tools against the diameter of the hole. Included in the figure (and the calculation of the regression) are the six tools that they tried to use and then discarded before manufacturing another to obtain the food. Note that all these discarded tools lie below the dotted line (the maximum tool diameter which would fit in the hole). In fact, all the discarded tools were unsuitable because they were too short to push the food cup to the point where it would fall down the vertical pipe [mean length (cm) \pm SEM=5.84 \pm 0.50, compared to 12.49 \pm 0.79 for the successful tools]. A linear regression was fitted to the data (including only the tools that were not modified after first use, and only the first-made tools in the 6 trials where the first-made tool was discarded: $n=27$), and the slope of this line was significantly different from zero ($F_{1,25}=8.216$, $P=0.0083$; $Y=2.006+0.311\times X$, $R^2(\text{adjusted})=0.247$). This proves that the crows manufacture tools that vary in diameter according to the size of hole in which the tools will be used.

Discussion

We have shown that the female crow actively sought her preferred tool, and dismantled the bundle of rods only when this was necessary to obtain the tool. Both crows also manufactured tools with an appropriate diameter for the task in which they were to be used.

In experiment 1, we could not define the optimal tool choice independent of the bird's behaviour, because two factors were clearly involved: the ergonomic suitability of the tool (the bird strongly preferred the thinnest rod) and its availability (the bird had to work for around 100 s to dismantle the bundle). Given that dismantling the bundle incurred a time cost, she behaved economically with respect to her preferred choice of tool, only dismantling the bundle if the thin rod was not freely available. This experiment, however, provided no evidence for an ability to take the hole diameter into account: the preferred tool was usable in all three diameters used.

In experiment 2, we tested for the birds' attention to tool diameter by allowing both crows to make their own tools. We found that in every trial but one, the crows made tools that were narrow enough to insert into the hole, on only two occasions by modifying their initial attempt at making a tool. Furthermore, the maximum diameter of the "working end" of the tool increased with the diameter of the hole, indicating that they were tracking the diameter of the hole and adjusting the diameter of the tool appropriately. Very thin tools are more flexible (and therefore less effective as pushing tools), and also more prone to breaking (unlike the human-made tools we provided in experiment 1), so making wider tools when the diameter of the hole allows it, rather than always manufacturing a very thin tool, is a good strategy. Their ability to manufacture such a well-fitting tool is impressive given the very uneven nature of oak twigs and sticks. There are numerous angles and projections that must either be removed or taken into account when selecting material to make a tool. Furthermore, some of the tools made for the 9 mm hole would have been too wide to fit into the 4 mm hole. These results add to the developing picture of New Caledonian crows as sophisticated tool users and manufacturers, showing that their tool behaviour is characterised by selectivity, flexibility and some level of understanding of the requirements of the task (Chappell and Kacelnik 2002; Weir et al. 2002).

We have previously shown that the crows are able to select an appropriate length of tool for a task (Chappell and Kacelnik 2002), and the observations in the current experiment support these findings. However, one might ask why on six occasions, the crows made tools which, while they were of a suitable diameter to fit the hole and were long enough to reach the food, were not long enough to push it out. There are two possible explanations. First, pulling food out of a hole corresponds closely to the natural action of tool use in the wild, whereas pushing food away does not (note that the crows are still able to successfully use this action, even though it does not form part

of their known natural repertoire). Thus, they may find it more difficult to judge the required length in the latter case. Second, all but one of the tools made were between 5.2 cm and 7.8 cm long: long enough to reach the food cup, but too short to reach the outlet hole, so that they may have been judging the distance between the input hole and food. Further to this observation, in some trials the crows succeeded in obtaining the food with short tools by using a similar action to that employed when using a snooker cue, resulting in the cup being knocked out of the pipe with some force. So, making a tool of insufficient length was less of an impediment to success in this experiment (unlike the arrangement in Chappell and Kacelnik 2002) than one with too large a diameter.

Few experiments have tested selectivity for the shape or size of a tool in any animal (Thouless et al. 1989; Aumann 1990; Anderson and Henneman 1994; Visalberghi et al. 1995; Chappell and Kacelnik 2002), and these studies offered the subjects a choice between tools prepared and provided by the experimenter. The experiments reported here are the first to demonstrate clear evidence of manufacture of an appropriate tool for a task. They also show active modification of tools in use to "fine tune" their specifications, a very rare observation indeed, but known in Galápagos finches (Bowman 1961) and several species of primates (see for example Westergaard and Suomi 1994; Bermejo and Illera 1999; Boysen et al. 1999; Fox et al. 1999; Lavalley 1999). In the wild, crows do use different tools to extract different prey (Hunt 1996, 2000a, 2000b; Hunt et al. 2001), but – because it seems that different tools are made at different sites – it is not yet clear whether the differences in the tools used are specifically due to differences in their functionality, rather than local culturally transmitted tool-making styles, or differences in the availability of materials or prey. As yet there are no field studies showing use of various tool shapes by the same individual crow in different situations. Here, we have shown that crows certainly have the capacity to adjust the specifications of the tools they make to suit the task at hand. Furthermore, they appear to understand some aspects of the function of tools, and (at least one of the captive crows) can make appropriate tools using novel manufacturing techniques and materials (Weir et al. 2002), an ability that is extremely rare if not absent even in primates (Povinelli 2000).

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References

- Anderson JR, Henneman MC (1994) Solutions to a tool-use problem in a pair of *Cebus apella*. *Mammalia* 58:351–361

- Aumann T (1990) Use of stones by the Black-breasted Buzzard *Hamirostra melanosternon* to gain access to egg contents for food. *Emu* 90:141–144
- Beck BB (1980) Animal tool use: the use and manufacture of tools by animals. Garland, New York
- Bermejo M, Illera G (1999) Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40:619–627
- Bowman R (1961) Morphological differentiation and adaptation in the Galapagos finches. *Univ Calif Publ Zool* 58:1–326
- Boysen ST, Kuhlmeier VA, Halliday P, Halliday YM (1999) Tool use in captive gorillas. In: Parker ST, Mitchell RW (eds) *The mentalities of gorillas and orangutans: comparative perspectives*. Cambridge University Press, New York, N.Y., pp 179–187
- Chappell J, Kacelnik A (2002) Tool selectivity in a non-mammal, the New Caledonian crow (*Corvus moneduloides*). *Anim Cogn* 5:71–78
- Fox EA, Sitompul AF, Van Schaik CP (1999) Intelligent tool use in wild Sumatran orangutans. In: Parker ST, Mitchell RW (eds) *The mentalities of gorillas and orangutans: comparative perspectives*. Cambridge University Press, New York, N.Y., pp 99–116
- Hunt GR (1996) Manufacture and use of hook-tools by New Caledonian crows. *Nature* 379:249–251
- Hunt GR (2000a) Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proc R Soc Lond B* 267:403–413
- Hunt GR (2000b) Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu* 100:109–114
- Hunt GR, Gray RD (2002) Species-wide manufacture of stick-type tools by New Caledonian Crows. *Emu* 102:349–353
- Hunt GR, Gray RD (2003) Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc R Soc Lond B* 270:867–874
- Hunt GR, Corballis MC, Gray RD (2001) Laterality in tool manufacture by crows. *Nature* 414:707
- Lavallee AC (1999) Capuchin (*Cebus apella*) tool use in a captive naturalistic environment. *Int J Primatol* 20:399–414
- Lefebvre L, Nicolakakis N, Boire D (2002) Tools and brains in birds. *Behaviour* 139:939–973
- Parker ST, Gibson KR (1977) Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *J Hum Evol* 6:623–641
- Povinelli DJ (2000) *Folk physics for apes: a chimpanzee's theory of how the world works*. Oxford University Press, Oxford
- Thouless CR, Fanshawe JH, Bertram BCR (1989) Egyptian vultures *Neophron percnopterus* and Ostrich *Struthio camelus* eggs – the origins of stone-throwing behavior. *Ibis* 131:9–15
- Tomasello M, Call J (1997) *Primate cognition*. Oxford University Press, New York
- Visalberghi E, Frigaszy DM, Savage-Rumbaugh ES (1995) Performance in a tool-using task by common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), an orangutan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*). *J Comp Psychol* 109:52–60
- Weir AAS, Chappell J, Kacelnik A (2002) Shaping of hooks in New Caledonian crows. *Science* 297:981
- Westergaard GC, Suomi SJ (1994) The use and modification of bone tools by capuchin monkeys. *Curr Anthropol* 35:75–77