The Role of Experience in Problem Solving and Innovative Tool Use in Crows

Auguste M.P. von Bayern,1,2,* Robert J.P. Heathcote,1,2 Christian Rutz,1 and Alex Kacelnik1,*
1Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

Summary

Creative problem solving and innovative tool use in animals are often seen as indicators of advanced intelligence because they seem to imply causal reasoning abilities [1]. However, complex behavior can also arise from relatively simple mechanisms [2, 3], and the cognitive operations underlying seemingly “insightful” behavior are rarely examined [4]. By controlling and varying prior experience, it is possible to determine the minimum information animals require to solve a given problem [5]. We investigated how pretesting experience affects the performance of New Caledonian crows (Corvus moneduloides) when facing a novel problem. The task (developed by Bird and Emery [6]) required dropping stones into a vertical tube to collapse an out-of-reach platform in a transparent box and release a food reward. After establishing that the birds had no preexisting tendency to drop stones into holes, subjects were assigned to two experimental groups that were given different kinds of experience with the affordances of the apparatus. Crows that had learned about the mechanism (collapsibility) of the platform without the use of stones passed the task, just like the subjects that had previously been trained to drop stones. This demonstrates that successful innovation was also possible after acquaintance with just the functional properties of the task.

Results and Discussion

Innovative tool use and “insightful” problem solving have recently been reported in naturally non-tool-using rooks (Corvus frugilegus). Following training, during which they nudged stones into a tube and/or saw others do it [6], five subjects picked up stones and used them as tools to release food from a transparent dispenser. They subsequently solved several transfer tasks, involving the appropriate selection and modification of different tools [6] and the dropping of stones into a water-filled tube to reach floating bait [7]. However, because all rooks had seen stones falling into the tube prior to facing these problems, the role of previous experience on their performance remains unknown (the importance of experience is well established in humans; see [8]). Therefore, several simpler cognitive operations or processes—such as associative learning, chaining, or (mediated) generalization across stimuli [2, 3, 9–11]—cannot be excluded as explanations for this initial successful tool use, as acknowledged by Bird and Emery [6] (cf. [7]). To this end, we investigated what experience another corvid, the New Caledonian crow, requires to solve the same stone-dropping task. This species habitually uses stick and leaf tools in the wild and drops nuts onto hard surfaces to crack them open, but it is not known to use stone tools [12]. We tested six crows with a replica of the apparatus used in the rook study [6] but assigned subjects to two experimental groups that were given different pretesting experiences (see Experimental Procedures for details). The apparatus consisted of a tube placed on top of a transparent box, which contained a hinged, out-of-reach platform baited with food (Figure 1A). The platform collapsed if light pressure (see Experimental Procedures) was applied from above (i.e., through the tube). In the critical tests, stones were available nearby. We first conducted an important control experiment (pretest), testing all subjects without prior experience with the apparatus (Table 1). Although five of the six naive birds took stones to the apparatus and made contact with the box, none of them dropped stones to collapse the platform within 4 hr of exposure, establishing that they had no preexisting tendency to drop stones into holes. Subsequently, two crows were trained, like the rooks in the earlier study [6], to nudge stones into the apparatus from a plate mounted around the mouth of the tube (“stone-nudging”), so that the stones dislodged the platform and released the food (Figure 1B). When these birds were reexposed to the critical test condition with the plate removed, both of them, just like the rooks, picked up stones and dropped them into the tube, collapsing the platform (Table 1). The four birds in our second experimental group were trained, in the absence of stones, to push down and collapse the platform directly with their beaks by reaching through a shortened tube (“platform-pushing”) (Figure 1C; see also Movie S1 available online). When re-exposed to the critical test, two of these subjects picked up stones and dropped them into the tube, despite having never used stones as tools or seen stones being dropped into the apparatus (see Experimental Procedures for information about the subjects’ previous exposure to stones; Table 1; Movie S1). Curiously, one of the successful platform-pushing birds dropped a small (<2 cm) feather into the tube between its first and second successful trials of the test, showing that it was not exclusively committed to dropping only suitably heavy items. The remaining two stone-naive subjects did not solve the task in the permitted time. However, one of them successfully used stones in a retest after having spontaneously pushed the platform with sticks in a stick/stone choice experiment (following the first test; see Experimental Procedures and Table 1).

Our results show that, for New Caledonian crows, learning about some functional affordances of the task (collapsibility of the platform through force or contact) is essential, whereas learning about specific visual stimuli (stones acting on the platform) or actions (picking up and dropping stones) is not. In most other studies reporting innovative tool use of non-tool-using birds, such as pigeons (Columba livia) [9], American crows (Corvus brachyrhynchos) [13], blue jays (Cyanocitta cristata) [14], or rooks [6, 7], subjects had previously been trained with actions and/or stimuli resembling those required for the final behavior [6, 7, 9, 13] or had the chance to learn the final action itself through trial and error [14]. These routes

*Correspondence: auguste.bayern@zoo.ox.ac.uk (A.M.P.v.B.), alex.kacelnik@zoo.ox.ac.uk (A.K.)

These authors contributed equally to this work.
were unavailable to our two subjects that solved the task without direct or vicarious experience with stone dropping, i.e., without having been reinforced in relation to stones. By excluding several simple mechanisms that may explain seemingly insightful behavior in animals (see above), our experiment succeeded in narrowing down the possible cognitive operations used by New Caledonian crows to solve this task. However, exactly what happens when the cognitive trace of previous experience is reorganized [1] to allow for innovative actions that appear “insightful” remains unaccounted for. Here, our birds may have learned that force needed to be applied to the platform, and after tapping into their general experience that falling objects exert force, their creative operation may have been to link these two pieces of information. The fact that one bird once dropped a light feather into the tube hints at an alternative possibility, namely that the platform-pushing birds formed the (erroneous) concept that any form of direct or remote contact with the platform would cause it to collapse. Recent work with rooks [15] shows that these birds seem to be able to form concepts about object relations that involve the positional effects of gravity (they pay additional attention when static objects do not have support from below), but how much they understand about forces is still open to inquiry. The ability to reason about invisible forces has not yet been convincingly demonstrated in nonhuman animals [10], but these recent observations with corvids may encourage future experiments.

In our opinion, “insight” can never be a satisfactory explanation for an animal’s innovative performance because this label avoids identifying the exact processes by which a solution is obtained. Whether in relation to innovative tool use or any other form of creative behavior that is examined to unravel problem-solving capabilities, the big challenge for animal cognition research is to devise controls that progressively restrict the information-processing operations that can account for any emergent behaviors.

Experimental Procedures

Subjects
Subjects were six New Caledonian crows (Corvus moneduloides): three females (Annie-Claude, Ebony, and Uék) and three males (Boycott, Corbeau, and Tino). Corbeau and Uék were bred and hand raised in captivity, whereas the others were wild caught (for details, see [16, 17]). All crows had had exposure to stones and other objects such as wood pieces (see Housing Conditions, below) and therefore, like any adult experimental subject, must have had prior experience with falling objects and food (through picking things up and releasing them or observing others doing it). All had participated in earlier experiments, some of which involved retrieving food from clear plastic tubes, but they had never been required to drop objects into tubes. Crucially, none of the birds had (to our knowledge) been taught to do it. All had participated in earlier experiments, some of which involved retrieving food from clear plastic tubes, but they had never been required to drop objects into tubes. Crucially, none of the birds had (to our knowledge)

Table 1. Overview of the Sequence of Experimental Testing, with Summary of the Main Results

<table>
<thead>
<tr>
<th>Bird</th>
<th>Pretest Experience</th>
<th>Critical Test</th>
<th>Stick/Stone Choice</th>
<th>Retest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uék</td>
<td>fail (0/24)</td>
<td>pass (24/24) stick (8/8)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Corbeau</td>
<td>fail (0/24)</td>
<td>fail (0/24) stick (8/8)</td>
<td>pass (24/24)</td>
<td></td>
</tr>
<tr>
<td>Annie-Claude</td>
<td>fail (0/24)</td>
<td>pass (21/24) stick (8/8)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Boycott</td>
<td>fail (0/24)</td>
<td>fail (0/24) stick (8/8)</td>
<td>fail (0/24)</td>
<td></td>
</tr>
<tr>
<td>Ebony</td>
<td>fail (0/24)</td>
<td>pass (23/24)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Tino</td>
<td>fail (0/24)</td>
<td>pass (24/24)</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>

The “Experience” column indicates the assignment of subjects to experimental groups (i.e., the training birds received after having been pretested naively). The pretest, the critical test, and the retest consisted of eight 30 min sessions per bird. Within each session, up to three trials could be completed, resulting in a maximum of 24 trials per test. The number of passed trials out of the total trials per bird is indicated in parentheses. The stick/stone choice test comprised two sessions with four trials each, hence eight trials in total, which could be solved by the use of either stones or sticks (or both). In fact, the birds only used sticks and passed all eight trials each, as indicated in the associated column. NA stands for not applicable.
prior experience with dropping objects to act on other objects, and, as our pretest control established, none of our experimental subjects had a preexisting tendency to drop stones into tubes (see Results and Discussion and below). Subjects were randomly assigned to two experimental groups: Annie-Claude and Tino were in the stone-nudging group, and the remaining birds were in the platform-pushing group (see description of the experience phase below).

Housing Conditions
The birds were housed in pairs (Corbeau and Uék, Annie-Claude and Boycott, and Ebony and Tino) in outdoor aviaries (~60 m² each) with associated indoor enclosures (~8 m² each). The indoor bedding material consisted of newspapers and wood chips, whereas the outdoor bedding was natural soil covered with wood bark chips, containing some stones and gravel of different sizes.

Apparatus and Experimental Setup
Testing took place in visually isolated experimental rooms (width × length × height, 1 m × 2 m × 1.75 m), which were adjacent to each subject’s indoor enclosure. The experimental rooms were always cleared of all potential tools prior to testing. The apparatus was set up, out of sight of the subjects, on a partial white plastic table (diameter 1 m), with a pile of eight stones on each side of the apparatus, at ~20 cm distance (Figure 1A). The stones were compact and of similar size, ranging between 1.6–2 cm in diameter and 9–14 g in mass. All stones were heavy enough to collapse the platform. The apparatus was an exact replica of that used by Bird and Emery [6] and consisted of a transparent Perspex box (~11 cm × 11 cm × 11 cm) with an open tube on top (length 11 cm; diameter ~5 cm) (Figure 1A). A collapsible platform (~8 cm × 11 cm) made of opaque white plastic was hinged inside the transparent box and placed in hole by two small magnetic strips. Application of some force was required to overcome the resistance of the magnets and cause them to detach. In contrast to procedures used by Bird and Emery [6], food pieces were placed off center so they were not located directly under the tube’s aperture. This change was implemented for two reasons. First, during the platform-pushing training, the area of platform directly under the aperture was accessible through the short tube, and the subjects could have taken the reward without collapsing the platform (see below). Second, this arrangement ensured that birds had to direct their pecking behavior toward the platform, rather than directly at the food reward. Food rewards were either newborn mice (commercially available as frozen pinkies) or giant mealworms (Zophobas morio), depending on the preference and motivation of the subjects.

Familiarization
Prior to the experiment, subjects were accustomed to the experimental chamber and apparatus (unbaited with hinged platform and placed under a cage) during three 30 min sessions.

Pretest
Before providing the birds with specific experience (prior to the critical test), a control was conducted with the naive subjects. The apparatus was set up and baited, and stones were placed on the table as described above, out of view of the subjects, before each session. The pretest consisted of eight 30 min sessions (i.e., 4 hr in total). If the subjects had retrieved a reward within 30 min (which never happened), the apparatus would have been baited up to two more times per session, like in the critical test (see description below).

Experience
After the pretest, subjects were assigned to one of two experimental groups. The two individuals in the stone-nudging group were trained to nudge stones into the apparatus from a rimmed (1 cm) square plate (10 cm × 10 cm) with a central hole, which was mounted around the top of the tube (Figure 1B). Initially, one stone was placed right at the edge of the tube opening so that the subjects caused it to fall into the tube accidentally. Once the birds had learned that the falling stone released food and had readily nudged it from the edge into the tube, the stone was gradually placed further away from the tube opening until it was finally placed near the rim of the square plate. The four subjects in the platform-pushing group were trained to reach with their beaks into a shortened tube of 3 cm length (Figure 1C) to collapse the platform (Movie S1). Initially, the food was positioned partly under the aperture of the tube so that the subject could still reach it with its beak and thereby accidentally cause the platform to collapse. The food was then gradually placed further off center until it was entirely out of reach and could only be obtained by pushing the platform down (see above). This experience stage was completed after the subject had retrieved food from the modified apparatus 30 times (counting from the moment the subjects had reached the final training stage, i.e., stone at the border of the plate or food only accessible by pushing). During the training, neither stones nor sticks were available in the experimental room.

Critical Test
The critical test was conducted after the subjects had completed their training (experience). The experimental setup and the procedure were identical to that of the pretest for both experimental groups. Thus, stones were available for both the stone-experienced stone-nudging group and the stone-naive platform-pushing group. Again, the birds were tested in eight sessions that lasted up to 30 min each. If a subject retrieved the reward within these 30 min, the apparatus was baited for up to two more times with ~2 min intervals between trials, resulting in a maximum of 24 trials. In order to rebait the apparatus within a session, the experimenter entered the room, obstructing with their body the subject’s view of the apparatus. The experimenter then quickly moved the bait onto the platform by reaching with two fingers through the opening in the lower part of the box (which was inaccessible to the birds) and pushed the platform up again in order to reattach the magnets (the apparatus was never baited by dropping food into the tube). Stones that had been removed from the piles were put back in place.

Stick/Stone Choice Test
Following the critical test, the birds participated in another test examining their preference when given a choice between two different tool types (sticks and stones), which were presented simultaneously next to the apparatus. Four stones and four sticks (of different lengths: 5 cm, 8 cm, 11 cm, and 14 cm, all of which were long enough for reaching the platform) were placed in an alternating, randomly changing sequence at each side of the baited apparatus, at a distance of ~5–25 cm. The choice test consisted of two sessions of four trials each.

Re-test
Finally, birds that had failed the critical test were tested again after they had had the opportunity to use stick tools (in the stick/stone choice test), a tool type New Caledonian crows use habitually in the wild [12]. Again, the experimental setup and procedure were the same as in the pretest and the critical test.

All experiments were in accordance with the animal welfare regulations of the Department of Zoology, University of Oxford, UK.

Supplemental Data
Supplemental data include one movie and can be found online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01858-2.

Acknowledgments
R.J.P.H. was supported by a bursary from the Schools Competition Act Settlement Trust. C.R. is a Biotechnology and Biological Sciences Research Council David Phillips Fellow (grant BB/G023913/1). We would like to thank C. Bird, I. Federspiel, and N. Emery for sharing their apparatus with us.

Received: September 4, 2009
Revised: October 9, 2009
Accepted: October 9, 2009
Published online: November 12, 2009

References