

# What You See Is What You Get—Reloaded: Can Jackdaws (*Corvus monedula*) Find Hidden Food Through Exclusion?

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Choice by exclusion, that is, the ability to base the choice of a target on the rejection of potential alternatives, is becoming increasingly interesting for comparative cognition research. Recently, ravens have been shown to solve an exclusion task and it had been suggested that this ability might benefit ravens in a food-caching context. To investigate this possibility, the raven study was replicated with a closely related, but noncaching, species, the jackdaw (*Corvus monedula*). In the first test, the birds had to find food hidden in one of two differently shaped tubes. The results suggest that the jackdaws found the food through intensive search behavior, with little evidence for exclusion abilities. In a follow-up experiment, the tubes were replaced by cups, and before the birds made a choice, one of the cups was lifted to inform them about its content. In a final task, this procedure was modified to control for the influence of local enhancement. In both experiments, the jackdaws were successful only if they had seen the food before. These findings are in contrast to the previous results on ravens and support the idea that exclusion abilities may have evolved as specific adaptations to food caching.

*Keywords:* exclusion, inference, reasoning, jackdaws, *Corvus monedula*, comparative cognition

Reasoning abilities of nonhuman animals have gained increasing interest recently (e.g., Blaisdell, Sawa, Leising, & Waldmann, 2006; Kaminski, Call, & Fischer, 2004; Kennedy & Fragaszy, 2008; Taylor, Hunt, Holzhaider, & Gray, 2007; Taylor, Hunt, Medina, & Gray, 2008). One potential way of demonstrating reasoning abilities is to choose via exclusion (Schloegl, Bugnyar, & Aust, 2009). A variety of experimental paradigms has been used, but the general procedure requires the subjects to base their choice on an exclusion of potential alternatives; for example, in a two-choice procedure, subjects have to detect hidden food after having seen which potential hiding place is empty (e.g., Call, 2004; Erdőhegyi, Topál, Virányi, & Miklósi, 2007; Sabbatini & Visalberghi, 2008; Schloegl, Dierks, et al., 2009). Great apes, in general, and chimpanzees (*Pan troglodytes*), in particular, are highly proficient in such tasks (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, 2004, 2006) and solve them in two sensory modalities. When chimpanzees were shown that one of two boxes did not contain any food, they reliably chose the opposite box.

Similarly, when they saw a box being shaken, they could use the presence and absence of a rattling sound to identify the baited box, that is, when hearing a sound, they chose this box, whereas they avoided the shaken box if no sound was audible (Call, 2004). Importantly, the chimpanzees apparently inferred that the sound was produced by the movement of the food in the box, because they chose at random when they heard a playback of the sound without the boxes being shaken.

In the visual domain, capuchin monkeys (*Cebus apella*; Paukner, Huntsberry, & Suomi, 2009; Sabbatini & Visalberghi, 2008), Tonkean macaques (*Macaca tonkeana*; Petit, Call, & Thierry, 2005), and olive baboons (*Papio hamadryas anubis*; Schmitt & Fischer, 2009), solved this task as well, whereas in the auditory domain, all species required additional training (Sabbatini & Visalberghi, 2008) or failed entirely (Paukner et al., 2009; Petit et al., 2005; Schmitt & Fischer, 2009). Recently (Schloegl, Dierks, et al., 2009), we showed similar exclusion abilities in the visual domain in ravens (*Corvus corax*) but not in keas (*Nestor notabilis*), which are equally large-brained and possess cognitively advanced abilities (Huber & Gajdon, 2006; Iwaniuk, Dean, & Nelson, 2005; Iwaniuk & Hurd, 2005; Werdenich & Huber, 2006). Finally, dogs' (*Canis familiaris*) performances are also usually inferior to primates' in exclusion tasks (Bräuer et al., 2006), because they respond mainly to social manipulations (the handling of the boxes) rather than according to the causal information provided (presence or absence of the food; Erdőhegyi et al., 2007).

These species differences are important for our understanding of the functions of cognitive abilities and the mechanisms leading to its evolution. Historically, three theories have been proposed to explain the evolution of cognitive abilities (Burghardt, 1973). The "phylogenetic discontinuity approach" (Bitterman, 1965) argued that the cognitive abilities of species vary with the phylogenetic distance between them and according to differences in brain de-

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velopment. However, this hypothesis is not supported by recent data (e.g., Emery, 2006; Jarvis et al., 2005; Tebbich, Bshary, & Grutter, 2002) and today is considered as outdated (Burghardt, 1973). Instead, two contrasting hypotheses are discussed. The “adaptive specialization hypothesis” (de Kort, Tebbich, Dally, Emery, & Clayton, 2006; Kamil, 1987) proposes that each species possesses a specific set of cognitive abilities, which evolved as an adaptation to the species’ social and ecological requirements. In contrast, proponents of a “general intelligence hypothesis” (Bolhuis & Macphail, 2001) suggest that evolutionary pressures will lead to the development of a general set of cognitive tools.

We had argued that the differences we had found between ravens and keas would support the “adaptive specialization hypothesis” (Schloegl, Dierks, et al., 2009). Ravens are food-caching scavengers that face high inter- and intraspecific competition over food caches (Heinrich, 1989, 1999); in addition, cache pilferage provides them with ample experience with hidden food. In a competitive situation, the preferred foraging strategy of ravens would be to explore only those cache sites that may contain food and to avoid apparently empty cache sites. In contrast, keas face only limited competition over food, as they forage in groups and mainly feed on fruits and roots (Diamond & Bond, 1999); further, they are well known for their complete lack of neophobia and intensive play and manipulatory behavior (Diamond & Bond, 1999, 2004). In turn, the preferred foraging strategy of keas may be intensive exploration of a large variety of locations. Consequently, the feeding ecology of ravens may favor the cognitive and motivational requirements of an exclusion task more than the feeding ecology of keas.

Even though suggestive, a comparison between a corvid and a parrot species does not provide the most powerful framework for such an analysis, based on the evolutionary distance between the two taxa (Hackett et al., 2008). A more convincing evidence for the adaptive specialization hypothesis would be if similar differences could be shown between two closely related species that differ in their socioecology. To investigate the impact of caching behavior on cognitive abilities, jackdaws (*Corvus monedula*) are suitable subjects for comparisons with the closely related ravens. According to a phylogenetic reconstruction of caching in the corvid family, they lost their caching behavior secondarily, as jackdaws and white-throated magpie jays (*Calocitta formosa*) are the only two corvid species not known to cache food (de Kort & Clayton, 2006). While anecdotal reports on caching in jackdaws exist (Henty, 1975), it is virtually absent in our group of jackdaws, and all observed caching events seem to lack important functional aspects (i.e., the covering of the hidden food with substrate or later retrieval of the cached items; pers. obs.).

The goal of the present study was therefore to replicate the original study on ravens and keas (Schloegl, Dierks, et al., 2009) with jackdaws. In the first experiment, the birds had to find hidden food in one of two tubes. Before they made their choice, the birds could see either the food being present or absent in one of the two tubes. A bent and a straight tube were used to investigate if the birds would appreciate that an empty straight tube is indeed empty, whereas an apparently empty bent tube may not, because the food could still be behind the bend (see also Flavell, Green, Herrera, & Flavell, 1991). In the second experiment, food was hidden underneath one of two cups and the birds were allowed to see the content of one of the cups prior to choosing. The working hypothesis is

that if experiences with food caching would benefit the ability to choose by exclusion, the jackdaws’ performance should be inferior to the ravens’ but more similar to the keas’. In contrast, the jackdaws’ performance should be similar to the ravens’ if a general intelligence evolved in corvids.

## Experiment 1: Food Hidden in Tubes

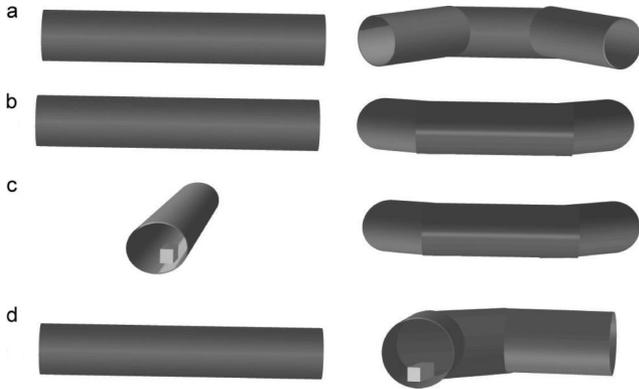
### Method

**Subjects.** Eight jackdaws (four males, four females) served as subjects. All birds had been hand raised in 2007; the hand-rearing conditions were similar to those of the ravens used in the original study (for details, see Kabicher & Fritz, 1996). At the start of testing, the birds were approximately five months old, which is younger than the ravens; however, jackdaws mature faster than ravens and all subjects were tested in the autumn before they reached sexual maturity. The birds were kept in a 60-m<sup>2</sup> outdoor aviary at the Konrad Lorenz Research Station, Grünau im Almtal, Austria. The aviary was composed of two outdoor sections and five small testing compartments that were visually isolated from the other parts of the aviary. The outdoor parts of the aviary contained natural grass vegetation, feeding platforms, nest boxes, and a few perches. The indoor testing compartments had a gravel floor and a few perches. In these testing compartments, the main room (approximately 3 × 2 m) and one of its neighboring rooms (approx. 1.5 m × 1 m) were both equipped with adjacent platforms (approx. 40 × 70 and 30 × 60 cm, respectively; 1.5 m above ground), which were connected through a wire gliding door. If not experimentally tested, birds were allowed to range freely in the entire complex. Prior to this study, the birds had participated in a gaze following study (Schloegl, Schmidt, Scheid, Kotrschal, & Bugnyar, 2008) and two studies on neophobia and cooperative behavior (Schwab, Swoboda, Bugnyar & Kotrschal, in preparation).

**Testing procedure.** Tests were conducted from October through December 2007. Birds were not food deprived but were tested before feedings. Water was available ad libitum. To keep birds motivated, small pieces of cheese—a highly favored food that was not available outside the experimental context—served as reward.

All birds were tested individually on the platforms in the testing compartments. The experimenter (E) was situated in the main room, and the bird was sitting on the platform in the adjacent room. At the onset of a trial, the bird watched E through the closed wire gliding door, with the approximate distance between the tubes and the bird 20–50 cm (depending on the position of the bird on the platform). After the presentation of the setup, E opened the gliding door and the bird could walk into the testing compartment and make its choice. It then returned to the smaller room and E closed the gliding door. Approximately one week prior to the start of the experiment, the birds were provided with the tubes to allow full habituation.

**Tubes.** Two gray opaque PVC tubes were used (Figure 1a); to adjust the size of the tubes to the smaller body size of jackdaws compared to ravens and keas, smaller tubes were used than in the original study; the tubes were of approximately 17 cm in length and a diameter of 3.5 cm. One tube was straight and the second tube had two 45° angles, preventing the birds from looking



**Figure 1.** Illustrations of the tubes used in Experiment 1. (a) Straight and bent tubes as used throughout the experiment. (b-d) Tubes aligned as in (b) ST trials, (c) Straight+ and Straight- trials (note that no food is visible in Straight- trials), and (d) Bent+ and Bent- trials (note that no food is visible in Bent- trials).

through the tube (Figure 1a). During the approach training with the tubes positioned on the platform, it turned out that several of the jackdaws did not reliably bend down to look into the tubes. Therefore, the setup was modified and the tubes were mounted on small wooden blocks (6 cm × 4.5 cm; 4 cm high) to facilitate the visibility of the tube content.

**Training.** The birds received training sessions to familiarize them with having to choose one of the tubes. E placed both tubes simultaneously on the platform at its rear end; the openings of the tubes were at a 90° angle away from the bird so that it could not see the content of either tube (Figure 1b). The bent and straight tubes were positioned left and right randomly, with the restriction that they were not on the same side consecutively more than twice. Then E called the bird's name, showed the food reward to the bird, and placed the reward (visible to the bird) in one of the two tubes. The food was positioned within 3–4 cm of the entrance of the tube. Next, E opened the door and the bird was allowed to approach both tubes and look into them. A choice was considered to have been made as soon as the bird touched one tube either with the beak or the foot, irrespective of whether it was the baited or the unbaited tube. A choice of the baited tube was considered as a success and the bird was allowed to retrieve the food; if it chose the unbaited tube, E stepped forward and removed both tubes to prevent the bird from obtaining the food. During the whole procedure, E stayed approximately 1 m behind the platform, looking straight ahead.

After the retrieval of the food, the bird returned to its room and the next trial started. The intertrial interval was set to at least 15 s, with the exact time dependent on the behavior of the bird. Each training session consisted of a maximum of 10 trials, depending on the motivation of the birds. To assess if the birds had learned to make a choice, only training sessions with the modified tubes mounted on the wooden blocks were considered. In comparison to our original study, the criterion of the approach training was modified (a) to account for the preexperience the birds had with the tubes without the blocks, and (b) because the number of trials a bird was willing to work in succession differed strikingly between subjects: the birds were advanced to testing if they chose the baited tube in  $\geq 80\%$  of the trials over two consecutive training

sessions with at least 15 trials, which is a significant preference for the baited tube according to a binomial distribution. In these two consecutive sessions (range: 15–20 trials), the birds chose correctly on  $90.69 \pm 6.5\%$  of the trials ( $\bar{x} \pm SD$ , range: 80–100%,  $p_s \leq .035$ ).

**Testing.** The birds were tested once per day. In contrast to the training trials, the food was hidden out of view of the birds underneath the platform. After the baiting, E placed the tubes simultaneously on the platform, with a distance of approximately 20 cm between the tubes. When moving the tubes, E held the tubes horizontally, paying explicit attention that food did not move inside the tubes and that it could not be seen by the bird.

After the positioning of the tubes, the bird could observe the setup for 3–5 s before E opened the door to allow the bird to choose one tube. If the bird chose the baited tube, it was allowed to retrieve the food and eat it. If it chose the unbaited tube, E stepped forward and removed both tubes, the subject returned to its room, and E closed the wire mesh door. E then baited the tubes again and a new trial started. The birds received a maximum of 10 trials per session (depending on the birds' motivation), and the food was hidden semirandomly in the two tubes, with the restriction that the food was not hidden on the same side (left or right) or in the same tube (bent or straight) for more than two consecutive trials. This stipulation was used because previous experiments showed that jackdaws develop side-biases rapidly.

There were five conditions, comprised of one standard-trial condition and four probe trial-conditions:

- Standard trials (ST), where tubes are positioned as in training trials, the openings are turned 90° away from the bird, and the content of the tubes is not visible (Figure 1b). This condition served as baseline and is the only condition in which the birds could look into both tubes simultaneously.

- Probe trials, where one tube was turned by 90° compared to ST trials, allowing the bird to see the content of the tube before approaching the setup (Figure 1c, d). In total, four different probe trial conditions were applied:

- Straight tube with food visible (Straight+): Food was visible inside the straight tube (Figure 1c).

- Bent tube with food visible (Bent+): Food was visible inside the bent tube (Figure 1d).

- Straight tube without food visible (Straight-): The inside of the straight tube was visible, but the tube was empty; the food was positioned in the bent tube.

- Bent tube without food visible (Bent-): The inside of the bent tube was visible, but no food was visible. In 50% of the trials, the food was in the straight tube; in the other 50% of the trials, the food was behind the bend inside the bent tube. The food was randomly assigned to the bent and the straight tube, with the exception that the food was not placed in the same tube more than twice in a row.

During pretesting, it became obvious that several jackdaws did not maintain their motivation for longer periods. Therefore, the testing procedure was adjusted by reducing the total number of ST trials (from 192 in the original study to 72 in the present study) and by increasing the number of probe trials per block from two to four.

Blocks of 10 trials were created and per block the birds received six ST trials and four probe trials (one per condition). A total of 12 trials per probe trial condition and 72 ST trials were administered for a total

of 120 trials per bird. Birds received up to 10 trials (one block) per day, and they received as many sessions as required to conduct all trials. In all,  $14.25 \pm 1.95$  sessions ( $\bar{x} \pm SD$ ) were conducted.

The following parameters were measured (identical to the procedure of Schloegl, Dierks, et al., 2009):

- Success rate was used as an indicator of the overall performance of the birds and was defined as the percentage of trials in which they chose the baited tube.

- To assess in more detail how the birds solved the task, the birds' strategies to find the food were analyzed. The measured parameters consisted of the following:

- Rate of inspections, defined as looking into a tube before making a choice. An inspection was assessed if the birds approached a side of a tube and—before inserting the beak into the tube or grasping it—clearly paused in front of the tube and looked into it.

- Timing of inspection, which was distinguished between simultaneous inspections of both tubes and serial inspections. Simultaneous inspections were defined as approaching the tubes, slowing down in pace, standing in the middle,  $+/-$  equidistantly between both tubes and—by lowering the head—looking into both tubes  $+/-$  simultaneously (due to their laterally placed eyes, birds can easily look into both tubes at the same time). Note that simultaneous inspections were only possible in ST trials. Due to the position of the tubes (see Figure 1c, d), it was not possible to look into both tubes simultaneously when standing between the two tubes in probe trials. In serial inspections, the birds approached one tube at a time and looked into them consecutively. For serial inspections, the birds could also stand in the middle between the two tubes but with their head clearly turned toward one tube at a time.

- The inspection pattern was measured to assess whether the birds appreciated the impact of the shapes of the tubes on the visual access to the food. For each tube, it was distinguished whether the birds looked into it from one side or from both sides. Following our definition of "looking," as previously described, a bird had to pause in front of the tube to look into it. Consequently, if, for example, a bird looked into one side of the tube, walked to the other side of the tube, and instantaneously inserted the beak into the tube (or grasped it), it was assessed as looking into the tube from one side only. If the birds appreciate the difference between the bent and the straight tube, they should look into the bent tube more often than into the straight tube from both sides.

Three instances were considered as indication that the birds relied on exclusion to choose a particular tube:

- In Straight- trials, if the birds chose the bent tube without prior inspection of any of the tubes (i.e., their choice behavior would be similar to the chimpanzees' behavior in Call, 2004). In other words, the birds would approach and choose the baited tube without any inspections.

- In Straight- trials, if the birds chose the bent tube without looking into it, after having looked into the straight tube (i.e., their behavior would be similar to the chimpanzees' behavior in Call & Carpenter, 2001). In other words, the birds would first look in the straight tube but would then take the other tube without looking into it.

- In ST trials, if the birds exhibited serial inspections, looked first into the empty tube, and then chose the other tube without

inspecting it (i.e., their behavior would be similar to the chimpanzees' behavior in Call & Carpenter, 2001).

All sessions were videotaped and analyzed from tape. A second person not involved in this study coded 100 trials and the inter-observer reliability (following Bakeman & Gottman, 1997) was excellent (Cohen's  $K = 0.93$ ).

**Predictions.** If the birds are capable of exclusion and can assess the difference between the two tube types, the following behavioral responses would be predicted:

- Standard trials (ST): The birds should inspect the tubes before making a choice, either by looking in both tubes simultaneously or in serial order.

- Straight tube with food visible (Straight+): The birds are expected to approach the straight tube directly and retrieve the food without prior inspection of any tube.

- Bent tube with food visible (Bent+): The birds are expected to approach the bent tube directly and retrieve the food without prior inspection of any tube.

- Straight tube without food visible (Straight-): The birds should avoid the straight tube and choose the bent tube without inspecting it first, that is, their inspection behavior should be similar to Straight+ and Bent+ trials.

- Bent tube without food visible (Bent-): The birds should inspect the tubes before choosing, that is, their inspection behavior should be similar to ST trials.

**Analysis.** Not all data sets were normally distributed (according to the Kolmogorov-Smirnov procedure) and, consequently, nonparametric statistics were applied throughout. To assess differences between the conditions and tube types, Friedman tests were used; for post hoc comparisons, the Student-Newman-Keuls (SNK) procedure was preferred over the more conservative Tukey test to reduce the risk of committing a Type II error based on the small sample size (Nakagawa, 2004). The performances in the first half and the second half of the experiment were compared with the Wilcoxon signed-rank test. All tests were conducted two-tailed and alpha was set to 0.05. Effect sizes (Cohen's  $d$ ) and 95% confidence intervals (CI) are reported in tables or in the main text. Due to the small sample size, exact  $p$  values are reported (Mundry & Fischer, 1998). Data analysis was conducted using SigmaPlot 11. Effect sizes and confidence intervals were calculated using SPSS 11.5 and the Effect Size Generator Free Edition (Deville, 2004). As the data is not normally distributed, box plots are used for graphical illustration.

## Results

The birds needed  $22.25 \pm 8.5$  ( $\bar{x} \pm SD$ , range: 15–40) trials to reach the training criterion.

**Success rate.** The jackdaws chose the baited tube above chance level in all five conditions (Wilcoxon tests:  $N = 8$ ,  $ps \leq .016$ ). Still, their performance differed across conditions (Friedman:  $N = 8$ ,  $\chi^2 = 28.987$ ,  $df = 4$ ,  $p < .001$ ). Post hoc analyses showed that the birds were most successful when they saw the food before approaching the tubes (conditions Bent+ and Straight+) compared to all other conditions ( $ps \leq .05$ ). Further, they were more successful in trials in which they did not see the content of any of the tubes (ST trials) than in trials in which they saw one tube empty (ST vs. Bent- and ST vs. Straight-;  $ps < .05$ ), but no difference could be found between the conditions Bent- and

Straight- ( $p > .05$ ; Figure 2; Table 1). The performance of the jackdaws did not change over the course of the experiment (all conditions, Wilcoxon tests:  $N = 8$ ,  $ps \geq .148$ ).

**Inspections.** The high success rates described here, even in conditions in which the birds could not see the location of the food at the start of a trial, were due to the high inspection rates (see Figure 3). For example, in the ST condition, in which the location of the food is unknown and not deducible, seven of the eight birds made a choice without prior inspection in  $\leq 5$  trials only.

Significant differences in inspection rates between the conditions were found (Friedman:  $N = 8$ ,  $\chi^2 = 29.369$ ,  $df = 4$ ,  $p < .001$ ; Table 1). Post hoc comparisons showed that the jackdaws inspected the tubes more frequently in ST trials compared to all other conditions (for all comparisons,  $ps < .05$ ). Inspection rates in the Straight- and Bent- trials were only slightly reduced in comparison to ST trials but did not differ from each other ( $p > .05$ ). In contrast, the jackdaws infrequently inspected the tubes if the food could be seen before the birds approached the setup (all comparisons of “+” trials vs. “-” trials,  $ps < .05$ ), but no difference was found between Straight+ and Bent+ trials ( $p > .05$ ). When comparing the first and the second half of the experiment, no change occurred in any of the conditions (Wilcoxon tests:  $N = 8$ ,  $ps \geq .188$ ).

**Timing of inspections.** When inspecting the tubes in ST trials, the jackdaws inspected both tubes simultaneously in  $59.84 \pm 15.74\%$  ( $\bar{x} \pm SD$ , 95% CI [46.68, 73.0]) of the trials and one tube at a time on  $40.16 \pm 15.74\%$  ( $\bar{x} \pm SD$ , 95% CI [27.0, 53.32]) of the trials, but this difference was not significant (Wilcoxon test:  $N = 8$ ,  $T^+ = 6$ ,  $p = .109$ ; Table 1); no change occurred over the course of the experiment (Wilcoxon test:  $N = 8$ ,  $T^+ = 9$ ,  $p = .25$ ).

**Inspection patterns.** The rate of inspections in the probe trial conditions differed between conditions (Friedman:  $N = 8$ ,  $\chi^2 = 20.143$ ,  $df = 3$ ,  $p < .001$ ). With both tube types, the jackdaws looked into the tubes from one side significantly more often than from both sides (SNK:  $ps < .05$ ); looking from one side occurred at comparable rates at the bent and at the straight tube ( $p > .05$ );

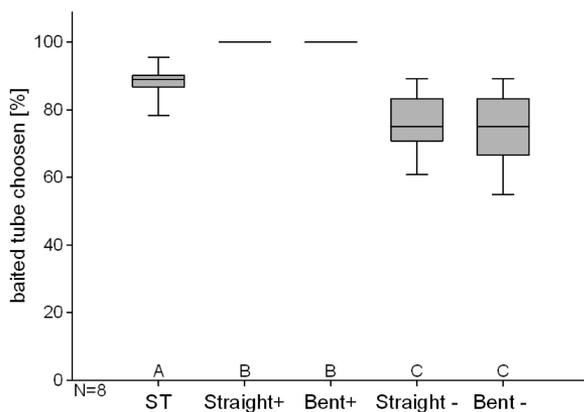


Figure 2. Experiment 1: Percentage of trials in which the baited tube was chosen in the different conditions. Box plots show median and upper and lower quartile. Whiskers indicate 10th and 90th percentiles. Differences between conditions are indicated by different letters below the bars. Bars marked with different letters differ significantly from each other (post hoc Student-Newman-Keuls test).

and the same pattern was found for looks from both sides ( $p > .05$ ; Figure 4; Table 1). Over the course of the experiment, the birds tended to increase the frequency of looks into the bent tube from both sides (Wilcoxon test:  $N = 8$ ,  $T^+ = 15$ ,  $p = .063$ ), whereas all other patterns remained unchanged (Wilcoxon tests:  $ps \geq .313$ ).

**Exclusion.** Throughout the experiment, only limited evidence for exclusion abilities was found. In only five ST trials (out of a total of 576), a bird chose the baited tube without prior inspection after inspecting the empty tube first. Additionally, in 8.3% of all Straight- trials did the jackdaws choose according to an exclusion strategy: On seven trials, four birds chose the baited tube without any prior inspection (one bird doing so on four trials), and on one trial, one bird looked first into the empty tube and then chose the other tube without looking into it. Taking all these instances together, the jackdaws chose by exclusion in  $7.99 \pm 11.32\%$  ( $\bar{x} \pm SD$ , 95% CI [-1.47, -17.45]) of all trials in which this was possible (i.e., in Straight- trials and ST trials with serial inspections, in which the empty tube was inspected first). The number of cases was too small to allow a systematic analysis of changes over time but three instances were observed in the first and second session. Two birds chose by exclusion on their first and second Straight- trial, respectively, and one of these birds also chose by exclusion on its third ST trial; however, 61.5% (8 out of 13) of all potential exclusion performances took place in the second half of the experiment.

## Discussion

Similar to the ravens and keas in the previous study (Schloegl, Dierks, et al., 2009), the jackdaws solved this task with ease, which is underlined by their high success rates. Again, similar to ravens and keas, the jackdaws chose the baited tube instantaneously if the food was visible already before they started to approach the setup (Straight+ and Bent+ conditions). However, if the food was not visible from the beginning, they solved this task largely through intense inspections of the tubes. Interestingly, the inspection pattern of the jackdaws was very similar to the ravens': Both corvid species usually approached the setup and inspected both tubes at the same time, using simultaneous inspections at virtually identical rates (jackdaws, 59.84%; ravens, 56.19%). In contrast, the keas preferentially inspected the tubes sequentially and often looked into both tubes from both sides; these double inspections were mainly absent in the jackdaws and the ravens.

The jackdaws and the keas reduced their inspection rates only slightly in the Straight- and Bent- conditions, whereas the ravens showed a steeper decrease. Irrespective of the steepness of the decrease, all three species did not treat the two tube types differently in the “-” conditions. This suggests that the jackdaws also did not differentiate between the two tubes and may not have been aware of the impact of the shape of the tubes on the visibility of the food (Flavell et al., 1991); however, the jackdaws (as the keas, but in contrast to the ravens) learned, to some degree, to appreciate these differences, as they increased the inspections of the bent tube from both sides.

The decreased inspection rates in the “-” conditions, when the food was not visible for the birds, was sharper in the ravens than in the jackdaws. This difference between the two corvid species is further obvious in the lower rates of exclusion shown by the jackdaws, which chose by exclusion in approximately 8% of all

Table 1  
*Effect Sizes and 95% Confidence Intervals for Statistical Comparisons of Experiment 1*

Comparison	Effect size (Cohen's <i>d</i> )	95% CI	
		LL	UL
1. Success rate			
<b>ST vs. Straight+</b>	<b>2.71</b>	<b>1.35</b>	<b>4.06</b>
<b>ST vs. Bent+</b>	<b>2.71</b>	<b>1.35</b>	<b>4.06</b>
<b>ST vs. Straight-</b>	<b>1.40</b>	<b>0.30</b>	<b>2.49</b>
<b>ST vs. Bent-</b>	<b>1.38</b>	<b>0.29</b>	<b>2.48</b>
<b>Straight+ vs. Straight-</b>	<b>3.26</b>	<b>1.77</b>	<b>4.76</b>
Straight+ vs. Bent+	0	0	0
<b>Straight+ vs. Bent-</b>	<b>2.85</b>	<b>1.46</b>	<b>4.24</b>
<b>Bent+ vs. Straight-</b>	<b>3.26</b>	<b>1.77</b>	<b>4.76</b>
<b>Bent+ vs. Bent-</b>	<b>2.85</b>	<b>1.46</b>	<b>4.24</b>
Straight- vs. Bent-	0.17	-0.80	1.16
2. Inspections			
<b>ST vs. Straight+</b>	<b>10.56</b>	<b>6.77</b>	<b>13.36</b>
<b>ST vs. Bent+</b>	<b>12.53</b>	<b>8.08</b>	<b>16.98</b>
<b>ST vs. Straight-</b>	<b>1.61</b>	<b>0.48</b>	<b>2.74</b>
<b>ST vs. Bent-</b>	<b>0.95</b>	<b>-0.07</b>	<b>1.99</b>
<b>Straight+ vs. Straight-</b>	<b>5.90</b>	<b>3.64</b>	<b>8.17</b>
Straight+ vs. Bent+	0.21	-0.77	1.20
<b>Straight+ vs. Bent-</b>	<b>5.81</b>	<b>3.57</b>	<b>8.05</b>
<b>Bent+ vs. Straight-</b>	<b>6.22</b>	<b>3.85</b>	<b>8.59</b>
<b>Bent+ vs. Bent-</b>	<b>6.04</b>	<b>3.73</b>	<b>8.36</b>
Straight- vs. Bent-	0.36	-0.62	1.35
3. Timing of inspections			
Simultaneous vs. sequential	1.19	0.12	2.25
4. Inspection patterns			
<b>Bent tube, one side vs. both sides</b>	<b>8.80</b>	<b>5.60</b>	<b>12.01</b>
<b>Straight tube, one side vs. both sides</b>	<b>11.63</b>	<b>7.48</b>	<b>15.77</b>
One side, bent vs. straight tube	0.28	-0.95	1.01
Both sides, bent vs. straight tube	0.07	-0.91	1.05
<b>Bent tube, one side vs. straight tube, both sides</b>	<b>8.43</b>	<b>5.35</b>	<b>11.51</b>
<b>Straight tube, one side vs. bent tube, both sides</b>	<b>12.58</b>	<b>8.11</b>	<b>17.05</b>

*Note.* Comparisons in bold were significant according to a Friedman test with post hoc Student-Newman-Keuls comparison. CI = confidence interval; LL = lower limit; UL = upper limit.

possible trials, compared to approximately 19% of the trials in the ravens; the keas applied this strategy even less frequently (approximately 4% of the trials).

In this test paradigm, inspection of the tubes was associated with little or no costs; consequently, the jackdaws' strategy of inspection rather than exclusion may be seen as the "safe" option, as inspections decrease the likelihood of making a mistake (Schloegl, Dierks, et al., 2009). Finally, to adjust the setup to the smaller body size of the jackdaws, smaller tubes had to be used, which may have reduced the visibility inside the tubes. While this obviously did not have an impact in those conditions in which food was visible (Bent+ and Straight+), it may have influenced the birds in the other conditions.

Exclusion seems not to be a common strategy in jackdaws, at least when searching is possible; like the jackdaws, capuchin monkeys did not demonstrate any exclusion abilities in a tube task similar to the present one (Paukner, Anderson, & Fujita, 2006) but showed exclusion in a different, more straightforward paradigm (Paukner et al., 2009; Sabbatini & Visalberghi, 2008). In this task, food was hidden underneath one of two bowls, instead of tubes, and in the crucial "exclusion" condition, the subjects were informed about the absence of food in one of the bowls. The important difference between this experiment and the tube tasks is

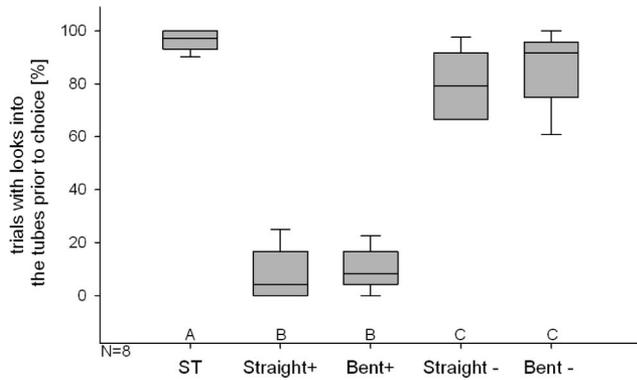
that, in the bowl task, the subjects have to choose by exclusion to solve the task, whereas its use is facultative in the tube task. It had been argued that species may value competing search strategies differently (Erdőhegyi et al., 2007; Schloegl, Dierks, et al., 2009), and different performances may be due to motivational rather than cognitive differences; for example, dogs preferentially choose according to social rather than causal information (Erdőhegyi et al., 2007; see also Bräuer et al., 2006), if both types of information are available. The same may be true for jackdaws, and this possibility was investigated in a second experiment in which the bowl task was replicated.

## Experiment 2: Food Hidden in Cups

### Methods

**Subjects.** Nine jackdaws (four males, five females) served as subjects; five of these birds had also participated in Experiment 1. The four additional birds (two males, two females) were of the same age and rearing history but had been unwilling to participate in Experiment 1.

**Testing procedure.** Tests were conducted in August 2008, approximately eight months after the end of Experiment 1. They



**Figure 3.** Experiment 1: Percentage of trials in which birds inspected at least one tube before making a choice. Box plots show median and upper and lower quartile. Whiskers indicate 10th and 90th percentiles. Differences between conditions are indicated by different letters below the bars, and bars marked with different letters differ significantly from another (post hoc Student-Newman-Keuls test).

were conducted in the same compartments, but, for this experiment, the birds were positioned in the larger central room and the experimenter in the smaller, adjacent room. Two identical plastic cups (6.5 cm in diameter and 7.5 cm in height) were used instead of tubes. The cups were positioned at the front end of the platform close to the gliding door so that the birds could see the setup as close as possible. In the original study (Schloegl, Dierks, et al., 2009), the cups were placed on a wooden board, but the jackdaws did not habituate to the movement of the board; instead, two white, square plastic cards (approximately  $8 \times 8$  cm) were used as a base for the cups.

In general, the birds waited on the platform in their compartment until the cue presentation had ended. However, two birds were highly impatient and approached the setup too early; for these two birds, the gliding door separating the two compartments was closed during cue presentation, whereas the door was open for the other birds. Those two birds took more trials to reach the training criterion but did not differ from the other birds in their test performance.

**Training.** Prior to testing, the birds were familiarized with having to make a choice. At the start of a trial, E called the bird's name and placed a food reward (a small piece of cheese) on one of the plastic cards, which were positioned on the experimental platform. Then E put the cups onto the plastic cards, with a distance of approximately 40 cm between them; the distance between the cups and the bird was approximately 15–50 cm, depending on the position of the bird on the platform. The food was positioned randomly on the left or on the right, with the exception that it was not positioned on the same side consecutively more than twice in a row.

As soon as E had stopped touching the cups, the bird was allowed to approach both cups and to turn around one of them. If the bird chose the baited cup, it was allowed to retrieve the food; if the bird attempted to approach the second cup, E removed both cups. During the whole procedure, E stayed approximately .5 m behind the experimental platform, looking straight ahead. The next trial started as soon as the bird had returned to the central room. The intertrial interval was set to at least 20 s, with the exact time

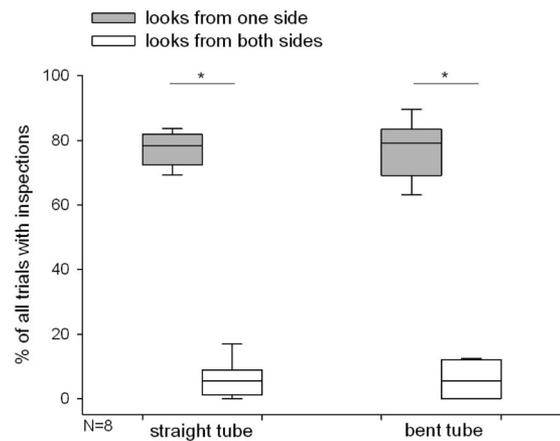
dependent on the behavior of the bird. Training sessions were planned to consist of 10 trials each. However, the birds' motivation to participate varied greatly from day to day, and the training sessions were opportunistically prolonged up to a maximum of 24 trials (range: 3–24 trials). As in Experiment 1, the birds were advanced to testing if they chose the baited cup in at least 80% of the trials, over two consecutive training sessions with at least 15 trials, which is a significant preference for the baited cup according to a binomial distribution. In these two consecutive sessions (range: 19–28 trials), they chose correctly on  $89.86 \pm 7.1\%$  of the trials ( $\bar{x} \pm SD$ , range: 81.8–100%,  $p_s \leq .004$ ).

**Testing.** The birds received one session per day. For testing, the food was hidden out of view of the birds under the experimental platform. After the baiting, E placed the cups (positioned on the plastic cards) on the platform. The distance to the wire mesh door separating the two compartments was approximately 10 cm. After the positioning of the cups, E called the bird's name and then provided one of four different cues:

- **Lifting both cups:** E touched both cups with his arms extended and lifted the cups to a height of approximately 20 cm above the platform and then returned the cups to the starting position.
- **Lifting the baited cup:** E touched both cups but lifted only the baited cup so that the food could be seen lying on the plastic card. During the presentation, E continued to touch the unbaited cup.
- **Lifting the unbaited cup:** As before, with the exception that the unbaited cup was lifted.
- **Control:** No cup was lifted but both cups were touched by E.

Each cue lasted for 5 s and E looked straight ahead during the presentation of the cue. The bird was allowed to choose a cup as soon as E had stopped touching the cups (or the gliding door was open, see "Testing procedure"). If the bird chose the baited cup, it was allowed to open it and to retrieve and eat the food. If it chose the unbaited cup, it was allowed to open this cup; then E stepped forward and removed both cups. A new trial started as soon as the bird had returned to the observation room.

Test sessions were restricted to 10 trials each. In contrast to the original study, two warm-up trials, which were identical to training



**Figure 4.** Experiment 1: Frequency of looking into a tube from one side or both sides. Box plots show median and upper and lower quartile. Whiskers indicate 10th and 90th percentiles. Asterisks indicate significant differences according to a post hoc Student-Newman-Keuls test.

trials, were conducted at the start of each session. This procedure was introduced because the jackdaws appeared to be less focused than the ravens and keas at the start of a session. After these two trials, eight test trials, with two trials per condition, were presented in randomized order. All sessions were videotaped and later analyzed from tape. To assess interobserver reliability, a second coder unaware of the purpose of the experiment independently analyzed five sessions and the two observers agreed on the choice of the bird in 100% of the trials.

**Analysis.** Differences between conditions were analyzed using the Friedman test and post hoc SNK comparisons. To assess learning effects, the performance in the first half and in the second half of the experiment was compared with the Wilcoxon test. Due to the variable number of training trials, the number of correct trials per condition and the number of training trials were correlated using Spearman correlations.

## Results

The jackdaws received  $61.3 \pm 29.2$  ( $\bar{x} \pm SD$ , range: 20–105) trials until they reached the training criterion. The two birds tested with the closed gliding door took the most trials to reach the criterion (104 and 105 trials, respectively; all other birds,  $\leq 80$  trials).

In the test sessions, the performance of the birds differed between the conditions (Friedman:  $N = 9$ ,  $\chi^2 = 18.818$ ,  $df = 3$ ,  $p < .001$ ). Post hoc analysis revealed that the jackdaws were most successful when both cups were lifted (comparisons against all other conditions:  $ps < .05$ ; Figure 5; Table 2); additionally, they were also more successful when they saw the food in the “baited cup lifted” condition compared to the “unbaited cup lifted” and the control conditions (for both comparisons,  $p < .05$ ). In contrast, their performance did not differ between the “unbaited cup lifted” and the control conditions ( $p > .05$ ; Figure 5; Table 2).

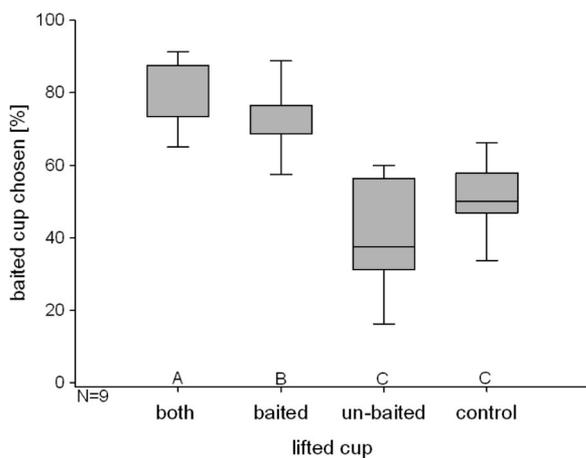


Figure 5. Experiment 2: Percentage of trials in which the baited cup was chosen. Box plots show median and upper and lower quartile. Whiskers indicate 10th and 90th percentiles. Differences between conditions are indicated by different letters below the bars, and bars marked with different letters differ significantly from another (post hoc Student-Newman-Keuls test).

Table 2  
Effect Sizes and 95% Confidence Intervals for Statistical Comparisons of Experiment 2

Comparison	Effect size (Cohen's <i>d</i> )	95% CI	
		LL	UL
<b>Both vs. baited</b>	<b>0.82</b>	<b>-0.15</b>	<b>1.78</b>
<b>Both vs. unbaited</b>	<b>2.81</b>	<b>1.51</b>	<b>4.11</b>
<b>Both vs. control</b>	<b>2.80</b>	<b>1.50</b>	<b>4.1</b>
<b>Baited vs. unbaited</b>	<b>2.10</b>	<b>0.95</b>	<b>3.25</b>
<b>Baited vs. control</b>	<b>1.86</b>	<b>0.75</b>	<b>2.96</b>
Unbaited vs. control	0.66	-0.29	1.61

Note. Comparisons shown in bold were significant according to a Friedman test with post hoc Student-Newman-Keuls comparison. CI = confidence interval; LL = lower limit; UL = upper limit.

Overall, the birds' performance did not change over the course of the experiment, even though the increase in accuracy in the “both cups lifted” condition only marginally failed to reach significance (Wilcoxon test:  $N = 9$ ,  $T^+ = 19.5$ ,  $p = .063$ ; all other comparisons,  $ps \geq .219$ ). However, in the “unbaited cup lifted” condition, two birds revealed a dramatic drop in performance, from 62.5% and 87.5% correct in the first half of the experiment to 0% and 25% correct in the second half, respectively (see Table 3 for individual performance data).

The number of training trials and the number of correct choices in the test did not correlate for the “lifting both cups” condition (Spearman:  $N = 9$ ,  $r = -0.162$ ,  $p = .643$ ) and the “lifting the unbaited cup” condition (Spearman:  $N = 9$ ,  $r = -0.072$ ,  $p = .844$ ). Those jackdaws that needed fewer trials to reach the training criterion performed significantly better in the “lifting the baited cup” condition than those birds that needed more training trials (Spearman:  $N = 9$ ,  $r = -0.716$ ,  $p = .0248$ ).

## Discussion

Only very limited evidence for exclusion capabilities could be found in this experiment. As in Experiment 1, the jackdaws were highly successful if they could see the food before they made their choice. However, if they did not see the food, they performed at chance level, indicating that they could not infer the position of the food under the second cup. Surprisingly, two subjects were rather successful in this condition in the initial phase of the experiment, but their performances dropped dramatically. These birds were not tested on the same days, suggesting that external reasons are unlikely to account for this decline in performance.

The jackdaws' performance was clearly distinct from the performance of the ravens. First, as a group, only the ravens made use of the information about the absence of the food in one location and inferred where the food was hidden. Second, all raven subjects selected the baited cup in more than 50% of the “unbaited cup lifted” trials, whereas only three of the nine jackdaws did so (Table 3). This relative preference for the lifted cup suggests that jackdaws may be highly susceptible to local enhancement (i.e., the movement of the cup); similarly, von Bayern and Emery (2009) reported that jackdaws are highly responsive to human-given cues in an object-choice task.

Table 3  
*Individual Performances of the Subjects in Experiment 2*

Subject	Overall				Sessions 1–4				Sessions 5–8			
	Both	Baited	Unbaited	Control	Both	Baited	Unbaited	Control	Both	Baited	Unbaited	Control
A	<b>87.5</b>	<b>93.75</b>	50	31.25	75	87.5	50	50	100	100	50	12.5
B	68.75	68.75	31.25	50	75	87.5	25	37.5	62.5	50	37.5	62.5
C	62.5	68.75	56.25	50	50	75	50	75	75	62.5	62.5	25
F	<b>93.75</b>	75	31.25	68.75	87.5	62.5	62.5	75	100	87.5	0	62.5
H*	<b>87.5</b>	50	62.5	62.5	87.5	37.5	75	62.5	87.5	62.5	50	62.5
I	<b>87.5</b>	68.75	37.5	50	75	62.5	37.5	50	100	75	37.5	50
K*	75	68.75	<b>6.25</b>	56.25	75	62.5	12.5	75	75	75	0	37.5
U	<b>87.5</b>	<b>81.25</b>	56.25	37.25	87.5	62.5	87.5	25	87.5	100	25	50
X	<b>81.25</b>	75	37.5	50	62.5	75	25	62.5	100	75	50	37.5

*Note.* Given is the percentage of correct choices in the entire experiment as well as in the first half (Sessions 1–4) and in the second half (Sessions 5–8) of the experiment. Due to the small number of trials per condition ( $n = 16$ ), a meaningful analysis of individual performance based on binomial tests can only be conducted for overall performance. Significant deviations from chance level in overall performance are printed in bold.

\*Subjects saw the cue with the gliding door closed.

A preference for the lifted cup was also found in a study on dogs, and it was suggested that this may overshadow the use of causal information (i.e., the absence of the food; Erdőhegyi et al., 2007). In a follow-up experiment, the dogs were tested in a situation in which the food underneath the cup was covered by a smaller, internal cup. In other words, the dogs again saw two cups, which were now lifted simultaneously. Underneath one of these (external) cups, the dogs saw an additional internal cup. In one condition, the food was still visible and the internal cup was empty. This condition corresponded to the “baited cup” lifted condition. In the condition corresponding to the “unbaited cup lifted” condition, the food was hidden underneath the internal cup, whereas the other cup remained empty. This modification avoided a bias toward one lifted cup, as both external cups were lifted simultaneously, and the internal cup prevented the dogs from seeing the food.

The dogs were able to find the food in both conditions, suggesting that they inferred the location of the food and chose by exclusion (Erdőhegyi et al., 2007). Unfortunately, an alternative explanation exists: In the exclusion condition, the dogs may not have inferred the location of the food underneath the internal cup but may have made the best out of a bad situation and may have chosen the cup itself. In this case, they may have found the food accidentally.

For the third experiment, the setup of the dog study was adapted but modified in the way that two internal cups, one transparent and one opaque, were introduced.

### Experiment 3: Controlling for Local Enhancement

#### Method

**Subjects.** The same nine jackdaws and an additional one-year-old female, with identical rearing background, served as subjects.

**Testing procedure.** Tests were conducted in succession of Experiment 2, and the test procedure was identical to Experiment 2 with one exception. Underneath the cups from Experiment 2 (in the following: external cups), two small internal cups were positioned (approximately 4 cm in diameter and 4 cm in height). These cups were made of transparent plastic, and opaque cups

were wrapped with blue tape. When introduced to the birds, only one bird (see “Training”) was at first reluctant to approach and manipulate these cups.

**Training.** As this experiment was conducted in direct succession of Experiment 2 and the same cups were used, it was assumed that the birds were familiar with the procedure and no training sessions were conducted. Only the bird that had not participated in Experiment 2 received training sessions identical to those conducted in the previous experiment. As this bird was shyer than the other birds, and first hesitated to approach the internal cups, it received two additional training sessions with the internal cups only (using one opaque and one transparent cup on each trial); this was necessary to ensure that the presence of these cups would not deteriorate its performance. Again, the training criterion was set to correct choices of the baited cup in at least 80% of the trials over two consecutive training sessions with at least 15 trials; this is a significant preference for the baited cup according to a binomial distribution. In the first training step, the bird reached the criterion after 60 training trials. Over the last two sessions, it was correct on 19 out of 20 trials (binomial test,  $p < .001$ ); with the internal cups, it reached the criterion within the minimum of two sessions (correct on 16 out of 20 trials,  $p = .012$ ).

**Testing.** In each test trial, two internal cups were positioned underneath the external cups; otherwise, the testing procedure was identical to Experiment 2. At the start of each session, two warm-up trials were conducted, using one opaque and one transparent internal cup.

Again, four conditions were created through the use of different sets of internal cups:

- Full information: two transparent internal cups.
- Baited Only: one transparent and one opaque internal cup, where the reward could be seen underneath the transparent cup.
- Unbaited Only: same as Baited Only, but the food was underneath the opaque cup.
- Control: two opaque cups.

In all conditions, the external cups were lifted for 5 s to a height of approximately 20 cm above the platform.

To investigate if short-term-memory effects influenced the birds' choices, the subjects were split randomly in two groups. Five birds were tested as described, and five birds received the same procedure without the external cups. Hence, the first group had to base their choice behavior on what they had seen previously, whereas the second group could base their choices on what they saw while they made their choice.

**Analysis.** Friedman tests with post hoc SNK tests were used for the main analysis. The performance in the first half and in the second half of the experiment and the performances in Experiments 2 and 3 were compared using the Wilcoxon test. The performance of the two groups of birds was compared using Mann-Whitney *U* tests. Individual performances were analyzed using binomial tests.

## Results

The two test groups (with or without external cups) did not differ in their performance in any of the conditions (Mann-Whitney *U* tests;  $ps > .548$ ) and were therefore combined. The birds' performance differed across the conditions (Friedman:  $N = 10$ ,  $\chi^2 = 18.160$ ,  $df = 3$ ,  $p < .001$ ; Figure 6, Table 4); post hoc analyses revealed that the birds were more successful in those two conditions in which the food was visible ("full information" and "baited only") than in the other two conditions (all comparisons,  $ps < .05$ ). In contrast to Experiment 2, no difference between the two conditions with food visible was detectable ( $p > .05$ ), but as in Experiment 2, the birds were not more successful in the "unbaited only" condition than in the control condition ( $p > .05$ ). No change in performance was detectable over the course of the experiment in any condition (Wilcoxon tests:  $ps \geq .129$ ).

Interestingly, those two individuals that were relatively successful in the first four sessions of the "lifting the unbaited cup" condition of Experiment 2 (subjects F and U; Table 3) were again successful in the "unbaited only" condition in this experiment (see Table 5 for individual performance data). Both birds chose the

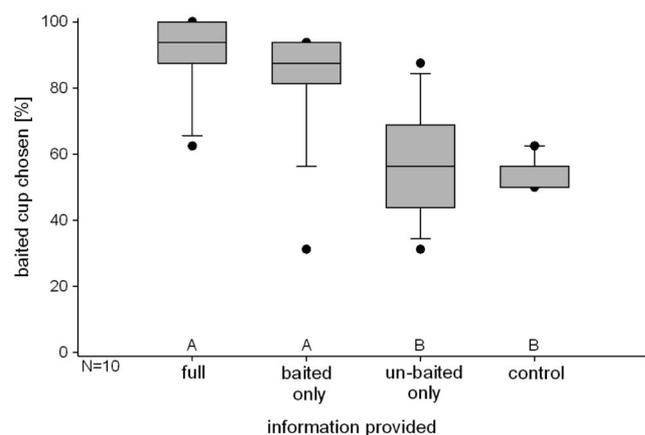


Figure 6. Experiment 3: Percentage of trials in which the baited cup was chosen. Box plots show median and upper and lower quartile. Whiskers indicate 10th and 90th percentiles, and circles show 5th and 95th percentiles. Differences between conditions are indicated by different letters below the bars, and bars marked with different letters differ significantly from another (post hoc Student-Newman-Keuls test).

Table 4  
Effect Sizes and 95% Confidence Intervals for Statistical Comparisons of Experiment 3

Comparison	Effect size (Cohen's <i>d</i> )	95% CI	
		LL	UL
1. Lift vs. nonlift			
"Full," lift vs. nonlift	0.57	-0.70	1.83
"Baited only," lift vs. nonlift	0.59	-0.67	1.86
"Unbaited only," lift vs. nonlift	0.46	-0.8	1.71
"Control," lift vs. nonlift	0	-1.24	1.24
2. Comparison of conditions			
Full vs. baited only	0.35	-0.54	1.23
<b>Full vs. unbaited only</b>	<b>1.89</b>	<b>0.84</b>	<b>2.96</b>
<b>Full vs. control</b>	<b>3.5</b>	<b>21.11</b>	<b>4.9</b>
<b>Baited only vs. unbaited only</b>	<b>1.33</b>	<b>0.36</b>	<b>2.3</b>
<b>Baited only vs. control</b>	<b>2.12</b>	<b>1.02</b>	<b>3.21</b>
Unbaited only vs. control	0.32	-0.56	1.20

Note. Comparisons shown in bold were significant according to a Friedman test with post hoc Student-Newman-Keuls comparison. CI = confidence interval; LL = lower limit; UL = upper limit.

correct cup significantly above chance when they saw the transparent cup empty (13 and 14 correct out of 16; binomial test:  $p = .021$  and  $p = .004$ , respectively). However, only subject U was also successful in the "baited cup only" condition (15 out of 16 correct,  $p = .001$ ), whereas bird F was correct on 5 out of 16 trials only ( $p = .210$ ; Table 5).

Finally, a comparison of the performance of those nine birds that participated in Experiments 2 and 3 (excluding bird N; Table 5) revealed that they were more successful in Experiment 3 than in Experiment 2 in the condition in which they received information about both cups (Wilcoxon test:  $N = 9$ ,  $T^+ = 34.5$ ,  $p = .016$ ), and in the condition in which they saw the content of the unbaited cup (Wilcoxon test:  $N = 9$ ,  $T^+ = 40.5$ ,  $p = .027$ ), but not when they saw only the content of the baited cup (Wilcoxon test:  $N = 9$ ,  $T^+ = 28.5$ ,  $p = .148$ ) or in the control condition (Wilcoxon test:  $N = 9$ ,  $T^+ = 9$ ,  $p = .813$ ).

## Discussion

Similar to the previous experiments, the jackdaws were highly successful if they saw the food before they made their choice. Additionally, the introduction of the internal cups helped them to improve their performance in some conditions; interestingly, they significantly improved their performance in the exclusion condition, but mainly because they lost their preference for one cup. However, in contrast to the previous experiments, two birds reliably chose the baited cup in the exclusion condition, even though only one of them chose by exclusion. The failure of the second bird in the "baited only" condition suggests that it had learned a rule to choose the opaque cup if a transparent and an opaque cup are presented. This finding demonstrates that individual subjects may be capable of exclusion under certain circumstances, but the underlying mechanisms remain unclear.

## General Discussion

The results of these three experiments clearly demonstrate differences between closely related jackdaws and the previously

Table 5  
*Individual Performances of the Subjects in Experiment 3*

Subject	Overall				Sessions 1–4				Sessions 5–8			
	Full	Baited	Unbaited	Control	Full	Baited	Unbaited	Control	Full	Baited	Unbaited	Control
A	<b>100</b>	<b>93.75</b>	31.25	50	100	87.5	25	37.5	100	100	37.5	62.5
B	<b>93.75</b>	<b>93.75</b>	50	50	87.5	87.5	50	50	100	100	50	50
C	62.5	<b>81.25</b>	68.75	50	75	62.5	75	62.5	50	100	62.5	37.5
F*	<b>87.5</b>	31.25	<b>87.5</b>	62.5	75	50	75	62.5	100	12.5	100	62.5
H*	<b>93.75</b>	<b>93.75</b>	68.75	56.25	87.5	87.5	62.5	50	100	100	75	62.5
I*	<b>100</b>	<b>87.5</b>	62.5	50	100	87.5	75	37.5	100	87.5	50	62.5
K*	<b>87.5</b>	<b>87.5</b>	50	50	87.5	87.5	25	50	87.5	87.5	75	50
U	<b>100</b>	<b>93.75</b>	<b>81.25</b>	56.25	100	87.5	75	50	100	100	87.5	62.5
X*	<b>93.75</b>	<b>87.5</b>	43.75	50	100	87.5	37.5	50	87.5	87.5	50	50
N	68.75	<b>81.25</b>	37.5	62.5	87.5	87.5	12.5	75	50	75	62.5	50

Note. Given is the percentage of correct choices in the entire experiment as well as in the first half (Sessions 1–4) and in the second half (Sessions 5–8) of the experiment. Due to the small number of trials per condition ( $n = 16$ ), a meaningful analysis of individual performance based on binomial tests can only be conducted for overall performance. Significant deviations from chance level in overall performance are printed bold.

\* Subjects tested without external cups.

tested ravens (Schloegl, Dierks, et al., 2009). The ravens demonstrated exclusion abilities repeatedly, whereas the jackdaws did not; further, the jackdaws failed not only in the identical experiments the ravens had mastered but also in a third experiment controlling for enhancement effects. Even though absence of evidence should not be mistaken for evidence of absence, these findings at least demonstrate that jackdaws do not use potentially existing exclusion abilities as reliably as ravens do.

However, even though they failed to demonstrate exclusion abilities, the jackdaws did not perform identically to the keas. First, the keas were less inclined to respond to enhancement or social information, that is, the movement of the cups. Second, the search patterns of the jackdaws in Experiment 1 were very similar to the patterns shown by the ravens. This common search strategy of the two corvid species is characterized by simultaneous inspections of both tubes and a limited number of inspections, whereas the keas demonstrated mostly serial inspections and more thorough explorations with frequent double inspections of the tubes.

The lack of evidence for exclusion capabilities in the jackdaws adds to the growing evidence that these choice tasks are cognitively demanding and not easy to solve (e.g., Erdőhegyi et al., 2007; Paukner et al., 2006; Schloegl, Dierks, et al., 2009; Schmitt & Fischer, 2009), but the mechanisms underlying the animals' choices are not fully understood (Schloegl, Bugnyar, et al., 2009; Schmitt & Fischer, 2009). Originally, it had been argued that these tasks are solved through inferential reasoning (e.g., Call, 2004), that is, that the animals are aware of the presence of the food in the alternative box or cup. However, some authors have recently suggested that some capuchin monkeys and olive baboons may solve this task through avoidance rather than inference (Paukner et al., 2009; Schmitt & Fischer, 2009). Additionally, most species failed to solve the cup task in the auditory domain, in which the information about the content of the cup is provided through the presence or absence of noise when the cup is shaken. This task is considered to be more demanding, because the choice cannot be based on directly perceived information (absence of food) but must be inferred from indirect information (i.e., that food produces noise and no noise means that no food is present). To date, this task has been solved instantaneously only by chimpanzees (Call, 2004).

A single bird demonstrated exclusion abilities from the start of the third experiment, suggesting that under the circumstances of this experiment, it may have been able to infer the location of the hidden food. However, this bird had gained ample experience over the course of the study; additionally, a second bird's success was clearly due to a learned rule based on differential discrimination of the two types of cups. Taken together, this makes a learned response the most parsimonious explanation, even though such discriminations may not be easily achieved, given the low number of birds doing so.

The differences between jackdaws and ravens are in line with the assumptions of the "adaptive specialization hypothesis" (e.g., Kamil, 1987), and the different feeding ecologies of the two species may provide a straightforward framework for explaining the different performances. Importantly, this does not necessarily imply differences in cognitive abilities; instead, motivational and attentional aspects may be of importance. Ravens mainly feed on carcasses and cache food, usually by digging a hole in the ground, inserting the food, and then covering the food with substrate (Heinrich, 1989). They are highly attentive to changes made to their own and others' caches that they had seen being made (Bugnyar, unpublished data). Jackdaws prey on insects on the ground and in the air, probe in the ground and turn stones when foraging (pers. obs.), but do not cache food. In a radial-arm maze, jackdaws revisited empty feeding locations (holes drilled in the ground) more frequently than food-storing jays and nutcrackers (Gould-Beierle, 2000). The author argued that nonstoring species might return to previously baited holes to search for further food, whereas storing species would not return because they would not expect them to be refilled. Accordingly, ravens may value information about the absence of food differently than jackdaws, as it may provide them with information about the fate of caches. Further, jackdaws may hold their attention for shorter periods (see also Scheid, Range, & Bugnyar, 2007), as their prey is quick and mobile. Insect-feeding cotton-top tamarins (*Saguinus oedipus*) are more impulsive and less patient than gum-feeding common marmosets (*Callithrix jacchus*) in temporal discounting tasks (Stevens, Hallinan, & Hauser, 2005), and higher impulsiveness and different

attention patterns may explain the differences between jackdaws and ravens.

Even though our ravens and jackdaws were hand raised and kept as similarly as possible, other differences between the two species exist beyond feeding ecology. For example, jackdaws live in colonies lifelong, whereas adult ravens live in pairs, and sociality has been used to explain differences in social learning preferences between ravens and jackdaws (Schwab, Bugnyar, & Kotrschal, 2008; Schwab, Bugnyar, Schloegl, & Kotrschal, 2008). Finally, the ravens in the previous study have had more experience with experimental testing than the jackdaws and had participated in a large number of choice tasks (e.g., Schloegl, Kotrschal, & Bugnyar, 2008a, 2008b). Thereby, they may have learned a general concept of choice tasks, which may have facilitated the use of an exclusion strategy. Future studies may therefore systematically modify the preexperience of the subjects to be tested. Also, comparisons incorporating more than two species and considering fine-tuned differences in caching behavior would be beneficial. While jackdaws and the white-throated magpie jay are the only two noncaching corvid species, large differences in caching strategies exist in corvids (e.g., seasonal vs. year-round caching species or long-term vs. short-term cachers), and Gould-Beierle (2000) suggested cognitive differences between Old World and New World corvids.

Not only the cognitive but also the neurological basis of these potential species differences is not clear. Jackdaws possess a smaller hippocampus than the food-caching corvids (Clayton & Krebs, 1994a), which manifests in differences in spatial memory (Clayton & Krebs, 1994a), associative memory (Clayton & Krebs, 1994b), and observational spatial memory (Scheid & Bugnyar, 2008). Given that the tasks presented here are, in their nature, spatial tasks, an involvement of the hippocampus is possible, even though speculative.

Taken together, these experiments clearly demonstrate differences between jackdaws, ravens, and keas in their ability to choose by exclusion in choice tasks. Interestingly, these differences were restricted to choices by exclusion, while ravens and jackdaws demonstrated very similar strategies when searching for food. Whereas alternative explanations still exist, feeding ecology and caching behavior may provide the most straightforward framework for explaining these differences as examples of specific adaptations.

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