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Daniels, Sarah E.; Fanelli, Rachel E.; Gilbert, Amy; and Sarah Benson - Amram, Sarah, "Behavioral flexibility of a generalist carnivore" (2019). *USDA National Wildlife Research Center - Staff Publications*. 2245.
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Behavioral flexibility of a generalist carnivore

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Received: 31 August 2018 / Revised: 1 February 2019 / Accepted: 15 February 2019 / Published online: 25 February 2019
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Abstract

Innovative problem solving, repeated innovation, learning, and inhibitory control are cognitive abilities commonly regarded as important components of behaviorally flexible species. Animals exhibiting these cognitive abilities may be more likely to adapt to the unique demands of living in novel and rapidly changing environments, such as urbanized landscapes. Raccoons (*Procyon lotor*) are an abundant, generalist species frequently found in urban habitats, and are capable of innovative problem solving, which makes them an ideal species to assess their behavioral flexibility. We gave 20 captive raccoons a multi-access puzzle box to investigate which behavioral and cognitive mechanisms enable the generation of innovative and flexible behaviors in this species. Over two-thirds of raccoons tested were not only capable of innovative problem solving, but displayed repeated innovation by solving more than one solution on the multi-access puzzle box and demonstrated that they learned multiple solutions to a novel problem. Although we found no relationship between our measure of inhibitory control and a raccoon's ability to exhibit repeated innovations, we did find a positive relationship between the diversity of behaviors that an individual exhibited when interacting with the problem and the number of solution types that they solved. We identified other predictors of problem-solving performance, including neophobia and persistence. Finally, we examine the implications of our results in the context of the cognitive-buffer hypothesis and consider whether the widespread success of an adaptive generalist carnivore could be due in part to having these cognitive and behavioral traits.

Keywords Repeated innovation · Learning · Inhibitory control · Cognition · Raccoon · *Procyon lotor*

Introduction

Anthropogenic influences are causing many habitats to change at rates that can outpace an animal's ability to adapt (Wong and Candolin 2015). A variety of factors may contribute to an animal's success in novel and changing environments, such as exaptation of preexisting traits to new environmental conditions (Gould and Vrba 1982; Hu and Cardoso 2009) or being a habitat or dietary generalist

(Bonier et al. 2007). If animals can adapt to novelty, changes in behavior are typically some of the first and most common adaptations (Wong and Candolin 2015). There are many examples of behavioral adaptation to disturbance. From shifts in activity and foraging patterns as a result of increased human activity (Tigas et al. 2002; Legagneux and Ducatez 2013; Gaynor et al. 2018), to changes in call amplitude as a response to noise pollution (Parks et al. 2010), many species can alter behaviors to respond to changing environments.

The cognitive-buffer hypothesis posits that large brains evolved primarily to buffer animals against mortality-causing events by facilitating the production of behavioral responses when animals are faced with novelty or change (Sol 2009a). Animals with enlarged brains relative to their body size are hypothesized to be more behaviorally flexible and exhibit enhanced domain general cognitive abilities compared to animals with smaller relative brain sizes (Sol 2009a, b). Behavioral flexibility is defined as an individual's ability to alter its behavior in response to environmental stimuli (Jones 2005; Coppens et al. 2010). It is considered

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10071-019-01252-7>) contains supplementary material, which is available to authorized users.

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a multi-faceted concept that includes an animal's ability to be innovative, learn from previous experience, and demonstrate inhibitory control (Griffin and Guez 2014b). Innovation, defined as an animal's ability to apply previous knowledge to a novel problem or apply novel techniques to an old problem (Kummer and Goodall 1985; Reader and Laland 2003), produces novel behavioral adaptations. Animals incorporate innovations into their behavioral repertoire through learning; without this cognitive mechanism, a behavior is an improvisation (or accident) that cannot be utilized by that animal in the future (Reader and Laland 2003; Ramsey et al. 2007). Repeated innovation occurs when an individual demonstrates multiple unique innovations across trials when faced with a novel problem with several different solution types (Johnson-Ulrich et al. 2018). Inhibitory control is hypothesized to be particularly important for the expression of behavioral flexibility, because animals must be able to discard previous and no longer accurate information to continuously, or repeatedly, innovate novel solutions to changing problems (Manrique et al. 2013; MacLean et al. 2014). Inhibitory control has been measured in innovative problem-solving tasks as an animal's ability to inhibit behaviors that were previously successful, but are no longer useful to solve new problems (Auersperg et al. 2012; Manrique et al. 2013; Johnson-Ulrich et al. 2018).

Cities represent some of the most rapidly changing and ecologically novel environments that animals are currently facing (Hendry et al. 2008). As predicted by the cognitive-buffer hypothesis, recent work has found evidence for the importance of advanced cognitive abilities, such as behavioral flexibility, in the success of species living in urbanized habitats (Echeverría and Vassallo 2008; Møller 2008, 2009; Maklakov et al. 2011; Samia et al. 2015, 2017; Audet et al. 2016; Ducatez et al. 2017). This work is limited in scope, however, as urban cognitive ecology is a relatively new area of study, and the studies that have been conducted have focused on birds. To date, evidence is lacking for these critical abilities in other taxa, such as carnivores [but see (Johnson-Ulrich et al. 2018)], which are also living successfully among humans. In this study, we assess the behavioral flexibility of an abundant, generalist carnivore, the North American raccoon (*Procyon lotor*), by testing for innovative problem solving, learning, inhibitory control, and repeated innovations in raccoons that are presented with a novel problem-solving task. We also examine the behavioral mechanisms that enable the creation of novel behaviors in raccoons.

Anecdotal evidence illustrates raccoons as highly intelligent animals. Raccoons have infiltrated nearly every corner of the United States, including habitats with vastly different temperatures, levels of urbanization, vegetation types, and elevation (Zeweloff 2002). Raccoons are dietary and habitat generalists (Zeweloff 2002), and ecological generalists tend

to be more innovative (Overington et al. 2011). Despite their assumed intelligence, very few studies have experimentally assessed cognitive abilities in raccoons [but see (Johnson and Michels 1958; Michels et al. 1961; Davis 1984; MacDonald and Ritvo 2016; Stanton et al. 2017)]. One of the few studies to address raccoon problem-solving abilities looked at causal understanding in eight captive raccoons using the Aesop's Fable Paradigm (Stanton et al. 2017). However, the ability of raccoons to behave flexibly when faced with change has not been tested. Thus, it remains unclear whether raccoons are proficient problem solvers and whether the cognitive abilities of raccoons can help to explain their great success inhabiting urban environments.

The multi-access puzzle box is an established tool to measure behavioral flexibility in animals, because it allows researchers to measure not only an individual's innovative propensity but also its learning, inhibitory control, and ability to exhibit repeated innovations (Auersperg et al. 2011, 2012; Manrique et al. 2013; Johnson-Ulrich et al. 2018). We designed a multi-access puzzle box with three solution types to assess several cognitive (e.g., learning, innovative problem solving, and inhibitory control) and behavioral traits (e.g., neophobia, exploratory diversity, and persistence) that may underlie behavioral flexibility [see (Griffin and Guez 2014b) for a complete review] in raccoons. We expected raccoons to be innovative problem solvers, defined as successfully opening at least one solution type multiple times (Manrique et al. 2013; Johnson-Ulrich et al. 2018). In addition, we examined whether factors that have been identified as important predictors of innovative problem solving in other species are also significant predictors of innovative problem solving in raccoons [e.g., (Benson-Amram and Holekamp 2012; Griffin and Guez 2014b; Benson-Amram et al. 2016)].

We predicted that:

1. Raccoons with a higher exploratory diversity score, also known as motor diversity (Griffin and Guez 2014a), which is measured as the total number of unique behaviors directed at investigating and opening the box, would be more successful than raccoons that did not demonstrate as many diverse behaviors (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013);
2. Raccoons that were more persistent, or spent more time working on the puzzle box before solving it for the first time, would be more successful than less persistent raccoons (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013; Johnson-Ulrich et al. 2018);
3. Raccoons that exhibited greater neophobia, a fear of novelty measured as the latency to approach the puzzle box in the first trial, would be less likely to open the puzzle box than individuals that exhibited less neophobia (Webster and Lefebvre 2001; Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013); and

4. Raccoons that paced, a stereotypic repetitive behavior commonly found in captive animals (Rose et al. 2017), would be less likely to open the puzzle box, since this behavior would detract from exploration of, and interactions with, the task.

Once raccoons found a solution for the first time, we predicted that those raccoons would demonstrate learning by extracting the food reward more quickly from the puzzle on subsequent exposures to the apparatus on the same night (Benson-Amram and Holekamp 2012). We also expected these raccoons to demonstrate learning by becoming more selective with their behavioral choices over time, resulting in a decrease in their exploratory diversity scores across trials (Benson-Amram and Holekamp 2012).

Once raccoons demonstrated that they learned a solution type, we blocked the solution(s) the raccoons had solved previously. We predicted that raccoons that demonstrated inhibitory control, or spent less time trying to open a blocked solution, would be more likely to demonstrate repeated innovations, defined as opening the puzzle box using multiple solution types, than raccoons that spent more time on a locked solution (Manrique et al. 2013; Johnson-Ulrich et al. 2018).

Methods

Ethical note and housing

This study was approved by the Animal Review Board at the USDA National Wildlife Research Center (NWRC) in Fort Collins, CO (Study Protocol QA-2492). Eighteen raccoons were live-trapped near Fort Collins and were in captivity for up to two years prior to participation in this study for an unrelated research project [see (Johnson et al. 2016)]. One wild-caught female gave birth after capture, and two of her captive-born offspring were included in this study for a total sample of 20 raccoons (8 males and 12 females, age range: 2–5 years, $M=2.9$). Raccoons were individually housed and tested in outdoor enclosures (3 × 3 × 2.5 m).

Problem-solving apparatus

To assess problem-solving abilities, we designed a novel extractive foraging task—a multi-access puzzle box—which is an established method for evoking repeated innovations (Auersperg et al. 2011; Manrique et al. 2013; Johnson-Ulrich et al. 2018). The Plexiglass box contained one clear panel with no solution and three solution panels, including: (1) a door, (2) a slide latch, and (3) a window [Fig. 1; design inspired by: (Auersperg et al. 2011, 2012; Benson-Amram and Holekamp 2012)]. Each solution could be locked, making the solution inaccessible, and each panel could be moved to counterbalance solution presentation across the raccoons. The puzzle box was baited in two ways: (1) sardine juice spread evenly along the outside of each panel as an olfactory cue; and (2) a single prune that was soaked in sardine juice within the box as a food reward. In addition, one sardine was placed outside of the box in each animal's enclosure prior to the start of its first trial on the initial night of testing.

Procedure

Raccoons were not food deprived prior to participation and were provided with their standard meal of Omnivore Chow, at 11:00 AM by the animal care staff. Raccoons could eat and drink *ad libitum* until the food was fully depleted, which varied by individual. Trials occurred in Summer 2015 between approximately 8:30 PM and 4:00 AM, when the raccoons were most active. Trials lasted until a solution was solved, with a maximum duration of 40 min, with approximately 5–10 min between trials, and were recorded with a mounted Sony HDR-CX405 located outside the enclosure.

We gave each raccoon a minimum of three trials, but not more than six per night for up to five nights (total trials over the course of the experiment ranged from 3 to 19, mean = 9.65). Each raccoon was given an unlocked puzzle box with all three solution types available on the first night of testing (Fig. 2). If a raccoon solved a solution during one of the first three trials, the raccoon continued receiving the puzzle box until it solved the same solution three times or had three consecutive trials in which it did not open a solution. Successful raccoons, those that opened one solution

Fig. 1 **a** The multi-access puzzle box administered to 20 raccoons at the National Wildlife Research Center in Fort Collins, CO. This apparatus contained three solution types to retrieve a food reward inside: a window (left), slide latch (center), and door (right). **b** Raccoon with the puzzle box

Fig. 2 A schematic of the possible outcomes of all trials for the typical raccoon in this study. On the first night, all three solution types could be used by a raccoon to unlock the puzzle box and retrieve the food reward. To successfully solve a solution type and move on to the next phase of testing, each raccoon must open the same solution type

three times. Successful raccoons were tested again on a subsequent night with the previously solved solution type locked, leaving two solution types available. The raccoon must then open a second solution type three times to continue to the final night of testing. On the last night of testing, only the final, unsolved solution type is unlocked

type three times, were tested again on a subsequent night, with the previously solved solution type locked. Raccoons then needed to open a different solution type three times to continue to the final night of the study. The final night of testing modeled the preceding nights, but with the two previously solved solutions locked. If a raccoon opened two or three different solution types three times each during one night of testing, then the solution type that it most frequently opened first was locked for the next night of testing, and the other solution types remained open.

Eight raccoons were retested after failing to solve a solution three times on their first night of testing because of possible confounding effects, such as human presence inside the testing building, that may have been disruptive to these raccoons (see Table 1 in the ESM for a detailed accounting of all trials and retests). These raccoons were given the puzzle box with all three solutions as viable options a second time 7.11 ± 2.15 (mean $\pm$ SE) nights after their first night of testing. We considered human presence in the building as a factor that may have affected problem-solving performance in our statistical analyses.

There were also a few instances of technical issues, which resulted in three raccoons receiving extra trials. One raccoon broke our two copies of the puzzle box on what would have been its final night of testing, so we gave that animal a retest 6 days later after we repaired the boxes. Another animal received one extra trial when the video camera died. This animal was unsuccessful in all four trials that it received and did not receive any additional nights of testing. A third animal was retested after receiving only one trial on its first night of testing due to the camera breaking. Finally, two

animals received extra trials because these animals appeared to be asleep for the duration of the first three trials that night (Table 1 ESM).

Behavioral and cognitive measurements

The presence and duration of all behaviors were extracted from video footage by SED and REF (inter-rater reliability across all measures included in this study for 20% of the video footage, Spearman's rank correlation: $R = 0.95$).

Exploratory diversity

We calculated exploratory diversity as the number of unique behaviors an individual directed at the box in the first trial (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013, 2014; Johnson-Ulrich et al. 2018). The exploratory diversity score accounts for behaviors that increase an animal's knowledge of the puzzle box (e.g., sniffing the apparatus), as well as behaviors like touching and biting the box that could result in opening a solution (Table 1). This metric was calculated for the initial trial for each night of participation for analyses examining whether exploratory diversity predicts success. This metric was also calculated for all trials on the first night of testing for successful individuals to examine learning.

Persistence

Persistence was calculated as the total duration of all exploratory behaviors expressed by each individual raccoon

Table 1 Ethogram of all observed behaviors exhibited by raccoons during puzzle box trials

Behavior	Definition
Bite	Open mouth and close teeth around a puzzle box feature
Circle	Move around puzzle box within arm's length
Climb	Raise body vertically along the puzzle box
Eat	Place prune into mouth and swallow
Lick	Open mouth and move tongue onto a puzzle box feature
Pace	Moving back and forth repetitively with no clear purpose
Pull box	Use limbs to move puzzle box toward self
Pull knob	Use mouth or paws to move knob of door solution toward self
Push with arms	Use limbs to move puzzle box away from self
Push with head	Place head against puzzle box and move forward
Push with nose	Place nostrils against puzzle box and move forward
Raise	Use nose or paws to move ledge of window solution up
Reach with head	Place head through open solution panel to detect and retrieve food reward
Reach with paw	Place paw through open solution panel to retrieve food reward
Slide	Use mouth or paw to move knob of slide solution to the left
Sniff	Draw in air through the nostrils to detect a scent
Stand on	Position body on top of the puzzle box
Touch	Place paw on a puzzle box feature

All behaviors listed here, except for pacing (which was analyzed separately), were used to calculate individual exploratory behavior scores, which were a metric of the total number of unique behaviors directed at the novel apparatus

towards the puzzle box, also known as 'work time' (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013, 2014). This metric was calculated for the initial trial for each night of participation. Subjects that spend more time working on the puzzle box in any given trial demonstrate higher persistence and are generally more successful (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013, 2014).

Neophobia

Neophobia was measured in two ways: a raccoon's latency to approach (within arm's length) and contact (first touch) the puzzle box during the first trial on the first night (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2016).

Pacing

Pacing was measured as the total time a raccoon spent moving back and forth in an abnormal repetitive manner (Rose et al. 2017). Pacing was calculated for the initial trial for each night of participation.

Learning

We measured learning for successful raccoons in two ways. We measured how long raccoons interacted with the puzzle box (persistence or work time) and the number of behaviors

(exploratory diversity) that the raccoons exhibited during each trial in their first night of testing (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2014; Johnson-Ulrich et al. 2018). Raccoons that learn a solution to the puzzle box should open the box faster (work time should decrease) and exhibit fewer behaviors across trials.

Inhibitory control

To measure inhibitory control, we timed how long a raccoon spent interacting with a locked strategy (Johnson-Ulrich et al. 2018) on the initial trial of both the second and third nights of the study.

Data analysis

Means are reported with standard error. *P* values less than 0.05 are considered statistically significant. We used Wilcoxon Rank Sum tests to measure if the total number of solutions found (0–3) was influenced by sex or origin (wild or captive born). We used generalized linear models (GLMs) and generalized linear mixed-effects models (GLMMs) to test which behavioral measures (exploratory diversity, neophobia, persistence, and pacing) best predicted successfully finding at least one solution. We calculated Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for each model and reported ΔAIC_c , df, Akaike weights, residual deviation, and model fit to evaluate model performance.

We constructed mean learning curves to assess how quickly raccoons learned to solve a solution and track changes in the average exploratory diversity score across trials on the first night of testing. We used a GLM and assessed model fit to determine the roles that inhibitory control, neophobia, persistence, and exploratory diversity play in predicting multi-solution success. We examined the effect of human presence in the building during the first trial on our measures of neophobia and success by including human presence (Y/N) as a covariate in our model. We found no evidence of human presence on raccoon performance ($F=0.21$, $p=0.653$) and we, therefore, did not analyze these individuals separately in our subsequent analyses. This means that these raccoons effectively received an extra night of trials. To account for this, we used only the data from the trials that occurred on the retest night in our analyses, because the performance of the raccoons during these trials determined their success and whether or not they participated in subsequent nights of testing.

Finally, the difficulty of each solution may influence variability in problem-solving success. We compared the expected versus observed frequencies using a chi-squared test for the first and second nights to see if any solutions were solved more or less frequently than expected by chance. Due to small observed and expected frequencies, we used Yates' Chi-squared and corrected p values. Post hoc comparisons were completed using binomial probabilities.

Results

We had seven raccoons that did not solve any solutions (35%), zero that solved one solution (0%), six that solved two solutions (30%), and seven that solved all three (35%). Success did not depend on sex (Wilcoxon Rank Sum test: $n=20$, $W=41.5$, $p=0.86$) or origin (i.e., wild-caught versus captive-born; Wilcoxon Rank Sum test: $n=20$, $W=24$, $p=0.36$).

Behavioral and demographic predictors of success

Our predictors of success were assessed with a sample size of 19 raccoons (12 successful individuals and 7 unsuccessful individuals) due to footage loss for one successful animal. We examined the roles of exploratory diversity, persistence, and pacing on puzzle box success using AICc model comparisons. Our top model included exploratory diversity alone as the best predictor of puzzle box success in the first trial ($\Delta\text{AICc}=0.0$; model fit: $X^2=2.27$, $p<0.0001$, Fig. 3; Table 2). Specifically, raccoons that exhibited a greater diversity of motor action patterns during their first trial with the puzzle box were more successful than raccoons that exhibited less exploratory diversity ($r^2=0.56$, $p<0.001$).

Fig. 3 Estimated logistic regression relationship between Exploratory Diversity Score (the number of exploratory behaviors exhibited by raccoons in the first trial) and the probability of problem-solving success ($p<0.0001$). The gray region represents a 95% confidence interval

Neophobia, as measured by contact on the first night, was also a strong predictor of raccoon problem-solving success (Table 2). Raccoons that were less neophobic were more successful than raccoons that took longer to approach the puzzle box during their first trial ($r^2=0.56$, $p<0.001$). More persistent raccoons were also more successful at solving the puzzle box than less persistent raccoons ($r^2=0.56$, $p<0.001$). Pacing did not interfere with performance on the problem-solving task ($t=-1.74$, $p=0.08$).

Learning

We examined learning in successful raccoons ($n=12$ due to footage loss for one animal), by determining whether successful animals decreased their work time and/or their exploratory diversity across all trials on the first night. On average, raccoons solved each subsequent trial 18.28 ± 27.4 s faster than the previous trial, and time to success decreased with trial number ($n=12$; model fit: $X^2=13,802$, $p<0.01$; Fig. 4a). Successful raccoons became more behaviorally selective across trials the first night, as demonstrated by decreases in their exploratory diversity scores over time ($n=12$; model fit: $X^2=7.56$, $p<0.0001$, Fig. 4b). Finally, the success of a raccoon in their initial trial predicted that individual's overall success in future trials (Spearman's Rank Correlation: $R=0.89$).

Inhibitory control

Since no raccoons found only one solution, we were unable to compare one-time innovators to multi-solution

Table 2 The top five models for examining the relationship between behavioral metrics (exploratory diversity, neophobia, persistence, and pacing) and success. These models greatly outperformed all other competing combinations of factors

Models	AICc	AICc	df	Weight	Res. deviation	r^2	p value
Exploratory diversity	17.08	0.0	3	0.50	1.8	0.56	<0.001
Exploratory diversity + neophobia	17.47	2.0	4	0.19	1.8	0.56	<0.001
Exploratory diversity + neophobia + persistence	19.25	3.8	5	0.08	1.8	0.56	<0.01
Exploratory diversity + persistence	20.11	1.8	4	0.21	1.8	0.56	<0.01
Exploratory diversity + pacing	20.20	8.9	3	0.01	1.8	0.56	<0.01

Fig. 4 With increased exposure to the puzzle box over the first night, successful raccoons solved the puzzle box more quickly on each subsequent trial than the previous trial (a) and became more selective in their behaviors over time (b). Above each point is the number of raccoons contributing to each mean, shown with standard error. The sample sizes above each point in a are the same for b

problem-solvers. We did, however, see if inhibitory control predicted the difference between two- and three-solution solvers. We did not find a relationship between the amount of time spent working on a locked solution and third night success ($n = 12$; model fit: $X^2 = 0.69$, $p = 0.42$).

Because differences in repeated innovation were not explained by inhibitory control, we also looked at persistence and exploratory diversity. Although third night success cannot be explained by a raccoon's persistence in the first trial of the third night ($n = 12$; model fit: $X^2 = 0.11$, $p = 0.53$), third night exploratory diversity scores positively predict

third night success ($n = 12$; model fit: $X^2 = 0.95$, $p = 0.02$). Raccoons that found all three solutions exhibited 9.5 behaviors on average in the first trial of the third night, while raccoons that did not find a third solution exhibited 6.4 behaviors, on average.

Solution difficulty

On the first night, raccoons did not open each solution type at a level expected by chance ($n = 13$; $X^2 = 5.693$, $p = 0.05$). While four raccoons opened the slide solution (binomial tests: $p = 0.55$), eight raccoons opened the door solution (binomial tests: $p = 0.03$) and only one raccoon opened the window solution (binomial tests: $p = 0.03$). On the second night, we compared the observed versus expected frequencies for a raccoon to solve a knob solution (door or slide) compared to solving the window solution for raccoons that had these choices available (excludes one raccoon). Again, we found a bias against the window solution, where this solution type was opened less than expected by chance ($n = 12$; $X^2 = 6.75$, $p < 0.001$). When the window was the only solution left for 11 of the successful raccoons on the third night, six raccoons solved the window solution (55%). Overall, 8 of the 13 successful raccoons solved the window solution across all three nights (62%).

Discussion

We evaluated evidence for behavioral flexibility in a highly successful urban carnivore by investigating whether raccoons exhibit repeated innovation, learning, and inhibitory control when presented with a novel multi-access puzzle box. We present evidence consistent with the cognitive-buffer hypothesis (Sol 2009a), which relates urban success to advanced cognitive abilities. Employing new behavioral strategies when the previous actions fail is likely to be critical for success in novel and changing environments. The cognitive-buffer hypothesis predicts that highly successful urban species, such as raccoons, should, therefore, exhibit high levels of behavioral flexibility. We found that raccoons are not only innovative problem solvers, but also capable of repeated innovations during a novel foraging task and

that individuals vary in their innovative propensities, with the majority of raccoons in this study finding two or three solutions to a multi-access puzzle box. Raccoons demonstrated evidence of learning, both in terms of the speed with which they solved the puzzle over time, and in their selective expression of behaviors as they gained experience with the problem. We also found persistence, exploratory diversity, and neophobia to be key factors in the generation of innovative behavior and in the degree to which raccoons exhibit repeated innovations. Exploratory diversity has been shown to be a critical determinant of innovative problem-solving abilities in other generalist and opportunistic species (Griffin and Guez 2014b), such as both wild (Benson-Amram and Holekamp 2012) and captive spotted hyenas (Benson-Amram et al. 2013), Noisy miners (Griffin and Diquelou 2015), and Indian mynas (Griffin et al. 2014; Griffin and Diquelou 2015). In all of these studies, individuals that exhibited a greater number of distinct motor actions were more successful at solving a novel problem-solving task. Despite its importance in innovative problem solving, exploratory diversity had not previously been identified as a key behavioral mechanism underlying the expression of behavioral flexibility more generally. In this study, we show that individuals that exhibit a greater diversity of motor action patterns are more likely to exhibit repeated innovations, finding multiple, different, solutions to a novel problem.

We expected both neophobia (Benson-Amram and Holekamp 2012) and pacing to negatively predict problem-solving success, but we only found this to be true with neophobia. Even though pacing could interfere with the amount of time raccoons spend interacting with the task, we did not find a relationship between pacing and success. We were unable to compare the inhibitory abilities of repeat innovators with one-time innovators, since no raccoons opened only one solution. Inhibitory control did not predict the varying degrees of repeated innovation that we observed. This may be because raccoons already demonstrated inhibitory control by finding multiple solutions, so there is likely little difference in the inhibitory abilities between two- and three-solution solvers. Instead, exploratory diversity predicted third night problem-solving success, demonstrating that exploratory diversity continues to be important beyond first time innovations.

Based on raccoon performance on our puzzle box task, we believe that our three solutions were not equally challenging. This imbalance allowed us to observe variation in problem-solving abilities that we might not have documented otherwise. Ours is not the first study to find differences in solution difficulty. For example, the previous multi-access puzzle box work with New Caledonian crows and keas showed a clear preference for one solution type over another, suggesting differing levels of difficulty in the task

and possible species-level differences in problem-solving ability (Auersperg et al. 2011). Importantly, not all problems in the wild are equally challenging and behavioral flexibility should be critically important for species encountering novel problems, even when those problems vary in their degree of difficulty.

Raccoons are famous for their high degree of manual dexterity and it is possible that dexterity gives raccoons a large advantage in urban environments, where raccoons forage in trash cans and break into houses in search of food and shelter. If a high degree of dexterity, and not cognition, is the major contributing factor driving the widespread success of raccoons, then we would expect all raccoons to open all solutions. Instead, our puzzle box design and the variation in raccoon success that we observed allowed us to demonstrate that manual dexterity alone cannot explain raccoon innovation. We believe our task to be especially relevant for assessing raccoon cognition. Any “artificial” problem-solving apparatus used on raccoons, and other urban-dwelling individuals, is highly ecologically relevant when we consider the types of man-made challenges that these animals face co-existing with humans.

The majority of raccoons (90%) used in this study were wild caught, so we cannot know or control for the previous experiences of our study subjects. However, we think that testing wild individuals in a controlled setting strengthens our results. In a recent review of innovative problem-solving, 14 out of 24 (58%) reviewed studies included captive testing of wild-caught animals (Griffin and Guez 2014b), allowing researchers to carefully test for abilities in wild animals that are difficult to test for in natural habitats. This captive study laid the groundwork for analyzing the cognitive abilities of an elusive, nocturnal animal, and the logical next step is to replicate these findings in the wild.

We have presented evidence of behavioral flexibility in an under-studied and successful carnivore. Our results illustrate that raccoons are highly capable problem-solvers. Successful raccoons employed a wide variety of behaviors, showed high persistence, were less neophobic, demonstrated evidence of learning with increased exposure to the task, and found multiple solutions to a novel problem. Understanding the roles of innovation, learning, and inhibitory control in the cognitive repertoires of urban-dwelling animals is an important step in understanding the behavioral mechanisms that enable some species to behave flexibly and to persist and thrive in human-altered habitats.

Acknowledgements We thank the NWRC for their collaboration on this project. We also thank the Division of Research Support at the University of Wyoming for constructing our puzzle box. This research was supported by a grant from the Animal Behavior Society to SED and two NSF EPSCoR grants to REF. We are grateful for suggestions and revisions on this manuscript from members of the Animal Behavior and Cognition Lab at the University of Wyoming.

Author contributions SED designed the study, ran experimental trials, conducted statistical analyses, and wrote the manuscript; REF ran experimental trials and wrote the manuscript; AG provided access to the study site and subjects; SBA designed the study and wrote the manuscript. All authors gave final approval for publication.

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