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ORIGINAL ARTICLE

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Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*)

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Abstract We present an experiment showing that New Caledonian crows are able to choose tools of the appropriate size for a novel task, without trial-and-error learning. This species is almost unique amongst all animal species (together with a few primates) in the degree of use and manufacture of polymorphic tools in the wild. However, until now, the flexibility of their tool use has not been tested. Flexibility, including the ability to select an appropriate tool for a task, is considered to be a hallmark of complex cognitive adaptations for tool use. In experiment 1, we tested the ability of two captive birds (one male, one female), to select a stick (from a range of lengths provided) matching the distance to food placed in a horizontal transparent pipe. Both birds chose tools matching the distance to their target significantly more often than would be expected by chance. In experiment 2, we used a similar task, but with the tools placed out of sight of the food pipe, such that the birds had to remember the distance of the food before selecting a tool. The task was completed only by the male, who chose a tool of sufficient length significantly more often than chance but did not show a preference for a matching length.

Keywords Tool manufacture · Selectivity · New Caledonian crow · Tool length

Introduction

We investigate the ability of New Caledonian crows *Corvus moneduloides* to select appropriate tools according to the needs of the task. Tool use and manufacture has been defined in a variety of ways (Beck 1980; Griffin 2001), and consequently, the number of species that can be said to be exhibiting tool use varies depending on the exact definition used. In addition, some reports of tool use in a species arise from a single individual on one occasion, or only from observations in captivity (surveyed by Beck 1980). Nonetheless, the general impression remains that tool use is a relatively rare occurrence taxonomically. For example, only 26 of an estimated 8,600 known species of birds have ever been shown to use any kind of tool, and in many of those cases, only a small fraction of individuals do so (Boswall 1977). Tool manufacture (implying substantial modification of a substrate to produce a tool) is even less common and is only routinely found in two genera of primates, *Pan* and *Pongo* (van Schaik et al. 1999), African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants (Chevalier-Skolnikoff and Liska 1993; Hart et al. 2001), woodpecker finches (*Cactospiza pallida*) (Millikan and Bowman 1967; Tebbich et al. 2001), and New Caledonian crows (Hunt 1996, 2000a). While New Caledonian crows have only recently been the object of scientific study, the evidence for habitual tool use in this species is stronger than would be suggested by the number of studies involved. Tool use in the wild appears to occur with sufficient frequency that local people often comment upon the abilities of the crows (personal observation) and the behaviour has recently been used as the motif of a postal stamp from New Caledonia.[1]

The paucity of species suggests that the conditions necessary for the emergence of tool manufacturing (the selective pressures favouring tool-related behaviour and/or the requisite phenotypic traits) might themselves be rare. To identify what these conditions might be, it is necessary to understand the limits and specificity of this kind of behaviour. It is necessary, for instance, to elucidate its relation to general intelligence, of which tool use could be both the cause and expression. Tool use and manufacture could occur at a number of different levels,

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[1] http://timbre.opt.nc/

differing in complexity and patterns of behavioural development. In terms of level of sophistication, animals may or may not manufacture morphologically and functionally variable tools, showing selectivity amongst them so that a functionally appropriate tool is chosen for a task (Parker and Gibson 1977; Anderson and Henneman 1994; Visalberghi et al. 1995; Tomasello and Call 1997). If they do, this ability may or may not evidence an understanding of the functional properties of tools, such that modifications to a tool that affect its function influence the animal's choice, but modifications to non-functional elements (such as colour) do not (Hauser 1997; Hauser et al. 1999; Hauser 2001).

New Caledonian crows offer an excellent opportunity to examine the specificity of cognitive adaptations associated with tool use because of their uniqueness among non-primate species in the intensity and sophistication of their tool-oriented behaviour. They manufacture and use several types of tools for extractive foraging on invertebrates, including straight and hooked sticks, and complex stepped-cut flat tools made from leaves of *Pandanus* spp. (Hunt 1996, 2000a, b). The latter have some of the hallmarks of complex tool manufacture: form is imposed on the raw material with control of various shape variables, a skilled tool-making technique is involved, and there is morphological standardisation of the finished tools (Hunt 2000a).

To our knowledge, there are only two reports of tool selectivity in non-primates. Working with one captive black-breasted buzzard (*Hamirostra melanosternon*) that dropped stones on domestic hens' eggs, Aumann (1990) reported that the animal preferred a 40 g stone from a range of stones weighing 15–65 g (the 40 g stone was used in nine of ten egg-breaking attempts over five trials), and Thouless et al. (1989) tested wild and two captive Egyptian vultures (*Neophron percnopterus*), providing them with models of ostrich eggs and a range of stone sizes (27–232 g). The authors showed that the vultures preferred 46-g stones. Ours is the first report in which the task (and therefore the tool required) is varied from trial to trial and the experimental protocol allows for computation of the random expectation for each case.

Experiment 1

Methods

Subjects

Subjects were two captive New Caledonian crows (one male and one female), held at the University of Oxford Field Station. The female crow was trapped by us at Yaté, New Caledonia in March 2000 using a Larsen-type trap and removed from the trap within 1 h of capture. This did not cause any injury to the bird and did not appear to cause undue distress. The male bird was also wild caught but had been kept for many years without any training at a local zoo in the Parc Forestier, Noumea, New Caledonia before coming to our laboratory. Both birds were then immediately transported to Oxford.

Housing

The birds are housed together (free-flying) in a room (4.29×2.94×3.0 m, L×W×H), with access to an outdoor aviary (2×4×2.5 m) during the day. They were separated for the duration of each trial by closing the door connecting the room and the outdoor aviary, so that the bird to be tested was confined to the indoor room while the other bird was in the outdoor aviary. None of the experiments described in this article involved deprivation of food or water. The birds are maintained on a 12L:12D lighting schedule.

Previous experience and training

Given that both subjects are wild caught and that they immediately showed extensive and spontaneous use of tools in our laboratory, no task can be said to be free from possible generalisation from previous experience. For this reason we give the information available in this respect in some detail.

In experiment 1, both birds were tested on a food-extraction task novel to them, while being offered a set of pre-prepared objects that could serve as tools. Since their arrival in our laboratory, the birds have been housed in the room and attached aviary described above that had been enriched to create a complex environment. The outdoor aviary contains four large wooden perches, in which the birds dig holes, and is floored with pebbles (which the female sometimes transports into the indoor room or places into other containers). There is also a large plastic tray for drinking and bathing. The immediately adjacent aviary houses two jackdaws (*Corvus monedula*). The indoor room contains various perches at different heights made from natural wood and building timber, including a thick pole that contains numerous drilled holes and radial perches. There is a covered water drinker, an open plastic tray for bathing, and a metal tray containing grit. We also provide various natural and man-made objects for enrichment such as hollow plastic shapes, lengths of tubing (flexible and rigid), and rubber toys for dogs.

Within hours of their initial release into the room, both birds broke off twigs and pieces of wood from the natural perches and used them to probe in any hole or crevice in the room (including the main power plugs, fire alarm, and wiring cases, which had to be shielded). When the objects were introduced, the birds treated them in a similar way, using them as containers in which to store food, probing sites, and general play objects. We have noted that the female has spontaneously nested the small plastic containers on several occasions, again apparently with no apparent reinforcement other than that gained from the action itself. An anthropomorphic description of their behaviour would be that they appear to explore and play with the objects.

We place the majority of food in open plastic or steel dishes, but we distribute a small amount of the favoured food items (meat and mealworms) around the room. This is done partly to give the birds some active food seeking opportunities but mainly to prevent the adult from monopolising the food source.

Experimental task and general procedure

Like any other animal grown under natural conditions, the two subjects clearly had a rich repertoire of experiences from which to generalise solutions to any new task, but we think it unlikely that either bird had previously encountered a physical setup close to that used in our present experiments.

The task consisted of extracting food from a transparent section of horizontal pipe closed at one end (30 cm long, 4 cm diameter) and mounted in a wooden stand with the centre of the pipe 12 cm above the ground. Ten sticks of 2 mm diameter, ranging in length from 8 to 26 cm at 2 cm intervals, were cut from lengths of bamboo skewer and displayed standing vertically in length order in a wooden block drilled with holes (see Fig. 1). This range of tool lengths is well within the range observed during spontaneous tool manufacture by both individuals in our laboratory. The pipe assemblage and the tool dispenser were placed in the centre of a table, with the tool block placed lengthwise adjacent to the pipe, so that they could approach the apparatus from any direction.

The tool block was reversed on each trial, so that the longest and shortest tools were alternately closest to the opening of the pipe, and the sticks were cleaned of any residual meat between trials. The food (a piece of ox heart weighing 0.5±0.1 g) was placed in the pipe using forceps (this was done outside the experimental room and therefore out of sight of the subjects) at one of ten distances from the opening, ranging from 8 to 26 cm. The food distances were randomly arranged among two sessions of ten trials each, so that each distance was presented once per session and twice in total. The adult bird's two sessions were on consecutive days, and the juvenile's on the same day. Within each session, the interval between trials (while the apparatus was being prepared for a new trial) was approximately 1 min. We deliberately limited the number of trials as it was our intention to test the abilities of the subjects to solve new problems, rather than their ability to improve in solving the task by practice and reinforcement; thus we wanted to minimise the opportunity for learning over the course of the experiment.

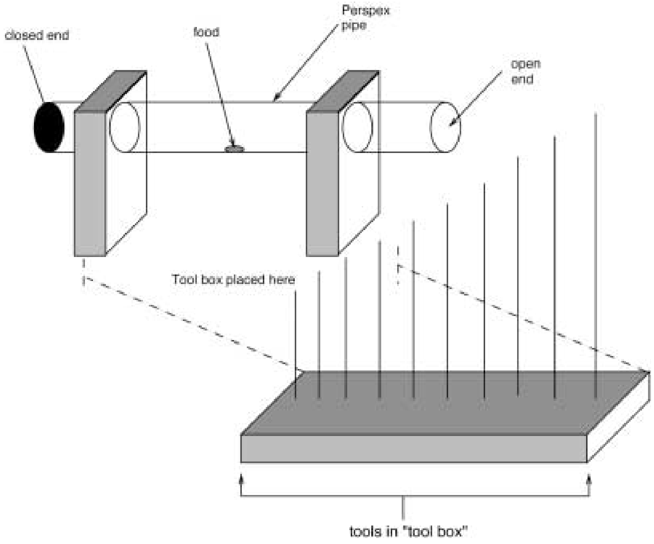


Fig. 1 A schematic representation of the apparatus used in experiment 1. The display of tool lengths was reversed on each trial so that the longest tool was alternately nearest or furthest from the opening of the pipe. The "tool box" is shown displaced to the right for clarity. In experiment 2, the tool box was placed approximately 3.5 m from the food pipe, with barriers adjacent to the tool box (0.71 m high) and food pipe (1.1 m high) preventing simultaneous viewing of both objects

Observations were made from behind a one-way window. The choice of tool was taken as the first stick to be inserted into the pipe. If the bird had selected a tool that was too short to reach the food, this was recorded as its choice, but it was allowed to select further tools until it was successful. In all such cases, the bird successfully removed the meat within 5 min of the start of the trial.

Results

Both birds showed similar behaviour in this experiment. They started by inspecting the position of the meat in the pipe, from the side (through the transparent walls of the pipe) and from the open end. They later approached the tool kit and picked one of the sticks. We suspect that in most cases, they could see the meat through the walls of the pipe from a distance before approaching either the pipe or tools, even if they did not closely inspect the position of the meat from the side once on the table. Thus, it is not possible from this data set to assess the relative contribution of the two different methods of inspection to the results observed.

There was no previous exposure to the setup before the trials analysed below. As described in the Methods, the tool the subject first inserted into the pipe was recorded as that trial's choice, but both birds sometimes initially removed other sticks from the tool box and immediately discarded them before taking one to the open end of the pipe. They held the sticks in one of two distinct ways, either by holding the stick at the proximal end so that it was in line with the beak, or, more frequently, holding it some distance down its length, with the excess at the proximal end pressed against the side of the head. It may be that this latter method offers greater mechanical control over the tool and better lateral stability. If they used the "tip" method, they could insert their whole beak into the tube and gain extra reach even with a short tool. The adult's beak measured 5.1 cm and the juvenile's 4.2 cm, so they could use a tool that was 4 cm shorter than the distance to the food and still successfully reach it. In practice, they did not do so (in this experiment, but see experiment 2),

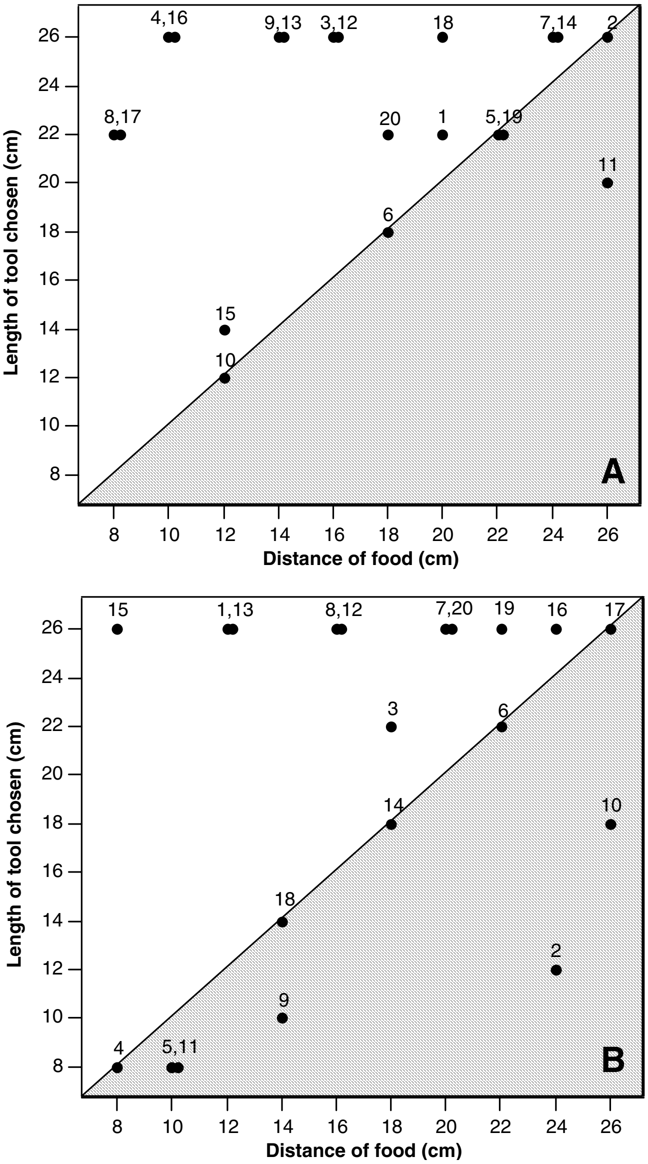


Fig. 2A, B Choice of stick as a function of distance of the food in experiment 1. Choices of tools are shown for the male (**A**) and the female bird (**B**). The small *numeric label* on each point is the number of the trial on which the choice was made. Choices of sticks that fell within the *hatched area* were too short to reach the food, those on the *diagonal line* matched the distance to food, and those in the *unhatched area* were longer than necessary to reach the food

perhaps because they preferred the second more lateral method of grasping the stick, or because they were fearful of inserting their head into the opening of the pipe. Both techniques involve using some stick length for holding. Since this was not quantified, we report all analyses with reference to the absolute length of the tools and depth of the food. A tool perfectly matching in length the depth of the food requires that the tip of the bird's beak is inserted into the entrance of the tube by an equivalent of the holding length lost.

Figure 2 shows the birds' choices of tool as a function of the distance of the food. The choices of the tool matching the distance to food (i.e. the diagonal of the plots) are distributed fairly evenly among the different food distances. Both birds chose the longest tool on 10 of the 20 trials, and the matching tool on 5 of the 20 trials. Their choice of one or other of these strategies did not seem to depend upon the distance of the food. In addition, the trial numbers show that the birds did not appear to change their strategy over the course of the trials. It is difficult to judge visually from Fig. 2 the extent to which the choices departed from random. To facilitate this comparison, Fig. 3 shows the same data as the proportion of trials on which the birds chose tools with specified deviations from the distance at which the food was placed, superimposed with the random expectation.

Both birds chose the matching tool (zero on the abscissa) significantly more often than expected by chance (5/20 trials; binomial parameters n, p equal to 20, 0.1 respectively; $P=0.032$. Both birds also chose the longest available tool significantly more often than random (10/20 trials, binomial parameters n, p equal to 20, 0.1 respectively, $P<0.00001$). In fact, the only "wrong" choices of tool (resulting in the subject being unable to get the food) were those showing negative deviations.

To give a more complete picture of how the subjects' choices compared to what one might expect if they were choosing randomly, we calculated the random probability that the crows would choose a tool of length equal to or longer than that necessary to reach the food. To do this, we needed to take into account that the random probability of choosing a longer than matching tool is greater the shorter the distance to the food. We found that the probability of committing as few errors as observed under random choice was less than 0.0001 for the male, and equal to 0.025 for the female. However, the distribution of choices does not seem to be due to the crows learning, over the course of the experiment, that "longer is better". A general linear model of the effect of trial on the length of tool chosen confirms the impression given by Fig. 2: there was no significant effect of trial number in the male and only a weak improvement in the female (male: $F_{1,9}=0.75$, $P=0.409$; female: $F_{1,9}=4.85$, $P=0.055$). This negative result does not mean that the birds were learning nothing. All we can say is that there is no indication in the data that learning took place during the experiments and that the pattern observed is not due to a substantial improvement during the experiment.

Throughout the entire period the crows seemed to use a bimodal rule: "Either choose a stick closely matching the distance of the food, or choose the longest tool in the set". Both strategies resulted in the crow getting the food (but so would using any tools longer than the minimum). Both crows used one or the other of the strategies on 70% (14/20) of the trials, when the random expectation would be 19% (binomial parameters n, p equal to 20, 0.19, respectively, $P<0.00001$). The random expectation ($p=0.19$) is calculated thus: in the two trials each bird experienced with food at the longest distance, the matching and longest tool is the same, so that the random probability of choosing this tool is 10%. In the remaining 18 trials, the

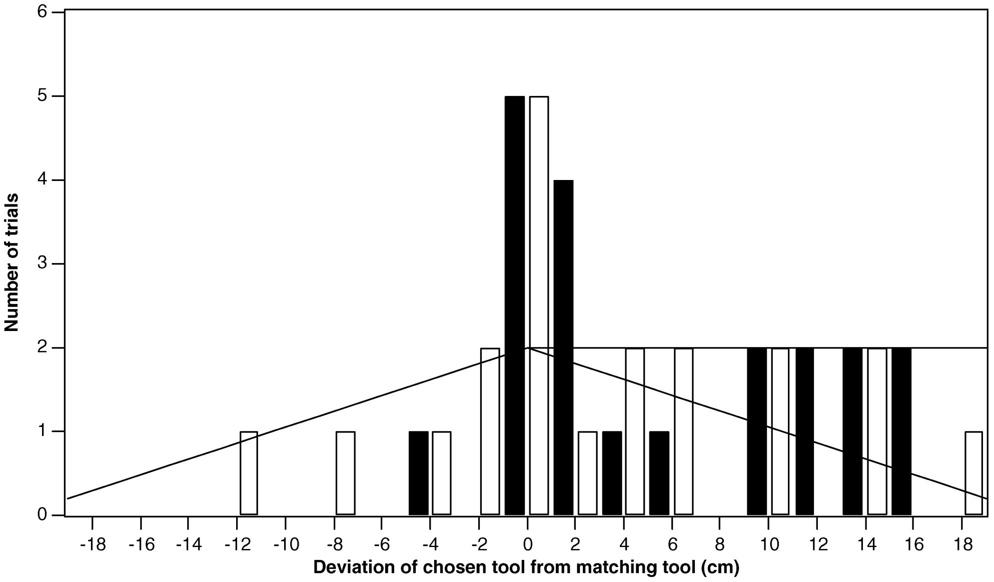


Fig. 3 Results of experiment 1. The *bars* show the number of trials in which the male (*black bars*) and the female (*white bars*) selected tools deviating by the length shown on the abscissa from the length of tool exactly matching the distance to food. For comparison, the figure shows the predicted number of trials if the birds selected tools at random (*solid line*), or always the longest (*dashed line*)

random expectation is double this value because two tools with random expectation of 10% each fit the rule (the matching one and the longest one), hence the total probability of following the dual strategy is 20%. This gives an overall random probability of using the dual strategy per trial of 19% {[(18×0.2)+(2×0.1)]/20=0.19}. The female bird committed more errors (choosing a shorter-than-matching tool) than the male, but we cannot interpret the potential developmental significance of this observation with a sample size of two.

Experiment 2

Methods

In experiment 1, the tools were immediately adjacent to the food pipe. In the wild and in spontaneous tool use and manufacturing in our laboratory, however, the food sources are not normally located next to the source of potential tools, and birds may have to remember the requirements of a task and then search for an appropriate tool at a different location. In experiment 2, we simulated this situation by repeating the experiment with the tools located away from the feeding site. The tool block was placed on the other side of the room, and two barriers prevented the subjects from viewing the food pipe from the tool block position and vice versa. A time limit of 2 h per trial was set for attempts to start the task, and if it took longer than this, trials were discontinued for that day.

This experiment was evidently much more taxing: the female did not complete any trials within the time limit. However, it was not inactive. During this time, the bird was actively using other materials in the room as tools in various places, and indeed it removed some of the provided sticks from the display to use in other locations. However, it did not attempt to use the provided sticks in the food pipe, and so it could not be used in this experiment. We cannot distinguish between motivational and cognitive reasons for this bird's failure to perform. The male took much longer than in experiment 1 to complete the extractions (mean latency±SEM=40.76±5.41 min, whereas in experiment 1 the maximum latency was less than 5 min for both subjects), so that the 20 trials took 30 days to complete.

Results

The male bird's behaviour in this experiment was rather interesting. The increase in time taken to complete the task noted above was almost exclusively due to the time taken to make any response at all. Once it had started to respond (i.e. left the perch and approached the table with the food pipe on it), it then solved the task with a comparable speed to that shown in experiment 1 (i.e. in a maximum of 5 min). The order of its actions was the same on every trial: after a lengthy period of waiting on a perch as described above, it went to the food pipe and looked at the position of the food within the pipe, both from the open end of the pipe and from the side. It then flew to the location of the tools, selected one, and returned to the food pipe. It then used the tool to remove the food. On two of the four occasions on which it selected a tool that was shorter than the distance to the food, it still successfully removed the food with the tool (in both cases, the tool selected was only 2 cm shorter than the distance to the food). This was possible because it used the "tip" holding technique and held the tool very close to the end, inserting part of its beak into the pipe. In the remaining two unsuccessful trials, the bird selected tools that were 4 and 6 cm shorter than the distance to the food, and it was not able to reach the food. On these two occasions, it returned very rapidly to the location of the tools and selected a longer tool, with which it successfully reached the food.

Figure 4 shows the male bird's choice of tool as a function of the distance of the food. The choices of the tool

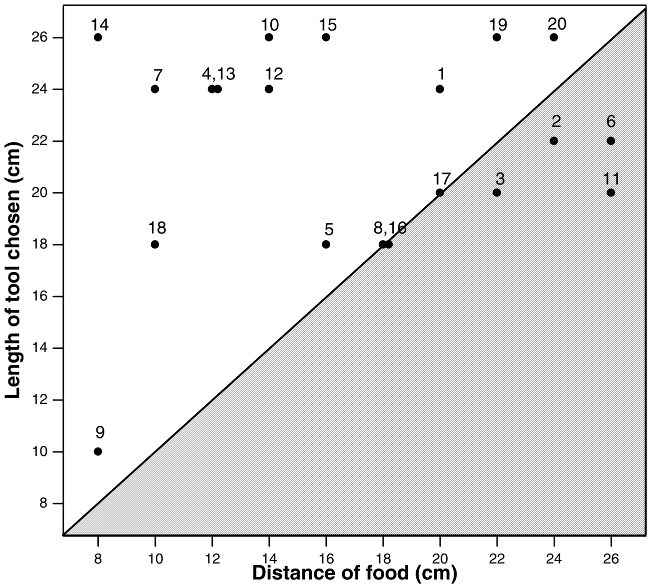


Fig. 4 Choice of stick as a function of distance of the food in experiment 2 by the male bird. See legend for Fig. 2 for details

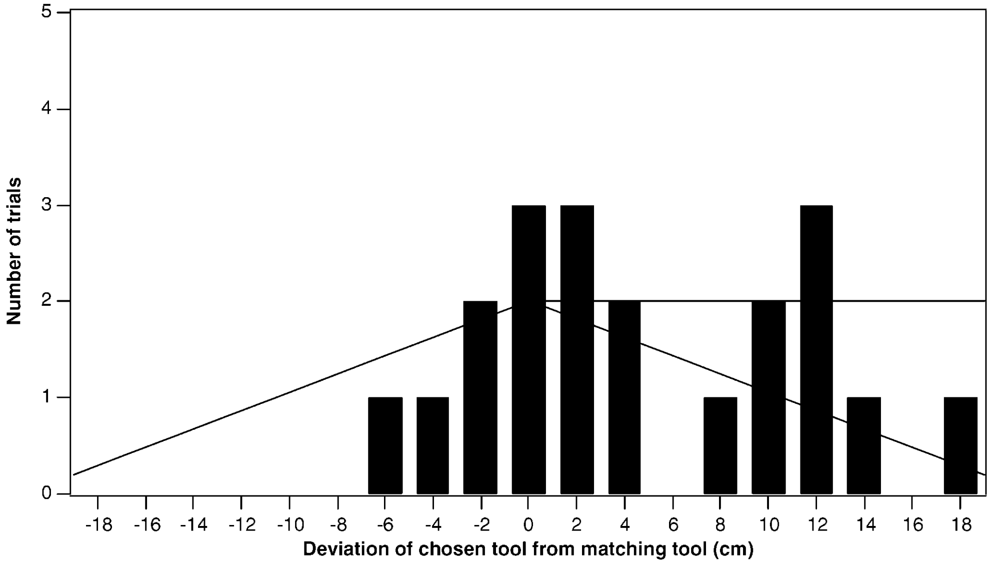
matching the distance to food are distributed fairly evenly among the different food distances. The bird chose the longest tool on 5 of the 20 trials, and the matching tool on 3 of the 20 trials. Again, the trial numbers show that the bird did not appear to change its strategy over the course of the trials.

Figure 5 shows how the bird's choices compared to random, and to a strategy of always choosing the longest tool. As in experiment 1, we calculated the probability of choosing a tool of length equal to or longer than that necessary to reach the food as often as observed. This was less than 0.025, hence performance is significantly better than random. The longest available tool was chosen significantly more often than random (5/20 trials, binomial parameters *n*, *p* equal to 20, 0.1, respectively, P=0.032). The number of choices of a tool exactly matching the minimum necessary length was not significantly better than random (3/20 trials; binomial parameters *n*, *p* equal to 20, 0.1, respectively, P=0.19). This suggests either that this task is more demanding than the one in experiment 1, or that the subject under these conditions was not interested in the challenge imposed by matching tool to food distance, drifting to the approach of always taking a tool from among the longer ones, without reference to the position of the food. The effect was not due to learning to choose always the longest stick, as the percentage of choices of the longest tool dropped from 50% in experiment 1 to 25% in experiment 2. Of the 20 trials, 20% were errors (tool shorter than minimum required). This performance is better than chance (45%), but poorer than the single error (5%) shown by the same subject in experiment 1. Again, the subject did not change its performance substantially over the course of the experiment. A general linear model of the effect of trial on the length of tool chosen revealed no significant effect ($F_{1,\,9}$=0.60, P=0.459).

Discussion

Experiment 1 showed that New Caledonian crows are capable of selectivity with respect to tool length when choosing tools for a task. It also showed that although they matched the distance to food significantly more often than would be expected at random, choosing the longest tool also appeared to be an important strategy. It remains to investigate what would be the longest tools used if the subjects had been presented with a set including tools beyond their usable range. We cannot claim that they were choosing optimal tool lengths, because it is difficult to specify what the optimal choice of length should have been. Any tool equal to or longer than the food distance could serve to solve the task, so that using a tool within

Fig. 5 Results of experiment 2. This experiment could only be completed with one subject (the male). The *bars* show the number of trials in which it selected tools deviating by the length shown on the abscissa from the length of tool exactly matching the distance to food (*symbols* are as in Fig. 2)



the set of longer ones (for instance the top half of lengths) would do better than random. In particular, always choosing the longest stick could have solved all tasks. In fact, choosing a tool that is slightly longer than the minimum may have been a good strategy, since we observed that both birds occasionally pushed the food further away in their attempts to pull it towards them, needing to pick a longer tool later to complete the extraction. Second, as discussed in the results of experiment 1, the birds are able to dynamically adjust the "working length" of longer tools.

One might speculate on why, if using a longer than necessary tool has some advantages, the crows often chose tool lengths matching the food distance, rather than choosing the longest available tool on all trials. It is likely that there are practical disadvantages to using a longer and hence heavier than necessary tool, such as the difficulty involved in manoeuvring a larger tool, perhaps translating into a longer time to finish the task. Any aiming error, tremor, or involuntary movement is amplified at the tip of a longer instrument. Even if the crow eventually grips the tool some distance down its length, it may take longer to get the tool into position and adjust the grip than it would with a shorter tool. Although we cannot eliminate this possibility, we believe that time costs are unlikely to have been important in intake rate terms. The trials did not form part of sessions with a long series of repetitions, so that short delays led to lost opportunity. They were more akin to one-shot chases of a single reward, where times other than the procurement interval dominate in computing the rate. The crows typically worked very fast and in the first experiment, started to interact with the apparatus as the experimenter was leaving the room. The extractions were completed within a few seconds, so that within the range of appropriate tools the time difference could not have caused a significant loss of foraging opportunity (the rationale for rate maximisation in foraging theory). However, the reason we cannot fully discard time as a factor is that in a one-shot task, even a small delay may have a strong psychological impact, because in the wild the extraction time may be particularly vulnerable to prey loss by competition, or by the potential escape of live prey. Although the functional reasons for preference of matching tools remain a matter of speculation, the results show that the crows do have the capacity to choose tools according to the specific task they face.

We cannot tell whether the task imposed in experiment 2 is at the limit of the crows' abilities, but even though this experiment was done later (and hence the subjects could have benefited from experience), the one subject that completed the experiment made more errors than in experiment 1. Nonetheless, although the results of experiment 2 do not support selectivity for a matching tool, the choices of the male bird were clearly non-random and biased towards choosing the longer tools. Moreover, this performance is even more impressive when compared to that of capuchin monkeys on an analogous task. Only 1 of 13 capuchins tested was able to transport tools successfully to a food source, although 7 of 13 were able to transport the food to the site of the tools (Jalles-Filho et al. 2001). Furthermore, the capuchins' task was somewhat simpler as they did not need to select an appropriate tool – all the tools provided were adequate to solve the task. Jalles-Filho et al. (2001) suggest that transportation of tools to use at a remote target requires a degree of abstract representation: a representation of the tool being sought and the intended goal must be coordinated, and the actions executed in the correct sequence. This is not necessarily the case when the food is transported to the tools, as the animal is in continuous sensory contact with the food, and this could evoke an associative link with the tools. Crows do transport tools in the wild (Hunt 1996) and may have a tool kit composed of different tools, though we do not as yet know what the different functions of the tools might be.

The ability of New Caledonian crows to select an appropriate tool on their first exposure to a task that is novel to them is impressive because hitherto, only primates have been shown to exhibit tool selectivity such as reported here (Anderson and Henneman 1994; Visalberghi et al. 1995; Hauser 1997; Hauser et al. 1999; Povinelli 2000). Furthermore, in the primate tests, performance typically improved gradually over a number of sessions, whereas here the birds solved the problems from the first exposure with no noticeable effect of experience. Although showing a capability for tool selection is impressive per se, as with other animals (see Hauser 2001), the extent to which New Caledonian crows' abilities in the tool domain are a specialisation for tool using or an expression of unusual cognitive ability in general can only be established by further experimentation.

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