

Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*

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(Received 21 January 2003; initial acceptance 6 March 2003;
final acceptance 7 August 2003; MS. number: 7589)

Woodpecker finches are famous for their spontaneous tool use behaviour in the wild. They use twigs or cactus spines to pry arthropods out of crevices and use this ability more than any other tool-using species known. We experimentally investigated the cognitive abilities related to tool use. We chose three experimental designs that have been used to test several primate species (trap tube task and modification task) and New Caledonian crows (tool length task). One of six woodpecker finches was able to solve the trap tube task, and several individuals modified tools and chose twigs of appropriate length. Most subjects mastered these new tasks quickly, but we found no evidence that they were able to assess the problems in advance. These findings resemble those obtained for primates in these tasks.

Comparative studies of cognitive aspects of behaviour, including social competence, imitation and tool use, have aimed to pinpoint important steps in the emergence of primate intelligence and the corresponding increase in brain volume (Byrne & Whiten 1988; Tomasello & Call 1997; Reader & Laland 2002). Tool use is considered to require special cognitive abilities, because it involves causally relating two or more objects that are external to one's own body (Piaget 1954; Parker & Gibson 1977). Research in monkeys and apes has revealed that the ability to learn by trial and error varies between species, and that success in using tools does not imply causal understanding (Tomasello & Call 1997; Visalberghi & Tomasello 1998; Povinelli 2000). Chimpanzees, *Pan troglodytes*, and orang-utans, *Pongo pygmaeus*, are outstanding in the primate world for their tool-manufacturing and tool-using behaviour both in the wild and in captivity (e.g. Lethmate 1982; Tomasello & Call 1997; Whiten et al. 1999; van Schaik et al. 2003). These results are consistent with the hypothesis that, at least in primates, brain size and tool use ability are causally linked (Reader & Laland 2002). However, tool use is not restricted to primates, but occurs in many other taxa, including insects and birds (Beck 1980). Habitual use of tools is known from several bird species: Egyptian vultures, *Neophron percnopterus*, drop stones on ostrich eggs (van Lawick-Goodall & van Lawick

1966); green-backed herons, *Butorides striatus*, use bait to catch fish (Walsh et al. 1985); satin bowerbirds, *Ptilonorhynchus violaceus*, use bark wads to paint their bower (Chaffer 1945); and New Caledonian crows, *Corvus moneduloides*, make and use at least three forms of tools to aid prey capture (Hunt 1996), and even manufacture hooks from wire to solve a specific task, exceeding even nonhuman primates with this ability (Weir et al. 2002).

As in primates, tool use abilities in birds are related to the size of selective neural structures. Tool use is positively correlated with the size of the neostriatum ventrale and hyperstriatum ventrale, indicating that special cognitive abilities are related to this skill (Lefebvre et al. 2002).

We investigated the cognitive abilities associated with tool use by the woodpecker finch, *Cactospiza pallida*. These birds use twigs or cactus spines to pry out arthropods from tree holes and crevices (Eibl-Eibesfeldt 1961). Woodpecker finches even modify their tools: they shorten twigs or break off side twigs that would prevent insertion into holes. Woodpecker finches spend more time using tools and acquire more food with them than do chimpanzees (Nishida & Hiraiwa 1982; Boesch et al. 1994; Yamakoshi 1998), which are the most proficient tool users among nonhuman primates. In the arid zone during the dry season, woodpecker finches spend half their foraging time using tools and obtain 50% of their prey this way (Tebbich et al. 2002). Therefore, this species seems to be an obvious candidate for investigating the cognitive abilities related to tool use. Several primatologists have proposed that only primates have special cognitive skills for using tools

(Parker & Gibson 1977; Bard 1995; van Schaik et al. 1999). Parker & Gibson (1977) classified tool use in the woodpecker finch as a context-specific, stereotyped behaviour, contrasting it with the intelligent tool use in apes. Experiments by Millikan & Bowman (1967), however, indicate that woodpecker finches are very flexible in their use of tools, and our own studies demonstrate that trial-and-error learning is involved in the acquisition of tool use in young, naïve woodpecker finches (Tebbich et al. 2001). We chose three experimental designs to investigate further the cognitive abilities related to the use of tools in this species. In the trap tube task (experiment 1), animals were confronted with a reward in a transparent or opaque tube that contained a hole connected to a vertically mounted trap (Limongelli et al. 1995). If a tool is applied from the wrong side of the tube, the reward falls into the trap and is lost. In the tool length task (experiment 2), food was presented in a transparent tube at different distances and woodpecker finches had to choose from five tools of different lengths. In the modification task (experiment 3), H-shaped tools were provided that had to be modified to fit into the tube (Visalberghi et al. 1995). We addressed the following questions. (1) Are woodpecker finches able to solve the trap tube task, and is there any indication that they have the ability to foresee the effect of their actions? (2) Are woodpecker finches able to choose a tool of exact or sufficient length? (3) Do woodpecker finches modify tools according to the task requirements, and are they able to assess the requirements of the task in advance? Given that woodpecker finches show spontaneous modification of tools in the wild, we expected them to master the last two tasks easily, but were not able to make predictions about their ability to assess these problems in advance.

The trap tube and modification tasks have been used to investigate similar questions in several primate species (Visalberghi & Trinca 1989; Visalberghi & Limongelli 1994; Limongelli et al. 1995; Visalberghi et al. 1995; Povinelli 2000), and the length task has been used to investigate cognitive abilities in New Caledonian crows (Chappell & Kacelnik 2002). Therefore, we expected these approaches to allow us to compare cognitive abilities involved in tool use between woodpecker finches and other tool-using species. Assuming that cognitive abilities may evolve in response to environmental challenges, we expected that woodpecker finches, which rely on the use of tools in times of food shortage, would be at least similar in their performance to other frequent tool users such as chimpanzees.

GENERAL METHODS

Study Area

The study was carried out at the Charles Darwin Station on Santa Cruz Island in the Galápagos Archipelago, Ecuador, from 15 September to 6 December 2001.

Housing

We mist-netted 17 woodpecker finches in the agricultural and arid zone of Santa Cruz. Finches were first kept

in a small cage (50×50 cm and 100 cm high) for 24 h. They were then housed singly in aviaries (2×1 m and 2 m high) that contained branches, a sawdust floor and food and water *ad libitum*. The finches were fed fresh insects and a mixture of minced beef, breadcrumbs and fresh cheese, with sand added to aid digestion. The tests were conducted in the housing aviaries. To prevent the possibility of observational learning, the aviaries were separated by opaque screens. All birds were released at the end of the experimental phase.

Tool Use Abilities of Woodpecker Finches

Since not all woodpecker finches use tools (Tebbich et al. 2001), after 4 days of habituation to the aviary, we tested their ability to recover food with the aid of tools by presenting a beetle larva in a wooden block with a crevice (5 mm wide×30 mm deep×80 mm long, open on top and on both sides). The wooden block was placed on a platform of concrete blocks. The larva was inaccessible without the help of tools. We put 10 twigs, 4–6 cm long, on the block. Each test lasted 30 min. Normal food was removed 1 h before the trial began. Individuals were tested singly, twice a day, for at least 25 days. The six birds that used tools frequently were used in the subsequent tests. Of the other 11 birds, one hardly used tools and 10 never did so; they were released after this initial test phase.

Subjects

Two of the six birds retained were juveniles (Blanco and Red1), approximately 5–8 months old. Juveniles can be identified by their beak colour, which changes from pink to black at the onset of the first breeding season. The ages of the adults (Rosa, Orange, Yellow, Blue2) could not be determined. One of the four adult finches (Blue2) was caught towards the end of our study period and therefore participated only in the covered trap tube experiment and the modification of natural tools. The other five birds participated in all experiments. All birds probably already had had some tool use experience in the wild, and we had observed three using tools before their capture.

Training

A Plexiglas tube (45 mm long×12 mm wide), open only at one end, was fixed horizontally on a wooden block (45 mm long×90 mm high). Several tools (toothpicks, 60 mm long, split lengthwise to reduce their weight) were placed near the opening on the wooden block. The side to which the open end pointed was randomized and counterbalanced. A beetle larva was placed near the closed end of the tube. To obtain the larva, woodpecker finches had to use a tool to pull it towards them. In the wild, woodpecker finches also lever or pull prey towards themselves and hardly ever push it away (S. Tebbich, personal observation). We required the finches to perform five correct responses before we proceeded to the next training step.

For this step, the Plexiglas tube was again fixed horizontally on the wooden block, but it was now open at both ends. Two tools 60 mm long were placed near the open side of the tube, and the larva was placed in the middle. We provided two tools because woodpecker finches often dropped tools to the ground. All finches solved this task within three trials. Each trial lasted up to 20 min. Again, we required the finches to perform five correct responses before we proceeded to the experiment.

Data Analysis and Statistics

In the trap tube experiment (experiment 1), unless stated otherwise, we analysed the performance of each finch in blocks of 20 trials to detect potential increases in performance. We scored only the successful retrieval of the food as a correct choice. We used a binomial test to assess the statistical significance of the results; the null hypothesis was 50% success. In the trap tube experiment and the two modification tasks (experiment 3), we used a Wilcoxon signed-ranks test to assess changes in the number of tool insertions, errors and time until success between the first and the last experimental block. The trials compared were in the same sequential order. In the tool length task, we used a Mann–Whitney U test to compare the tool length chosen by the finches in trials after failure versus trials after success in the previous trial. We used nonparametric statistics (Siegel & Castellan 1988) and SPSS 7.5.1 for Windows (SPSS Inc, Chicago, U.S.A.). All tests are two tailed.

Ethical Note

Permission to catch the birds and to conduct the study was given by the Galápagos National Park. The birds were kept for 30–75 days, depending on their tool use abilities. Woodpecker finches show no fear of humans and habituate easily to captivity. All individuals resumed feeding within 5 h of capture and maintained their weight throughout the study. The birds were released at the location of their capture shortly before the following breeding season. However, we were not able to follow these individuals after release because of the large territory size (up to 4 ha) and the low singing activity at this time of the year. In a previous study (Tebbich et al. 2001), several individuals were resighted up to 3 months after the release.

EXPERIMENT 1: TRAP TUBE TASK

Methods

Transparent trap tube

The trap tube apparatus consisted of a horizontally oriented clear tube (90 mm long \times 10 mm diameter) mounted on a platform by two vertical Plexiglas sheets. The tube contained a hole and a vertically oriented trap mounted lateral to the centre, 35 mm from the nearest end (Limongelli et al. 1995; Fig. 1a). Before the birds entered the aviary, we placed the food in the centre of the

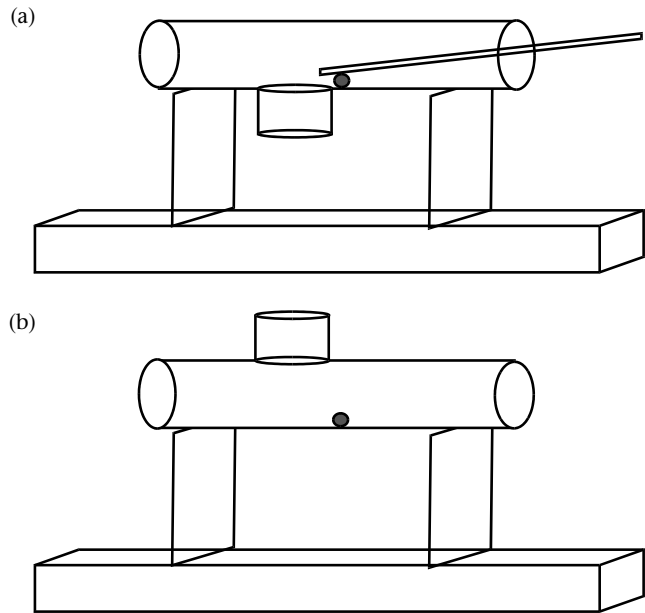


Figure 1. (a) Apparatus used in the trap tube task (experiment 1), consisting of a Plexiglas tube with a hole lateral to the centre and a trap underneath. (b) In the control condition the tube was rotated, so that the trap was ineffective.

tube. The food could be obtained either by inserting the tool at the end nearest to the trap and pushing the reward or by inserting it at the end furthest from the trap and pulling the reward. We chose to position the food centrally in the tube because we wanted to prevent the birds from using the relative distance of the food as a cue (Visalberghi & Trinca 1989). However, the relative distance of the trap could still have served as a cue to solve the task.

The orientation of the apparatus was changed trial by trial, so that the position of the trap was right or left of the centre according to a randomized, balanced schedule. Each finch therefore received the same number of trials with the trap to the left and right of the centre. Two tools 60 mm long were placed on the wooden block on each side of the tube. The experimenter placed the apparatus on the brick platform, and the session started as soon as the experimenter left the aviary. Each trial lasted 10 min at most. If the finch obtained the larva, the apparatus was removed and the next experiment started after the 10 min had elapsed. If it was not successful or the reward fell into the trap, the apparatus stayed in the aviary for the entire 10 min. This procedure ensured that food intake per time did not differ between successful individuals, which could have affected motivation. Each bird had five trials in the morning and five trials in the afternoon and at least 60 total trials. Rosa, Red1 and Orange, who had been caught earlier than the other birds, received 80 trials. Rosa had another 20 trials after the opaque trap tube task (below).

All trials were recorded with a digital video camera, operated by the experimenter behind a screen so that the experiment could be followed on the video mini screen without the bird seeing the experimenter. The observed behavioural variables were picking up a tool, number of

insertions into the tube, the side of insertion (defined from the observer's perspective), whether the animal pushed the larva away or pulled it towards itself, and the number of successful retrievals of food and failures (food pushed into the trap).

Opaque trap tube

During the trials with the transparent trap tube, we noticed that the finches often peered into the tube before they started to use tools, and that the hole leading to the trap was not clearly visible from this perspective. After finishing the transparent trap tube trials, we covered the horizontal tube completely with opaque tape but left the trap transparent. This technique enhanced the visual contrasts between the tube and the trap and made the hole leading to the trap more visible to the finches as they peered into the tube ($N = 80$ trials for Red1, Orange and Blue2, 60 trials for Blanco and Yellow and 40 trials for Rosa, using the same procedure as in the transparent trap tube task).

Control: inverted transparent and covered trap tube

As a control, we investigated the behaviour of the bird when the trap was ineffective. The trap tube was rotated 180° so that the trap was on top (Fig. 1b). As before, the orientation of the apparatus was changed according to a randomized and balanced schedule. Testing consisted of four blocks of five trials each for the transparent and covered conditions. Only Rosa was tested in this control condition.

Results

Transparent trap tube

All five birds made contact with the apparatus and inserted tools. Except Orange, all individuals showed high levels of motivation throughout the trials. Four of them predominantly pulled the reward towards themselves (Rosa: 99% of the trials; Orange: 92%; Red1: 74%; Yellow: 73%), and Blanco pushed and pulled equally often. In the first four experimental blocks, none of the five birds retrieved the food above chance level when we analysed blocks of 20 trials, and Yellow and Blanco performed significantly below chance level in one block (Fig. 2a).

The performance of Blanco merits more detailed attention. This bird had several long sequences in which it consistently failed or succeeded. In the beginning, it failed 11 times in a row, and later on it succeeded once eight times and once seven times in a row. In random sequences with $N = 66$, one sequence with 11 or more heads/tails in a row is very improbable ($P = 0.007$, S. Rands, unpublished software program to determine exact probabilities). Even a sequence with eight heads/tails is unlikely ($P = 0.056$). It therefore appears that the behaviour of Blanco was not random. In the long sequence of failures, Blanco avoided the side with the trap and pushed the reward. It subsequently switched from pushing to pulling the reward and was frequently successful, but did not stick consistently to this strategy.

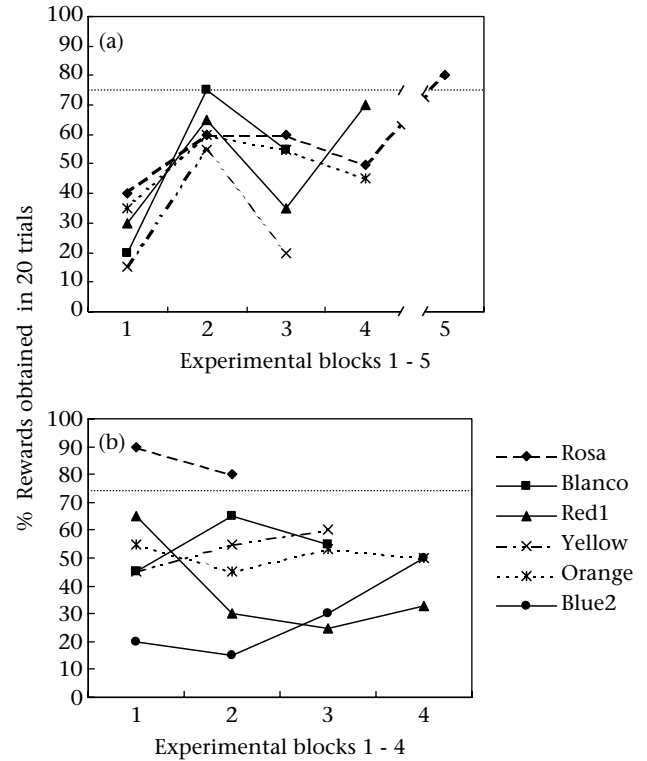


Figure 2. Percentage of rewards obtained in (a) the transparent trap tube task in experimental blocks 1–5 and (b) the opaque trap tube task in blocks 1–4 ($N = 20$ trials per block). Block 5 of the transparent trap tube task was performed after the opaque trap tube task. The dotted horizontal line marks the significance level at 75%.

Another procedural rule that finches could follow is to stick to one side. Scoring only the final insertion in each trial, Blanco and Rosa had a significant preference for one side in the last block of 20 trials (Blanco: 75% of insertions from the right side, binomial test: $P = 0.041$; Rosa: 90%, $P < 0.001$) and Red1 in the last two blocks (75% and 80%; $P = 0.041$ and $P = 0.012$).

After the subsequent experiment with the opaque tube, Rosa was tested once more with the transparent trap tube and retrieved the food significantly above chance level (binomial test: $P = 0.012$; Fig. 2).

Obtaining the food could be solved in two ways: a finch could first look at the position of the reward in relation to the trap and insert the tool accordingly. This would probably require a mental representation of the problem and require only one insertion of the tool. Alternatively, the bird could insert the tool and observe the effect of its own actions on the reward and adjust its own behaviour accordingly. In this case, more than one tool insertion and insertions from both sides would be likely. An analysis of Rosa's behaviour showed that it inserted the tool significantly more often, and more frequently from both sides of the tube, in the last 20 trials than in the first 20 trials (Wilcoxon signed-ranks test, number of insertions: $Z = -3.729$, $P < 0.001$; number of side changes: $Z = -2.547$, $P < 0.05$; Table 1). As the experiment proceeded, Rosa became very cautious when the reward was near the trap. It took significantly longer until loss or

Table 1. Median number (range) of insertions into the transparent trap tube, and side changes from one opening to the other, and mean (range) time (s) until loss or access of the reward in the first and last experimental blocks of the transparent trap tube task and the control task

| Experimental block ($N = 20$ trials) | No. of insertions | No. of side changes | Time until success |
|--|----------------------|------------------------|-----------------------|
| First | 1 (1–3) | 0 (0–1) | 16.2 (7–32) |
| Last | 7.5 (2–22) | 0.5 (0–4) | 57.1 (16–117) |
| Control | 8.5 (3–34) | 0 (0–6) | 41.9 (7–120) |

access of the reward in the last 20 trials than in the first 20 trials (Wilcoxon signed-ranks test: $Z = -3.884$, $P < 0.001$; Table 1).

Opaque trap tube

Rosa obtained the reward in 90% of the first 20 trials and in 80% of the following 20 trials (Fig. 2b). Blanco, Orange, Red1 and Yellow performed at chance level; Blue2 performed significantly below chance level in the first two blocks and at chance level in the last block (Fig. 2b). The initial failure of Blue2 did not occur because of a simple distance rule that the bird might have applied. For example, when Blue2 failed 12 times in a row, it both pulled from the side closer to the trap and pushed from the opposite side.

Trap tube control

When the trap was reversed, Rosa performed at chance level in 20 trials, both with the opaque and the transparent tube (45% and 55%, respectively). Rosa showed a significant preference for the right side (transparent tube: 75% insertion from the right side; binomial test: $P = 0.041$; opaque trap tube: 100%; $P < 0.001$).

EXPERIMENT 2: TOOL LENGTH

Methods

This experimental design was similar to that of Chappell & Kacelnik (2002). The aim of the experiment was to test whether woodpecker finches were able to choose a tool of proper length for a given task, and if so, whether they did so by choosing the exact length or any length that would solve the task. Five birds (Rosa, Blanco, Red1, Orange, Yellow) were presented with a horizontal, transparent tube (80 mm long \times 10 mm diameter and open on one side) mounted on a platform by two vertical Plexiglas sheets. A bait (1-cm-long segment of a beetle larva) was arranged in random sequence at five distances (20, 35, 50, 65 and 80 mm) from the opening. On another wooden block with drilled holes, five tools of different lengths (15, 30, 45, 60 and 75 mm) were presented vertically, ordered by length (Fig. 3). The mean length of a woodpecker finch beak is 12 mm, so birds were able to reach the bait with a tool slightly shorter than the distance. The length of the tools was in the range of tools used in natural situations (S. Tebbich, personal observation).

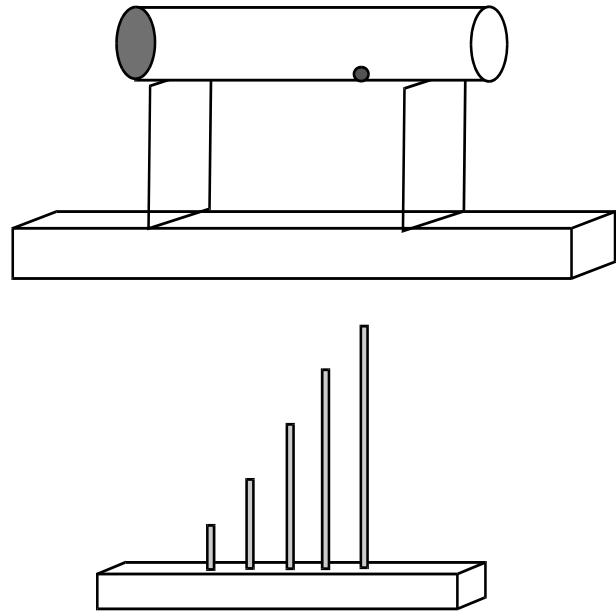


Figure 3. Apparatus used in the tool length experiment (experiment 2). Woodpecker finches could choose between five tools, mounted on a wooden block, to reach the reward that was presented at five distances to the opening in the transparent Plexiglas tube.

The orientation of the block with tools was randomized and balanced so that the distance of the shortest and longest tool to the tube opening was alternated. The birds were tested in four sessions with five successive trials for a total of 20 trials, so that each distance occurred four times. After success, which usually occurred within 1 min, we waited 5 min before beginning the next trial. The birds were tested on 2 successive days. We recorded all tools that the birds either successfully or unsuccessfully used to obtain the bait. The choice was classified according to the first tool inserted into the tube. Birds were able to reach the bait with a matching tool or one that was longer than the presented distance. If a bird chose a tool that was too short, we allowed it to choose further tools until it was successful.

Results

Did finches match tool length with position of food item?

There was no indication that any of the five birds tried to match tool length with the position of the food item in the tube. Exact matches occurred three to six times ($N = 20$ trials: expected by chance: 4 times; Table 2). We found no significant correlation between location of food and the length of the first tool chosen (Spearman rank correlation: $r_s = -0.06$ to 0.38 , all $N = 20$, all $P > 0.095$).

Were finches able to solve the task on their first attempts in each trial?

All five birds retrieved the food items eventually, but not necessarily with the first tool chosen. For the subsequent analysis, we included only the first chosen tool of each trial. In the position closest to the opening, the bait could

Table 2. Performance of five birds in a tool length task

| Subject | Match length | Sufficient length | Mean tool length | After failure | After success |
|---------|--------------|-------------------|------------------|---------------|---------------|
| Blanco | 6/20 | 13/16 | 62 | 75(3) | 59(16) |
| Orange | 5/20 | 9/16 | 50 | 56(7) | 47(12) |
| Red1 | 5/20 | 12/16 | 57 | 72(4) | 53(15) |
| Rosa | 4/20 | 13/16 | 62 | 60(3) | 62(16) |
| Yellow | 3/20 | 7/16 | 47 | 47(9) | 44(10) |

Data show how often each finch matched tool length with position of food in the tube, chose tools of sufficient length, mean tool length (mm) chosen, tool length in trials following a trial with initial failure and in trials following a trial with immediate success. Numbers in parentheses represent sample sizes for trials following trials with initial failures or immediate success.

be retrieved with all tools, so these trials were not included in the analysis. For the combined remaining four situations, the average probability that a bird would choose a tool that was long enough was 50% ($80 + 60 + 40 + 20\%/4$). However, the birds' performances in each situation could not be pooled and tested against a 50% chance probability, so we only describe the results. Three of the five birds tested chose an appropriate tool (exact or longer than necessary length) at the first attempt of each trial with high probability (Table 2). Blanco and Rosa chose an appropriate tool in 81% of their trials, and Red1 in 75%. Blanco made no mistakes in its last 11 trials. Yellow and Orange performed close to chance level (56% and 44%, respectively), and their success rate did not increase substantially between trials.

Could the finches use any obvious strategies to solve the task?

The high success rates of Blanco, Rosa and Red1 were not because of a general preference for long tools. In fact, all five birds chose sticks of the two shortest length classes in their respective first trials. In particular, Yellow started with the shortest tool and used it six times during the first 10 trials but not thereafter in trials 11–20 (Fisher's exact test: 6:4 against 0:10, $P = 0.011$). Two of the three highly successful birds, Blanco and Red1, appear to have used the decision rule 'if you failed initially in one trial, go for the safe option and choose the longest tool in the next trial'. Red1 used significantly longer tools in trials after a failure than in trials after success (Mann–Whitney U test: $U = 9.5$, $N_1 = 4$, $N_2 = 15$, $P = 0.047$) and Blanco showed a strong tendency in this direction (Mann–Whitney U test: $U = 9$, $N_1 = 3$, $N_2 = 16$, $P = 0.093$; Table 2).

EXPERIMENT 3: MODIFICATION TASK

Methods

Modifying artificial tools

Five birds (Rosa, Blanco, Red1, Yellow, Orange) were presented with an opaque tube 90 mm long \times 7 mm wide, open at both ends. The food item was placed in the middle of the tube. Two H-shaped tools were placed on the wooden block at either side of the tube. The H-shaped tools were toothpicks, split lengthways and 60 mm long, with two smaller sticks (20 mm long) affixed transversely at each end. The smaller pieces were fixed by splitting the

ends of the toothpick and inserting the transverse pieces. To insert the tool, the birds had to remove at least one transverse piece, either by wriggling it out or by breaking it off. Each bird received 30 trials, each lasting a maximum of 15 min. If a bird was successful in obtaining the larva, 5 min elapsed before the next trial began. We recorded the following: picking up a tool, attempted insertion of the H-shaped tool, attempted removal of the transverse piece, removal of the transverse piece, insertion of the transverse piece, removal of one transverse piece and attempted insertion with the wrong end, successful insertion of a modified tool, the latency (s) from the first contact with the tool until its first successful insertion into the tube. We used this measurement instead of time until success because the stickiness of the larva segments varied, affecting the difficulty of prey extraction for the birds.

Modifying natural tools

The apparatus (horizontal opaque tube) was the same as in the previous experiment and we tested all six birds. The tools were dry twigs of *Scutia spicata*, 60 mm long, with 15-mm-long thorns near both ends. These thorns pointed in opposite directions. As in experiment 2, the thorns prevented the insertion of the tool into the tube. To insert the tool, the finches had to break off at least one thorn and correctly orient the tool ($N = 15$ trials). We recorded the same behavioural parameters as in the previous experiment. Blue2 hardly approached the apparatus, picked up tools only 10 times and never attempted an insertion. This subject was therefore not included in the final data analysis.

Results

Modifying artificial tools

Rosa, Blanco and Red1 solved this task repeatedly. Rosa needed 21 trials until it first got the reward, and Blanco and Red1 were successful after 14 trials. Rosa and Red1 removed the transverse pieces by wriggling them out or breaking them off, and Blanco learned to remove them by shaking the tool or pushing the tool against obstacles. After this initial success, these three birds solved the task in all subsequent trials. However, all three individuals continued to make three types of errors before retrieving the food (Table 3). Two birds improved their performance from the first 10 to the last 10 trials in two ways. In the last

Table 3. Mean \pm SD latency (s) until successful insertion of a modified tool, and number of the three types of errors in the modification task with artificial tools

| Subject | Latency | | EH | | ES | | EO | | Total | |
|---------|--------------|--------------|----|----|----|----|----|----|-------|-----|
| | 1 | 3 | 1 | 3 | 1 | 3 | 1 | 3 | 1 | 3 |
| Rosa | | 47 \pm 12 | 51 | 7 | 8 | 0 | 19 | 0 | 78 | 7* |
| Blanco | 180 \pm 98 | 42 \pm 21* | 40 | 66 | 34 | 0 | 0 | 3 | 74 | 69 |
| Red1 | 74 \pm 49 | 48 \pm 36 | 37 | 39 | 10 | 47 | 6 | 24 | 53 | 110 |
| Yellow | | | 26 | 5 | 0 | 0 | 0 | 0 | 26 | 5* |
| Orange | | | 11 | 4 | 0 | 2 | 0 | 0 | 11 | 6 |

1, 3 represent the first and third blocks of 10 trials each. EH = insertion of the H-shaped tool; ES = insertion of the short transverse piece; EO = insertion of the T-shaped tool in wrong orientation. Rosa was not successful in the first block and Yellow and Orange not at all. Therefore, values for latencies are missing.

* $P < 0.05$; Wilcoxon signed-ranks test, comparison of latency and number of errors in the first and last block of trials.

10 trials Blanco inserted the modified tool in significantly less time (Wilcoxon signed-ranks test: $T = 57$, $P < 0.001$; all other individuals NS; Table 3) and Rosa made fewer errors (Wilcoxon signed-ranks test: $T = 1$, $P = 0.011$; Table 3). Rosa made no errors in the last seven trials.

Modifying natural tools

Rosa, Blanco, Red1 and Yellow modified the tool and retrieved the food in the first trial. Duration until the successful insertion and number of errors did not decrease between trials 1–7 and 8–14 (Table 4).

DISCUSSION

Our results reveal that woodpecker finches are similar to other tool-using species in their ability to solve the three given tasks. However, the way in which they solved these tasks both corresponded and differed between species.

In trap tube experiments similar to ours, where the trap was in the centre of the tube and the reward either left or right of it, three of 12 chimpanzees (Limongelli et al. 1995; Povinelli 2000) and one of four capuchin monkeys (Visalberghi & Limongelli 1994) solved the problem. However, when the trap was nonfunctional, in the control condition, the successful primates showed the same behaviour as in the test. Thus, they had learned to insert the tool into the opening furthest from the reward and showed no understanding of the physical problem (Visalberghi & Limongelli 1994). Similarly, only one of

six woodpecker finches, Rosa, was able to solve the trap tube problem in experiment 1. Rosa was the only finch that used one technique almost exclusively to obtain the reward, namely, pulling the food towards itself. It is possible that the mixed strategy of pulling and pushing made it more difficult for the other individuals to solve the task.

In contrast to all tested primates, Rosa behaved differently in the control condition with the inverted trap than during the conditions with the functional trap. When the trap was inverted, Rosa extracted the food predominantly from one side, regardless of where the trap was located. It is therefore unlikely that this bird used the relative distance of the trap as a cue to solve the task. However, this control condition did not confirm whether Rosa understood the function of the trap, because the condition can exclude only one of the several rules that Rosa might have learned.

Our results do not indicate that Rosa was able to form a mental representation of the problem and assess it in advance. Limongelli et al. (1995) showed that two chimpanzees solved the trap tube problem in a transfer task by directly approaching the correct side, which indicates their ability to assess the problem in advance. The multiple insertion of the tool from both sides in the successful trials instead supports the idea that Rosa observed the effect of its own tool manipulation on the reward. Especially in this respect, Rosa showed a behavioural similarity with the successful capuchin monkey described in Visalberghi & Limongelli (1994). The ability

Table 4. Mean \pm SD latency (s) until successful insertion of a modified tool, and total number of the three types of errors in the modification task with natural tools in first and second blocks ($N = 7$)

| Subject | Latency | | EH | | ES | | EO | | Total | |
|---------|--------------|--------------|-----|-----|----|---|----|----|-------|-----|
| | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| Rosa | 32 \pm 22 | 50 \pm 52 | 10 | 27 | 1 | 0 | 10 | 0 | 21 | 27 |
| Blanco | 148 \pm 96 | 89 \pm 50 | 127 | 109 | 6 | 2 | 7 | 4 | 140 | 115 |
| Red1 | 98 \pm 73 | 100 \pm 60 | 81 | 97 | 3 | 2 | 5 | 19 | 89 | 118 |
| Yellow | 113 \pm 71 | 72 \pm 25 | 28 | 15 | 4 | 0 | 1 | 0 | 33 | 15 |
| Orange | | | 29 | 0 | 0 | 0 | 1 | 0 | 30 | 0 |

EH = insertion of H-shaped tool; ES = insertion of short transverse piece; EO = insertion of T-shaped tool in wrong orientation.

to monitor the effect of the tool on the larva was also possible with the covered trap tube, because the finches peered into the opening of the tube. Under these conditions, the visibility of the trap may even have been enhanced, and they probably resembled a more natural situation. The change in Rosa's performance from random to 90% correct choices occurred abruptly with the use of the opaque tube. We therefore conclude that it was the new test condition that improved the bird's performance, and not a coincidence or an improvement over time from practice effects.

White, Yellow and Blue2 performed significantly below chance level in the first experimental blocks. They did not apply a distance rule like chimpanzees in series of failures (Limongelli et al. 1995) but approached the tube from both sides (close to or distant from the trap) and pushed or pulled, depending on their position. A plausible explanation for this behaviour is that the finches tried to push the larva into the visible hole of the trap, which they saw when peering into the tube. Perhaps, they had to learn that the hole led to a trap where the food was inaccessible.

In the tool length task (experiment 2), three birds chose tools of sufficient length with a high probability. Although they did not match the tools to the given distance, as shown in New Caledonian crows (Chappell & Kacelnik 2002), three finches obtained the prey with their first chosen tool with a high probability, and one similar to that of crows. Within the very short testing period, some finches were able to assess the necessary length in advance. This result, however, may have reflected a fast learning process. Like the New Caledonian crows, woodpecker finches had a tendency to choose tools longer than necessary but had no preference for the longest ones. Choosing a longer tool did not impose obvious costs on the finches. Furthermore, it is likely that the cost of error is asymmetric: in the wild, woodpecker finches normally break off their tool from a twig or cactus, insert it and shorten it if it is too long. If they bring a tool that is too short, they have to search for a new tool, which may take considerable time (S. Tebbich, personal observation).

In the modification task (experiment 3), the woodpecker finches' performance was similar to that of primates so far investigated (chimpanzees, bonobos, *Pan paniscus*, orang-utans and capuchin monkeys: Visalberghi et al. 1995). Most of these primates were able to solve the task, but their performance indicated that they were not able to understand in advance that an H-shaped tool does not fit into the tube. At first they tried to insert the unmodified tools in various ways. Although apes reduced the number of errors over time, the capuchin monkeys persisted in making them. In our first modification task, three of five birds learned to modify and use the tools correctly after a few trials. Like the apes, two finches improved their performance over time either by reducing the time until correct insertion or by reducing the number of errors. However, the other two birds persistently used the nonfunctional tools, even in the last trial. This result again indicates that the birds did not form a mental representation of the task and were unable to assess the problem in advance. The natural tools in the second modification task were easier to handle for the finches,

and one more individual was able to solve the task, but all of them committed errors until the end of the experiment.

Primates have a general tendency to manipulate objects that make the development of tool use likely (Povinelli 2000). Woodpecker finches also seem to have a specific predisposition for the acquisition of tool use (Tebich et al. 2001). This may be why they are also able to form associations related to tool use in new tasks quickly and easily. It remains to be determined whether these learning abilities are related only to tool use or whether they are more general. Furthermore, no information exists on the brain size or brain morphology of woodpecker finches. Comparative data on the learning ability and brain morphology of Darwin's finches may be useful to determine whether tool use demands special cognitive abilities.

In conclusion, tool use in the woodpecker finch is not a stereotypic behavioural pattern, but is open to modification by learning. Although we found no evidence for a mental representation of the physical problems, some of our subjects were able to solve the trap tube problem, modify tools for a specific task and choose tools of a sufficient length. Studies suggest that even chimpanzees do not reason about unobservable physical processes, but rather are fast learners (Tomasello & Call 1997; Povinelli 2000). Tool use in the woodpecker finch also seems to be guided by a rapid process of trial and error learning.

Acknowledgments

We thank the Galápagos National Park Service and the Charles Darwin Research Station for support, TAME for reduced ticket fares and especially W. Wickler for enabling this study. Santiago Torres Baéz, Carlos Vinuesa and Heide Tebbich helped in data collection, Nathan Emery and Kim Sterelny gave helpful advice on the manuscript, H. Prossinger and Sean Rands gave statistical advice and H. Bshary helped to catch the birds. J. Chappell and E. Visalberghi helped to improve the manuscript with constructive comments. The project was financed by the Max-Planck Institute for Behavioural Physiology Seewiesen. Both authors were also funded by the European Union (Marie Curie Fellowship).

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