Insightful problem solving and creative tool modification by captive nontool-using rooks

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The ability to use tools has been suggested to indicate advanced physical cognition in animals. Here we show that rooks, a member of the corvid family that do not appear to use tools in the wild are capable of insightful problem solving related to sophisticated tool use, including spontaneously modifying and using a variety of tools, shaping hooks out of wire, and using a series of tools in a sequence to gain a reward. It is remarkable that a species that does not use tools in the wild appears to possess an understanding of tools rivaling habitual tool users such as New Caledonian crows and chimpanzees. Our findings suggest that the ability to represent tools may be a domain-general cognitive capacity rather than an adaptive specialization and questions the relationship between physical intelligence and wild tool use.

cognition | intelligence | Corvus | frugilegus | hook

The ability to use tools, once thought to be unique to humans, has been suggested to indicate advanced physical cognition in animals (1, 2). True tool use is "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just before use and is responsible for the proper and effective orientation of the tool" (1). Recent studies on tool-using chimpanzees (3, 4) and nontool-using birds and monkeys (5, 6) have questioned the relationship between tool use and physical intelligence. Many species have been observed to use tools in the wild, including insects, sea otters, herons, Egyptian vultures, woodpecker finches, capuchin monkeys, orangutans, and chimpanzees (1, 2, 7); however, only chimpanzees, orangutans, New Caledonian crows, and woodpecker finches habitually use and manufacture tools in the wild (8–12, although see refs. 13, 14). In the laboratory, early experiments indicated that chimpanzees lack a functional understanding of tool properties (4); however, more recent studies suggest that these abilities may have been underestimated (15, 16). New Caledonian crows have also been shown to be capable of tool selection (17, 18), modification (19), and metatool use (i.e., using one tool to access another tool to access food) (20, 21).

Recent estimates suggest 39 cases of true tool use in birds, with corvids as the most proficient tool users (7). New Caledonian crows readily modify and use tools to extract grubs from small holes (10, 11) and a captive New Caledonian crow made hooks out of straight pieces of wire to retrieve food (19). It has been suggested that tool use may have evolved in this species as a result of cognitive specialization, ecological pressures, or morphological features (22). Rooks do not use tools in the wild but appear to have physical intelligence that rivals chimpanzees (5, 23, 24). We describe the spontaneous use of tools in captive rooks and investigate its causal underpinnings.

When given a completely novel apparatus containing a worm suspended on an out-of-reach platform only accessible by collapsing the platform (supporting information (SI) Fig. S1), 5 rooks dropped a stone down a vertical tube providing the necessary force to collapse the platform and acquire the worm (Movie S1). Subjects learned the affordances of the task by either nudging the stone into the tube (presumably accidentally in the first instance) or by observing another bird solve the task (at this pretraining phase, all subjects were tested together in the main aviary). Subjects were given 5 trials each in which the stone could be nudged into the tube. Having successfully completed these 5 trials, each subject was then given a further 5 trials whereby the stone was placed at the base of the tube. Upon this transfer, all subjects immediately picked up the stone and dropped it into the tube. Having completed 5 transfer trials, each subject was removed from the main aviary to allow another subject to access the apparatus. One subject (Fry) did not need any "nudging" trials but rather spontaneously picked up the stone and dropped it into the tube, having watched her partner Cook successfully complete the transfer task (she performed this behavior on Cook's fourth transfer trial). Therefore, although insight is not implicit in this initial behavior acquisition, the behavior fits current definitions of tool use (1, 25) and presents the opportunity to investigate insightful reasoning in subsequent tests.

The first 4 rooks to solve the task (Cook, Fry, Connelly, and Monroe, in this order) were subsequently presented with experiments to investigate the causal underpinnings of this behavior. It is likely that these 4 birds solved the task first as they were the 4 most dominant birds and monopolized the apparatus. The other birds in the group did not have the same opportunity to show the behavior.

For testing, subjects were individually isolated in testing areas separate from the main aviary. These areas each consisted of an indoor testing room connected to an outdoor "run." Subjects were free to move between the room and the run. When in the run, subjects could see the rest of the group, whilst when in the room they were visually isolated. Experiments followed the same general procedure. The apparatus was baited with a waxworm (wax moth larvae, *Achroia grisella*) and placed into the testing room; the bird performed the behavior or was timed out after 5 min if not successful, and the apparatus was removed. In experiments where subjects were given a choice of tools, the tools were placed next to the apparatus and the position of the tools was pseudorandomized so that no one tool was consistently closest to the apparatus. Each test consisted of between 10–60 trials per bird (see *Methods*).

Data were tested for normality using the Anderson Darling test ($P < 0.05$). Data that were not normalized were subject to nonparametric tests; however, data were mainly analyzed using a General Linear Model (GLM), the residuals of which were

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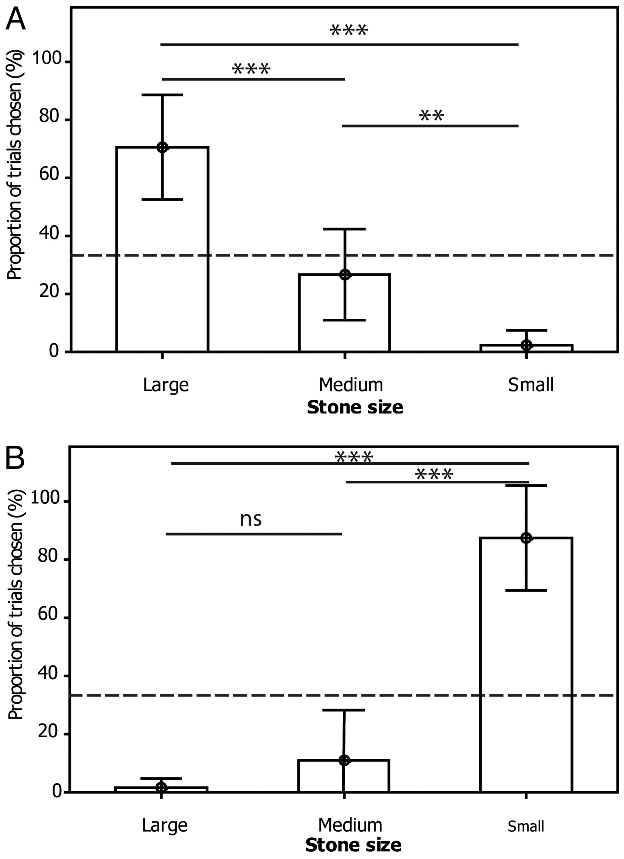

Fig. 1. Choice of appropriate stone size. Mean stone sizes ± SEM: large (23.5 ± 2.0 g), medium (11.2 ± 0.4 g), small (3.8 ± 0.5 g). Graphs display percentage mean choices of 4 subjects across all trials. (*A*) Stone size choice when presented with large diameter tube. Subjects preferred to use the large stones (GLM, stone size: $F_{2,28} = 51.83$, $P = 0.00$, [Tukey test: large–medium $T = 6.49$, $P = 0.00$, large–small $T = 10.04$, $P = 0.00$, medium–small $T = 3.55$, $P = 0.004$]), and this did not differ across blocks of trials (GLM, block: $F_{2,28} = 0.00$) or between subjects (GLM, subject: $F_{3,28} = 0.00$) (*B*) Stone size choice when presented with small diameter tube. Subjects switched their choice to the small size stones (GLM, stone size: $F_{2,28} = 258.88$, $P = 0.00$, [Tukey test: large–medium $T = 2.21$, $P = 0.086$, small–large $T = 20.72$, $P = 0.00$, small–medium $T = 18.51$, $P = 0.00$], block: $F_{2,28} = 0.00$, subject: $F_{3,28} = 0.00$). ** $P < 0.01$, *** $P < 0.001$. Dashed line represents 33% chance level.

tested for normality such that the model assumptions were met. Factors included in these analyses were the variable under question (e.g., tool functionality), block (to examine any effects of learning), and subject (to test for individual differences between the 4 birds). We also performed planned comparisons using Tukey tests in the experiments that provided a choice of 3 tools. Alpha was 0.05. Interobserver reliability was performed on a random subset of trials (10% of trials were analyzed by an independent reviewer). In choice tasks, the agreement of the 2 reviewers was 100%. Where other behaviors had to be scored (e.g., whether the stone was rotated, whether the stick was pushed down, etc.), reliability was 94 ± 3.2%. Where some other measure was required (e.g., stone weight or hook angle) reliability was calculated using the Pearson correlation coefficient; $r = 1.0$, $P = 0.00$.

Stone Size Test. When provided with a choice of different stone sizes, all 4 subjects preferred to use the largest stones (Fig. 1*A*; Movie S2; Fig. S2*A*). This preference was interesting as all of the stones offered in this choice experiment were functional; that is, they were all able to fit into the tube and were heavy enough to release the platform. The large stones may have been chosen in this case since they were more visually salient. When the diameter of the tube was reduced from 42 mm to 16 mm, such that the large- and medium-sized stones no longer fit, all subjects inhibited their initial preference by choosing the small stones significantly more often than the large or medium stones (Fig. 1*B*; Movie S2). Three of the 4 subjects made this choice on the first trial (Monroe chose the medium stone on the first trial and the small stone on the second trial) without trying the larger stones first (Fig. S2*B*). This transfer indicates that rooks are capable of selecting tools based on their functionally relevant properties in relation to specific task affordances; in this case size was functionally relevant. Although stone size and weight were confounded, all choice stones were heavy enough to collapse the platform, such that weight in itself was an irrelevant property.

Stone Retrieval Test. When not provided with stones, all 4 subjects left the testing room to the external run, selected a stone from the ground, and returned with a tool. When choosing the tool, the apparatus was out of sight; hence, selecting the appropriate sized tool required remembering which size tube had been provided. Subjects only needed to be selective in the stones they chose for the small tube, as both small and large stones were successful with the large tube. All 4 subjects chose significantly smaller stones for use with the small tube (4.1[mean] ± 0.7[SEM] g) than for use with the large tube (7.6 ± 0.8 g). A General Linear Model (GLM) showed a significant effect of tube size on the size of stones chosen ($F_{1,9} = 17.81$, $P = 0.002$), but no difference between subjects ($F_{3,9} = 1.05$, $P = 0.414$) or blocks ($F_{1,9} = 2.79$, $P = 0.126$). The size of stones chosen markedly decreased after trial 1 with the small tube, but not for the large tube (Figs. S3*A* and *B*), although there was no effect of interaction between tube size and block ($F_{1,9} = 0.51$, $P = 0.494$).

The shape of the stones was also important as large stones that were long and thin could be used successfully with the small tube if oriented vertically. Stones chosen for use with the small tube fell below the critical size (16 mm) in only 2 of the 3 dimensions (width and depth) on 66.3 ± 7.4% of successful trials.

Stone Orientation Test. When provided with the choice of a long, thin stone or a round stone, all subjects chose the long, thin stone regardless of tube size (small tube: 97.5 ± 1.4% of trials, large tube: 98.8 ± 1.3% of trials). Although the same stone was chosen for both tubes, the way in which it was manipulated differed. To fit the long, thin stone into the small tube, subjects rotated it into a vertical orientation. The stone was rotated significantly more often for the small tube than the large tube (GLM, effect of tube size: $F_{1,10} = 40.51$, $P = 0.00$, block: $F_{1,10} = 0.39$, $P = 0.55$, subject: $F_{3,10} = 2.80$, $P = 0.1$). This manipulation was performed by 3 of the 4 subjects on the first trial and 2 of subjects made the rotation without first trying the stone in the horizontal orientation (Movie S3, Fig. S4).

Stick Use Test. We carried out further experiments where the subjects could not access stones but were provided with a novel stick tool. Immediate transfer to using a new tool in the same apparatus would demonstrate flexibility and understanding of task affordances. Subjects were first given the apparatus with the large tube and provided with a 16.5 cm long stick. All subjects immediately used the sticks in place of the stones to solve the task. A particular technique was used for inserting the sticks, whereby subjects picked up the stick near to its end and placed it into the bottom of the tube first. When provided with a heavy, thick stick, subjects simply dropped the stick into the tube as they would stones (Fig. 2*A*; Movie S4*a*; Fig. S5*A*). However, when provided with a light, thin stick, subjects retained their hold once inserted and subsequently pushed down to provide the necessary force to collapse the platform and release the worm (Fig. 2*B*;

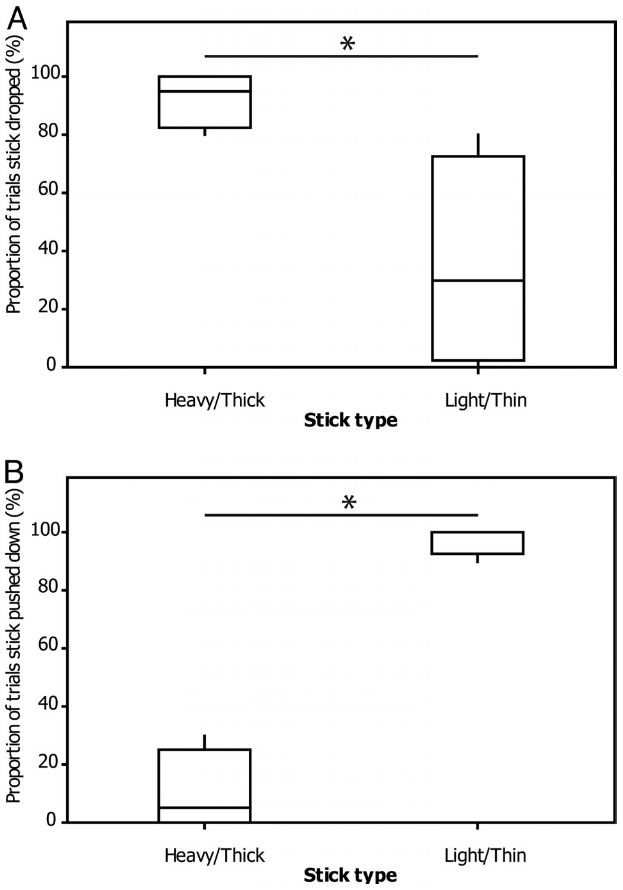

Fig. 2. Actions when using sticks as a tool. Heavy sticks were 3.5 g (165 mm × 8 mm) and light sticks were 0.5 g (165 mm × 2 mm). Mann-Whitney U tests were used to compare stick type for 2 different actions (dropping and pushing down). (*A*) Stick dropped. Box plot (median, IQR, 95% CI) showing proportion of trials stick dropped ($W = 25.5$, $n = 4$, $P = 0.043$). (*B*) Stick pushed down. Box plot (median, IQR, 95% CI) showing proportion of trials stick pushed down ($W = 10.0$, $n = 4$, $P = 0.03$). $*P < 0.05$

Movie S4*B*; Fig. S5*B*), suggesting a goal-directed action rather than a conditioned dropping response.

Functional Tool Type Test. In a further 2 choice tests using the small tube, subjects were provided with the 2 tool types (stick and stone) that were either functional or nonfunctional depending on whether they would fit in the tube. In the first combination, subjects were given a functional long stick (16.5 cm) and a nonfunctional large stone (20–30 g). In the second combination, subjects were given a nonfunctional short stick (7 cm, note that this short stick was not heavy enough to be successful when dropped) and a functional small stone (2–4 g), All 4 subjects chose the functional tool regardless of tool type; that is, they predominantly chose the stick in the first choice test (Fig. 3*A*; Movie S5) and the stone in the second choice test (Fig. 3*B*; Movie S5). All 4 subjects chose the functional tools on the first trial in both tests (Fig. S6). Although we can say that subjects chose the functional tool in both cases, we should also point out that subjects may have simply had a preference for a long stick over a large stone and a small stone over a short stick regardless of functionality. As subjects had previously showed a preference for large stones, this may seem unlikely, although this still leaves the possibility that sticks increase in attractiveness very steeply as a function of length. Although not run here, conditions where the large stone and short stick are functional while the long stick and small stone are not may help to answer this question.

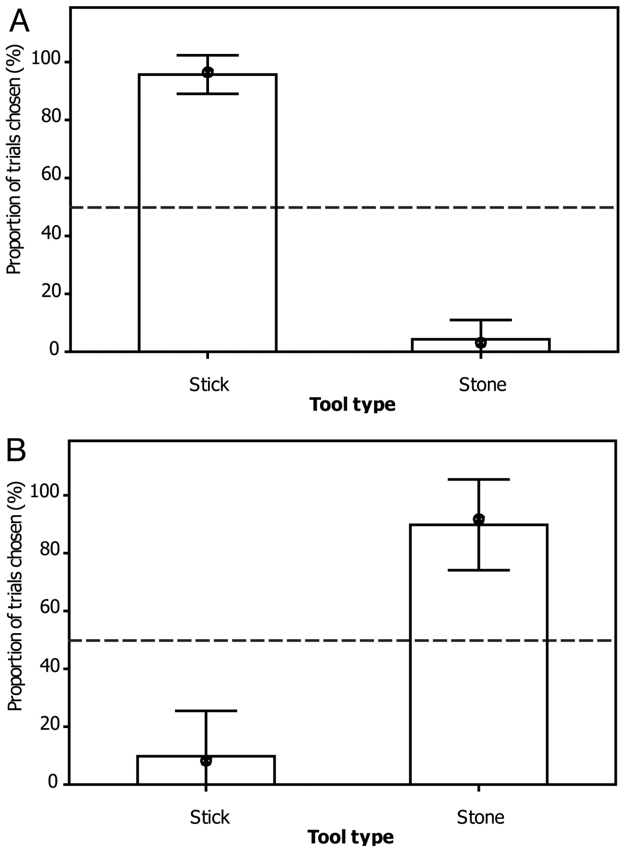

Fig. 3. Choice of tool type. Graphs display mean choice of 4 subjects across all trials. Subjects chose the functional tool (GLM, functional, or nonfunctional, $F_{1,40} = 771.56$, $P = 0.00$), regardless of tool type (stick or stone, $F_{1,40} = 3.56$, $P = 0.07$). There was no difference in choice between blocks of trials (GLM, block: $F_{2,40} = 0.00$) or subject (GLM, subject: $F_{3,40} = 0.00$). (*A*) Combination 1: functional stick versus non-functional stone. Subjects chose the stick nearly every time. (*B*) Combination 2: non-functional stick versus functional stone. Subjects chose the stone nearly every time. Dashed line represents 50% chance level.

Metatool Test. Use of "a tool that serves as a tool for another tool (ref. 24, p. 361)," or metatool use, is thought to be an important step in hominid evolution (25). Typically, metatool use has been examined using sequential tasks in which subjects have to use a tool to reach a second tool that can be used to access out-of-reach food (26, 27). Great apes and New Caledonian crows rapidly solve metatool tasks (20, 28), whereas monkeys have had limited success (29, 30). Difficulty in metatool use stems from 3 problems. First, the subject must recognize that one tool can be used on another or on nonfood items. Second, the subject must resist the immediate motivation to use the tool to attempt to access the food directly, and third, the individual must be capable of hierarchically organized behavior (20).

We tested the subjects on a spontaneous metatool use task, whereby they had to use a large stone to access a small stone that could be used to release the inaccessible food. Subjects were provided with an initial tool (large stone) and then a choice of 2 tools that could be accessed with it (Fig. S7). One choice of tool was another large stone; the other was a small stone, which could be used to access the food in the small tube (Movie S6). All 4 subjects solved the metatool use task from the very first trial (Fig. 4) and success rates were very high (96.7 ± 2.6%). Subjects rarely tried to access the food with the initial large stone (16.7 ± 4.7% of trials). Instead, they used this stone to access another tool, choosing to access the small stone significantly more often

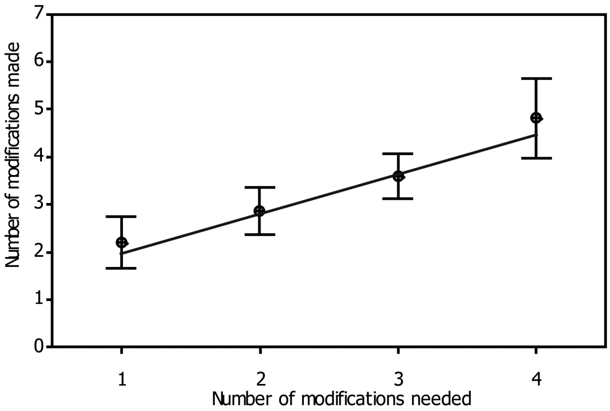

Fig. 4. Stick modification efficiency. Mean number (± SEM) of modifications made against number of modifications needed. Line shows linear regression ($r^2 = 0.23$, $F_{1,116} = 35.27$, $P = 0.00$).

than the other large stone (76.7 ± 1.4%, GLM; stone size, $F_{1,17} = 544.00$, $P = 0.00$; block, $F_{2,17} = 0.00$; subject $F_{3,17} = 0.00$). On trials where the small stone was accessed, this stone was immediately used to access the food on 97.5 ± 1.6% of trials. On trials where the large stone was chosen, subjects immediately rectified their mistake by using this stone to access the small stone 94.0 ± 3.0% of the time. Our metatool task improves on a previous metatool task reported for the New Caledonian crows (20) by providing a choice between 2 previously rewarded tools (large and small stones) so that our subjects had to attend to the functional features of the tool (21).

Stick Modification Test. The ability to select appropriate tool properties and to manipulate a tool may be important indicators for tool modification or manufacture. We therefore tested the rooks' ability to modify tools. Subjects were given the small tube and provided with a piece of elm tree consisting of a straight section (120–220 mm long) and a number of smaller side branches (Fig. S8 *A* and *B*). The straight section could not be used as a tool unless the side branches were broken off. Each subject received 30 trials in which the stick needed 1–4 modifications to become a functional tool. All 4 birds demonstrated tool modification and successful use of the modified tool to access the worm. Success rates were very high (97.5 ± 1.6% of trials). On most trials, modifications were made to the stick when it was partially inserted into the tube (96.5 ± 1.4% of trials). Subjects also modified the stick on the platform on 23.1 ± 3.9% of trials and performed the modification before first attempting to insert the stick on 3.5 ± 2.0% of trials. Placing the stick partially into the tube provided a very useful method for holding the stick stable whilst modifications were made (Movie S7; Fig. S8*C*). There was a highly significant linear relationship between the number of modifications needed and the number of modifications made to each stick (Fig. 5). All subjects were highly efficient in their modifications, directing their actions to the base of the side twigs to snap them off cleanly, and only making an average of 1.5 modifications for every 1 needed. In addition to this, subjects rotated the sticks to minimize the number of modifications needed on 29.2 ± 8.0% of trials and only tried to push down the stick before it was successfully modified on 33.5 ± 5.6% of trials.

Hook Use Test. In the final set of experiments, we tested our subjects on a different tool use task, similar to the type of tool use used by New Caledonian crows (10, 11). The task required the rooks to use a hook tool to retrieve an out of reach bucket containing a waxworm, located in a vertical clear tube (Fig. S9). In the initial task, we provided a hook tool next to the apparatus. This consisted of a 16 cm long stick with an arrow shaped hook on one end (Fig. S9*A*). Subjects were required to insert the tool the correct way round (hook end down), hook the tool onto the bucket handle and pull up (rather than push down as previous experiments had required). All 4 subjects successfully solved this task (success rate was 90.8 ± 4.4% of trials), with 3 of the 4 birds solving the task on trial 1 and the fourth bird solving the task from trial 2 (Movie S8 and Fig. S10*A*). All subjects inserted the hooked end into the tube significantly more often than the straight end (GLM; tool end $F_{1,17} = 4.54$, $P = 0.048$; subject $F_{3,17} = 1.60$, $P = 0.226$); however, this required some learning (block $F_{2,17} = 10.93$, $P = 0.001$).

Functional Hook Test. To further test the subjects understanding of hook shape on functionality, we carried out a second experiment whereby subjects were provided with a choice of 2 tools; one with a functional hook and the other with a nonfunctional (backwards) hook end (Fig. S9*B*). Subjects chose to insert the functional hook tool significantly more often than the nonfunctional hook tool (GLM; tool type $F_{1,17} = 41.65$, $P = 0.000$; subject $F_{3,17} = 0.00$, $P = 1.00$; block $F_{3,17} = 0.00$, $P = 1.00$).

Three of the 4 subjects chose the functional hook on the first trial, while the fourth subject (Cook) was successful from trial 3 (Fig. S10*B*). Although we cannot exclude the possibility that subjects simply perseverated on the same tool as used in the first experiment, we can say that subjects actively discriminated between the 2 possible hook shapes. This is interesting as the nonfunctional hook contains identical components as the functional hook but in an alternative, inappropriate arrangement and therefore is not chosen.

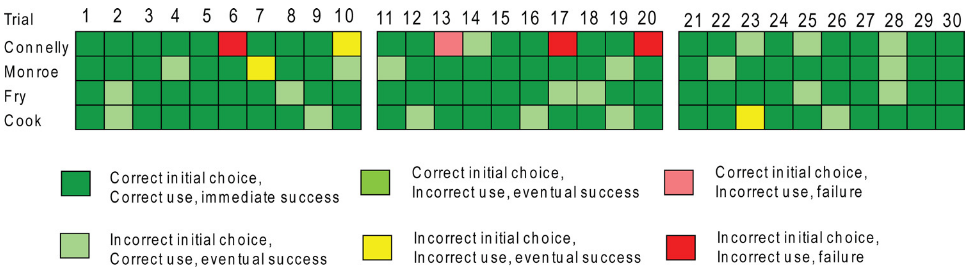

Fig. 5. Metatool use task; trial by trial description of behavior. Initial choice indicates whether the tool provided was used to acquire the small stone (correct) or the large stone (incorrect). If the small stone was chosen, this stone was either used to acquire the worm (correct use, immediate success); used to acquire the large stone and subsequently used to acquire the worm (incorrect use, eventual success), although this never happened; or taken away (incorrect use, failure). If the large stone was chosen, this stone was either used to acquire the small stone, which in turn was used to acquire the worm (correct use, eventual success), redropped into the empty tube before being used to acquire the small stone which was in turn used to acquire the worm (incorrect use, eventual success) or taken away (incorrect use, failure).

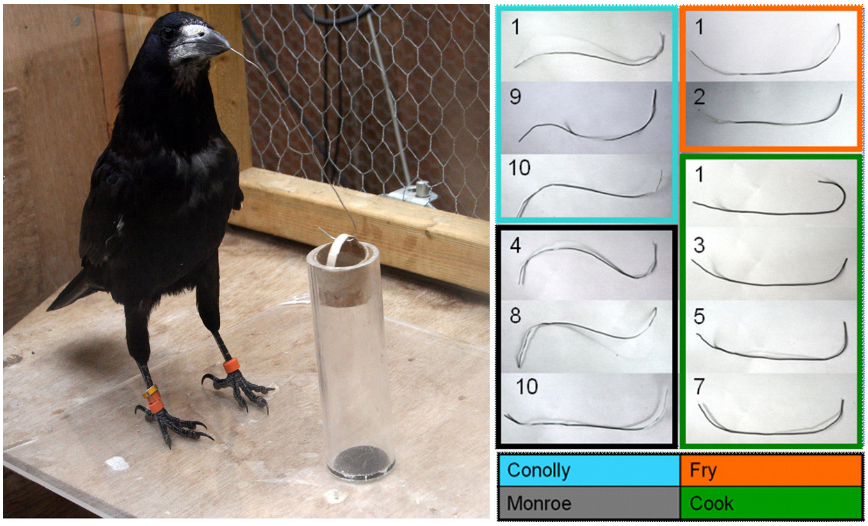

Fig. 6. Bending wire into hooks by rooks. (*Left*) Fry extracting the bucket containing a worm using a piece of wire she had just bent. This photo was taken after the experiment was completed but the hook and posture are typical of experimental trials. (*Right*) Photographs of the successful hooks used by all 4 subjects (excluding the 2 trials where the straight wire was used to stab the bucket), with the successfully used end facing right. Numbers indicate trial number.

Hook Manufacture Test. Finally, we tested whether rooks could fashion a hook from a novel material, a straight piece of wire (17 cm long, Fig. S9*C*) and use this to extract the bucket from the vertical tube. So far, this ability has only been demonstrated by a single New Caledonian crow, Betty (19). Remarkably, all 4 rooks spontaneously manufactured a hook and used it successfully to extract the bucket, 3 of the 4 subjects achieving this on the first trial with the fourth subject successful on trial 4 (Movie S9 and Fig. S10*C*). Subjects manufactured a hook on every trial; however, they successfully pulled out the bucket on 35 ± 2.9% of trials. This was likely due to the difficulty in stretching up to pull the bucket completely free of the tube. Subjects could only reach to a certain height and thus only hooks with a large degree of bend could retain hold of the bucket when pulled diagonally. Successful hooks had a bend of 100 ± 8.5° (Fig. 6), while unsuccessful hooks had a bend of 75 ± 4.5°. On 2 occasions (5% of trials), subjects were also successful by stabbing the bucket with the straight wire. This was similar to the report of Betty, the New Caledonian crow (19). Interestingly, the angle of the unsuccessful hooks manufactured by the rooks were within the successful range of Betty (74 ± 30°). Together, the 3 experiments demonstrate the ability of rooks to spontaneously manufacture and use hook tools that rivals the ability of the New Caledonian crows.

Discussion

Our results contradict suggestions that tool use was the driving force behind the evolution of advanced physical intelligence (2). It appears more likely that corvid tool use is a useful by-product of a domain-general "cognitive tool-kit" (31) rather than a domain-specific ability that evolved to solve tool related problems. Whether or not each species taps into this capacity for tool use may depend on their ecology (22, 32).

We suggest that these data also provide evidence for insight in the problem-solving abilities of rooks. Insight is the "sudden production of new adaptive responses not arrived at by trial behavior…or the solution of a problem by the sudden adaptive reorganization of experience (33, p. 110)," a concept developed to explain sophisticated behavior that could not be the result trial-and-error learning (34). In these experiments, our hand-raised rooks rapidly learned the affordances of the original task and transferred this understanding immediately to novel task configurations, novel tools, and novel materials. Although there may be some transfer of information from one task to another, the solutions could not be derived simply through "chaining" the actions of several independent tasks together. Epstein showed that pigeons were able to chain together independent behaviors to achieve solutions that appeared creative (35). However, in our experiments often the solution to one task (e.g., pulling up on a hook tool) was the opposite to that used on a previous task (e.g., pushing down on a stick tool).

The rooks even creatively designed a new hook tool in the same manner as a New Caledonian crow. These results are even more impressive because rooks have not been shown to use tools in the wild and have had limited experience of tools in captivity (5, 21, 22). Parallels can be drawn with capuchin monkeys that have been known for many years to be good tool users in the lab but scarcely at all in the field (36) and only in certain ecological conditions, such as when food is scarce (37). Rooks exploit a number of different, readily-available food sources, such as seeds, insects, carrion, and refuse and as such may lack the motivation to use tools in the wild.

As rooks are capable of using tools in captivity, but only New Caledonian crows habitually use and make tools in the wild, the question arises as to when the capacity for tool use developed in corvids. The majority of anecdotal reports of corvid tool use are from the *Corvus* genus suggesting that the common ancestor of *Corvus* possessed the necessary cognitive abilities (7). However, as there are reports of tool use in more distantly related members of the corvids (e.g., blue jays 38), we may postulate the capacity evolved even earlier.

Rooks are highly innovative, social foragers (39), using their cognitive abilities in a number of nontool related ways (40). Our findings provide further support for recent claims of convergent evolution in the cognitive abilities of corvids and apes (31). New Caledonian crows and now rooks have been shown to rival, and in some cases outperform, chimpanzees in physical tasks, leading us to question our understanding of the evolution of intelligence.

Methods

Subjects. The 4 rooks (*Corvus frugilegus*) used for the experimental tests were 2 males (Connelly, Cook) and 2 females (Fry, Monroe). All subjects were part of a group of 12 hand-raised rooks, housed at the University of Cambridge, Subdepartment of Animal Behavior, Madingley, United Kingdom. All subjects were 5 years old at the time of testing. Cook and Fry were the alpha-mated pair of the group while Connelly and Monroe were the beta-mated pair. Cook was the first bird to use the tools followed by Fry, then by Connelly, and finally by Monroe. All birds had previous experience pulling sticks already inserted inside clear plastic horizontal tubes [Connelly (23), Cook (5, 24), Fry (5, 24) and Monroe (23)] but no experience of vertical tubes. In addition, the floor of the aviary is lined with stones and is surrounded by wire mesh, and as such, subjects may have had some experience of manipulating stones, sticks, or wire. However, they had never used any of these materials in the context of tool use or in conjunction with similar apparatus and had no experience of sticks with a hooked end or pieces of wire detached from the aviary.

Pretesting. The apparatus was initially placed on a platform inside the main aviary (Fig. S1, Configuration 1). Connelly, Cook, and Monroe initially solved the task by nudging the stone into the tube. After 5 trials of nudging the stone, it was placed at the base of the apparatus and all 3 birds immediately picked up the stone, dropping it into the tube. Fry picked up the stone from the base of the tube and dropped it in without the nudging phase. Once each bird had solved the task 15 times (5 × nudging, 5 × stone at apparatus base, 5 × stone on aviary floor), they were moved into the testing compartment to allow the rest of the group access to the apparatus.

Testing. Tests consisted of the following number of trials: stone size test (60 trials), stone retrieval and stone orientation test (40 trials), Stick use test (20 trials), functional tool type test (60 trials), metatool test (30 trials), stick modification test (30 trials), hook use test (30 trials), functional hook test (30 trials), hook manufacture test (10 trials). Subjects were given blocks of 10 trials and each block used a different subset of tools. In experiments that used both the large and small tube, the order of the trials was pseudorandomized unless otherwise stated below.

Procedural Variations. Stone retrieval test: Connelly was given all 20 trials with the large tube before trials with the small tube (all other birds trials were pseudorandomized).

Functional versus nonfunctional tool type test: Cook and Fry received all 30 trials of combination 1 (functional stick vs. nonfunctional stone) before combination 2 trials (nonfunctional stick vs. functional stone).

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