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Adaptation of the Aesop's Fable paradigm for use with raccoons (*Procyon lotor*): considerations for future application in non-avian and non-primate species

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Abstract To gain a better understanding of the evolution of animal cognition, it is necessary to test and compare the cognitive abilities of a broad array of taxa. Meaningful interspecies comparisons are best achieved by employing universal paradigms that standardize testing among species. Many cognitive paradigms, however, have been tested in only a few taxa, mostly birds and primates. One such example, known as the Aesop's Fable paradigm, is designed to assess causal understanding in animals using water displacement. To evaluate the universal effectiveness of the Aesop's Fable paradigm, we applied this paradigm to a previously untested taxon, the raccoon (*Procyon lotor*). We first trained captive raccoons to drop stones into a tube of water to retrieve a floating food reward. Next, we presented successful raccoons with objects that differed in the amount of water they displaced to determine whether raccoons could select the most functional option. Raccoons performed differently than corvids and human children did in previous studies of Aesop's Fable, and we found raccoons to be innovative in many aspects of this task. We suggest that raccoon performance in this paradigm reflected differences in tangential

factors, such as behavior, morphology, and testing procedures, rather than cognitive deficiencies. We also present insight into previously undocumented challenges that should better inform future Aesop's Fable studies incorporating more diverse taxa.

Keywords Causal understanding · Tool use · Choice task · Innovation · Problem solving · Carnivora

Introduction

To understand how and why cognition has evolved across the animal kingdom, it is essential to assess cognitive abilities systematically across a wide range of taxa. Achieving this goal, however, is one of the more challenging obstacles in the field of comparative cognition (Shettleworth 2010). Variation in phylogeny, ecology, species-specific traits (e.g., behavior, morphology), and logistical considerations (e.g., sample size, testing environment) makes meaningful standardized testing difficult (Auersperg et al. 2012; Thornton and Lukas 2012). The development of universal paradigms, or standardized tests that can be successfully applied to a wide range of species, is a promising method to facilitate interspecies comparisons. Indeed, universal paradigms, such as the string-pulling task (see Jacobs and Osvath 2015 for review) and standardized apparatuses, such as single-solution puzzle boxes (Benson-Amram et al. 2016), have been successfully administered to many taxa in the investigation of cognitive evolution. Yet the effectiveness of most universal paradigms has not been fully evaluated. The Aesop's Fable paradigm, proposed to investigate the cognitive ability of causal understanding, is one such example.

Coined "Aesop's Fable" after Aesop's classic tale of The Crow and the Pitcher, this paradigm presents a subject with

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a clear cylinder that is partially filled with water. Floating on top of the water, inside the cylinder, is a desirable yet out-of-reach food reward. To bring the reward within reach, the subject must make selections between options that differ in functionality, such as objects that will either sink or float. If the subject chooses the more functional option (i.e., the option that is most effective at raising the water level) significantly more often than the less functional options, these choices could demonstrate that the subject has causal understanding of the physical properties of each option (Jelbert et al. 2015). Although general performance on the tasks presented in Aesop's Fable varies, corvids have demonstrated the ability to correctly discriminate in choice tasks at the same level as children ages five to seven (Cheke et al. 2012; Jelbert et al. 2015).

The Aesop's Fable paradigm has been proposed as a universal assessment of causal understanding across species because it is no more ecologically relevant for one species than another (e.g., Jelbert et al. 2014; Logan et al. 2014). This paradigm, however, has only been tested in birds and human children (Logan 2016; Miller et al. 2016). Use of similar, established paradigms designed to assess causal understanding, such as the trap-tube task (Visalberghi and Limongelli 1994) and the floating peanut task (Mendes et al. 2007), have also been largely constrained to birds and primates. The limited use of such established paradigms leaves two primary gaps in our knowledge as researchers of animal cognition: not only are we unaware of causal understanding in a broad array of species, but we also do not know if these paradigms are appropriate for use outside of birds and primates. To help address these gaps in knowledge, we applied the Aesop's Fable paradigm to a previously untested taxon, the raccoon (*Procyon lotor*).

Evidence from a small number of studies indicates that the general intelligence of raccoons surpasses domestic cats (*Felis catus*), but does not exceed rhesus macaques (*Macaca mulatta*) (e.g., Cole 1907; Davis 1907; but also Vonk and Leete 2017 for discussion) and that raccoons demonstrate innovative problem solving and behavioral flexibility (Daniels 2016). Furthermore, popular opinion based on anecdotal evidence also indicates that raccoons are a clever species capable of overcoming novel challenges (e.g., North 1966). Given the demonstrated capacity of raccoons for cognitive testing, and our basic understanding of their cognitive abilities, we predicted that:

1. Raccoons can learn to drop stones into a tube of water to retrieve a floating reward, and therefore the Aesop's Fable paradigm can be applied to carnivorans in addition to birds and primates.
2. When presented with choices that vary in functionality, raccoons will either select the correct choice at the start of trials, demonstrating that they have causal

understanding or will learn to choose the correct option over the course of several trials, indicating that this task requires trial-and-error learning.

Subjects and materials

Our study was conducted at the USDA National Wildlife Research Center (NWRC) in Fort Collins, CO under protocol QA-2490. The raccoons were also part of several other protocols at NWRC (QA-2111, QA-2290, QA-2440, and QA-2492). Half of the subjects ($N = 4$) were wild-caught adult raccoons brought into captivity for QA-2111 (see Johnson et al. 2016). The other half of the subjects ($N = 4$) were littermates born to a wild-caught mother (not tested) at the NWRC and were two years of age at the time of testing. Raccoons from both wild-caught and captive-born groups comprised an even sex ratio. The Aesop's Fable apparatus consisted of a 0.5-m vertical cylinder of clear polycarbonate attached to a 0.5 m × 0.14 m Arboron[®] platform base weighing 11.3 kg. An extended, circular rim measuring 0.19 m in diameter added to the top of the tube provided a ledge on which to balance stones. We used one marshmallow cut into smaller pieces as our floating reward and filled the tube with 500 mL of water (± 100 mL depending on the predetermined arm length of the individual being tested).

Procedure

Due to time limitations imposed by other protocols, we employed a similar, but not identical, procedure used in previous Aesop's Fable studies. In Phase I, each raccoon ($N = 8$) participated in three conditions: initial, learning, and final trials. All trials lasted a minimum of 20 min, and the number of trials per condition was dependent on the performance of the subject. During initial trials, we presented each subject with five stones on the platform of the apparatus to determine if raccoons could solve the task without any training (three trials). If the raccoons failed to drop the stones into the tube during initial trials, they immediately progressed into learning trials for stone-dropping training. During learning trials, we stacked and balanced stones on the extended rim at the opening of the tube and placed small pieces of food on the stones and apparatus for several trials (mean trial number = 12.5, range = 10–18 trials). If raccoons interacted with the apparatus, the stones would fall in accidentally and raise the water level (see video Online Resource 1). Raccoons could then form an association between the stones falling into the apparatus and the reward moving within reach. After learning trials were complete, the raccoons entered final trials (mean trial number = 4.5, range = 4–8 trials) where they had to pick up stones from

the ground and drop them into the tube to retrieve the reward (see Fig. 1).

Raccoons that learned to drop stones into the Aesop's Fable apparatus advanced into Phase II, which was comprised of four additional tasks: size, substrate, and density choice tasks based on previous Aesop's Fable studies (e.g., Bird and Emery 2009; Jelbert et al. 2014), and a novel tool use task that we introduced to expand the current Aesop's Fable paradigm with dexterous, long-limbed species (see ESM Fig. 1). In the size task (six trials), we presented raccoons with a single apparatus and six stones: three large and three small. In the substrate task (12 trials), raccoons were presented with the same five stones used in Phase I and two apparatuses: one containing water and another containing corncob litter (see video Online Resource 2). In the density task (12 trials), we presented raccoons with a single apparatus and six small, numbered tennis balls. Three of the balls were heavy and would sink when placed in water, while the other three were light and would float (see video Online Resource 3). Lastly, in the tool use task (12 trials), we presented raccoons with a single apparatus and a small, steel cup with a handle that could be used to scoop out the marshmallow reward (see video Online Resource 4). To ensure standardization of procedures, tasks were deployed in the following chronological order: size, substrate, tool use, and density.

We investigated the processes by which subjects learned to drop stones in the apparatus during Phase I by modeling the effects of subject ID and trial number on (1) changes in work time and (2) changes in exploratory diversity (Benson-Amram and Holekamp 2012; Chow et al. 2016). We also modeled the effect of subject ID and trial number on the proportion of correct versus incorrect choices made across trials

in Phase II, which would indicate whether raccoons learned to select the more functional options with greater experience. To assess preference for the more functional options across tasks, we used exact binomial tests to determine if (1) the first choice made in each trial (i.e., the first stone/object dropped, or the first apparatus the subject dropped a stone into) was correct more often than would be expected by chance, and (2) the overall number of correct choices made in each trial differed from chance. A detailed description of our methods, criteria, and analyses can be found in ESM.

Results

All of the raccoons approached the apparatus in at least two trials, and seven of the eight raccoons interacted with the experimental materials (e.g., touched and sniffed the apparatus, handled the stones). None of the raccoons solved Aesop's Fable in the initial trials. During learning trials, four subjects retrieved the marshmallow reward when balanced stones resting on top of the apparatus accidentally fell into the tube. In final trials, only two males (captive-born littermates: Raccoon 29 and Raccoon 40) retrieved the reward by picking up and dropping stones in the apparatus. Another captive-born female (Raccoon 22) also began dropping stones into the apparatus; however, she never extended her arm far enough into the tube to retrieve the reward, despite the reward being well within reach. During final trials, Raccoon 22 innovated a unique solution by gripping the inner rim of the apparatus with her forepaws and, while rocking her body back and forth, overturned the entire apparatus and retrieved the reward (see video Online Resource 5).

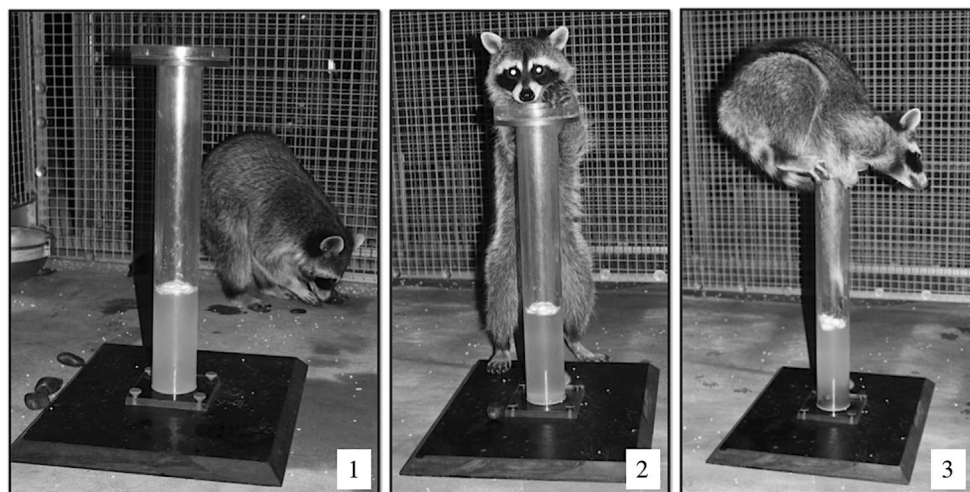


Fig. 1 Image of Raccoon 40 solving the Aesop's Fable task. (1) The raccoon collected stones, (2) placed them onto the rim and pushed them into the tube, and (3) reached into the tube with one arm and grabbed the marshmallow reward

Model selection was based on Akaike's information criterion corrected for small sample sizes. Our top model for changes in work time revealed that there was an interaction effect between subject ID and trial number (see ESM Table 1), and learning curves for each successful raccoon revealed different patterns. We found that work time decreased across trials for Raccoon 29, increased across trials for Raccoon 40, and remained consistent across trials for Raccoon 22 (see ESM Fig. 2). Likewise, our top exploratory diversity model (see ESM Table 1) indicated that the proportion of useful behaviors expressed improved across trials for Raccoons 29 and 40, whereas Raccoon 22 did not show improvement (see ESM Fig. 3).

Only Raccoons 29 and 40 progressed into Phase II based on their ability to drop stones into the apparatus to retrieve the reward. Our top models for each of the three choice tasks indicated that Raccoons 29 and 40 did not differ in performance, and their performance did not change as they gained experience with each of the choice tasks (see ESM Table 1). Exact binomial tests indicated there was no preference in the first choice made in each trial across tasks for either raccoon ($P \geq 0.07$ for all tasks). Overall, they did not show a preference for the large, more functional stones rather than the small, less functional stones in the size task (Raccoon 29: 46% correct drops, binomial test, $P = 0.71$; Raccoon 40: 52% correct drops, binomial test, $P = 0.50$; see ESM Fig. 4). In the substrate task, Raccoon 29 showed a preference for dropping stones into the water tube (77% correct drops, binomial test, $P < 0.0001$), but Raccoon 40 did not (50% correct drops, binomial test, $P = 0.56$; see ESM Fig. 5). However, when Trials 4 and 11 were removed from analysis (i.e., trials where Raccoon 40 stood on top of the corncob-filled tube and repeatedly dropped and removed the same stone multiple times), Raccoon 40 also showed a preference for the water-filled tube (75% correct drops, binomial test, $P = 0.01$). In the density task, the raccoons did not show a preference for the sinking balls over the floating balls (Raccoon 29: 44% correct drops, binomial test, $P = 0.86$; Raccoon 40: 50% correct of drops, binomial test, $P = 0.95$; see ESM Fig. 6). Unexpectedly, both raccoons increased the functionality of the floating balls by pushing down on them repeatedly in the tube, splashing small bits of marshmallow upward. In the tool use task, both raccoons failed to retrieve the reward using the cup in a continuous scooping motion. In one trial each, however, the raccoons captured marshmallow pieces by dropping the cup into the tube and quickly retrieving it before it sank (see video Online Resource 4).

Discussion

Our application of the Aesop's Fable paradigm not only in a new species, the raccoon, but in a new order, the

Carnivora, is an important first step in expanding the investigation of causal understanding. We found that raccoons did not spontaneously drop stones into a tube of water to retrieve a floating reward, however, Raccoons 29 and 40 learned to drop stones into the tube and Raccoon 22 innovated a different, novel solution. Although participation and learning by Raccoons 29 and 40 confirmed our first prediction that it is possible to engage raccoons in the Aesop's Fable paradigm, we successfully trained only two of eight subjects, which is less than that of other Aesop's Fable studies (e.g., 50% of subjects, Logan et al. 2016; ~80% of subjects, Cheke et al. 2011; Taylor et al. 2011). Despite seven of our eight subjects engaging with the task, our reduced training success could be explained by our inability to implement a distinct habituation period and/or additional training trials, as is common in the Aesop's Fable paradigm (Jelbert et al. 2015; Miller et al. 2016). It is possible that the interest and success of our top three participants are related to their captive-rearing background (see Thornton and Lukas 2012); however, we could not test for an effect of background statistically because of our low sample size.

Raccoon morphology allowed our subjects to pick up multiple objects at one time, which is similar to the abilities of primates but unlike the more limited abilities of birds to manipulate objects (Cheke et al. 2012). In the size and density tasks, it was common for raccoons to collect whichever stones and objects were closest as they approached the apparatus, place them on the rim, and move them around until one (or more) fell into the tube. As proposed by Cheke et al. (2012), the crowding of multiple stones and objects when falling into the tube could have negatively affected the ability of the raccoons to observe which were most effective and learn the differences in the functionality among all options. Raccoons did show a preference for the water tube during the substrate task, yet, unlike studies in birds and children (see Jelbert et al. 2015 for discussion), trial number did not seem to affect their choices. We therefore believe raccoons either learned the functionality of the water tube quickly because this task offered the most dichotomous choices, or that raccoons were biased toward the water tube because they had previous experience working with it. Similar biases have been proposed in the "object bias" hypothesis (Jelbert et al. 2015) and reported by Miller et al. (2016). In the tool use task, raccoons did not use the cup in a scooping motion to retrieve the reward. Although the proper scooping technique could have required extended time to develop, we do believe that raccoons would have been physically capable of completing this task based on the handling abilities we observed. Nevertheless, raccoons were able to retrieve the reward by quickly recovering the cup before it sank.

Future considerations

Although Aesop's Fable has a strong potential for inter-species comparisons (Jelbert et al. 2014; Logan et al. 2014), our experience using this paradigm revealed challenges when adapting it for a species that is morphologically and behaviorally different from those previously tested. For example, in following the traditional design of an Aesop's Fable apparatus, one important consideration was to accommodate the lengthy arms and small forepaws of raccoons by increasing the height of the tube. This height required vigorous involvement on the part of the subjects; raccoons either needed to stand tall on their toes or climb on top of the apparatus and then push their entire arm into the tube to reach the reward. Ultimately, the unwillingness of Raccoon 22 to fully extend her arm into the tube prevented her advancement to Phase II. The intentionally narrow diameter of the tube also made it difficult for raccoons to readily drop stones into the tube, and instead they had to align the stones appropriately for insertion, which could explain the abnormal learning curve of Raccoon 40 (see ESM for a brief discussion). To improve the traditional design for species with long forelimbs, we recommend the development of new apparatuses that incorporate water displacement, rather than a column of water.

The exploratory, tactile nature of raccoons may have confounded their performance in the Aesop's Fable paradigm. For example, during Phase II the behavior of Raccoons 29 and 40 did not seem to be goal-oriented, in the sense described in many other Aesop's Fable studies (e.g., Bird and Emery 2009). That is, they did not drop the exact number of stones necessary to retrieve the reward and continued dropping stones and exploring experimental materials after the reward had been retrieved. We recorded many instances where the raccoons washed the stones/objects in their water dish, buried the stones/objects in their litter box, carried the stones/objects into their den box, and seemingly played with the stones/objects for long periods of time. These observations are reminiscent of the Brelands' well-known attempt to train a raccoon to drop coins into a piggy bank (Breland and Breland 1961). The authors attributed the unsuccessful performance of their subject to "instinctual drift," whereby the raccoon's natural inclination to handle coins inhibited its ability to let go of them, even for a food reward. Raccoons 29 and 40 did not share this same rigid "misbehavior," as they readily dropped stones and objects into the tube. However, their tactile, instinctual tendencies likely affected the unique ways in which raccoons interacted with materials in this task. Thus, similar species-specific behaviors and sensory mechanisms should be considered in future adaptations of the Aesop's Fable paradigm, including interpretation of results.

Because our experiments were limited by time constraints and a relatively small sample size, the depth at which our

raccoon subjects understood the causal properties of this task remains uncertain and thus should be interpreted with caution. Yet we observed an expression of diverse, investigative behaviors that have not been previously reported in other Aesop's Fable experiments, and can, in part, explain raccoon performance in this paradigm. Perhaps animals such as raccoons, whose dexterity allows for increased engagement with their environment, require more time to fully investigate the physical features of a task to develop a preference than less dexterous species. Alternatively, it may be best to present such animals with more functionally dichotomous choices to elicit a strong preference. Nevertheless, applying the Aesop's Fable paradigm to raccoons has reaffirmed the innovativeness of raccoons as study subjects and highlighted important considerations when using the Aesop's Fable paradigm to assess causal understanding across diverse taxa in the future.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflicts of interest.

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