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Western scrub-jays do not appear to attend to functionality in Aesop's Fable experiments

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ABSTRACT

Western scrub-jays are known for their highly discriminatory and flexible behaviors in a caching (food storing) context. However, it is unknown whether their cognitive abilities are restricted to a caching context. To explore this question, we tested scrub-jays in a non-caching context using the Aesop's Fable paradigm, where a partially filled tube of water contains a floating food reward and objects must be inserted to displace the water and bring the food within reach. We found that scrub-jays did not attend to the functional properties of objects or tubes, and were not motivated to participate in these experiments, suggesting that either this paradigm was ecologically irrelevant or perhaps their flexibility is restricted to a caching context.

INTRODUCTION

Western scrub-jays (*Aphelocoma californica*; hereafter referred to as scrub-jays) are known for their highly discriminatory and flexible behaviors in a caching (food storing) context. For example, scrub-jays prefer to recover perishable food items sooner than non-perishable items (Clayton et al. 2001), they plan what they want for breakfast the next morning (Raby et al. 2007), and jays with prior experience stealing other's caches use cache protection strategies (Dally et al. 2006, see review in Grodzinski & Clayton 2010). However, it is unknown whether such abilities are restricted to a caching context - the context in which these abilities evolved (Grodzinski & Clayton 2010). To begin to answer this question, we tested scrub-jays in a non-caching context using the Aesop's Fable paradigm. In this paradigm, clear tubes that are partially filled with water contain a floating food reward that can only be reached by inserting objects into the tube to raise the water. In all other corvid species tested (the family including jays, magpies, and crows), some to all individuals tested using the Aesop's Fable paradigm were successful: they were sensitive to the functional properties of objects and tubes, preferring the more functional option to gain a food reward (3-4 out of 4 rooks [*Corvus frugilegus*] solved 3 experiments: Bird & Emery 2009a; 0-2 out of 5 Eurasian jays [*Garrulus glandarius*] solved 7 experiments: Cheke et al. 2011; New Caledonian crows [*Corvus moneduloides*]: 1 out of 4 crows succeeded at water vs. sand and 4 out of 4 crows succeeded on the rest of the experiments according to group averages in 5 experiments in Taylor et al. 2011, 0-6 out of 6 crows were successful in 6 experiments in Jelbert et al. 2015, 0-6 out of 6 crows were successful in 7 experiments in Logan et al. 2014). The only non-corvid bird tested so far, the great-tailed grackle (*Quiscalus mexicanus*), was also successful (0-6 out of 6 grackles in 3 experiments) and two individuals changed their preferences when circumstances changed, indicating behavioral flexibility (Logan 2015a). Of these species, the Eurasian jay is the only other caching specialist and it exhibited flexibility outside of a caching context (Brodin & Lundborg 2003, Pravosudov & de Kort 2006). This leaves an open question of whether scrub-jays can apply their flexibility outside of a caching context.

We gave scrub-jays five Aesop's Fable experiments that have been conducted on other bird species to make their performance comparable. In Experiment 1 (Water vs. Sand), one tube was partially filled with water and the other with sand; stones were available to solve the task by dropping them into the water tube (Bird & Emery 2009, Taylor et al. 2011, Jelbert et al. 2014, Logan et al. 2014). Experiment 2 (Heavy vs. Light) consisted of one water tube with more functional heavy objects and less functional light objects, while Experiment 3 (Heavy vs. Light Magic) was the same except the heavy objects became non-functional because they stuck to a magnet while the light objects became the functional option because they fell past the magnet (Logan 2015a). Behavioral flexibility, the ability to change preferences when the task changes, would be demonstrated if individuals that preferred heavy objects or had no object preference in

Experiment 2 changed their preference to either no preference or to preferring light objects in Experiment 3. Experiment 4 (Colored U-tube) consisted of two differently colored apparatuses, each with a small tube containing food, but too small to insert stones, and a large tube that could accommodate stones (Logan et al. 2014). One apparatus had a connector tube under the lid, therefore to succeed the bird must associate color with function to complete the task. This experiment was modified from its previous version (in Logan et al. 2014) by making each apparatus more visually distinct through expanding the color cues and shapes to include the whole apparatus and both tubes; this should facilitate the perception that both tubes belonged to one apparatus rather than being separate. Additionally, the water in the large tubes was tinted with food coloring such that when stones were dropped into the connected apparatus, water in the connected small tube would change color, therefore allowing the hidden mechanism (the connector tube) to be inferred (using the concept of water flow). Experiment 5 (Uncovered U-tube) was the same as Experiment 4 except all color cues were removed and the connector tube exposed so the bird could see how the apparatus worked (Logan et al. 2014).

If scrub-jays attend to the functional properties of objects and tubes and flexibly change their preferences when the task changes, as has been found in non-caching specialists and in one caching specialist bird, this would indicate that their highly discriminatory and flexible behavior generalizes to conditions outside of the context in which their cognitive abilities evolved.

METHODS

Animal Ethics

This research was carried out in accordance with the University of California, Los Angeles' (UCLA) Institutional Animal Care and Use Committee (protocol # 1995-026-63).

Subjects

Three wild adult male Western scrub-jays (*Aphelocoma californica*) were caught using Potter traps baited with peanuts in southern California (July-August 2013), and one female nestling (BB) was taken from the nest in the summer of 2012 and hand-raised (all captures were authorized under appropriate federal and state collecting permits). Birds were sexed genetically, and the validity of this measure was confirmed via inspection of gonads in another study (see Griffiths et al. 1998, Rensel et al. 2015). For these experiments, jays were housed singly, in visual but not auditory isolation of other birds, in aviaries measuring 5.3x1.2x1.9m. Jays had *ad libitum* access to water and access to food (Roudybush Daily Maintenance Diet, fruit, mealworms, and peanuts) for a minimum of 20 hours everyday, which was removed before and during testing when testing occurred. Birds were tested in two batches: BB and GG were tested from August 2014 to January 2015, and PA and H from June to November 2015.

Experimental Set Up

For each experiment, testing apparatuses were placed on a paper-covered table (0.3x1.1x0.6m) inside the aviary with perches placed above the table to allow easier access to the apparatuses. Testing lasted up to five hours per day between 0700 and 1600. If testing occurred in the morning, food was removed from the aviaries the night before (between 1800 and dusk). For afternoon test sessions, food was removed at 0700. Testing sessions lasted up to approximately 20 minutes. If a bird did not interact with the task after 4 minutes, the apparatus was removed from the testing aviary for at least 10 minutes before resuming the session. Water tubes were baited with peanut pieces attached to cork using a tie wrap to allow the food to float.

Experiments 1-5 consisted of 20 trials per bird. All experiments were recorded with a Sony Handycam HD camera on a tripod.

Color Learning for Side Bias Prevention

To prevent side bias during the water tube experiments involving two tubes, jays were required to learn to associate food with color, forcing them to attend to color rather than location (see Logan et al. 2014). A gold tube always contained food (small peanut fragments), while a silver tube never did. One gold and one silver tube were placed on the table, one on the left and one on the right (left side first, pseudorandomized for side) with the open ends of the tubes facing the side walls such that birds could not see which tube contained the food. Birds were habituated to the task using a blue tube (all tubes measured 50x50x67mm, outer diameter=26mm, inner diameter=19mm) until they learned to search for food even if it was not visible. After habituation, the color learning test began and jays got one choice per trial, marked as the first tube they look into, and proficiency was reached when an individual chose the gold tube at least 17 out of the most recent 20 trials (having achieved at least 8 out of 10 on each set of 10 contributing to the passing score). Pseudorandomization consisted of alternating sides for the first two trials and then allowing each tube to remain on the same side for a maximum of two consecutive trials. Between 20 and 80 trials were required for three birds to reach proficiency (Table 1), similar to grackles (Logan 2015a), Darwin's finches (Tebbich et al. 2010), and pigeons (Lissek et al. 2002), and faster than pinyon jays, Clark's nutcrackers, and previously tested Western scrub-jays (Bond et al. 2007). GG did not complete this training due to his lack of motivation. During two-tube water tube experiments (Experiments 1, 4, and 5), a side bias was considered to have developed if a bird approached the same side three or more times. At this point, the experiment was suspended and the subject was given the color learning test. If they chose gold at least 8 out of 10 trials, the experiment resumed. However, if they no longer had a color preference, they were tested until they chose gold at least 17 out of the most recent 20 trials (per the criteria above), and then the experiment resumed.

Stone Dropping Training

Birds were trained to lift stones off of the testing table, carry them to the perch, and drop them down the tube of an apparatus with a collapsible platform. The apparatus was a clear cast acrylic box (185x110x85mm) with a 90 mm tube (outer diameter: 51mm, inner diameter: 43mm) on top of the box and a platform inside that was held up by a magnet (Figure 1A; as in Bird & Emery 2009). Magnetic contact was broken upon impact from the stone dropped into the tube, allowing the platform to fall down and release food onto the table. Birds were first encouraged to accidentally push the stone into the tube by placing a small piece of peanut under the stone balanced on the edge of the rim, then they progressed to picking up and dropping the stone into the tube from anywhere on the table. Birds accessed the top of the tube by standing on a perch placed near the top of the tube rather than by standing on the ground because they were more willing to participate in this context. Proficient stone drops were defined as those in which the bird picked up the stone from the table and directly dropped it into the tube. Once proficiency was reached, 30 more trials were conducted to ensure their expertise on the task. BB and GG required 72 and 255 trials to pass this training, respectively, while PA and H never passed (we stopped their training at 536 and 507 trials, respectively; Table 1).

Multi-stone Dropping Training

After reaching proficiency on stone dropping training, birds received multi-stone dropping training to learn that solving a task might require dropping more than one object into the tube. The multi-stone apparatus was similar to the stone dropping training apparatus, but had a larger box (box: 200x180x150mm; tube: 95mm tall, 50mm outer diameter, 44mm inner diameter; Figure 1B; design in Logan et al. 2014) and the platform was balanced on a circular rod rather than being held up by a magnet. Counterweights placed at the rear of the platform ensured that 2-4 stones needed to drop down the tube, which then slid down a ramp to land on the front of the platform, before the platform would fall open, thus releasing the food. Individuals passed this training once they successfully solved 10 consecutive trials. BB and GG were immediately proficient, thus they completed all 10 trials proficiently.

Reachable Distance

The height at which a bird could reach the food in the tube was determined in advance to establish how high to set the water level in the experiments. This was necessary so that the food would be out of reach and require the desired number of objects to bring it within reach. The reachable distance was the distance from the bottom of the tube to the top of the food, which sat on top of a plastic sandwich bag stuffed with cotton in a standard tube used in the water experiments (a clear cast acrylic tube measuring 170mm tall, 50mm outer diameter, 43mm inner diameter and attached using super glue to a clear cast acrylic base measuring 300x300x3mm). Birds were allowed to access the food, initially well within reach, and then the distance was decreased until it was out of reach.

Experiment 1: Water vs. Sand

This experiment consisted of two standard tubes: one partially filled with sand and the other with water to the same height in each tube, to determine whether birds preferred to drop stones into the functional water tube rather than the non-functional sand tube (Figure 2; similar to Logan et al. 2014). First, birds were given a 10-trial training period in which any initial tube preferences were discouraged by heavily baiting the non-preferred tube. Tubes contained water and sand (and were pseudorandomized for side), but no floating food and the tops were taped over with bait (peanuts) placed on top and at the base of each tube. The tube the bird ate from first was recorded to determine whether a preference emerged. After these training trials, the experiment began and the sand and water tubes continued to be pseudorandomized for side. Four stones (weighing 14-21g and displacing 6-8mm water) were located between the two apparatuses: two on the base of one apparatus and two on the other.

Experiment 2: Heavy vs. Light

One standard water tube was given with 4 heavy (a steel rod encased in fimo clay, each weighing 10g and displacing 2-3mm of water) and 4 light (black plastic tube partially filled with fimo clay, each weighing 2g and displacing 1-1.5mm water) objects (Figure 3A; see Logan 2015a). Heavy objects displaced more water than light objects and therefore were more functional, however light objects were also functional if enough were inserted. First, birds were given a 3-trial training period in which any initial object preferences were discouraged0 by heavily baiting the non-preferred object. A heavy and a light object were placed next to each other on the table and bait was placed underneath and on top of both objects. The object the bird ate from first was recorded to determine whether a preference emerged, and the trial ended when the bird had interacted with both objects. After these trials, the experiment began and pairs of heavy and light objects were pseudorandomized for location.

Experiment 3: Heavy vs. Light Magic

This experiment was the same as Experiment 2, except here the heavy objects became non-functional to determine whether birds could change their preference from the previous experiment. A magnet was attached to the inside of the tube above the water level so that the heavy (metal) objects became non-functional (they stuck to the magnet if inserted into the tube), thus making the light (non-metal) objects the only functional option because they could fall past the magnet and into the water (Figure 3B). Three heavy and 3 light objects were placed in pseudorandomized pairs at the base of the tube because 4 heavy objects would not fit on the magnet.

Experiment 4: Colored U-tube

This experiment consisted of two apparatuses made of clear cast acrylic, each containing a standard tube and a small-diameter tube (small tube outer diameter=25.4mm, inner diameter=19mm) 25mm apart, with 160mm of tube above and 90mm below a clear cast acrylic lid (300x400x3mm) on a wooden box (Figure 4A). The small tubes contained out of reach floating peanuts (the reachable distance for each bird was obtained for the small tube prior to beginning the experiment), but were too small for stone insertion. On one apparatus, a tube under the lid connected the two water tubes such that inserting the stone into the standard tube resulted in the food rising in the small tube. The connected apparatus was indicated by a particular color (counterbalanced across birds) and was pseudorandomized for side. The apparatuses were the same as in Logan et al. (2014) with modifications to make the two tubes on each apparatus appear as part of the same apparatus and to distinguish the two apparatuses from each other. Instead of both apparatuses having a white paper background with differently colored shapes at the base of the standard tube as in a previous study (Logan et al. 2014), here each apparatus had a distinct background color (blue or brown). On top of these backgrounds, each apparatus had a different color and shape (pink triangle or yellow square) that extended around the base of the two tubes to further unify the tubes of each apparatus by making them appear more as a single unit, instead of only extending around the base of the standard tube. One white strip of electrical tape was placed on each apparatus to indicate that these are the same apparatuses in the next experiment. Any initial apparatus preferences were discouraged by heavily baiting the non-preferred object over the course of 10 trials as in Experiment 1. During the experiment, 20-30 drops of red (for pink) or yellow food coloring (the same as the colored paper on the connected tube) were placed into each wide tube such that when a stone was dropped into the connected apparatus, the flow of tint from the standard to the small tube would visibly indicate water flow. Four stones were placed between the apparatuses as in Experiment 1.

Experiment 5: Uncovered U-tube

This experiment was the same as Experiment 4 except all paper and color cues were removed and the boxes around the bases were removed on both apparatuses, thus exposing the connector tube under the lid of the connected apparatus (Figure 4B). Food coloring (the same color as that used for the connected color in Experiment 4) was used in the same way as before to show the water flow through the connector tube.

Statistical Analyses

Binomial tests were carried out in R v3.2.1 (R Core Team 2015), and, when there were multiple p-values per experiment, they were corrected using the Bonferroni-Holm method.

RESULTS

All choices per trial per bird are shown in Figure S1 (Supplemental Material) and a video showing the experiments is available online at: https://youtu.be/RCNENBwsbA8.

Experiment 1: Water vs. Sand

GG had no preference for which tube to drop the stones into (Table 1). BB did not complete this experiment: her motivation to participate declined because she received few food rewards (she primarily chose the sand tube). To prevent her from giving up on dropping objects down tubes entirely, she was given alternating sessions with a water tube and the multiple stone dropping apparatus and stones for four days until she regained motivation and began to participate again.

Experiment 2: Heavy vs. Light

BB and GG consistently successfully obtained the food using both heavy and light objects without a preference for the more functional heavy objects (Table 1).

Experiment 3: Heavy vs. Light Magic

BB had no preference for heavy or light objects, though it appeared that she was developing a preference for light objects near the end of her experiment so it is possible that the preference would have been significant given more trials (Table 1). GG stopped participating in experiments at this time at first because he was afraid of the magnet, but even after a successful magnet habituation period, his motivation for participating in tests did not recover.

Experiment 4: Colored U-tube

BB had no preference for dropping stones into the standard tube on the brown apparatus, which indicated the connected apparatus (Table 1).

Experiment 5: Uncovered U-tube

BB had no preference for dropping stones into the connected apparatus (Table 1).

DISCUSSION

Two scrub-jays successfully obtained the food in the Heavy vs. Light experiment because both objects were functional, however no scrub-jays attended to the functional differences between objects or tubes or changed their preference when the task changed. In every other species tested so far, including a caching specialist (Eurasian jay), at least some individuals attended to the functional differences between objects and/or tubes, thus making the scrub-jays the first species tested to lack such attention to function (Bird & Emery 2009a, Cheke et al. 2011, Taylor et al. 2011, Jelbert et al. 2014, Logan et al. 2014). While it appeared that BB was learning to prefer light objects in Heavy vs. Light Magic, she did not learn to significantly prefer this object type within the 20 trials that are standard for these experiments. In contrast, within 20 trials, 4 out of 6 great-tailed grackles preferred to drop heavy objects in Heavy vs. Light and two grackles changed their preference in Heavy vs. Light Magic (Logan 2015a). The color and water flow modifications to the Colored U-tube and Uncovered U-tube experiments did not appear to facilitate learning to prefer the connected apparatus.

The two scrub-jays that became proficient at stone dropping required a similar amount of training as required by grackles (6 grackles learned in 135-362 trials and 2 grackles never learned; Logan 2015a) and New Caledonian crows (12 crows learned in 1-116 trials and others never became proficient, unpublished data from Jelbert et al. 2014 and Logan et al. 2014). Using the same platform apparatus, Eurasian jays and rooks needed much less training to learn the task (4 Eurasian jays learned in 11-33 trials and 1 never became proficient, Cheke et al. 2011; whereas all 4 rooks learned in 5 trials, Bird & Emery 2009b). Two out of four scrub-jays never became proficient at stone dropping, and thus did not participate in stone dropping experiments, and both jays that participated in experiments did not participate in every experiment. It appeared that their lack of motivation for participating in these kinds of tasks slowed their learning and could have caused them to give up; alternatively they could have lacked motivation due to cognitive limitations preventing them from solving the tasks. The exception was BB who showed more motivation than the others and participated in more experiments, perhaps due to her being the only hand raised jay in this group – a developmental experience that has been shown to improve cognitive performance in other species (see Thornton & Lukas 2012).

The scrub-jays' lack of motivation combined with their lack of a preference for the functional options suggests that either the Aesop's Fable paradigm is too ecologically irrelevant for this species or that their highly discriminatory and flexible behaviors do not transfer to a non-caching context. Future studies using different non-caching paradigms are needed to determine which conclusion is correct.

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COMPETING INTERESTS

The authors declare that there are no competing interests.

DATA DEPOSITION

Data are available at the KNB Data Repository:
https://knb.ecoinformatics.org/#view/corina_logan.20.3 (Logan 2015b).

SUPPLEMENTAL INFORMATION

All choices per trial per bird are shown in Figure S1 (Supplemental Material) and a video showing the experiments is available online at: https://youtu.be/RCNENBwsbA8.

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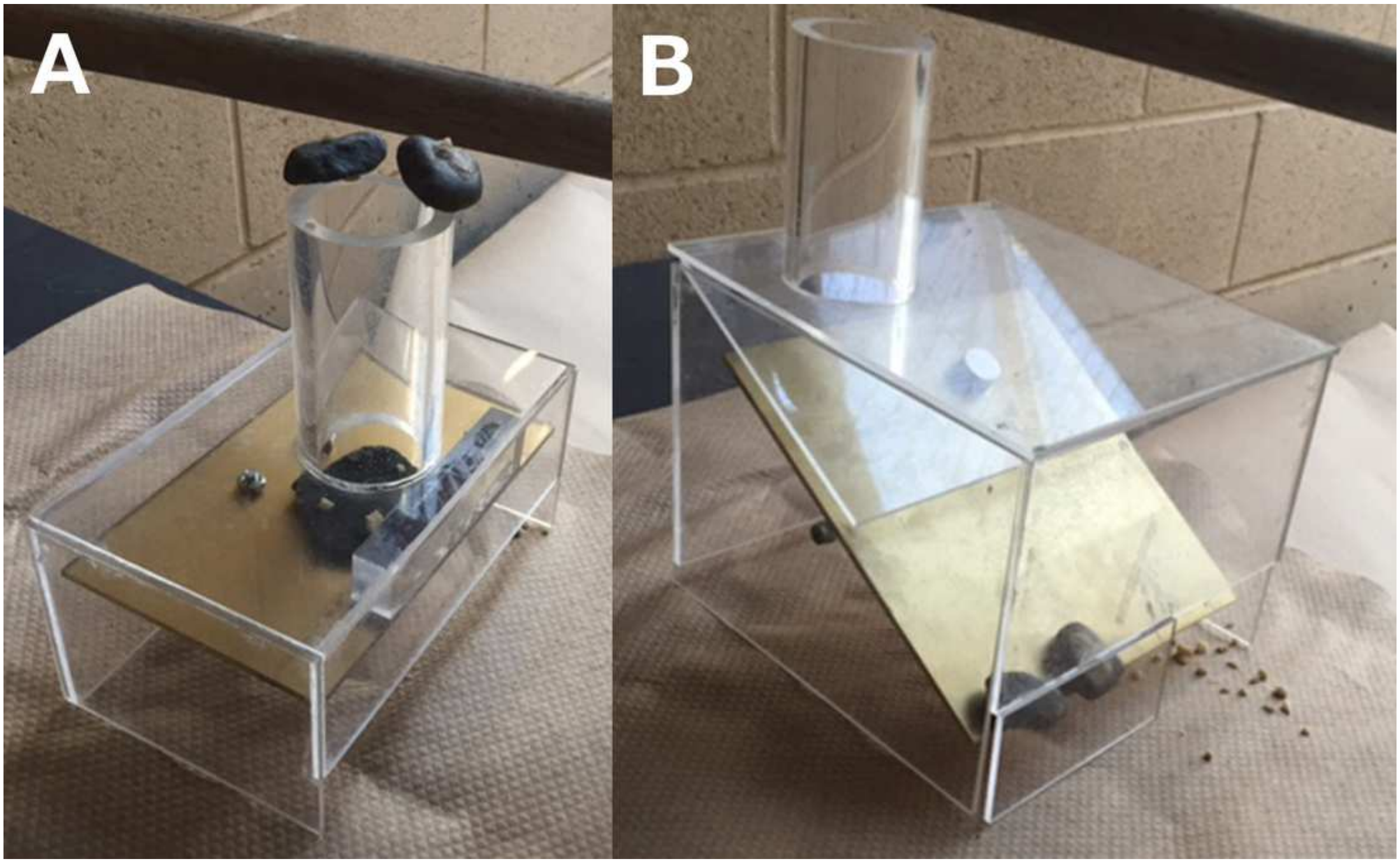
1

Single stone dropping apparatus (A) and multi-stone dropping apparatus (B)

Photo credit: Brigit Harvey.



2

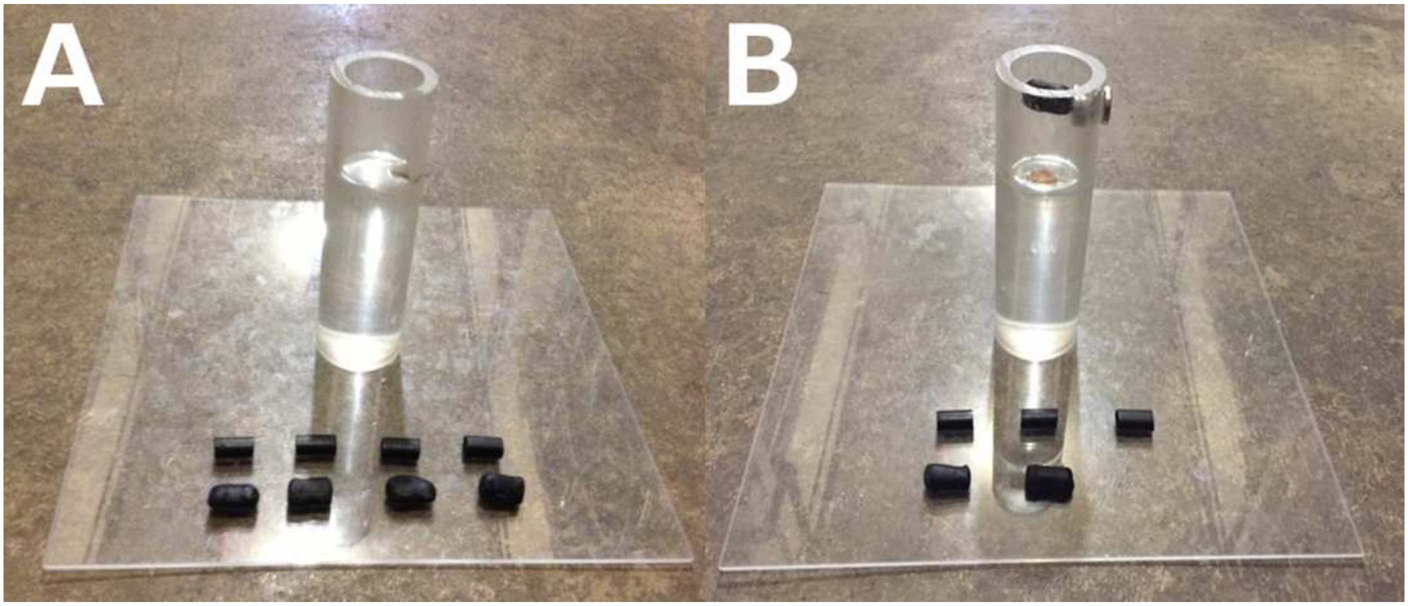
Water vs. sand experimental set up.

Photo credit: Brigit Harvey.

3

Heavy vs. light (A) and heavy vs. light magic (B) experimental set up. Notice the heavy object stuck to the magnet in B.

Photo credit: Brigit Harvey.



4

Colored u-tube (A) and uncovered u-tube (B) experimental set up. The connector tube is visible on the apparatus on the right in B.

Photo credit: Brigit Harvey.

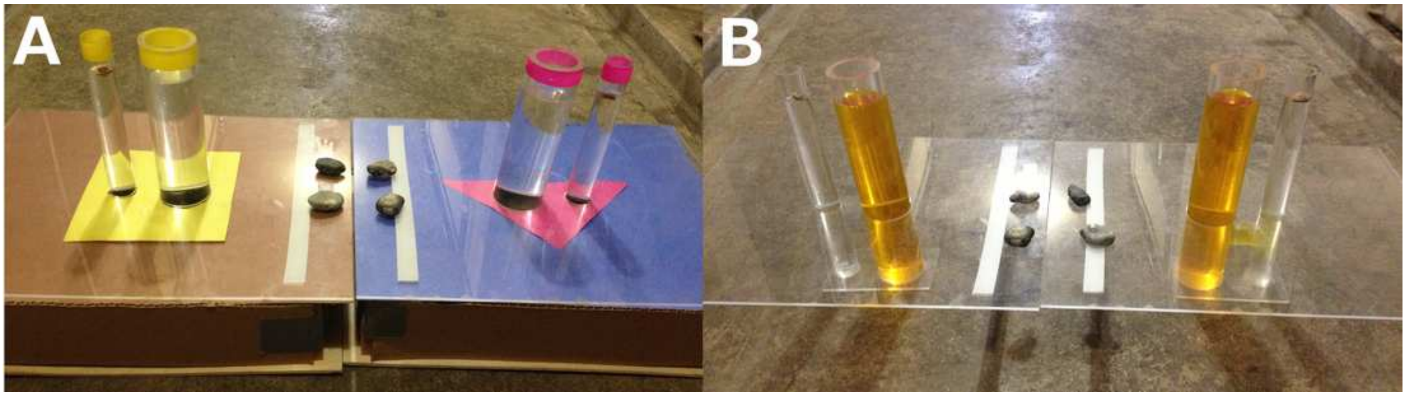


Table 1(on next page)

Summary of results

The number of trials required to learn to associate food with the gold tube (color learning; min. 17 out of 20 trials correct) and to become proficient at dropping stones down the platform apparatus (stone drop training; number of non-proficient stone falls plus 30 proficient stone drops); p-values from binomial tests for experiments 1-5 (the Bonferroni-Holm correction was applied to Experiment 2). X=bird did not complete this experiment, -=bird did not participate in this experiment.

Table 1. Summary of results: The number of trials required to learn to associate food with the gold tube (color learning; min. 17 out of 20 trials correct) and to become proficient at dropping stones down the platform apparatus (stone drop training; number of non-proficient stone falls plus 30 proficient stone drops); p-values from binomial tests for experiments 1-5 (the Bonferroni-Holm correction was applied to Experiment 2). X=bird did not complete this experiment, -=bird did not participate in this experiment.

Bird ID	Sex	Color learning	Stone drop training	Exp 1: Sand vs Water	Exp 2: Heavy vs light	Exp 3: Heavy vs light magic	Exp 4: Colored u-tube	Exp 5: Uncovered u-tube
BB	F	80	76	X	0.46	0.06	0.33	0.17
GG	M	X (28)	255	0.40	0.46	-	-	-
H	M	20	X (507)	-	-	-	-	-
PA	M	50	X (536)	-	-	-	-	-