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Exclusion in Corvids: The Performance of Food-Caching Eurasian Jays (*Garrulus glandarius*)

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Choice by exclusion involves selecting a rewarded stimulus by rejecting alternatives that are unlikely to be rewarded. It has been proposed that in corvids, exclusion is an adaptive specialization for caching that, together with object permanence and observational spatial memory, enhances a bird's ability to keep track of the contents of caches. Thus, caching species are predicted to perform well in tasks requiring exclusion. We tested this prediction by assessing the performance of Eurasian jays (*Garrulus glandarius*), a highly specialized cacher, in a two-way object choice task in which food was hidden in 1 of 2 cups. Consistent with the corvids' capacity for observational spatial memory, jays were highly accurate when shown the location of the food reward. However, the jays failed to exclude the empty cup when shown its contents. This failure to select the baited cup when shown the empty cup was possibly due to jays attending to the experimenter's movements and erroneously selecting the empty cup by responding to these local enhancement cues. To date, no corvids have been tested in an auditory two-way object choice task. Testing exclusion in the auditory domain requires that a bird use the noise produced when the baited cup is shaken to locate the reward. Although jays chose the baited cup more frequently than predicted by chance, their performance did not differ from trials controlling for the use of conflicting cues provided by the experimenter. Overall, our results provide little support for the hypothesis that caching has shaped exclusion abilities in corvids.

Keywords: Eurasian jay (*Garrulus glandarius*), exclusion, corvid, two-way object choice, acoustic cues

Animals may reduce foraging costs by using information available in the environment to exclude locations that are unlikely to contain a desired resource. A common paradigm for testing for such exclusion abilities in nonhuman animals is a two-way object choice task in which animals must find food hidden inside one of two containers (Call, 2004; Premack & Premack, 1994). In this task, an animal first learns across trials that only one container contains a hidden food reward. Subsequently, when the animal is informed about the empty container, it can potentially use one of two mechanisms to correctly choose the rewarded container: They can either avoid the empty container without mentally representing the contents of the rewarded container, or they can infer from the available information that if one container is empty, the other must contain the reward (Mikolasch, Kotrschal, & Schloegl, 2011; Paukner, Huntsberry, & Suomi, 2009; Schmitt & Fischer, 2009). Whereas both mechanisms require that the animal learn the rule that one container will always be rewarded and one will always be empty, the second relies on the animal's ability to inferentially reason about the location of the reward (Call, 2004). However, few studies of exclusion distinguish between these two mechanisms, namely exclusion by avoidance and exclusion by inference (Mikolasch et al., 2011; Paukner et al., 2009; Pepperberg, Koepke, Livingston, Girard, & Hartsfield, in press; Schmitt & Fischer, 2009).

Irrespective of the mechanism underlying a species' capacity for exclusion, the ecological factors that influence these exclusion abilities can be investigated with a comparative approach (Schloegl et al., 2009). The two-way object choice task and variants of this task have been used to evaluate the exclusion abilities of apes (Call, 2004, 2006; Hill, Collier-Baker, & Suddendorf, 2011; Premack & Premack, 1994), monkeys (Heimbauer, Antworth, & Owren, 2012; Hill et al., 2011; Sabbatini & Visalberghi, 2008; Schmitt & Fischer, 2009), prosimians (Maille & Roeder, 2012), human children (*Homo sapiens*; Hill, Collier-Baker, & Suddendorf, 2012), and dogs (*Canis lupus familiaris*; Aust, Range, Steurer, & Huber, 2008; Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Erdőhegyi, Topál, Virányi, & Miklósi, 2007). Recently, parrots (African Grey parrots, *Psittacus erithacus*; Mikolasch et al., 2011; Pepperberg et al., in press; Schloegl, Schmidt, Boeckle, Weiss, & Kotrschal, 2012; keas, *Nestor notabilis*; Schloegl et al., 2009) and corvids (carrion crows, *Corvus corone corone*; Mikolasch, Kotrschal, & Schloegl, 2012; ravens, *Corvus corax*; Schloegl et al., 2009; jackdaws, *Corvus monedula*; Schloegl, 2011) have also been tested using this paradigm.

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Among the corvid species tested in the two-way object choice task, ravens and crows demonstrate the capacity for exclusion and correctly select the rewarded container when shown the contents of the empty container (Mikolasch et al., 2012; Schloegl et al., 2009), but jackdaws do not (Schloegl, 2011). Both ravens and carrion crows are moderate cachers, and this trait has been secondarily lost from an ancestral state of caching in noncaching jackdaws (de Kort & Clayton, 2006). It has therefore been hypothesized that among corvids, exclusion abilities are an adaptive specialization for caching behavior, with cognitive demands associated with caching potentially giving rise to the capacity for exclusion (Mikolasch et al., 2012; Schloegl, 2011). Exclusion allows individuals to avoid locations that are unlikely to contain a desired resource without the need to extensively search in them. Thus, this ability may be enhanced in caching species that need to keep track of the contents of their caches and avoid revisiting sites they know to have been recovered or pilfered (Mikolasch et al., 2012; Schloegl, 2011). Accordingly, there is evidence that at least one species of corvid avoids caching in locations that are routinely pilfered (western scrub-jays, *Aphelocoma californica*; de Kort, Correia, Alexis, Dickinson, & Clayton, 2007).

The capacity for exclusion may also enhance corvid pilfering behavior. In contrast to food-caching species from other clades (e.g., black-capped chickadees, *Poecile atricapillus*; Baker et al., 1988), observational spatial memory has been demonstrated in food-caching corvids including western scrub-jays (Clayton, Griffiths, Emery, & Dickinson, 2001; Watanabe & Clayton, 2007), ravens (Bugnyar & Kotrschal, 2002), pinyon jays (*Gymnorhinus cyanocephalus*; Bednekoff & Balda, 1996b), Mexican jays (*Aphelocoma ultramarine*), and Clark's nutcrackers (*Nucifraga columbiana*; Bednekoff & Balda, 1996a). Corvids use observational spatial memory to remember the location of caches that they have seen another individual make. The capacity for exclusion may enable corvids to avoid targeting caches that they have seen being recovered or pilfered by another individual, reducing costly time spent searching for caches that are no longer available to pilfer. However, exclusion in corvids may not necessarily be an adaptive specialization related to feeding ecology. Instead, the capacity for exclusion may have emerged in the more closely related carrion crow and raven after their last common ancestor with the jackdaw (Mikolasch et al., 2012). Alternatively, exclusion may be a general ability possessed by all corvids, but the conditions under which it is usually tested favor certain predispositions or sensory biases in caching species (Schloegl, 2011). To elucidate the role of feeding ecology in promoting exclusion abilities, distantly related corvids with differing feeding ecologies must be tested (Schloegl, 2011).

The Eurasian jay (*Garrulus glandarius*) is from a distantly related genus to *Corvus*, namely *Garrulus*. In contrast to moderate cachers such as ravens and crows, which do not have strongly seasonal caching behavior and do not rely on caches as a staple food resource, Eurasian jays are highly specialized cachers that cache thousands of acorns in the autumn and rely on them as a staple food resource throughout the year (Bossema, 1979; de Kort & Clayton, 2006). Jays also use flexible cache protection and pilfering strategies (Shaw & Clayton, 2012). If their caching behavior involves adaptive specializations that also enhance exclusion performance, jays should demonstrate exclusion abilities that at least equal those of the more generalized caching species, the crow and the raven. Accordingly, jays should preferentially select a baited container when given information only about an empty container in a two-way object choice task.

In primates, exclusion abilities have been investigated in both the visual and the auditory domain (Call, 2004; Hill et al., 2011) and subjects' performance is typically poorer in the auditory domain (Heimbauer et al., 2012; Paukner et al., 2009; Schmitt & Fischer, 2009). However, prosimians are a notable exception, as they have been shown to perform better in auditory exclusion tasks than in visual tasks (Maille & Roeder, 2012). When tested in the auditory domain, subjects must first relate the presence and absence of noise to the location of a food reward, before being able to exclude a silent location and correctly select the baited cup (Call, 2004; Schloegl et al., 2012). For avian species, exclusion performance in an auditory version of the two-way object choice task has only been investigated in African Grey parrots (Schloegl et al., 2012). It has been suggested that the failure of many primate species in auditory exclusion tasks could be due to inattention to the auditory cues in the task (Schmitt & Fischer, 2009). However, Eurasian jays (Shaw & Clayton, 2013), like western scrub-jays (Stulp, Emery, Verhulst, & Clayton, 2009), are sensitive to acoustic cues both when caching and when pilfering and so may be capable of exclusion in the auditory domain. The critical first step to testing exclusion in the auditory domain is to demonstrate that a species can use auditory cues to find food. The aim of this study was therefore to test the visual exclusion performance of a specialized caching corvid and to establish whether this species could use auditory information to locate a food reward.

Method

We tested Eurasian jays (*Garrulus glandarius*) from two social groups that had never been in contact: Group A contained twelve 3-year-old birds and Group B contained nine 4-year-old birds. The two groups were housed in separate outdoor aviaries, each measuring 28 × 10 × 3 m (length × width × height). Aviaries were wood and mesh construction with gravel floors and contained several perches of varying height, width, and length. Each aviary contained smaller aviaries at one end (6 × 1 × 3 m or 6 × 2 × 3 m). Group A had three smaller aviaries and Group B had four smaller aviaries, each of which was accessible via a mesh door and could be closed off from the main aviary. Smaller, individual, indoor testing compartments (measuring approximately 1 × 1 × 2 m) were accessible from these small aviaries via opaque trap doors. Birds were obtained from a registered breeder (M. Ghobbain, Derbyshire, UK), hand raised, and kept for future behavioral experiments after the conclusion of this study. Jays had ad libitum access to water, maintenance diet (soaked dog biscuits, egg, cheese, bread, cooked vegetables, seeds, nuts, and fruit), and enrichment (small toys and other objects). The experiments were conducted under the UK Home Office project license PPL 80/2519.

Each experiment consisted of a training phase followed by a testing phase. For the visual experiment, we tested four jays from Group A and two jays from Group B. These trials took place between February 25 and June 10, 2012, and were conducted in the testing compartments. For the auditory experiment, we tested four jays from Group A and three jays from Group B. These trials took place between December 15, 2011, and April 5, 2012. Four jays participated in both experiments and all were tested in the auditory experiment first. For the auditory experiment, Group A jays were already familiar with being tested in the compartments in the presence of the experimenter (RCS), whereas Group B jays were not. We therefore tested Group B jays in the small aviaries and Group A jays in the compartments.

In all trials described below, a jay was enclosed in the compartment or small aviary and presented with two round (7 cm diameter × 2 cm high) metal cups with identical opaque white squares of Perspex resting on top as lids. These were positioned between the experimenter and jays, approximately 0.5 m apart, on a platform inside the testing compartment (see Figure 1) or on the floor of the small aviary. For each jay, the cups were placed in the same location for all trials within a block. During the presentation of the cups, jays sat on a perch 0.7 m above the platform in the compartments or used perches positioned between 0.7 and 2.0 m from the cups in the small aviaries. As the jays used in our experiments differed in their preference for perching location at the start of a trial, it was impossible to position the cups in a location where it was certain that the jays had a direct line of sight into the cup once the lid was removed. The experimenter therefore observed the jays during presentation to ensure that they had looked at the contents of both cups in all visual trials and auditory training trials (looking behavior was judged from the orientation of the jay's head and eyes relative to each cup) and to ensure that they were oriented toward the experimenter and cups during presentation in auditory experimental trials and all control trials. After presentation, the experimenter was careful to not directly observe the jays or cups and oriented her body such that she did not directly face the experimental set up until the jays had selected a cup.

Training

Visual. We gave jays blocks of 10 trials in which we showed them the contents of both cups. We use the term *block* to refer to consecutive trials that took place within a single day, usually in a single session. However, if a jay lost motivation and ceased approaching the cups, occasionally a block of trials was split across two sessions within a single day. Before a trial began, the experimenter turned her back to the jay and baited one cup out of view with either a peanut or a worm, depending on the preference of the jay. The experimenter then covered both cups before turning to face the jay, opening the small door that gave access to the compartment platform and placing the covered cups on the platform (see Figure 1a). The side on which the baited cup was placed (left or right) was pseudorandomized between trials, with one side baited in no more than two consecutive trials. The experimenter called the jay's name to gain its attention while touching both lids. Once the jay was attentive, the experimenter simultaneously withdrew the lids toward herself, allowing the bird to see inside both cups (see Figure 1b). If the jay attempted to approach before the cups were closed, the trial was aborted (to be repeated later) and both cups were removed before the jay could retrieve the food reward; jays therefore quickly ceased attempting to approach while the cups were open during the training sessions. After presentation, the experimenter replaced the lids, closed the compartment door, and allowed the jay 30 s to approach and touch or remove the lid of one cup only (see Figures 1c and 1d). After the jay had made its choice, both cups were removed and the procedure was repeated, or the jay was released, as necessary (jays given peanuts typically needed to be released to cache these between trials). Jays pro-

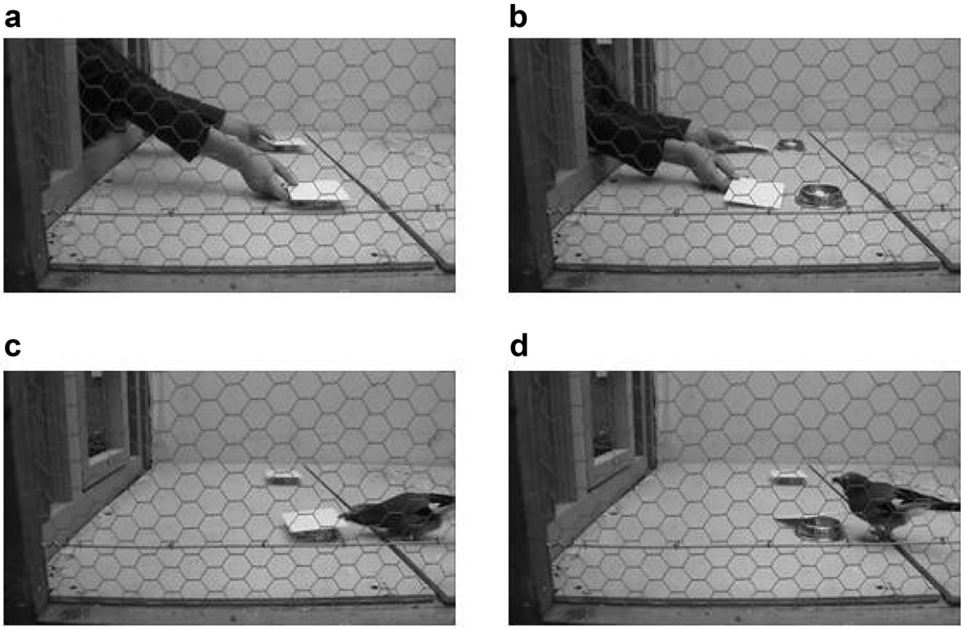

Figure 1. Figure of the testing compartment (Group A) and placement of cups and lids during a training trial in the visual experiment. The baited cups were placed approximately 50 cm apart on the platform (a), the lids were removed to show the contents of cups to the jay (b, jay out of view), the jay was allowed to approach one cup (c) to remove the lid and retrieve the food item (d).

ceeded to the testing phase of the visual experiment once they had selected the baited cup in at least eight of 10 trials within a block.

Auditory. Before testing jays in the auditory task, we first gave them blocks of 10 training trials to ensure that they would attempt to recover a reward from the cups when they had seen its location. During training trials in the auditory experiment, the jay watched the cup being baited. This difference in training methodology was because, in contrast to the visual experiment, some jays were tested in the small aviaries in the auditory experiment. The jays tested in the small aviaries were frequently at a greater distance from the cups at the start of a trial compared with jays tested in the compartments. Therefore, to ensure that the location of the reward remained salient in the small aviary, the experimenter showed the jay the reward being placed into the cup. At the beginning of a block, the experimenter first positioned the cups and then removed the lids and placed them behind the cups either on the compartment platform (Group A) or on the aviary floor (Group B). For Group A, a trial began with the experimenter opening the small door into the compartment platform and holding the nut in the air while calling the jay's name and repeating the word *look* to ensure that the jay was oriented toward the cups and experimenter. For Group B, the trial began with the experimenter approaching from the far end of the small aviary, kneeling down beside the cups, and attracting the jay's attention as described above. Once the jay was attentive, the experimenter placed the nut into one of the cups and then covered both cups simultaneously. Between trials, the order in which the left and right cups were baited was pseudorandomized, with the same side being baited in no more than two consecutive trials.

After baiting, the experimenter closed the compartment door and stepped to the side (Group A) or stood up and moved back to the far end of the small aviary (Group B) and allowed the jay up to 30 s to touch or remove the lid from one of the cups. After 30 s had elapsed, or after the jay had touched or removed the lid of a cup, the experimenter approached and returned both lids to their original position behind the cups. If the jay failed to select the baited cup, the food reward was removed and a new trial was begun by repeating the entire procedure (unless the block was complete). If the jay had selected the baited cup and retrieved the peanut, it was released to allow it to cache before being reenclosed in the compartment (Group A) or small aviary (Group B) to continue the block if necessary. Jays proceeded to the testing phase of the auditory experiment once they had selected the baited cup in at least eight of 10 trials.

Testing

Visual. Before a block of trials in the visual experiment, jays were given "refresher" trials. These were identical to training phase trials and their purpose was to ensure that jays did not have a preference for a particular side and remained attentive to the location of the food reward. Jays correct on the first four refresher trials were tested immediately; jays that scored less than four correct refresher trials were given 10 trials and were tested only if they were correct in eight of these trials. Only one jay (Ohuruogu) failed to reach criterion on one occasion and was not tested further on that day; instead, it was tested the subsequent day. The testing blocks in the visual experiment consisted of four "baited" and four "empty" trials. The procedure for these trials was almost identical to the training and "refresher" trials. The only difference was that while touching both lids, the experimenter withdrew the lid from one cup only: the empty cup lid in "empty" trials and the baited cup lid in "baited" trials. Within a block, all four possible combinations of baited cup location and cup shown (empty or baited) were used twice. Between blocks, the order of the different combinations of side baited and cup shown was pseudorandomized, with the baited cup being on the same side in no more than two consecutive trials.

At the end of each block, jays were given two "control" trials, in which both lids were touched for approximately 3 s and no lids were removed. The purpose of these was to ensure that jays were not responding to unintentional cues given by the experimenter about the location of the food item or to other possible cues such as olfactory cues. We were limited in the number of control trials we could give jays, as jays rapidly became unmotivated to approach the cups in the absence of any cues given by the experimenter. Jays received four blocks in total during the testing phase of the visual experiment, with no more than two blocks per day and no more than a 4-day break between consecutive blocks.

Auditory. The testing blocks in the auditory experiment consisted of eight trials in which each closed cup was shaken in turn. At the beginning of a trial, the experimenter faced away from the jay and held both cups and lids out of view to place a single peanut in either the left or right cup. The experimenter then turned to face the jay, opened the door into the compartment, and held the cups above their usual locations on the platform (Group A) or walked toward the jay, knelt down, and held cups above their usual location on the ground (Group B). The experimenter called the jay's name to gain its attention before shaking each of the cups in turn for 4 s each (cups were moved side to side for maximum rattling effect) and subsequently placing the cups on the platform or ground. The experimenter then retreated in the same manner as described for training trials and allowed the jay up to 30 s to touch or remove the lid from one of the cups. After 30 s had elapsed, the cups and lids were retrieved and the procedure was repeated or the jay was released, as necessary. The right-side cup was baited four times within a block. The side that was baited and the order in which cups were shaken were pseudorandomized between blocks and between jays: The same side was baited in no more than two consecutive trials, and the same cup was shaken first in no more than two consecutive trials.

We gave jays four blocks of trials in the auditory experiment. Similar to the testing phase of the visual experiment, at the end of each block, jays received two "control" trials. In these, the cups were held for approximately 3 s and were not shaken before being placed on the platform or ground. Jays received no more than two blocks of 10 trials per day and had no more than a 4-day break between consecutive blocks. In the small aviaries, one jay side-biased (choosing the left-side cup in at least nine trials) in two blocks of trials and one jay side-biased (choosing the left-side cup in 10 trials) in one block. These blocks were excluded from the analyses, and both jays received additional blocks to give a total of four blocks in which side-biasing did not occur. However, we also report the results of an analysis of the data set that includes these side-biasing blocks and excludes the additional blocks.

Analysis

For the visual experiment, we compared the proportion of trials in which the baited cup was chosen between the baited, empty, and control conditions using a Friedman analysis of variance. Wilcoxon signed-ranks test for matched pairs were used for pairwise planned contrasts of the control condition with the baited condition and with the empty condition (visual experiment) and the control condition with the auditory condition (auditory experiment). For the testing phase of both experiments, in each condition we compared the jays' performance with the chance expectation that they would select the baited cup in 50% of trials using one-sample Wilcoxon's tests. Given the small sample sizes, all tests were exact and were calculated by hand (Mundry & Fischer, 1998). All tests were two-tailed and the alpha level was set at .05.

Results

Visual Performance

During the training phase of the visual experiment, the six jays received an average of 1.4 ± 0.3 (mean ± *SE*) training blocks until they chose the baited cup in at least eight of 10 trials within a block (mean trials of 10 correct = 8.83 ± 0.40). The jays' performance when shown the contents of both cups remained consistent throughout the visual experiment, and jays correctly chose the baited cup more frequently than expected by chance in their refresher trials (see Table 1 for individual performance in all experimental trials and Table 2 for the number of refresher trials that jays had at the start of each test block; Wilcoxon's test: $n = 6$, $T^- = 0.00$, $p < .05$).

In the test phase of the visual experiment, the jays' performance differed between trials in which they were shown the baited cup's contents (baited condition), trials in which they were shown the empty cup's contents (empty condition), and trials in which they were not shown the contents of either cup (control condition; Friedman: $n = 6$, $\chi^2 = 11.57$, $p = .003$; see Figure 2). Jays chose the baited cup more often in the baited condition than in the control condition (Wilcoxon's test: $n = 6$, $T^+ = 0.00$, $p < .05$). Moreover, within the baited condition, jays correctly chose the baited cup more often than predicted by chance (Wilcoxon's test: $n = 6$, $T^- = 0.00$, $p < .05$; see Figure 2). By contrast, jays did not choose the baited cup more frequently in the empty condition than in the control condition (Wilcoxon's test: $n = 6$, $T^- = 5.00$, $p > .10$). There was a trend for jays selecting the baited cup less frequently than predicted by chance in the empty condition (Wilcoxon's test: $n = 6$, $T^- = 1.00$, $.10 > p > .05$; see Figure 2). In the control condition, three of the six jays selected the baited cup in exactly 50% of trials (see Table 1); therefore, the number of jays with a non-zero difference between chance and their performance was less than the minimum necessary for a Wilcoxon's test. Finally, there was no evidence of a learning effect across trials; the jays' choice of the baited cup did not differ between the first two blocks and last two blocks in any of the conditions (see Table 1; Wilcoxon's test: empty condition, $n = 5$, $T^- = 1.5$, $p > .1$. In the baited and control conditions, several jays had the exact same performance in the first and second half of the experiment; because of these ties, statistical analysis was not feasible).

Auditory Performance

During the training phase of the auditory experiment, the seven jays received a mean of 1.4 ± 0.2 training blocks before correctly selecting the cup containing the reward in at least eight of 10 trials in a block (mean trials of 10 correct = 8.57 ± 0.20). In the testing phase, jays did not differ in their accuracy between the auditory and control conditions (Wilcoxon's test: $n = 7$, $T^+ = 12.50$, $p > .10$; see Figure 3). However, jays correctly selected the baited cup more frequently than predicted by chance (chance = 50% of trials) in the 32 auditory trials (Wilcoxon's test: $n = 7$, $T^- = 0.00$, $p < .02$; see Figure 3), whereas in the control condition three jays selected the baited cup in exactly 50% of trials (see Table 3), such that the number of jays with a non-zero difference when comparing their performance with chance was less than the minimum sample size necessary for a Wilcoxon's test. Analyzing the data set that included blocks in which side-biasing occurred (and excluded the additional replacement blocks) yielded results that were identical to those described above.

The jays' performance in the first two blocks could not be statistically compared with their performance in the last two blocks of trials, as too few jays changed in their performance to permit the use of a paired Wilcoxon's test (see Table 3). Two jays were more accurate in the second half of trials, two jays were less accurate, and three jays showed no change (see Table 3). In the first 16 trials in the auditory task, there was a trend for jays performing above chance (median % correct = 56.25; Wilcoxon's test: $n = 5$, $T^- = 0.00$, $p < .10$), and this reached significance in the last 16 trials

Table 1
Individual Performance (Percentage Correct of Total Trials) in the Refresher, Baited, Empty, and Control Trials of the Visual Experiment

	Overall				Blocks 1 and 2				Blocks 3 and 4			
Jay	Refresh	Baited	Empty	Control	Refresh	Baited	Empty	Control	Refresh	Baited	Empty	Control
Lima	*92.5*	100.0	37.5	50.0	*95.0*	100.0	12.5	50.0	*90.0*	100.0	62.5	50.0
Ohuruogu	*97.5*	87.5	56.25	37.5	*95.0*	87.5	62.5	50.0	100.0	87.5	50.0	25.0
Pendleton	100.0	93.75	31.25	50.0	100.0	100.0	25.0	75.0	100.0	87.5	37.5	25.0
Romero	*85.0*	75.0	37.5	25.0	*90.0*	62.5	25.0	25.0	*80.0*	87.5	50.0	25.0
Washington	100.0	87.5	25.0	50.0	100.0	87.5	12.5	50.0	100.0	87.5	37.5	50.0
Wilson	*90.0*	93.75	37.5	62.5	*90.0*	87.5	37.5	50.0	*90.0*	100.0	37.5	75.0

Note. Jays in bold participated in both experiments. Values in italics for the refresher trials denote that a jay received 10 trials for at least one block.

Table 2
Number of Refresher Trials That Each Jay Received at the Beginning of Each Block in the Visual Experiment

	Block			
Jay	1	2	3	4
Lima	4	10	10	10
Ohuruogu	4	10	4	4
Pendleton	4	4	4	4
Romero	10	4	10	10
Washington	4	4	4	4
Wilson	10	4	10	4

Note. Jays in bold participated in both the visual and auditory experiments.

(median % correct = 56.25; Wilcoxon's test: $n = 6$, $T^{-} = 0.00$, $p < .05$).

Discussion

The adaptive specialization hypothesis predicts that species that cache food should perform better at tasks requiring exclusion than species that do not (e.g., Kamil, 1987; Krebs, 1990). However, we found no evidence that the Eurasian jay, a specialized cacher, could correctly select the baited cup in the visual two-way object choice task after being shown the contents of the empty cup. Consistent with previous studies demonstrating object permanence in the Eurasian jay (Zucca, Milos, & Vallortigara, 2007), and with evidence that many corvids possess well-developed observational spatial memory (reviewed in Shaw & Clayton, 2012), when shown the baited cup, the jays were more accurate in their choice of this cup than predicted by chance and compared with control trials. By contrast, when shown the empty cup, jays tended to preferentially choose this cup. Furthermore, the jays' performance did not change over the course of the experiment, suggesting that they did not learn the causal cues (e.g., using the presence or absence of the food reward inside the cup to determine which cup to choose) required to solve the task.

In a two-way object choice task, the movements of a human experimenter may unintentionally distract the subject from the information relevant to the task (Erdőhegyi et al., 2007). By lifting or moving the empty cup to reveal its contents to the subject, the experimenter may draw the subject's attention to this cup, distracting it from the causal cues relevant to the task and confounding its ability to exclude this unrewarded location and correctly select the baited cup. Accordingly, dogs tested in a two-way object choice task were more likely to incorrectly select the empty container when shown its contents by a human experimenter and only switched to correctly selecting the baited container once the task had been modified such that the human experimenter did not touch either container when showing their contents to the subject (Erdőhegyi et al., 2007). Similarly, the jays in our study tended to incorrectly choose the empty cup in trials in which the human experimenter removed the lid of this cup. Potentially, the experimenter's movements drew the jays' attention to the empty cup, possibly via local enhancement or a similar mechanism, and these social cues were more salient to the jays than the relevant cue (i.e., the absence of the food reward) that they needed to respond to in order to exclude the empty cup and select the baited cup.

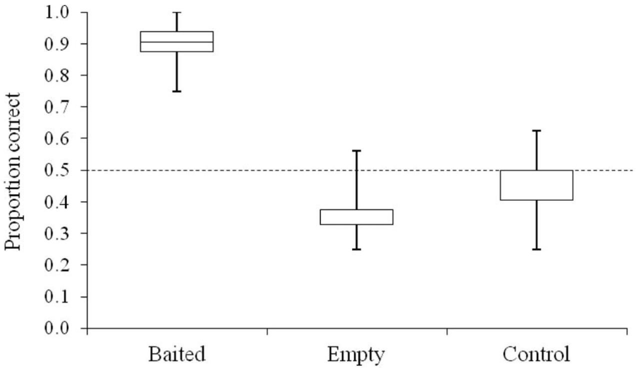

Figure 2. The proportion of trials within each condition (baited, empty, and control) in which jays correctly chose the cup containing the food reward (bars show the range, and boxes show the median and the interquartile range). The dashed line indicates the chance expectation that the cup containing the food reward would be chosen.

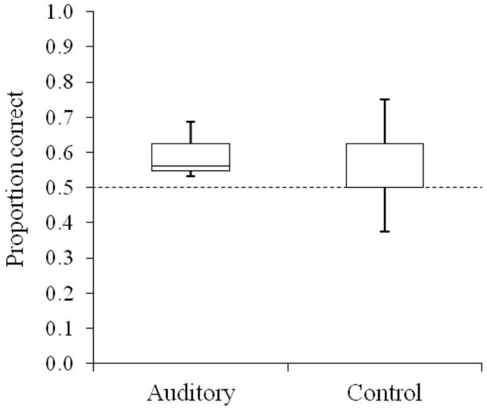

Figure 3. The proportion of trials in which jays correctly chose the cup containing the reward in the auditory and control trials (bars show the range, and boxes show the median and the interquartile range). The dashed line indicates the chance expectation that the cup containing the food reward would be chosen.

In a previous, visual, two-way object choice experiment, hand-raised ravens correctly selected the baited cup when shown the contents of the empty cup, whereas keas failed to do so (Schloegl

Table 3
Individual Performance (Percentage Correct of Total Trials) in the Auditory and Control Trials of the Auditory Experiment

	Overall		Blocks 1 and 2		Blocks 3 and 4	
Jay	Auditory	Control	Auditory	Control	Auditory	Control
Caracas	53.125	50.00	50.00	50.00	56.25	50.00
Hoy	56.25	62.50	50.00	50.00	62.50	75.00
Lima	62.50	75.00	62.50	75.00	62.50	75.00
Ohuruogu	53.125	50.00	56.25	50.00	50.00	50.00
Pendleton	68.75	37.50	68.75	50.00	68.75	25.00
Rome	62.50	50.00	68.75	50.00	56.25	50.00
Wilson	56.25	62.50	56.25	75.00	56.25	50.00

Note. Jays in bold participated in both experiments.

et al., 2009). This species difference in performance led the authors to suggest that, like dogs (Erdőhegyi et al., 2007), keas may have been more responsive to social cues than to the causal cues relevant to the task (Schloegl et al., 2009). Likewise, when the experimenter manipulated only one cup in each trial, the Eurasian jays in our study, carrion crows (Mikolasch et al., 2012), and jackdaws (Schloegl, 2011) failed to select the baited cup in trials in which they were shown the contents of the empty cup. An additional experiment in the crow study revealed that crows preferred to select the last cup that an experimenter had manipulated, even when the manipulation consisted of the experimenter removing the food reward (Mikolasch et al., 2012). Therefore, similar to keas (Schloegl et al., 2009), the failure to use exclusion by jays, crows, and jackdaws in the two-way object choice task in which the experimenter manipulates only one cup in a trial may be due to subjects attending to social rather than causal cues, potentially masking the true exclusion abilities of these species.

The two-way object choice task was therefore modified in the crow and jackdaw studies to remove local enhancement cues by having the experimenter manipulate both containers equally in every trial (Mikolasch et al., 2012; Schloegl, 2011). In this modified paradigm, the particular arrangement of opaque and transparent cups underneath larger opaque cups allowed experimenters to reveal the presence or absence of a food reward by simultaneously lifting both large external cups. Subsequently, the crows' exclusion performance improved and they correctly selected the baited cup more frequently when shown the empty cup's contents than in control trials, but remained less successful than in trials in which they had been shown the contents of the baited cup (Mikolasch et al., 2012). By contrast, there was only limited evidence that jackdaws were capable of exclusion in the modified task, with only one jackdaw improving its ability to correctly select the baited cup when shown the empty cup's contents (Schloegl, 2011). If Eurasian jays are in fact capable of exclusion, but these abilities are masked by their response to local enhancement cues, then their performance in the two-way object choice task should improve if confounding social cues are controlled or removed in a similar manner (Mikolasch et al., 2012). Such evidence for exclusion abilities in a specialized caching species would fit the prediction of the hypothesis that differences in caching ecology may explain differences in exclusion performance among corvids (Mikolasch et al., 2012; Schloegl, 2011). However, the cups and lids to which our jays were accustomed (see Figure 1) could not be modified to fit smaller interior cups that the jays were able to lift, such as those used in the crow and jackdaw studies, to remove potentially confounding social cues provided by the experimenter.

In contrast to previous studies with great apes (Call, 2004; Hill et al., 2011), lemurs (*Eulemur macaco* and *Eulemur fulvus*; Maille & Roeder, 2012), and African Grey parrots (Schloegl et al., 2012), we found no clear evidence that Eurasian jays could use a sound cue to locate a food reward. As the first step in investigating exclusion performance in the auditory domain is demonstrating that an animal can use sound cues to locate a food reward (Heimbauer et al., 2012), we therefore did not proceed to test jays in an auditory version of the two-way object choice task. The jays did select the baited cup more frequently than predicted by chance, indicating that they could potentially associate the rattling sound with the location of a food reward. However, as the jays' performance did not differ between the auditory and control conditions, we cannot rule out the possibility that jays responded to inadvertent cues provided by the experimenter.

Many species fail to use auditory cues to locate food, despite succeeding in a visual version of the task (e.g., olive baboon, *Papio hamadryas Anubis*; Schmitt & Fischer, 2009). Foraging ecology, combined with the ease with which species can manually manipulate objects, may affect their performance in the task. Capuchin monkeys (*Cebus apella*), for example, use weight and sound cues to determine the contents of closed nut shells before attempting to open these (Visalberghi & Neel, 2003). Moreover, capuchins become more accurate in using auditory cues to select a reward container in a two-way object choice task after receiving training trials in which they have the opportunity to manipulate baited and empty containers to produce sound themselves (Sabbatini & Visalberghi, 2008). By contrast, there is no evidence that investigation of the acoustic properties of objects plays an important role in corvid foraging strategies, and this could potentially lead to corvids performing poorly in the acoustic version of the two-way object choice task (Schmitt & Fischer, 2009). However, both Eurasian jays and western scrub-jays suppress noises associated with caching in the presence of a conspecific that can hear but cannot see them (Shaw & Clayton, 2013; Stulp et al., 2009), indicating that corvids may be attentive to acoustic cues in some foraging contexts. Given that the jays' performance in the auditory condition of our study was above chance, it remains possible that jays can use sound to locate food. However, as small sample sizes can increase the likelihood of both Type I and Type II errors, caution is needed when interpreting the jays' performance in the auditory task.

Although it remains possible that the Eurasian jays' exclusion performance may improve if conflicting enhancement cues are controlled for in the two-way object choice task (e.g., Erdőhegyi et al., 2007; Mikolasch et al., 2012), our current results for this specialized caching species provide little support for the hypothesis that the capacity for exclusion is an adaptive specialization for food caching in corvids. Thus, it is possible that within the *Corvus* genus, exclusion abilities emerged in the more closely related crows and ravens after their split from a common ancestor shared with jackdaws (Mikolasch et al., 2012). To evaluate this intriguing possibility, more species belonging to both *Corvus* and to other corvid genera that are distantly related to *Corvus* must be tested in the two-way object choice task. Although the results of our study add valuable data to our existing knowledge of the exclusion abilities of corvids, testing additional species to further investigate exclusion in the auditory domain and the selective pressures that led to the emergence of exclusion abilities in corvids remains exciting avenues for future research.

References

Aust, U., Range, F., Steurer, M., & Huber, L. (2008). Inferential reasoning by exclusion in pigeons, dogs, and humans. *Animal Cognition, 11,* 587–597. doi:10.1007/s10071-008-0149-0

Baker, M. C., Stone, E., Baker, A. E. M., Shelden, R. J., Skillicorn, P., & Mantych, M. D. (1988). Evidence against observational learning in storage and recovery of seeds by black-capped chickadees. *The Auk, 105,* 492–497.

Bednekoff, P. A., & Balda, R. P. (1996a). Observational spatial memory in Clark's nutcrackers and Mexican jays. *Animal Behaviour, 52,* 833–839. doi:10.1006/anbe.1996.0228

Bednekoff, P. A., & Balda, R. P. (1996b). Social caching and observational spatial memory in pinyon jays. *Behaviour, 133,* 807–826. doi:10.1163/156853996X00251

Bossema, I. (1979). Jays and oaks: An eco-ethological study of a symbiosis. *Behaviour, 70,* 1–116. doi:10.1163/156853979X00016

Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology, 120,* 38–47. doi:10.1037/0735-7036.120.1.38

Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, Corvus corax: Is it "tactical" deception? *Animal Behaviour, 64,* 185–195. doi:10.1006/anbe.2002.3056

Call, J. (2004). Inferences about the location of food in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo pygmaeus*). *Journal of Comparative Psychology, 118,* 232–241. doi:10.1037/0735-7036.118.2.232

Call, J. (2006). Inferences by exclusion in the great apes: The effect of age and species. *Animal Cognition, 9,* 393–403. doi:10.1007/s10071-006-0037-4

Clayton, N. S., Griffiths, D. P., Emery, N. J., & Dickinson, A. (2001). Elements of episodic-like memory in animals. *Philosophical Transactions of the Royal Society of London, Series B, 356,* 1483–1491. doi:10.1098/rstb.2001.0947

de Kort, S. R., & Clayton, N. S. (2006). An evolutionary perspective on caching by corvids. *Proceedings of the Royal Society B: Biological Sciences, 273,* 417–423. doi:10.1098/rspb.2005.3350

de Kort, S. R., Correia, S. P. C., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). The control of food-caching behavior by western scrub-jays (*Aphelocoma californica*). *Journal of Experimental Psychology: Animal Behavior Processes, 33,* 361–370. doi:10.1037/0097-7403.33.4.361

Erdőhegyi, Á., Topál, J., Virányi, Z., & Miklósi, Á. (2007). Dog-logic: Inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour, 74,* 725–737. doi:10.1016/j.anbehav.2007.03.004

Heimbauer, L. A., Antworth, R. L., & Owren, M. J. (2012). Capuchin monkeys (*Cebus apella*) use positive, but not negative, auditory cues to infer food location. *Animal Cognition, 15,* 45–55. doi:10.1007/s10071-011-0430-5

Hill, A., Collier-Baker, E., & Suddendorf, T. (2011). Inferential reasoning by exclusion in great apes, lesser apes, and spider monkeys. *Journal of Comparative Psychology, 125,* 91–103. doi:10.1037/a0020867

Hill, A., Collier-Baker, E., & Suddendorf, T. (2012). Inferential reasoning by exclusion in children (*Homo sapiens*). *Journal of Comparative Psychology, 126,* 243–254. doi:10.1037/a0024449

Kamil, A. C. (1987). A synthetic approach to the study of animal intelligence. *Nebraska Symposium on Motivation, 35,* 257–308.

Krebs, J. R. (1990). Food-storing birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions of the Royal Society of London, Series B, 329,* 153–160. doi:10.1098/rstb.1990.0160

Maille, A., & Roeder, J. J. (2012). Inferences about the location of food in lemurs (*Eulemur macaco and Eulemur fulvus*): A comparison with apes and monkeys. *Animal Cognition, 15,* 1075–1083. doi:10.1007/s10071-012-0531-9

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2011). African Grey parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food. *Biology Letters, 7,* 875–877. doi:10.1098/rsbl.2011.0500

Mikolasch, S., Kotrschal, K., & Schloegl, C. (2012). Is caching the key to exclusion in corvids? The case of carrion crows (*Corvus corone corone*). *Animal Cognition, 15,* 73–82. doi:10.1007/s10071-011-0434-1

Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: Examples from *Animal Behaviour*. *Animal Behaviour, 56,* 256–259. doi:10.1006/anbe.1998.0756

Paukner, A., Huntsberry, M. E., & Suomi, S. J. (2009). Tufted capuchin monkeys (*Cebus apella*) spontaneously use visual but not acoustic information to find hidden food items. *Journal of Comparative Psychology, 123,* 26–33. doi:10.1037/a0013128

Pepperberg, I. M., Koepke, A., Livingston, P., Girard, M., & Hartsfield, L. A. (in press). Reasoning by inference: Further studies on exclusion in grey parrots (*Psittacus erithacus*). *Journal of Comparative Psychology*.

Premack, D., & Premack, A. J. (1994). Levels of causal understanding in chimpanzees and children. *Cognition, 50,* 347–362. doi:10.1016/0010-0277(94)90035-3

Sabbatini, G., & Visalberghi, E. (2008). Inferences about the location of food in capuchin monkeys (*Cebus apella*) in two sensory modalities. *Journal of Comparative Psychology, 122,* 156–166. doi:10.1037/0735-7036.122.2.156

Schloegl, C. (2011). What you see is what you get—reloaded: Can jackdaws (*Corvus monedula*) find hidden food through exclusion? *Journal of Comparative Psychology, 125,* 162–174. doi:10.1037/a0023045

Schloegl, C., Dierks, A., Gajdon, G. K., Huber, L., Kotrschal, K., & Bugnyar, T. (2009). What you see is what you get? Exclusion performances in ravens and keas. *PLoS One, 4,* doi:10.1371/journal.pone.0006368

Schloegl, C., Schmidt, J., Boeckle, M., Weiss, B. M., & Kotrschal, K. (2012). Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings of the Royal Society B: Biological Sciences, 279,* 4135–4142. doi:10.1098/rspb.2012.1292

Schmitt, V., & Fischer, J. (2009). Inferential reasoning and modality dependent discrimination learning in olive baboons (*Papio hamadryas anubis*). *Journal of Comparative Psychology, 123,* 316–325. doi:10.1037/a0016218

Shaw, R. C., & Clayton, N. S. (2012). Eurasian jays, *Garrulus glandarius*, flexibly switch caching and pilfering tactics in response to social context. *Animal Behaviour, 84,* 1191–1200. doi:10.1016/j.anbehav.2012.08.023

Shaw, R. C., & Clayton, N. S. (2013). Careful cachers and prying pilferers: Eurasian jays (*Garrulus glandarius*) limit auditory information available to competitors. *Proceedings of the Royal Society B: Biological Sciences, 280*. doi:10.1098/rspb.2012.2238

Stulp, G., Emery, N. J., Verhulst, S., & Clayton, N. S. (2009). Western scrub-jays conceal auditory information when competitors can hear but cannot see. *Biology Letters, 5,* 583–585. doi:10.1098/rsbl.2009.0330

Visalberghi, E., & Neel, C. (2003). Tufted capuchins (*Cebus apella*) use weight and sound to choose between full and empty nuts. *Ecological Psychology, 15,* 215–228. doi:10.1207/S15326969ECO1503_2

Watanabe, S., & Clayton, N. S. (2007). Observational visuospatial encoding of the cache locations of others by western scrub-jays (*Aphelocoma californica*). *Journal of Ethology, 25,* 271–279. doi:10.1007/s10164-006-0023-y

Zucca, P., Milos, N., & Vallortigara, G. (2007). Piagetian object permanence and its development in Eurasian jays (*Garrulus glandarius*). *Animal Cognition, 10,* 243–258. doi:10.1007/s10071-006-0063-2

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