Task Aspects Triggering Observational Learning in Jackdaws (*Corvus monedula*)

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Abstract – Complex novel tasks are often used in animal cognition research to allow discrimination between various learning mechanisms. Successful performance relies on the capacity to identify informational cues from features in the environment. Additionally, observational learning is often considered more beneficial for survival than individual learning. Despite the importance of controlling task complexity, it can often be challenging to operationalize. This study investigated whether jackdaws, a highly social corvid species, can learn to drop stones inside a tube to release a reward after observing a trained conspecific. Additionally, it aimed to identify the underlying learning mechanisms and to detect the informational cues triggering learning. A research design was developed to highlight different aspects of the required action sequence. Experimental conditions included a conspecific model demonstrating the full sequence, parts of the sequence, consuming the reward without solving the task, and consuming the reward after the solution was demonstrated without a visible model. None of the 12 naïve jackdaws solved the task in pretests. Two subjects started solving in test sessions and they developed modified versions of the demonstrated action. Observing the full action sequence performed by a conspecific seemed to trigger learning. The majority of the subjects exhibited changes in their stone-oriented behavior, most likely due to stimulus and/or local enhancement. As predicted, jackdaws were influenced by conspecific model demonstrations when manipulating a complex novel foraging task. Factors contributing to the apparent task difficulty and directions for future studies are discussed within a tri-dimensional framework including the task, setup, and individuals.

Keywords – corvid, jackdaw, observational learning, task complexity, informational cues

The acquisition of skilled performance is dependent on the capacity to accurately identify and utilize informational cues from features in the environment (Brouwers et al., 2016), thereby enabling the discrimination of relevant cues (Weiss & Shanteau, 2003). Animals can learn individually through exploratory behavior, a broad category for interactions with the environment, including both search and exploration (Reader, 2015). Alternatively, they can extract informational cues by observational learning, after observing either a novel action performed by another individual or only the products of this activity (Zentall, 2012). The adaptive value of observational learning is based on flexibility and cost reduction when compared to predisposed or individual learning (Boyd & Richerson, 1988; Nicol, 2006). Investigations of the mechanisms involved in observational learning improve our understanding of the factors underlying cognitive processing of social information (Hoppitt & Laland, 2013). Ultimately, they also provide insights

into the evolution of geographical variations in behavior and cultural diversity (van de Waal et al., 2013; Whiten et al., 2011; for a review, see Galef, 2012).

Many classifications have been proposed to describe the mechanisms underlying observational learning in human and non-human animals (Heyes, 1994; Hopper, 2010; Nicol, 1995; Whiten et al., 2004; Zentall, 2012). In terms of increasing complexity, the mechanisms can be categorized into social influence, associative learning in a social context, and social learning of demonstrated behavior (Zentall, 2012). Social influence occurs when the actions of a demonstrator draw the attention of an observer to a location associated with reinforcement (local enhancement: Roberts, 1941; after Zentall, 2001) or an object/part of an object (stimulus enhancement: Spence, 1937). Associative learning in a social context involves individual trial-and-error learning facilitated by observing a social model. This category includes 'emulative' learning, which describes achieving the same end-state of a demonstrated behavior while employing a different technique (Wood, 1989). Finally, social learning of behavior involves reproducing the exact form of a demonstrated action (imitation: Whiten & Ham, 1992), which cannot be explained by alternative motivational, attentional, or simple learning processes.

Cognitive skills evolved as adaptations to specific ecological niches and complex environments (Clarin et al., 2013; for a review, see Mettke-Hofmann, 2014). Jackdaws (*Corvus monedula*) are semi-colonial, monogamous corvids that form long-term pair bonds and exhibit prolonged offspring care (Henderson et al., 2000; Lorenz, 1931; Röell, 1978). Their advanced cognitive skills and social complexity make them an attractive model species for investigating mechanisms underlying observational learning (Emery & Clayton, 2004; Güntürkün & Bugnyar, 2016; Katzir, 1982, 1983; Olkowicz et al., 2016; Röell, 1978).

In Europe, the primary habitats of jackdaws are grasslands with scattered trees, agricultural towns, as well as coastal and inland cliffs (Lockie, 1955; Madge & Burn, 2013). They opportunistically feed on a variety of readily available animals and plant matter, including insects, snails, berries, small seeds, grain, vegetables, fruit, and even parasites of farm animals, such as ticks collected from sheep (Hogstedt, 1980; Holyoak, 1968; Lockie, 1955, 1956; Madge & Burn, 2013). The observed diversity of feeding locations highlights the behavioral flexibility of jackdaws, i.e., the ability to conquer several ecological niches (Madge & Burn, 2013; for a review, see Seed et al., 2009).

The feeding methods used by jackdaws focus mainly on the ground surface and sometimes also extend to the forest canopy and air (Lockie, 1955; Madge & Burn, 2013). Interestingly, although jackdaws attempt deep-probing to reach underground prey, it does not seem an efficient technique (Lockie, 1956). The most likely explanation is the physical constraint of their relatively short beaks (Hogstedt, 1980; Lockie, 1956). Food caching in wild jackdaws is either not present (Waite, 1985) or rare in case deep crevices are available near the feeding site (Henty, 1975). In terms of object dropping behavior, jackdaws were observed to feed on horse-chestnuts (*Aesculus hippocastanum*) by dropping them on the pavement from approximately 10 m height (Gibson, 1992). Jackdaws usually forage in open flocks for defense against interspecific aggression and increased feeding efficiency for individual flock members through the acquisition of social information about new food sources (Röell, 1978).

Experimental studies support naturalistic observations in which jackdaws benefit from the social context to maximize their foraging success. Social information is also used when assessing the risk of anthropogenic stimuli, such as novel food, startling objects, or individual humans (Greggor et al., 2016; Lee et al., 2019). Protocols testing the effect of observational learning on the acquisition of novel foraging techniques in jackdaws included locating food hidden in various containers (Röell, 1978) and learning to push down a lever vs. pull a disc (Wechsler, 1988) or to lift vs. push a small ball (Federspiel et al., 2019) to receive a reward. In all studies, local and stimulus enhancement seemed to be the most potent learning mechanism as jackdaws barely approached the experimental setup and did not learn to obtain rewards before observing others manipulating the novel devices. Additionally, juvenile jackdaws seem to be more successful than adults in learning novel techniques, most likely due to engaging in more exploratory behaviors (Federspiel et al., 2019). Remaining to be investigated is whether the spread of foraging innovations within a social group extends from simple one-step manipulations to more complex sequences of actions and object use.

One of the research paradigms employing sequential actions in novel foraging tasks requires subjects to perform object dropping. This behavior is present in nature in multiple bird species, both in foraging and non-foraging contexts (Cristol & Switzer, 1999; Hunt et al., 2002; Lefebvre et al., 2002). Foraging observations include dropping prey items (such as eggs, mollusks, bones, nuts, and small animals) on hard surfaces, dropping stones on eggs, and dropping bread or insects into the water for fish bait. Observations in the non-foraging context include nest defense and nest predation by dropping stones, twigs, or other pieces of vegetation. In captivity, jackdaws carry, manipulate, and even cache small non-edible objects (Auersperg et al., 2014; Jacobs et al., 2013; von Bayern et al., 2007), but they rarely drop or insert objects into tubes (Auersperg et al., 2014).

Two experimental approaches incorporate stone-dropping behavior in comparative physical cognition research. The first approach uses a platform-release apparatus that consists of a vertical transparent tube positioned above a collapsible platform holding an out-of-reach reward. Subjects are required to drop an object inside the tube to release the platform and obtain the reward (for a revolving platform task requiring insertion of objects, see Taylor et al., 2014). Bird and Emery (2009) designed the platform-release apparatus for a study on rooks (*Corvus frugilegus*) where the subjects were trained to drop stones inside the tube before being presented with various tasks investigating the causal basis of this behavior. All subjects learned to solve the task after being shaped to nudge a stone into the tube. One subject presumably also learned after observing a conspecific performing the stone-dropping action. Similarly, successful performance in New Caledonian crows (*Corvus moneduloides*) was facilitated by training to either nudge a stone into the tube or to release the platform directly by pushing it down with the beak (von Bayern et al., 2009). Within a social context, relatively asocial Eurasian jays (*Garrulus glandarius*) did not use social information to solve the task. However, they were also successful after being trained to nudge stones into the tube (Miller et al., 2016).

The second experimental approach to incorporate stone dropping uses a vertical transparent tube filled with water that contains a floating, out-of-reach reward. Subjects are required to drop stones into the tube to raise the water level and reach the reward. Rooks (Bird & Emery, 2009), Eurasian jays (Cheke et al., 2011), and New Caledonian crows (Jelbert et al., 2014; Logan et al., 2014; Taylor et al., 2011) were successful in solving this task. However, they often required training on the platform-release task to reinforce the dropping behavior in a different context.

Initially, the platform-release task was described as requiring the use of stones as tools (Bird & Emery, 2009). The classic definition describes 'tool use' as manipulating unattached objects to change "the form, position, or condition of another object" (Beck, 1980, p. 10). However, more recent definitions emphasize that 'a tool' should be controlled to change the physical characteristics of a target through a mechanical interaction (St Amant & Horton, 2008). Furthermore, some authors consider only such "body–plus–object systems" as 'tooling' (Fragaszy & Mangalam, 2018, p. 18) and exclude aimed throwing or dropping of objects from their definition.

Problem-solving tasks are widely used in both human and non-human animal cognition research to investigate performance and behavior (Liu & Li, 2012; van Horik & Madden, 2016). Interaction between task, subject, and environmental characteristics was suggested to influence and predict performance. While preparation of experimental design includes some clearly defined areas, such as randomization or treatment effects (Bateson & Martin, 2007), controlling task characteristics, such as complexity or salience, is often less straightforward (Hærem et al., 2015; Rumbaugh et al., 2007).

A task was initially separated from the performing individual (*task qua task*; Wood, 1986) while including an interaction between objective task and subjective individual characteristics (Campbell, 1988). A more recent definition also incorporates the characteristics of an individual's behavior and the context of a task (Hærem et al., 2015). Following the influential framework presented by Wood (1986), tasks can be divided into three essential components: products, (required) acts, and informational cues. Products are items created by behaviors that are observable and independent of the acts that produced them. An act is a pattern of activities (e.g., closing a beak) forming a distinct behavior with an identifiable direction that separates one act from another (e.g., lifting vs. inserting an object). Informational cues are features of the task components that are used by individuals to make discriminations during the performance of a task. They are the most challenging task characteristic to formally operationalize within a study design because

they rely on subjects' perception of the attributes of stimulus objects and have to be assumed a priori to testing (Wood, 1986). The presence of subtasks additionally characterizes complex tasks (March & Simon, 1958; after Campbell, 1988) and sequence organization of subtasks in animal behavior was suggested as an estimate of the underlying complexity of cognitive processes (Byrne et al., 2001).

Complex novel tasks are often used in research designs to allow discrimination between various observational learning mechanisms (e.g., Custance et al., 1999; Logan et al., 2016). In practice, it is difficult to identify truly novel behavior because some features of any action an individual is capable of performing are likely to have been present in some form in its previous behavioral repertoire. Instead, responses with a very low probability of occurrence in the absence of observed demonstration by a model (Thorpe, 1961; Zentall, 2012) or that are difficult to acquire by individual trial-and-error learning (Seed & Byrne, 2010) are more feasible to control.

The present study was designed to investigate whether jackdaws can learn to use objects in a novel foraging context after observing trained conspecifics. The platform-release task was selected because jackdaws are unlikely to solve it opportunistically. An experimental protocol was developed to highlight different aspects of the demonstrated action sequence. It also aimed to empirically identify the informational cues triggering skill learning and the underlying learning mechanisms. Successful performance only after observing a full demonstration would indicate imitation or emulation learning, depending on the form of the reproduced action. Success after observing partial action demonstrations would point to stimulus or local enhancement. Success after observing a model feeding on a pre-released reward would suggest increased appetitive motivation to interact with the task. Lastly, successful performance after observing a 'ghost display' (where the task is solved without a visible social model: for a review, see Hopper, 2010) would suggest that observing only the movement of the stone provides sufficient informational cues to elicit successful performance. Based on the socio-ecological and cognitive profile of jackdaws, changes in their task-oriented behavior were expected after observing conspecific model demonstrations of the novel action sequence.

Method

Subjects

The subjects were 12 hand-raised jackdaws, without prior experience with object-dropping tasks and tested outside of the breeding season. Juvenile and sub-adult individuals were selected because younger jackdaws are more likely than adults to learn novel foraging techniques (Federspiel et al., 2019). Since hatching, the birds were group-housed at the Avian Cognition Research Station of the University of Oxford, United Kingdom, hosted by and associated with the Max Planck Institute for Ornithology, Germany. The facility consisted of a large outdoor aviary (10 m x 12 m x 2.5 m) with adjacent experimental compartments. Natural stones of various sizes were present in the aviary. The daily diet consisted of a meat-curd-rice formula (including egg powder, dried insects, oils, vitamins, and minerals), cereals, fruit, and soaked cat biscuits or Versele Laga Beo® pearls. Fresh water was available ad libitum. The station followed applicable international, national, and institutional guidelines for the care and use of animals in research. In accordance with the German Animal Welfare Act (Section V, Article 7; Borchert, 1998), no specific research permissions were required for this non-invasive study.

Models

Two adult jackdaws (a male and a female, both 7 years old) were used as models and pseudo-randomly assigned across subjects and conditions. They were familiar, but not affiliated, with the subjects and were trained over approximately 100 trials to drop stones into the tube. During testing, models promptly performed the required action, collected the reward, and left the cage. They were always rewarded for their actions to facilitate learning of novel complex skills through observed reinforcement (Akins & Zentall, 1998; Giraldeau & Templeton, 1991; Rendell et al., 2011) and to increase the incentive motivation in observers (Caldwell & Whiten, 2003). These particular models were selected because research suggests that juveniles

are more likely to learn from adults than from younger individuals (Holzhaider et al., 2010; Rendell et al., 2011). However, to investigate the effect of a juvenile model, a successful subject (Apache) was demonstrating for Sioux, Chimney, and Cherokee in the third round of testing as well as for Cherokee in the fourth round of testing.

Experimental Setup

The experiment was conducted inside a test room (2.5 m x 2 m) with occluded walls facing the adjacent home aviary of the subjects. A dual-cage (113 cm wide x 100 cm long x 90 cm high), an established method in observational learning research developed by Warden and Jackson (1935), was placed approximately 90 cm above the ground. It consisted of two duplicate chambers divided by a slide-in partition made of wire-mesh that permitted a clear view of the demonstrated actions. Additionally, it ensured close and equal proximity between observers and models across sessions. The front of the dual-cage included small flap doors that allowed access for models during testing. An experimenter was visible and sat approximately 50 cm in front of the cage.

The equipment inside the dual-cage (see Figure 1) included: a transparent Perspex apparatus consisting of a tube (5 cm wide x 11 cm high) and a box (12 cm wide x 11 cm long x 6 cm high), eight pebble stones (approximately 12 g each) placed in front of the apparatus, a turned over transparent glass bowl (14 cm diameter x 5 cm high), and a wooden tube cover (18 cm wide x 30 cm high). The apparatus was baited with a visible dead Morio worm (larvae of *Zophobas morio* beetle), a preferred food with high incentive value for jackdaws, placed on an opaque collapsible platform inside the box. Dropping a stone into the tube would release the platform from a small magnet. The reward would then emerge, together with the dropped stone, through a slot in the front of the apparatus.

Two sets of the apparatuses and stones were placed on removable boards (each 100 cm long x 30 cm wide x 1 cm thick), covered with a thin polystyrene layer to reduce sound cues of dropping stones inside the cage. The boards allowed for randomization of the relative positions of the two apparatuses during pretest and test sessions (see below) to control for location effects, attract attention, and potentially facilitate learning through setup changes (Rumbaugh et al., 2007; Schwab et al., 2008).
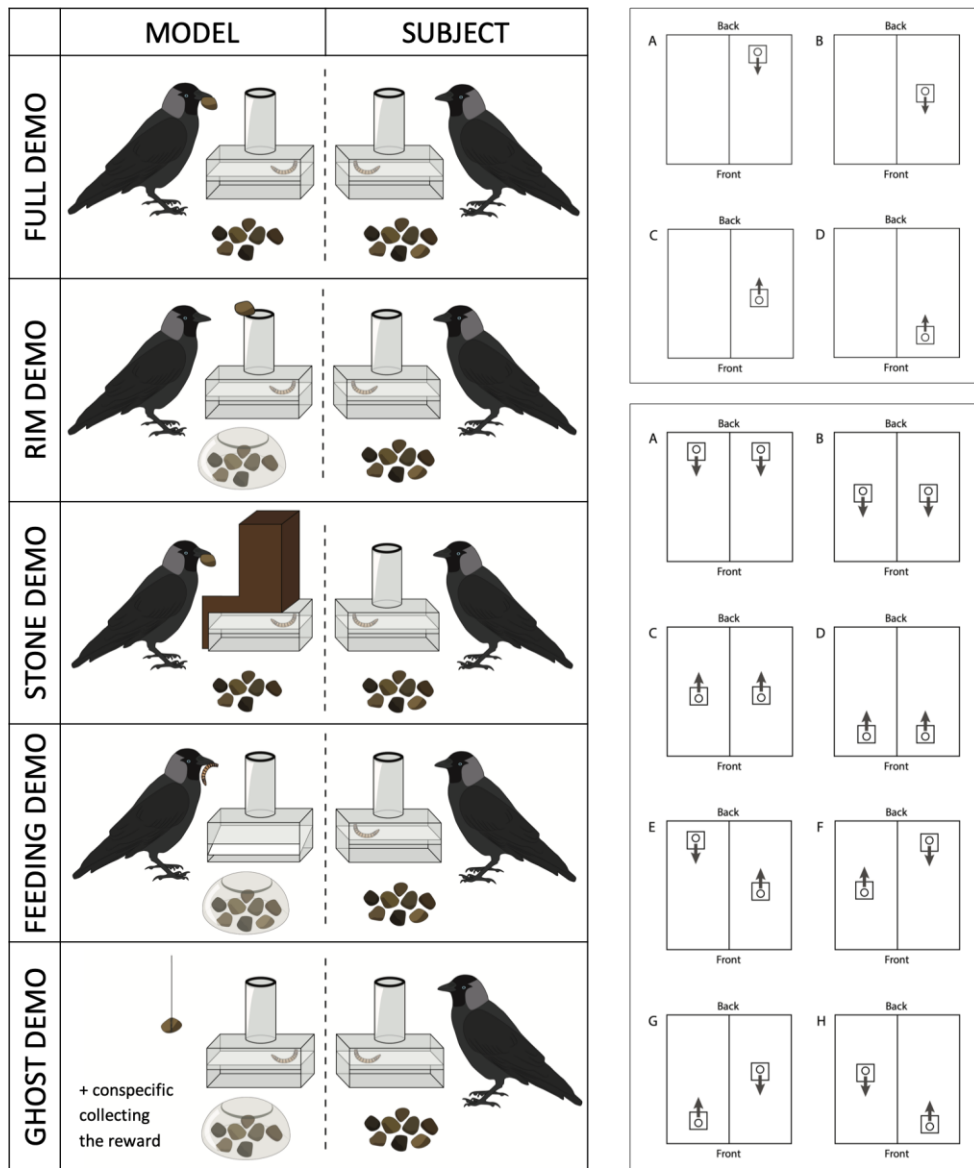
Experimental Phases

Habituation

Subjects were already habituated and trained to enter the dual-cage during a previous study. They were individually familiarized with the setup following a short period (30 min) without food to control their energetic state and ensure motivation for feeding. Cereals and Morio worms were provided in front of the released platform of the apparatus. Subjects entered the dual-cage for a couple of minutes, which time was gradually extended to match the length of a test session. They proceeded to the next experimental phase when they displayed no signs of neophobia inside the dual-cage and fed on the provided food.

Pretests

Pretests were conducted to verify that subjects had no predisposition to place stones inside or on the apparatus. Each subject received seven pretests of 20 min, following a short period (30 min) without food to ensure motivation for retrieving the reward. Each individual received only one pretest per day. Between sessions, the positions of the apparatus in the dual-cage were pseudo-randomized across four predetermined locations to control for possible side/location effects (see Figure 1, right-hand upper side).

Figure 1

A Graphic Overview of the Experimental Conditions and Positions of the Apparatus

Note. **Left-hand side:** Experimental conditions inside the dual-cage. The setup on the side of the subject always included a baited apparatus, eight stones, a turned over glass bowl, and a tube cover. The bowl and the tube cover were present in both chambers of the dual-cage during all conditions but for clarity purposes, they are only represented as part of the demonstration setup. **Right-hand upper side:** Positions of the apparatus inside the dual-cage during pretests: (A) top-down, (B) middle-down, (C) middle-up, (D) bottom-up. The arrows indicate the direction in which the apparatus was facing. **Right-hand lower side:** Relative positions of the two apparatuses inside the dual-cage during tests. Symmetric positions: (A) top-down, top-down, (B) middle-down, middle-down, (C) middle-up, middle-up, (D) bottom-up, bottom-up. Asymmetric positions: (E) top-down, middle-up, (F) middle-up, top-down, (G) bottom-up, middle-down, (H) middle-down, bottom-up. The arrows indicate the direction in which the apparatus was facing.

Tests

Each test session lasted approximately 35 min, following a short period (30 min) without food to ensure subjects were motivated to attend to the behavior of a conspecific (Dorrance & Zentall, 2001) and to

retrieve the reward. The success criterion was defined as six consecutive actions of deliberately dropping a stone inside the tube, which would indicate that the behavior was learned and reliably repeated. During testing, the experimental equipment was always available to the subjects, allowing continuous exploration and instant reaction in response to the observed actions. The relative positions of the apparatuses were pseudo-randomized across sessions to eliminate possible locations effects (see Figure 1, right-hand lower side).

A test session included four demonstration trials. Each demonstration trial consisted of a demonstration and acquisition time (4 min), during which a subject could interact with the equipment without being interrupted. Once the acquisition time had passed, the apparatus in the demonstration chamber was re-baited for the subsequent demonstration trial. In the middle of a test session, the observation and demonstration sides of the dual-cage were switched to control for local enhancement specific to the demonstration apparatus (Zentall, 2012). During the side-switch, subjects were offered a dead Morio worm in front of the released platform of the demonstration apparatus. The freely available reward aimed to maintain subjects' motivation and to potentially facilitate learning by allowing them to experience the results of the demonstrated action (Berry, 1908; Del Russo, 1971; Miller & Dollard, 1941). After the side-switch and at the beginning of a test session, subjects were given 2 min to settle.

Experimental Conditions

Subjects were divided into two test groups: conspecific model and ghost model demonstrations. In the conspecific model demonstration group, eight juvenile individuals (four females and four males, approximate age at the start of testing: 4 months) were pseudo-randomly assigned to a maximum of four test rounds. Within each round, subjects experienced 10 test sessions of different experimental conditions that highlighted various aspects of the required action sequence: (1) 'Full Demo', (2) 'Rim Demo', (3) 'Stone Demo', and (4) 'Feeding Demo' (for an overview, see Table 1; for a study presenting various types of demonstrations in a cumulative experimental design, see Hopper et al., 2014). In the ghost model demonstration group, four sub-adult individuals (sexes undetermined, approximate age at the start of testing: 12 months; available only at the later stages of the project) participated in (5) 'Ghost Demo' only.

Table 1

An overview of the Test Groups and the order of Experimental Conditions

Group	Subject	Sex	Pretest	Round 1	Round 2	Round 3	Round 4
Conspecific model	Apache	Female	Pretest	Full[a]			
	Choctaw	Female	Pretest	Full	Rim[d]		
	Blackfoot	Male	Pretest	Rim	Stone	Full	
	Chimney	Male	Pretest	Rim	Stone	Full	
	Chapa	Female	Pretest	Stone	Rim	Full	
	Sioux	Female	Pretest	Stone[b]	Rim	Full[c]	
	Cherokee	Male	Pretest	Feeding	Rim	Stone	Full
	Mohawk	Male	Pretest	Feeding	Stone	Rim	Full
Ghost model	Bunny	Und.	Pretest	Ghost			
	Gru	Und.	Pretest	Ghost			
	Monkey	Und.	Pretest	Ghost			
	Snake	Und.	Pretest	Ghost			

Note. [a] Solved the task and replicated the success.
[b] Solved the task for the first time but did not replicate the success in subsequent trials.
[c] Started solving again but never reached the success criterion.
[d] One individual (Choctaw), which started with the Full Demo, also received the Rim Demo to investigate whether this partial action demonstration following the full demonstration would elicit solving.

In (1) the Full Demo condition, subjects observed the complete sequence of actions necessary for solving the task: They observed the model collecting, carrying, and dropping a stone into the tube. In (2) the Rim Demo, subjects observed only a partial action where the model pushed a stone attached to the rim of the tube; the remaining stones were placed underneath a glass bowl to prevent further demonstrations. Similarly, in (3) the Stone Demo, subjects also observed only a partial action where the model collected a stone and carried it towards the apparatus; the action of dropping the stone inside the tube was occluded by a cover mounted on top of the box. In (4) the Feeding Demo, subjects only saw the model consuming the reward in front of the released platform; stones were present but placed underneath the glass bowl to prevent stone-dropping demonstrations. In (5) the Ghost Demo, a stone was moved by the experimenter on a thin transparent nylon string: It was lifted from the top of the glass bowl covering the remaining stones, slowly moved towards the apparatus, and dropped inside the tube. Once the reward was released, a conspecific would briefly enter the cage to collect the reward which rendered this condition an 'enhanced' ghost demonstration (Fawcett et al., 2002; Hopper et al., 2008; for a graphic overview of the experimental conditions, see Figure 1, left-hand side).

Scoring and Statistical Analysis

All pretest and test sessions were recorded on two camcorders (Sony Handycam DCR-SX65). The measurements of subject behavior were scored from the video recordings. Interest in stones was coded as the total time (in seconds) of stone manipulation by either beak or feet and the frequency of carrying stones (collecting a stone and making at least one step). Stone-related behaviors aimed at the apparatus were coded as frequencies of holding a stone near/inside the tube, placing a stone at the box, or placing a stone inside the slot of the apparatus.

Statistical tests were used to analyze whether: (1) the proportion of successful actions differed between observer and demonstration chambers, (2) time spent manipulating stones differed between subjects presented with the Full Demo during the first or last round of testing, (3) time spent manipulating stones differed between pretests and tests for each test condition, and (4) the frequency of stone-related behaviors aimed at the apparatus differed significantly between all conditions. A binomial test was used to analyze differences between solving proportions in observer and demonstration chambers. Linear mixed models were used to investigate the effect of experimental conditions and trials on log-transformed time spent manipulating stones, including subjects as a random factor to account for repeated observations of the same individuals. Log-transformation was used to satisfy model assumptions regarding normality of residuals. Model selections were based on stepwise backward model refinement from a full model and comparisons of the Akaike Information Criterion (AIC). Associations between conditions and frequencies of stone-related behaviors were compared via χ^2 contingency tests.

All statistical analyses were conducted in R software version 3.4.3 (R Core Team, 2018). Statistical models were conducted by employing the 'lme4' package and model assumptions were confirmed visually through the 'mcp.fnc' function of the 'lmer.convenience' package. Graphs were created by employing the 'ggplot' function (Wickham, 2009) and the 'mosaic' function of the 'vdc' package (Meyer et al., 2006).

Results

The habituation phase lasted five days until subjects were feeding inside the dual-cage. None of the subjects solved the task in pretests and all proceeded into testing. Two subjects (named Apache and Sioux, both females) learned how to solve the task during test sessions, but only Apache reached the success criterion. Additionally, both subjects developed modified techniques for solving the task that differed from the demonstrated action of placing a stone into the tube while standing on the ground.

Successful Subjects

Apache solved the task in the first round of testing, Full Demo, Test Session 4, once after Demo 1 (total of 13 demonstrations; see Video 1) and once after Demo 4 (total of 16 demonstrations). She started

solving continuously in Test Session 5, Demo 1 (total of 17 demonstrations) until reaching the success criterion. The employed method was dropping stones while standing on top of the tube. However, Apache started solving while standing on the ground after demonstrating in Rim Demo.

Sioux solved the task for the first time in the first round of testing, Stone Demo, Test Session 9, once after Demo 4 (total of 36 demonstrations; see Video 2). However, she did not replicate this success until reaching the third round of testing, Full Demo, Test Session 21 (see Video 3). In this session, Sioux solved the task once before Demo 1 (total of 0 Full demonstrations, preceded by 40 Stone and 40 Rim demonstrations), after Demo 3, and before Demo 4 (total of 3 demonstrations). Subsequently, she started solving again in Test Session 24, before Demo 1 (total of 12 demonstrations). However, she failed to reach the success criterion due to an accidental manner of the performed stone-dropping actions (for an overview, see Table 1). Sioux also started solving while standing on top of the tube. However, she would hold a stone in her foot and drop it upon flying away or while manipulating it between the feet. Rather than inspecting the front of the apparatus for the released reward, Sioux often departed from the apparatus and returned only after discovering the available reward. On two occasions, she held and subsequently released a stone outside the tube (see Video 4).

Behavioral Effects of Test Conditions

There was no difference in the proportion of successful actions between observer and demonstration chambers, $\chi^2(1) = 0.01$, $p = .93$. The subjects presented with the Full Demo during the last round of testing did not differ in the time spent manipulating stones from the subjects presented with the Full Demo during the first round of testing, LMM: $\beta = -0.36$, $SE = 0.64$, $t = -0.57$, $p = .57$. The time spent manipulating stones was significantly affected by condition, $\chi^2(5) = 30.70$, $p < .001$, but not by session number, $\chi^2(1) = 2.30$, $p = .13$. There was significantly more stone manipulation in Full, Rim, Stone, and Feeding Demo conditions as compared to pretests and significantly less stone manipulation in the Ghost Demo as compared to the Full Demo (for detailed results, see Table 2 and Figure 2). Similarly, frequencies of stone-related behaviors differed significantly between test conditions, $\chi^2(15) = 183.10$, $p < .001$. There was more activity near the tube of the apparatus in the Full Demo, more activity near the slot in the Rim Demo, more activity at the box in the Stone and the Feeding Demo, and more carrying of stones in pretests than expected if the frequencies were evenly distributed across all conditions and activities (see Figure 3).
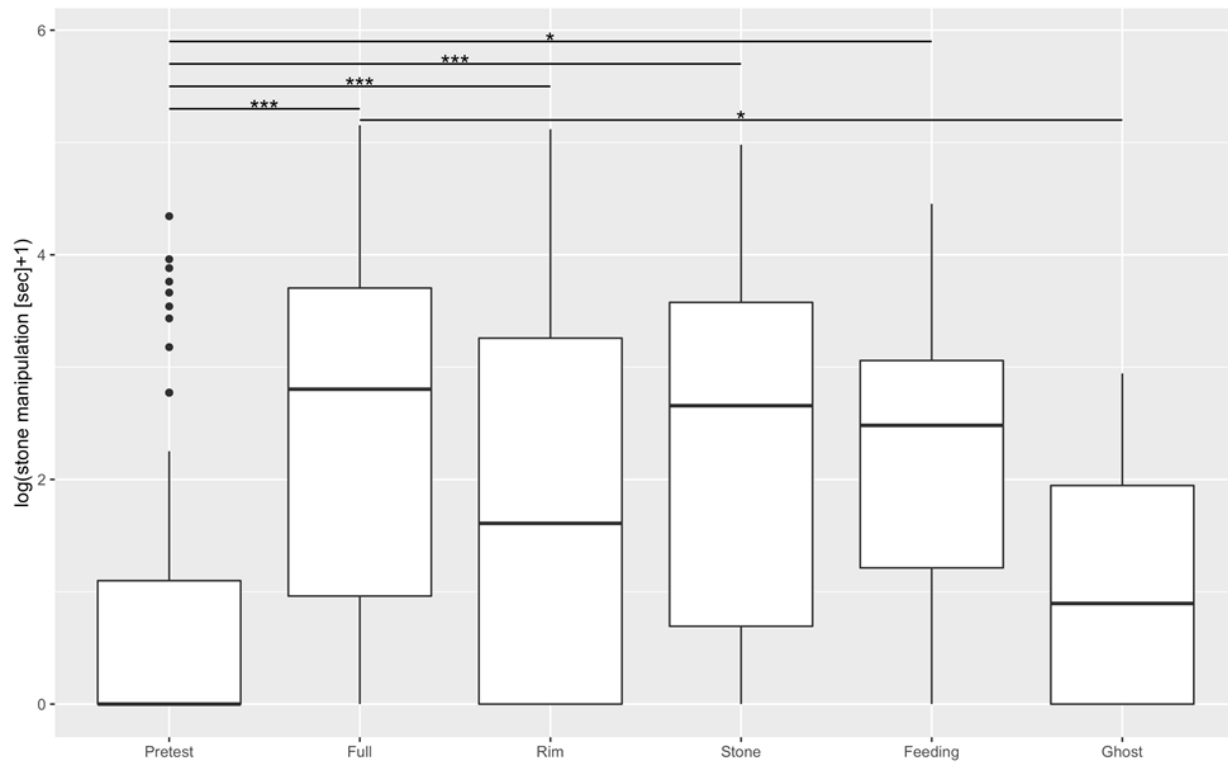
Table 2

Multiple Comparisons of Time Spent Manipulating Stones (in Seconds) in Different Experimental Conditions

			β	SE	t	p
Full	-	Feeding	0.41	0.36	1.13	0.86
Ghost	-	Feeding	-0.69	0.46	-1.50	0.65
Pretest	-	Feeding	-1.17	0.37	-3.16	0.02
Rim	-	Feeding	-0.21	0.36	-0.59	0.99
Stone	-	Feeding	0.32	0.36	0.87	0.95
Ghost	-	Full	-1.10	0.36	-3.06	0.03
Pretest	-	Full	-1.58	0.24	-6.70	<.001
Rim	-	Full	-0.62	0.23	-2.74	0.06
Stone	-	Full	-0.09	0.24	-0.39	0.99
Pretest	-	Ghost	-0.48	0.30	-1.59	0.59
Rim	-	Ghost	0.48	0.36	1.32	0.76
Stone	-	Ghost	1.01	0.37	2.74	0.06
Rim	-	Pretest	0.96	0.24	3.99	<.001
Stone	-	Pretest	1.49	0.25	5.99	<.001
Stone	-	Rim	0.53	0.24	2.25	0.20

Note. Model: log(Manip.stones + 1) ~ Condition + (1 | Subject).

Figure 2

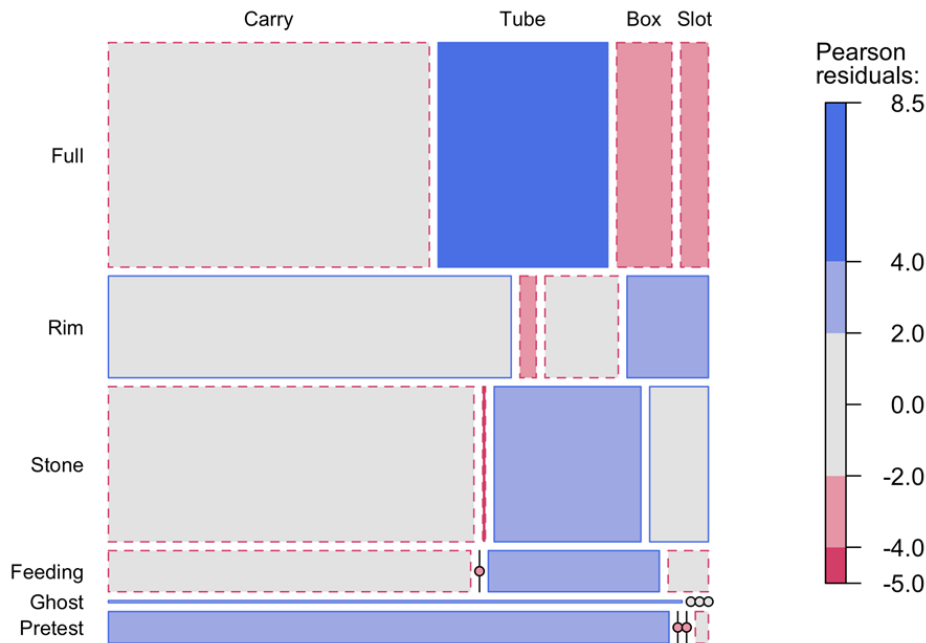*Stone Manipulation Time (log seconds) for each Experimental Condition*

Note. ***p < .001, **p < .01, *p < .1;* black dots in the graph represent outliers, bold horizontal lines indicate median values; boxes span the first to third quartiles and whiskers represent 95% confidence intervals.

Discussion

None of the subjects solved the task in pretests. Additionally, the demonstrators required extensive training, indicating that jackdaws do not have a predisposition for dropping stones into tubes and that the platform-release task was not easily solved by individual learning. Subjects were influenced by conspecific model demonstrations in their stone manipulations, thus confirming the study predictions. More time was spent manipulating stones in Full, Rim, Stone, and Feeding Demos than in pretests, as well as in the Full Demo than in the Ghost Demo condition. In terms of learning how to solve the platform-release task, one subject (Apache) was successful in the Full Demo condition and another subject (Sioux) started repeatedly solving in the Full Demo condition but did not reach the success criterion.

Figure 3

Mosaic Plot of Stone-Related Behaviors in Different Experimental Conditions

Note. The size of each rectangle represents the frequency of activities. Shading indicates levels of significant deviation in the frequencies of stone-related behaviors as compared to equally distributed frequencies (dark shading for residuals > ±4, light shading for residuals > ±2, grey shading for no significance). Continuous lines indicate higher frequencies than expected and broken lines indicate lower frequencies than expected in an equiprobability model.

Informational Cues

Cognition has evolved in specific environments to extract information efficiently (Mettke-Hofmann, 2014). Furthermore, organisms attend to environmental stimuli and events in line with their genomes and developmental histories (Rumbaugh et al., 2007). Therefore, the difference between successful and non-successful subjects could be attributed to their ability to perceive informational cues (Overington et al., 2011). Examination of the behavioral effects of test conditions reveals which aspects of the demonstrations were perceived as most salient and contributes to our understanding of how task complexity influences the learning process.

Significant differences in the stone-related behaviors were observed as compared to evenly distributed frequencies across all conditions and activities. After the Full Demo, more stone activity was aimed at the tube, after the Rim Demo, more stone activity was aimed at the slot, after the Stone and the Feeding Demo, more stone activity was aimed at the box, and in the pretests, there was more stone carrying. Therefore, it seems that only observing the full demonstration performed by a conspecific model influenced the emergence of behavioral changes relevant for solving the task. Regarding the remaining conditions, the visibility of the reward inside the box and the presence of the released reward inside/near the slot might have increased salience and response-eliciting properties of these non-functional parts of the apparatus (Rumbaugh et al., 2007). Observing a feeding conspecific seemed to increase appetitive motivation to interact with the task. The presence of stone carrying in pretests might be explained by object play behavior, defined as divertive interactions with objects (such as exploratory manipulations; Auersperg et al., 2014).

The Ghost Demo did not influence the subjects' behavior when compared to pretests. Additionally, this condition seemed to negate the effect of observing a conspecific consuming the reward. This reduced performance could be a result of neophobia as non-animate objects that violate expectations for movement were suggested to be startling to wild jackdaws (Greggor et al., 2018). However, it is unlikely that the hand-risen subjects in this study were afraid of the ghost display because they participated in repeated exposures to the procedure and exhibited no signs of distress during testing. A more likely explanation is distraction of the subjects' attention due to the unnatural character of a moving stone. The decreased motivation to copy a ghost display potentially indicates that demonstrations of conspecific models with agency were more salient than moving but nonliving objects (Hopper, 2010; Hopper et al., 2014; Zentall, 2012).

Learning Mechanisms

Interestingly, the two subjects that started dropping stones inside the tube developed alternative techniques from the ones demonstrated. During the first successful performance, Apache carried a stone across the experimental cage directly to the apparatus, jumped on top of the tube (instead of standing on the ground), and released the stone inside the tube, seemingly without trial-and-error learning. Three explanations are possible for this observed behavior: emulative learning, stimulus and/or local enhancement, or physical limitations of the subject.

Emulative learning could be a potential underlying mechanism as it involves achieving the result of a demonstrated action by employing a method different from the one presented (Whiten et al., 2004). However, the low success rate among subjects in this study precludes strong conclusions. Alternatively, a more parsimonious explanation of the observed behavior includes stimulus and/or local enhancement. In experimental studies, it is often not possible to differentiate between these two learning mechanisms because the target object might have a fixed location within an apparatus (Zentall, 2012), as was the case with the tube in the platform-release task. However, enhancement effects usually refer to simple actions, such as discovering a route around a barrier, or are paired with individual trial-and-error learning of directing predisposed actions, such as pecking at a paper cover to access a reward (for a review, see Zentall, 2012). Finally, Apache was younger and slightly smaller than the adult models. This size difference might have potentially contributed to standing on top of the tube while solving the task. However, Apache was able to drop stones inside the tube while standing on the ground after she demonstrated in the Rim Demo.

The second subject, Sioux, was more interested in the stones and the tube, although seemingly without a functional understanding of how to solve the task. This limitation was indicated by the large gap between her first and second solving, the failure to replicate the correct behavior consecutively, and the accidental manner of the performed stone-dropping actions (i.e., dropping a stone held in a foot when flying away from the tube). Therefore, the most likely underlying mechanism of the observed behavior was stimulus/local enhancement. Similarly, in the study by Wechsler (1988) jackdaws acquiring a novel foraging technique also would not consistently repeat rewarded actions. Instead, they only gradually focused their manipulations on the relevant parts of the apparatus which led to improved solving efficiency.

Jackdaws are known to be highly susceptible to the influence of local and/or stimulus enhancement after observing conspecifics demonstrating novel food-acquisition techniques (Röell, 1978; Tamm, 1977; Wechsler, 1988) or humans presenting food locations (Mikolasch et al., 2012; Schloegl, 2011). However, the strong enhancement effect was also suggested as potentially masking their capacity to perform cognitively demanding tasks (Mikolasch et al., 2012). In nature, jackdaws are opportunistic foragers who explore their environment for freely available food sources. Therefore, simple social influence mechanisms, such as local and/or stimulus enhancement, might be sufficiently inducing jackdaws to follow conspecifics to food sources that are readily available upon arrival. Additionally, relying on simple learning mechanisms fulfills the survival need to locate food without having to invest more energy into detailed conspecific observation. It also decreases the risk of predation or accessing a potentially depleted food source.

Factors Influencing Task Difficulty

The majority of the subjects were unsuccessful in solving the platform-release task. The apparent difficulty and the directions for future research will be discussed within a framework for examining complex problem-solving. The tri-dimensional framework includes the task, situation (setup), and person (individual; Beckmann & Goode, 2017).

Task

Perceptually, the conditions used in this study might have increased the complexity, and thus difficulty, of the platform-release task by introducing stimuli (wooden tube cover, glass bowl, nylon string) that were not supposed to function as informational cues. Additionally, the salience of a relevant stimulus is crucial for learning to occur. Salience may be determined by the natural properties of a stimulus, such as size or color, or by the outcomes produced by the organism's past behavior (Rumbaugh et al., 2007). For the subjects in this study, the strength of perceived informational cues might have been weakened by the cumulative experience of not being able to solve the task.

Subjects directed their stone-related behaviors towards the parts of the apparatus where the reward was either visibly stored (box) or released together with a stone (slot). Placement of stones on the box might suggest poor inhibitory control of the tendency to reach for food directly through the transparent apparatus (MacLean et al., 2014). Unfortunately, subjects seemed distracted from attending to the functionally relevant part of the apparatus (tube). The division of attention when approaching novel tasks was suggested to decrease performance (Dukas & Kamil, 2001; Overington et al., 2011). Indeed, in a study by Wood and Whiten (2017), solving success was reduced after subjects observed a demonstration that was spatially distant from the reward, most likely due to a conflict in attentional focus. Similarly, Wechsler (1988) reported that jackdaws rarely interacted with the relevant parts of a food dispenser after observing skilled conspecifics. Instead, they explored the food-release area and randomly pecked at the equipment.

Additionally, the key to eliciting novel problem-solving behavior is sensory-motor integration. It is crucial to activate the sensory association areas of the brain together with the neural circuits between the sensory areas and the motor association areas (Nomura & Izawa, 2017; Rose & Colombo, 2005). Dopamine enhances this process because it allows the rewarding properties of the behavior to be detected and thus causes the rewarded behavior to share its strong salience with the associated discriminative stimuli that initially had weaker salience (Berridge, 2007; Puig et al., 2014; Rumbaugh et al., 2007). However, the relevant connection between carrying a stone towards the tube and the reward seemed not prominent enough to elicit successful performance. The demonstration of the action sequence and the crucial release of a stone into the tube might have happened too fast for observational learning to occur (Swaney et al., 2001). It was likely the case in the Rim Demo where the stone was already placed at the tube, thus reducing visible manipulation time.

The incentive magnitude of the reward, a single Morio worm, might also have been too small to motivate the subjects to expend energy to obtain it (Collier, 2005; Crespi, 1942). In a study by Rose et al. (2009), common pigeons performed better in a simple discrimination task when a large reward was provided than with a smaller contingent reward. The effect was suggested to be caused by more substantial rewards creating larger prediction-errors and therefore leading to faster learning.

Setup

Another area of potential difficulties relates to the setup complexity of presenting the novel task. A common characteristic of the dual-cage paradigm is the presentation of the experimental equipment in both the observation and the demonstration chamber. This design might have directed subjects' attention towards the apparatus operated by a model and potentially decreased the enhancement effect of the apparatus in the observation chamber as well as acquisition of stone dropping. Alternatively, the similarities between the two apparatuses might have directed subjects' attention to their own apparatus. Potential underlying mechanisms could include stimulus enhancement and stimulus generalization between the features of both

sets of equipment (Zentall, 2012). Indeed, jackdaws seem to possess the capacity for the latter, as there was no difference in the successful performance between the observer and the demonstration chambers. Stimulus generalization can potentially also explain why the majority of successful performance occurred in the Full Demo, where both sets of equipment were identical. The additional elements used in other conditions, such as the tube cover or the glass bowl, might have produced differences in the perception of the setup (even though all equipment was always present in the dual-cage in all experimental conditions). Explicit or implicit similarity comparisons and structure mapping influence cognitive processes (Gentner, 2003; Rumbaugh et al., 2007). Similarities and differences between two stimuli, events, or situations are identified by determining the maximal alignment between their mental representations in the form of connected neural circuits. Therefore, comparisons between the equipment in the observation and the demonstration chamber in test conditions other than the Full Demo might have created different perceptions of the setup.

Individual

The cognitive demands of the platform-release task exposed individual variation in information processing among jackdaws, with Apache potentially representing an outlier from the species' mean. Rather than being a universal species-specific capacity, accumulating evidence suggests a systematic individual variation in observational learning skills within various species (Mesoudi et al., 2016; for a review, see Thornton & Lukas, 2012). When presented with novel tasks, subjects with relatively higher capacity for cue utilization should perform better than subjects with lower capacity (for a review, see Brouwers et al., 2016). Likewise, temperament traits, such as individual variation in exploratory behavior, were linked empirically to fitness (Réale et al., 2007).

When faced with a novel foraging task, individuals can either explore and potentially obtain valuable information or exploit their existing behavioral repertoire and potentially obtain resources (the 'exploration-exploitation trade-off'; Reader, 2015; for a review, see Mehlhorn et al., 2015). Additionally, successful exploration may add a new, profitable act to the behavioral repertoire. In contrast, failed exploration, such as placing stones on the box or inside the slot of the apparatus, can indicate no profitability of a new act (Reader, 2015). The side-switch procedure used in this study, including a freely available reward, could have potentially served as a low effort opportunity for exploitation.

In terms of motivation, the fact that subjects were offered a reward during the side-switch procedure might have decreased their general activity and learning. Additionally, it could have prompted a strategy of waiting until being provided access to a reward. This behavior would always lead to receiving a reward and through cumulative positive transfer across test sessions it potentially could have become the correct response for the subjects. Indeed, scrounging (joining the discoveries of others) was suggested to provide less variable feeding rates than producing (locating resources by individual search; Caraco & Giraldeau, 1991; Lendvai et al., 2004) and therefore might have been preferred by subjects in this study. Similarly, common pigeons (*Columba livia*) that scrounged on food rewards produced by demonstrators did not learn novel foraging techniques (Giraldeau & Lefebvre, 1987; Giraldeau & Templeton, 1991). Accumulated exposure to the setup might also have negatively influenced the motivation to participate in testing by gradually decreasing subjects' activity. However, this explanation is unlikely as there were no differences between the first and last round of testing in the time subjects spent manipulating stones.

Future Directions

Task

Modifications of the presented methodology could focus on improving the salience of informational cues while controlling the complexity of the task. The discrimination learning literature argues that stimulus dimensions might differentially attract subjects' attention (Mackintosh, 1975; Rumbaugh et al., 2007). Indeed, the relatively large tube cover used in the Stone Demo might have attracted more attention than the stones and therefore could be reduced in size. In contrast, highly noticeable properties of stimuli, such as

bright colors, seem to support faster concept learning than do less noticeable properties. It remains to be investigated whether brightly colored stones and/or the edge of the tube would facilitate learning to solve the platform-release task. A modified version of the apparatus could prevent the stone from being released together with the reward to avoid distracting subjects' attention by a rolling stone. Further studies could also investigate the effect of reinforced observation in which the subject receives a model-contingent reward during the demonstration, i.e., the reward is released simultaneously from both apparatuses (Del Russo, 1971). Additionally, exchanging the transparent box of the apparatus for an opaque one might eliminate the distraction of a visible reward.

Setup

Regarding test protocol adjustments, the side-switch procedure could be removed because jackdaws seem to be able to generalize between equipment placed in two separate chambers. More importantly, it would also eliminate the potential reinforcement effect of a freely available reward. The brain prioritizes specific classes of stimuli based on their significance for adaptation in a specific ecological niche (Rumbaugh & Washburn, 2003). The limited successful performance observed in this study might suggest that the novel foraging task was not relevant to the subjects. Additionally, outcomes are coded in relation to their resource value and the potential to obtain these outcomes in the future (Rumbaugh et al., 2007). Although the platform-release apparatus was baited with a high-preference reward, subjects were tested only once per day to control for potential confounding factors. Conducting more daily tests per subject could potentially increase the perceived relevance of the novel task and lead to acquisition of the stone-dropping behavior.

Individual

Regarding individual characteristics influencing the performance, future studies could explore the effect of age. Delays in avian brain maturation were suggested to promote behavioral flexibility (Charvet & Striedter, 2011). Therefore, testing adult jackdaws would benefit the assessment of whether the capacity to discriminate informational cues in novel tasks increases or decreases with age. The influence of individual characteristics of the models (such as sex, age, familiarity; for a review, see Rendell et al., 2011) could also be investigated, provided a larger sample size was available.

Concluding Summary

This study indicates that jackdaws can learn from conspecifics some aspects of how to use objects in a novel problem-solving task, although successful completion of the task was limited to only a few instances. Stimulus and/or local enhancement was most likely the learning mechanism underlying the successful performance, although emulative learning could also be involved. The results further suggest that jackdaws might be more focused on the location of a food reward than the specific behavior of a foraging conspecific. Task complexity and informational cues are crucial to consider when designing experimental protocols in animal cognition research.

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Conceptualization: AMPvB (study idea formulation, study design), BM (Ghost Demo design); Implementation: AMPvB (provision of study materials and animals), BM (setup construction, data collection), XS (setup construction, data collection), AB (Ghost Demo data collection); Statistical analysis: BM, MOH; Manuscript preparation: BM, AMPvB, IGF, AMIA, MOH.

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Appendix

The following video links provide examples of some of the stone-dropping behaviors performed by the successful subjects.

Video 1. First time solving: Apache, Round 1, Full Demo, Test Session 4. In this video, Apache collects a stone from the side of the dual-cage (placed there earlier during her stone manipulation), carries it towards the apparatus, steps on the rim of the tube, places the stone inside the tube, drops the stone, and collects the released reward.

Video 2. First time solving: Sioux, Round 1, Stone Demo, Test Session 9. In this video, Sioux collects a stone, brings it towards the apparatus, jumps on the rim of the tube, moves the stone towards the feet, drops the stone inside the tube, and collects the released reward.

Video 3. Second time solving: Sioux, Round 3, Full Demo, Test Session 21. In this video, Sioux collects a stone, steps on the rim of the tube, places the stone under her feet, manipulates the stone, and pecks at the rim of the tube. Subsequently, she drops the stone inside the tube while bending to peck at the box of the apparatus and collects the released reward.

Video 4. Accidental solving: Sioux, Round 3, Full Demo, Test Session 24. In this video, Sioux collects a stone, steps on the rim of the tube, places the stone in her foot, moves the foot outside of the tube, manipulates and drops the stone on the floor of the dual-cage. Subsequently, she collects the stone again, steps on the rim of the tube, places the stone under her feet, pecks at the stone, and drops it inside the tube when flying away.