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# Variation in reversal learning by three generalist mesocarnivores

Lauren A. Stanton<sup>1,2</sup> · Eli S. Bridge<sup>3</sup> · Joost Huizinga<sup>4</sup> · Shylo R. Johnson<sup>5</sup> · Julie K. Young<sup>6</sup> · Sarah Benson-Amram<sup>1,2</sup>

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## Abstract

Urbanization imposes novel challenges for wildlife, but also provides new opportunities for exploitation. Generalist species are commonly found in urban habitats, but the cognitive mechanisms facilitating their successful behavioral adaptations and exploitations are largely under-investigated. Cognitive flexibility is thought to enable generalists to be more plastic in their behavior, thereby increasing their adaptability to a variety of environments, including urban habitats. Yet direct measures of cognitive flexibility across urban wildlife are lacking. We used a classic reversal-learning paradigm to investigate the cognitive flexibility of three generalist mesocarnivores commonly found in urban habitats: striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*). We developed an automated device and testing protocol that allowed us to administer tests of reversal learning in captivity without extensive training or experimenter involvement. Although most subjects were able to rapidly form and reverse learned associations, we found moderate variation in performance and behavior during trials. Most notably, we observed heightened neophobia and a lack of habituation expressed by coyotes. We discuss the implications of such differences among generalists with regard to urban adaptation and we identify goals for future research. This study is an important step in investigating the relationships between cognition, generalism, and urban adaptation.

**Keywords** Behavioral adaptation · Comparative cognition · Carnivore · Flexibility · Generalism · Urbanization

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## Introduction

Urbanization is rapidly changing the planet and has been linked to extinctions and evolutionary change in organisms across the globe (Pimm et al. 2014; Alberti et al. 2016). Given the projected biodiversity loss stemming from urbanization (Seto et al. 2012), understanding the mechanisms that affect a species' propensity to avoid or adapt to urban habitats remains a priority for conservation and urban planning (Johnson and Munshi-South 2017). Urban habitats are typically characterized by the same broad environmental transformations: an increase in humans and artificial entities (e.g., lights, acoustics, substrates, vehicles, trash, chemicals) and a decrease in natural resources and landscape connectivity (Grimm et al. 2008; Sih et al. 2011). The anthropogenic disturbances that occur in urban habitats impose new challenges for wildlife, but anthropogenic resources (e.g., food, shelter) also provide new opportunities for exploitation (Lowry et al. 2013). Consequently, some species not only persist but actually thrive in urbanized habitats (McKinney 2006). These successful species are usually found to be

ecological generalists, characterized by their ability to use a diversity of food and habitat types (Devictor et al. 2008; Ducatez et al. 2018). Yet the mechanisms underlying the adaptive, exploitative skills of generalists represents a critical gap in our knowledge (Overington et al. 2011).

Ecological generalism may have coevolved with a suite of cognitive abilities that allow generalists to cope with environmental variability (Lefebvre et al. 1997; Sol 2009; Overington et al. 2011; Ducatez et al. 2015; Sol et al. 2016; Navarrete et al. 2016). The cognitive buffer hypothesis suggests that advanced cognitive abilities associated with large relative brain size, such as rapid learning, innovation, and flexibility, allow animals to modify their behavior in adaptive ways when confronted with challenges in their environment (Sol 2009). In accordance with the cognitive buffer hypothesis, generalists are exposed to diverse environmental conditions that require a capacity for rapid, flexible responses to new or local cues (Mettke-Hofmann 2014; Sol et al. 2016). Such a capacity includes the exploitation of various habitats, foods, and shelters while avoiding the novel dangers associated with such transitions, such as the consumption of noxious foods or increased risk of predation (Greenberg 2003; Sol 2003; Robertson et al. 2013). Cognitive flexibility may, therefore, allow generalists to be plastic in their behavior, which increases their adaptability (Godfrey-Smith 1996; Sol and Lefebvre 2000; Sol et al. 2002, 2013; Wright et al. 2010; Mettke-Hofmann 2014) and serves as a potential mechanism for urban adaptation (Maklakov et al. 2011; Sih et al. 2011; Snell-Rood and Wick 2013; Sol et al. 2013). For example, both brain size and dietary innovation rate have been implicated in the success of many widespread species (Lefebvre et al. 1997; Sol and Lefebvre 2000; Sol et al. 2002, 2008; Maklakov et al. 2011; Overington et al. 2011; Snell-Rood and Wick 2013; Ducatez et al. 2015). Nevertheless, establishing the link between the cognitive traits of generalists and their successful adaptation to urbanization requires further empirical support.

The cognitive flexibility of an animal is commonly assessed using a test known as reversal learning, which was originally designed as an assessment of animal intelligence (Mackintosh et al. 1968). In this paradigm, previously learned reward associations are reversed and the ability of the animal to respond to the new contingency by changing its behavior remains a widely accepted measure of flexibility (Audet and Lefebvre 2017; Izquierdo et al. 2017). Reversal learning is thought to involve two different aspects of learning: an initial, more basic associative learning of a stimulus and a response (i.e., acquisition phase), and a second, more flexible reversed learning ability that requires additional executive control (i.e., reversal phase) (Lai et al. 1995; Chow et al. 2015; Buechel et al. 2018; Madden et al. 2018). Specifically, when an animal is presented with the challenge of a reversal, it must first inhibit its inclination

to select the previously correct response and then shift its attention to the new stimuli (Shettleworth 2010). Although most (if not all) animals can be expected to learn simple associations (Morand-Ferron 2017), less flexible individuals are expected to demonstrate difficulty responding to a reversed association and, therefore, make a high number of errors during the onset of a reversal event. In contrast, highly flexible individuals experience less difficulty in altering their behavior and, therefore, make fewer errors. As an animal learns the affordances of this task, it is also expected that they will make fewer errors across reversals and perhaps even demonstrate an optimal, more advanced learning strategy, wherein only one error is made per reversal (i.e., win stay–lose shift strategy; Mackintosh et al. 1968; Macphail and Bolhuis 2001; Shettleworth 2010). Thus, the cognitive flexibility of an animal can be measured by the onset of a single reversal event or across serial reversals; tests that may emulate challenges found in complex or changing environments, such as switching foraging strategies (Tebbich and Teschke 2014), resource tracking (Hermer et al. 2018), or maintaining social competency (Bond et al. 2007). Indeed, performance in reversal learning has been linked to many cognitive and ecological traits of interest, including brain size (Buechel et al. 2018), social complexity (Bond et al. 2007; Ashton et al. 2018), and habitat unpredictability (Tebbich and Teschke 2014; but see Croston et al. 2017; Hermer et al. 2018). Furthermore, the neural basis of reversal learning has been well-established in the lab (Izquierdo et al. 2017). Since reversal learning is a validated measure of the cognitive underpinnings of behavioral plasticity and parallels ecologically relevant challenges that animals face in novel, complex, or changing environments, it can serve as a tool to investigate the link between the cognition of generalists and urban adaptation.

Mammals comprise a rich and underutilized taxon for investigations of cognition and behavioral adaptation to urbanization. The evolution of intelligence in mammalian carnivores (i.e., mammals within the order Carnivora) may have been driven by ecological complexity (Holekamp and Benson-Amram 2017), and behavioral plasticity has been suggested as important for urban carnivores (Bateman and Fleming 2012; Barrett et al. 2019; Murray and St. Clair 2015; Young et al. 2019a). Large and small mammalian carnivores are underrepresented in urban areas (Bateman and Fleming 2012), and large carnivores are typically the first to disappear as a result of an increased human presence (McKinney 2002). In contrast, several medium-sized, generalist carnivores (i.e., “mesocarnivores”) in North America, such as striped skunks (*Mephitis mephitis*; henceforth “skunks”), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*) are successful at persisting despite often being targeted by humans as “nuisance species” (Gehrt 2004; Bateman and Fleming 2012; Barrett et al. 2019). Thus, these

species may offer new insight on the relationships between cognition, generalism and urban adaptation. Indeed, early comparative cognition research on mesocarnivores, including skunks and raccoons, suggests that these species are capable of discrimination and reversal learning (Fields 1936; Shell and Riopelle 1957; Johnson and Michels 1958; Warren and Warren 1962; Gossette et al. 1968; Doty and Combs 1969). However, these studies were conducted in a laboratory setting with heavy experimenter involvement and may have limited applicability to wild animals. Although fewer studies of traditional discrimination and reversal learning have been conducted with coyotes, captive coyotes have proven capable of discriminating between different quantities of food (Baker et al. 2011; but see Mahamane et al. 2014). Captive coyotes also have demonstrated skill in matching their behavior to changing reward contingencies, which is suggestive of behavioral plasticity (Gilbert-Norton et al. 2009). Despite the tenacity of urban mesocarnivores, the challenges of working with such species, especially in the wild, has hindered investigation of their cognitive flexibility (e.g., Pettit 2010; Stanton et al. 2017) and thus remains generally under-investigated in comparison to other taxa (e.g., birds; but see Gossette et al. 1968; Gilbert-Norton et al. 2009; Daniels et al. 2019).

To generate new insights on mesocarnivore cognition and thereby address critical gaps in knowledge regarding the link between the cognition of generalists and urban adaptation, we developed an automated device and protocol to directly measure the cognitive flexibility of skunks, raccoons, and coyotes in captivity using a classic reversal-learning paradigm. Although these mesocarnivores differ in many traits, including brain morphology, sociality, reproduction, and foraging strategies, all three species are considered to be predominately nocturnal, dietary and habitat generalists that are commonly found in cities in North America (Gehrt 2004; Gehrt et al. 2010; Jardim-Messeder et al. 2017; Stankowich and Romero 2017). Given that behavioral plasticity and ecological generalism may have coevolved, we expect that skunks, raccoons, and coyotes are cognitively flexible, and that this aids in their exploitation of urban habitats. Therefore, we predicted that all three species would form rapid associations and demonstrate cognitive flexibility as evidenced by a low number of errors made during the reversal of a learned behavior. Our methodology allowed us to assess the reversal-learning ability of mesocarnivores without any hands-on training, which has the potential for field applications. Although similar methodologies have been developed for reversal learning in studies of wild birds (Morand-Ferron, Hamblin, et al. 2015a, b; Cauchoix et al. 2017; Tello-Ramos et al. 2018; Bridge et al. 2019), to the best of our knowledge this methodology has yet to be applied to mammalian carnivores. Thus, our study extends the body of work on automated cognition testing to an understudied yet

remarkably successful guild, thereby advancing our ability to investigate the connections between generalism, cognition, and urban adaptation.

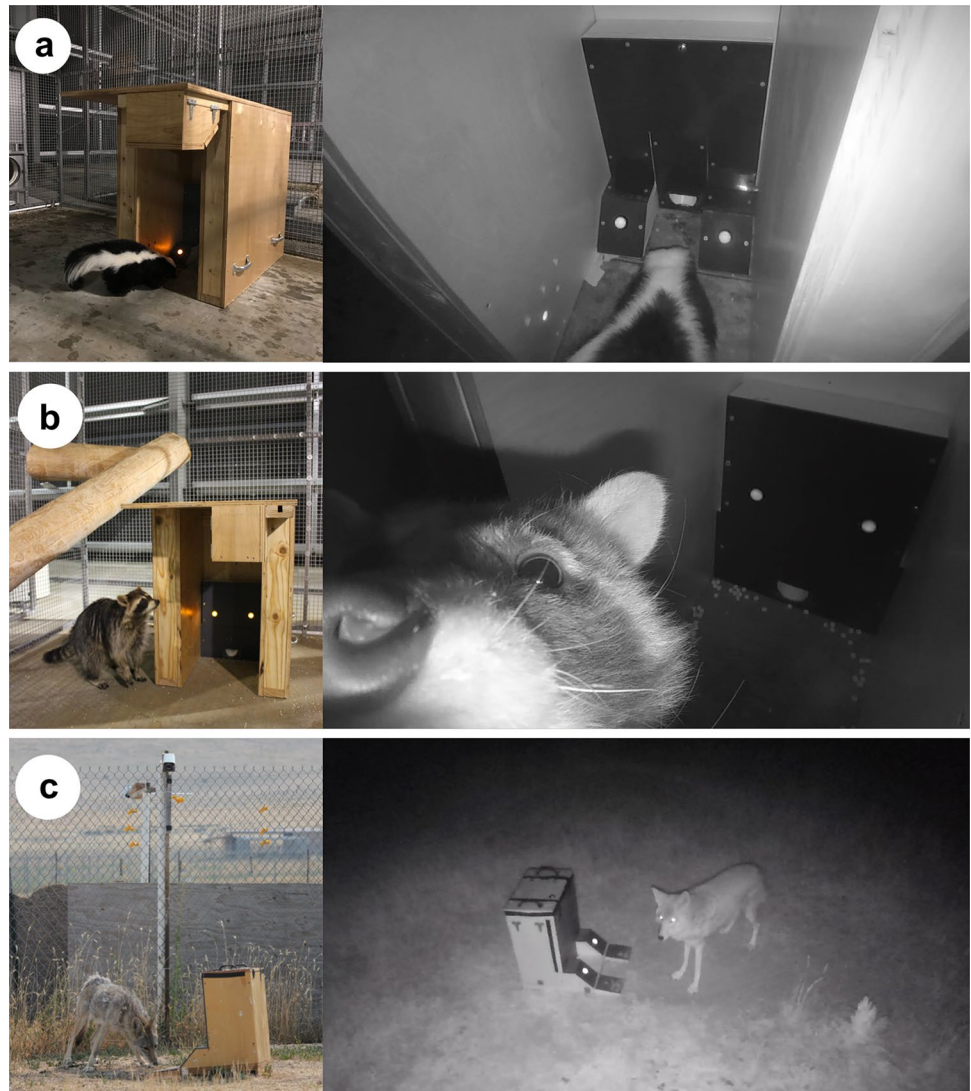
## Methods

### Study sites and general procedure

Trials were conducted at two USDA National Wildlife Research Center (NWRC) facilities and this study was approved by NWRC Institute for Animal Care and Use Committee (QA-2825). Skunks ( $n=4$ ) and raccoons ( $n=11$ ) were tested at the NWRC headquarters in Fort Collins, CO, whereas coyotes ( $n=6$ ) were tested at the NWRC's Predator Research Facility in Millville, UT (see Electronic Supplementary Material (ESM) for husbandry and housing information). Animal subjects were selected on their likelihood of voluntary participation (i.e., exhibited low levels of fear and high levels of food motivation; see ESM). Trials were administered by an automated device resembling a classic operant conditioning chamber or "Skinner Box" (Skinner 1938) using a two-choice, spatial paradigm. The device featured two round buttons (placed at an angle for skunks and placed vertically for raccoons) or rectangular foot pedals (placed on the ground for coyotes) on either side of a food dispensing chute (Fig. 1). Each button was associated with an LED light to indicate the device was on and active. Subjects were required to press one of the two buttons, either on the left or right side, to receive a food reward. When the subject pressed the correct button (i.e., positive stimulus), the device automatically released a small food reward. When the subject pressed the incorrect button (i.e., negative stimulus), the device initiated a brief 10 s time-out period, where the LED lights shut off and the device became unresponsive. Trials were delivered in blocks of 10, and subjects were required to meet a 90% learning criterion (i.e., select the correct button in 9 out of 10 consecutive trials) before a block was considered passed (Cauchoix et al. 2017). If the subject did not meet the 90% criterion, the block was considered a failure, and a new block of 10 trials began.

We considered the first test delivered every night, in which the subject had to make an initial discrimination between the two stimuli and meet the 90% criterion, to be a "pre-reversal block". The initial, correct stimulus (i.e., right vs. left button) in a subject's first pre-reversal block was randomly assigned. The rewarded stimulus in subsequent pre-reversal blocks was alternated across all testing sessions for a subject. Tests following the pre-reversal block within a single testing session were considered to be reversals. Whenever a block was passed, a reversal event was initiated by the device, whereby the current reward association was reversed (i.e., the negative

**Fig. 1** Images of the devices used to deliver trials to **a** skunks, **b** raccoons, and **c** coyotes. Buttons were placed in different positions so that they were easily accessible to each species, and the device used with coyotes was smaller than that used with skunks and raccoons



stimulus became the positive stimulus and vice-versa) and a new block of trials began. Subjects were not limited in the number of the reversals they could achieve in a single testing session, and our goal was to obtain a minimum of 30 reversals per individual over the course of several testing sessions so that performance could be assessed across time. Subjects were tested approximately once every 24 h for the duration of their trials (median = 24.17 h, range = 17.89–337.02 h), although this was subject to animal and researcher availability (see ESM). If a subject did not complete a pre-reversal or a reversal prior to the end of its testing session, this incomplete block was abandoned and the subject started a new pre-reversal block in its subsequent testing session. All trials were automated and filmed so that an experimenter was not present nor actively involved in trials (video footage from the skunk, raccoon, and coyote trials can be found in ESM Videos

1, 2, and 3, respectively). The device kept a record of all trials administered.

### Skunk and raccoon protocol

Skunks (4 males, 0 females) were all captive-bred subjects and raccoons (6 males, 5 females) were all wild-caught subjects (see ESM). Subjects were not food-deprived for this experiment and always had access to their food and water bowls during trials. They were tested individually, at night, and the testing device was placed in a subject's home enclosure at the beginning of a testing session and removed at the end of the session. The device used with skunks and raccoons was equipped with an infrared (night vision) camera and a break-beam sensor (Fig. 1a, b). The break-beam sensor was able to detect the presence of an animal inside of the device. We used this feature to both habituate subjects to

the device in their initial testing sessions by providing free rewards for simply entering the device, and to signal the start of trials upon their entry into the device for each subsequent testing session (see ESM).

The reward used for skunks and raccoons was a mix of cereal and dog kibble that differed from their normal diet (see ESM). To train the animals to target the buttons and discourage the development of a side bias, both right and left buttons were initially baited with a food cue during the subject's first testing session (see ESM). During this time, subjects could press either button and receive a reward for a maximum of 10 pushes before the first pre-reversal test began. Testing sessions initially lasted up to 300 min to allow for habituation but were reduced to 30–90 min after subjects had begun to engage in testing (see ESM). Skunks and raccoons received one testing session per night for a maximum of 14 nights or a minimum of 30 reversals achieved (whichever occurred first). However, if a subject never approached the device within its first five testing sessions or did not receive their free rewards within eight testing sessions, the subject was considered uninterested and was removed from further testing.

### Coyote protocol

Adult coyotes (5 males, 1 female) comprised a mix of wild-caught ( $n = 2$ ) and captive-born ( $n = 4$ ) individuals, but all received identical care after reaching 15 weeks of age (see ESM). Because coyotes have demonstrated neophobia toward large, novel objects (Mettler and Shivik 2007; Windberg 2008), several adjustments were made to our protocol and to the testing device upon the start of coyote trials. The device remained in the subject's enclosure full time for a minimum of 40 days, and testing sessions lasted for many hours, beginning at dusk and ending the following morning. Coyotes received a minimum of 25 testing sessions (i.e., when the device was active). The device was powered off while not in use, and a cover was placed over the interface so coyotes could not access the foot pedals outside of testing sessions. Unlike the devices used in the skunk and raccoon trials, the coyote device used was smaller, less like a chamber (i.e., no sides), and lacked a break-beam sensor and camera (Fig. 1c). Instead, the night vision camera used to film trials was mounted away from the device on the fencing of the animal's enclosure and remained present throughout the study. The reward was a mix of dog kibble and sausage, which differed from their normal diet (see ESM). For habituation, the device was programmed to automatically deliver food every 40 min throughout the initial testing sessions, regardless of where the coyote was in its enclosure. The foot pedals used for making a selection were constructed to lie flat on the ground and projected away from the device so that the coyotes could maintain some distance from the main

part of the device during testing. Pedals were heavily baited every night with high-value food rewards (e.g., chicken liver, sausage, mink food), and coyotes were allowed to push on the baited pedals for an extended period of time (i.e., several testing sessions) before trials began. Thus, the habituation period was extended beyond that allocated to the skunks and raccoons, and coyotes received longer testing sessions in general. To further motivate participation, some of the coyotes were transitioned from their highly preferred, meat-based diet to a kibble diet, and some coyotes were also tested both alone and with their mate present (see ESM Table 1).

Although extended testing sessions were necessary, we were concerned that prolonged gaps in time (i.e., potentially several hours) between selections would result in memory loss and that this would inhibit our ability to make comparisons in performance among study subjects. Therefore, to emulate the testing experience of the skunks and raccoons, we initiated a block reset if the device went untouched by a coyote for more than 40 min (i.e., the maximum amount of time between selections observed by the skunks and raccoons). In other words, if the device detected no selections for 40 min, any ongoing blocks were canceled, reset to 0, and not included in analysis. Furthermore, we found that the 10 s time-out period upon an incorrect selection was too long for coyotes and would cause abandonment of testing. We, therefore, dropped the time-out period from 10 to 2 s, which allowed us to better maintain coyote interest.

### Prior experience

In the development of appropriate methods for this experiment, including the construction of the testing devices, some of the subjects were exposed to pilot versions of the testing device. This exposure was necessary for us to create a device and an automated protocol that was most suitable for testing mesocarnivores. Due to the time and resource constraints of our study, we decided to continue testing individuals that may have had initial, prior experience, because they were already habituated to our experimental setup. We expected that this prior experience might have affected individual performance in this task. Specifically, we estimated that animals having more prior experience would make fewer errors during testing than individuals that lacked any prior experience (Izquierdo et al. 2017). We, therefore, assigned a category to each subject based on the level of prior experience they had with the devices: group A were subjects that had experience with one or more pilot devices and completed a small number (1–13) of blocks (i.e., moderate experience;  $n = 5$ ), group B had experience with one or more pilot devices but did not complete blocks (i.e., low experience;  $n = 5$ ), and group C had no prior experience ( $n = 11$ ).

## Statistical analysis

We tested (1) the ability of our subjects to improve their performance over time and (2) investigated factors that may have contributed to variation in performance. We measured performance by the number of errors an individual made before reaching criterion (i.e., before completing a reversal). All analyses were performed using Program R (R Core Team 2018). We first used Poisson regression to test how reversal number, individual ID, species, and prior experience (fixed effects) affected performance (i.e., number of errors made by subjects) using package lme4 (Bates et al. 2015). Although we intended to include additive models for all fixed effects, as well as additional traits such as sex and origin, we encountered data limitations that prevented us from building more complex models (see below). We evaluated model fit and parsimony using Akaike's Information Criterion corrected for small sample sizes (AICc) using package MuMIn (Bartoń 2018). Furthermore, we identified the amount of variation explained by each fixed effect by calculating  $R^2$  values for each model. We also assessed whether duration (number of hours) between testing sessions could have affected participation and testing performance. Although we found a weak trend that suggested subjects may have completed more reversals after a prolonged break from testing, these results were non-significant (see ESM).

To evaluate variation in individual performance, we next built individual learning curves using Poisson regression to compare the number of errors each individual made during the first reversal ( $y$ -intercept) and the rate at which the number of errors changed as reversal number increased (slope). We considered a subject to have improved in its performance if there was a decreasing trend in the number of errors made or the number of blocks an individual needed to meet learning criterion across reversals. Lastly, we tested each individual for a side bias, or the tendency for an individual to make more or fewer errors based on the side (left vs. right) assigned as the positive stimulus. To evaluate any side bias, we again used Poisson regression to model the effect of reversal number on the number of errors made while including the assigned positive stimulus (left or right) as a fixed effect.

To better understand the specific learning processes that subjects underwent in this experiment, we assessed the sequence of choices subjects made across testing sessions. As in other studies of reversal learning, we expected that subjects may develop an advanced, rule-based strategy to improve in performance, such as win stay–lose shift, or that subjects may experience a type of learning barrier that would inhibit improvement, such as proactive or retroactive interference (Anderson and Neeley 1996). Using analytical methods similar to those of recent reversal learning studies (Liu et al. 2016; Bridgeman and Tattersall 2019), we created

pairs of successive choices starting at the beginning of a testing session and ending at the last completed block of that testing session for all subjects (i.e., included the pre-reversal block and subsequent reversal blocks for a testing session). We labeled each pair of choices as one of four possibilities: win stay (first choice correct, next choice correct), lose shift (first choice incorrect, next choice correct), win shift (first choice correct, next choice incorrect), and lose stay (first choice incorrect, next choice incorrect). We calculated the number of pairs for each category and divided it by all of the pairs made in a testing session, resulting in the proportion of each category per testing session. We expected that if subjects developed a win stay–lose shift strategy, we would see the proportion of win stay and lose shift responses increase, while the alternative, incorrect responses (i.e., win shift–lose stay) decreased. However, if subjects were experiencing a learning barrier, such as proactive or retroactive interference, or lacked inhibitory control, then we generally expected to see a high proportion of incorrect responses. We, therefore, combined the proportion of win stay responses with lose shift responses and win shift responses with lose stay responses and modeled the effect of testing session on the proportion of each strategy exhibited by each species, while controlling for individual variation by allowing the intercept to vary among individuals (package glmmTMB; Brooks et al. 2017).

## Results

The majority of skunks (3 of 4) and raccoons (8 of 11) participated in the study and received an average of nine testing sessions (range = 6–12). Despite strong efforts to habituate coyotes to the experimental setup and motivate their participation, we only had one of six coyotes (male, Orion) participate in trials. With the exception of one coyote that was removed from testing prematurely due to stress (female, Vela), all other coyote subjects received an average of 55 testing days (range = 39–88) and 40 testing sessions (range = 26–65), during which they approached and touched the device at least once. Ultimately, we had a total sample size of 12 subjects across species (skunks:  $n = 3$ , raccoons:  $n = 8$ , coyotes:  $n = 1$ ) the majority of which had at least some prior experience (skunks: A:  $n = 1$ , B:  $n = 1$ , C:  $n = 1$ ; raccoons: A:  $n = 3$ , B:  $n = 2$ , C:  $n = 3$ ; coyotes: A:  $n = 1$ , B:  $n = 0$ , C:  $n = 0$ ). Subjects varied in the number of pre-reversals (range = 6–12) and reversals (range = 0–32) completed (Table 1). We experienced two instances of unexpected device malfunction during raccoon testing (once with Pollux and once with Rigel) and did not include data from these two instances in our analyses (see ESM).

Raccoons typically began interacting with the device during their first or second testing session (Fig. 2), completed

**Table 1** Individual traits and variation in performance of study subjects

| Name    | Species | Sex | Origin | Prior experience | Number of pre-reversals | Number of reversals | Side bias reversals | WSLS blocks | Reversal improvement* |
|---------|---------|-----|--------|------------------|-------------------------|---------------------|---------------------|-------------|-----------------------|
| Neptune | Skunk   | M   | CB     | A                | 12                      | 13                  | No                  | 0           | No                    |
| Saturn  | Skunk   | M   | CB     | B                | 10                      | 12                  | No                  | 2           | Yes                   |
| Jupiter | Skunk   | M   | CB     | C                | 6                       | 2                   | NA                  | 0           | NA                    |
| Mars    | Skunk   | M   | CB     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Luna    | Raccoon | F   | WC     | A                | 8                       | 4                   | NA                  | NA          | NA                    |
| Rigel   | Raccoon | M   | WC     | A                | 6                       | 20                  | Left                | 5           | Yes                   |
| Sirius  | Raccoon | M   | WC     | A                | 9                       | 23                  | No                  | 0           | Yes                   |
| Pollux  | Raccoon | M   | WC     | B                | 12                      | 32                  | No                  | 4           | Yes                   |
| Vega    | Raccoon | F   | WC     | B                | 9                       | 32                  | No                  | 5           | Yes                   |
| Astrid  | Raccoon | F   | WC     | C                | 12                      | 13                  | No                  | 0           | Yes                   |
| Castor  | Raccoon | M   | WC     | C                | 9                       | 31                  | Left                | 0           | Yes                   |
| Celeste | Raccoon | F   | WC     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Nova    | Raccoon | F   | WC     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Oberon  | Raccoon | M   | WC     | C                | 11                      | 28                  | No                  | 0           | Yes                   |
| Titan   | Raccoon | M   | WC     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Orion   | Coyote  | M   | WC     | A                | 12                      | 9                   | No                  | 2           | No                    |
| Cepheus | Coyote  | M   | CB     | B                | 0                       | 0                   | NA                  | NA          | NA                    |
| Draco   | Coyote  | M   | WC     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Leo     | Coyote  | M   | CB     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Perseus | Coyote  | M   | CB     | C                | 0                       | 0                   | NA                  | NA          | NA                    |
| Vela    | Coyote  | F   | CB     | C                | 0                       | 0                   | NA                  | NA          | NA                    |

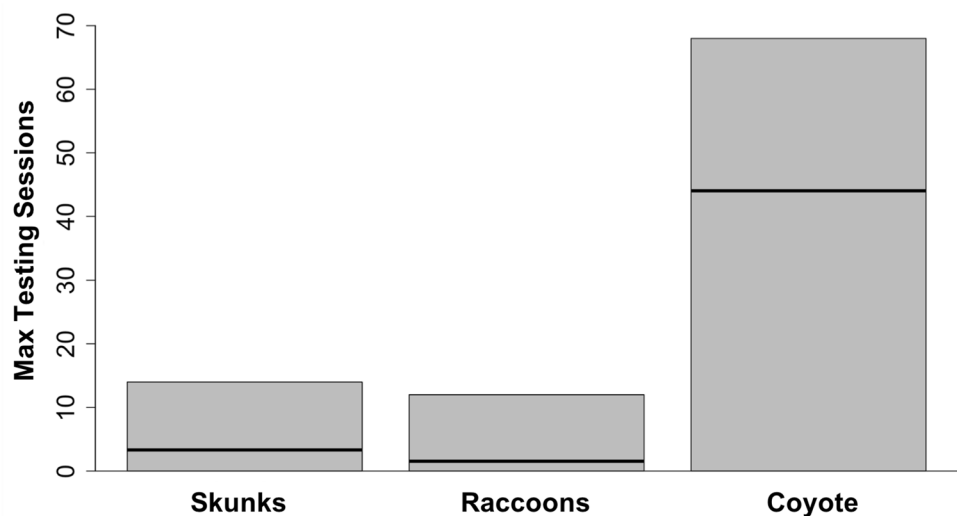
Sex: M = male, F = female; Origin: WC = wild-caught, CB = captive-born; NA = column not applicable to the individual

Prior Experience: A = moderate prior experience, B = low prior experience, C = no prior experience

WSLS blocks = Number of win stay–lose shift blocks (i.e., only 1 error made per block) performed in reversals

\*Improvement determined by *P* values and confidence intervals (see SI)

**Fig. 2** Maximum number of testing sessions allocated to skunks ( $n = 4$ ), raccoons ( $n = 11$ ), and coyotes ( $n = 6$ ). Black lines indicate the number of testing sessions administered before participants began interacting with the testing device (averages presented for raccoons and skunks). Although raccoon and skunk participants began interacting within the first few nights, Orion did not begin engaging with the device until his 44th testing session



an average of 2.4 reversals during each testing session (range = 0–6), and completed an average of 27 reversals in total (range = 4–32). Skunks also began interacting with

the device within their first few testing sessions (Fig. 2) but completed an average of 0.8 reversals per testing session (range = 0–2) and an average of nine reversals in total

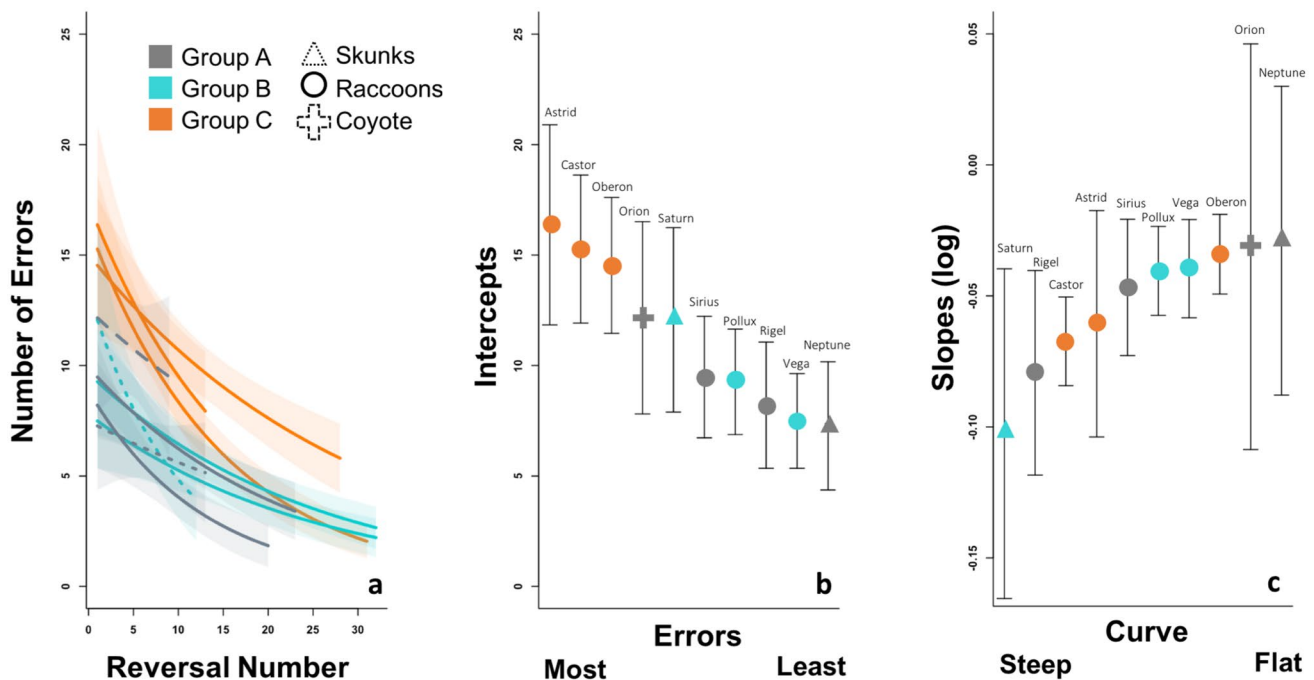


(range = 0–13). Our single coyote participant did not begin actively pushing on the pedals of the device until the 44th night (Fig. 2) and, similar to the skunks, typically achieved 0.5 reversals per testing session (range = 0–2) and completed nine reversals in total (Table 1).

Our analysis was limited by the number of individuals per species that participated in the study. Nevertheless, because we observed some behavioral differences among species in response to testing, and because our protocol varied slightly between the two testing facilities, we proceeded with investigation of the number of errors made by species groups (in addition to other factors that could explain variation in performance), but did so with caution. Our top model investigating predictors of performance included both reversal number and individual ID as fixed effects (see ESM Table 2 for all model selection results) and indicated that subjects improved across reversals ( $\beta = -0.05$ , 95% CI =  $-0.06$ ,  $-0.04$ ,  $P < 0.001$ ) (Fig. 3). Reversal number alone explained 26% of the variation in number of errors. Individual ID and prior experience explained an additional 16% and 11% (respectively) of the variation in the number of errors when included as fixed effects in the model alongside reversal number. In contrast, species identity explained only 2% of the variation in number of errors when included as a

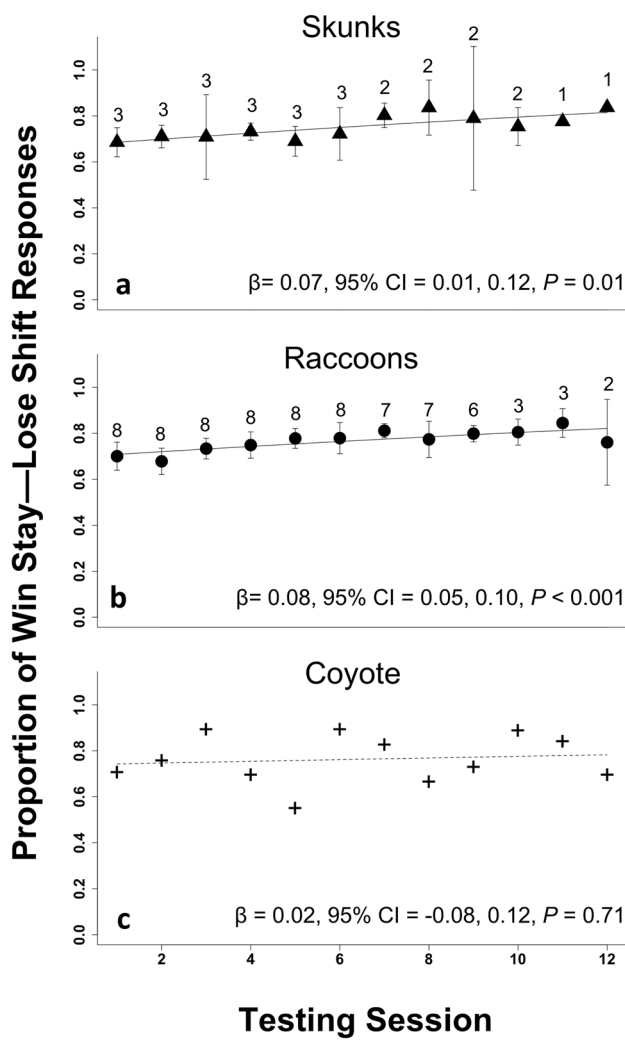
fixed effect in the model alongside reversal number, although again, this result should be interpreted with caution given our low sample size within each species group. In visually comparing the y-intercepts of each subject's learning curve (Fig. 3a), animals with no prior experience made a higher number of errors initially in reversals (Fig. 4b). However, no obvious patterns regarding prior experience emerged when visually comparing each subject's slope (Fig. 3c). We also did not observe any obvious patterns with regards to species in visual review of learning curves (Fig. 3a–c).

Poisson regression performed individually for each subject suggested that the majority of subjects improved across trials and thus was not constrained to groups with or without prior experience (Table 1; all individual models and accompanying metrics in ESM Table 3). One skunk (Saturn) and seven raccoons (Astrid, Castor, Oberon, Pollux, Rigel, Sirius, and Vega) showed improvement in reversals. In contrast, our single coyote participant (Orion) and one skunk (Neptune) did not show improvement. Except for one raccoon (Pollux), none of the subjects exhibited a decrease in the number of blocks needed to meet the learning criterion. Instead, we found that subjects typically required a low number of blocks to meet criterion in reversals (skunks: mean = 2.4, range = 1–4; raccoons: mean = 2.3, range = 1–6;



**Fig. 3** Learning curves ( $\pm$ SE) for each study participant during the reversal phase based on generalized linear models of individual performance (a). Panel (b) ranks the y-intercept of each participant's learning curve from the highest number of initial errors to the lowest number of initial errors made. Panel (c) ranks the slope of each learning curve from the steepest, indicating the greatest improvement made, to the flattest slope, indicating the least amount of improve-

ment. Reversal curves suggest that animals with no prior experience made a higher number of initial errors, but no clear pattern emerges with regards to species. Subjects are identified by species (line type and symbol) and level of prior experience (A = moderate prior experience, gray; B = low prior experience, blue; C = no prior experience, orange) (color figure online)



**Fig. 4** Win stay–lose shift analysis. Average proportion ( $\pm$ SE) of choice strategies employed by **a** skunk, **b** raccoon, and **c** coyote subjects across testing sessions with predicted linear model (includes data from all pre-reversals and reversals). Subjects primarily demonstrated a win stay strategy (60% of all choices) and win stay–lose shift increased slightly across trials for skunks and raccoons. The sample size (number of participants) per testing session is indicated (note: only one coyote participant)

coyote mean = 3.3, range = 1–6). The results of our side bias analyses suggested that two of our raccoon subjects (Rigel and Castor) may have had a left-side bias, but this did not inhibit their ability to improve in reversals (Table 1). One skunk (Jupiter) and one raccoon (Luna), only completed two and four reversals, respectively, and consequently had an insufficient amount of data to evaluate individual learning curves (see ESM).

With regards to the sequence of choices that subjects made across testing sessions, we found that win stay was the most common strategy (60% of all choices made by subjects). The proportion of win stay–lose shift responses increased across trials for raccoons ( $\beta = 0.08, 95\% \text{ CI} = 0.05,$

$0.10, P < 0.001$ ) and skunks ( $\beta = 0.07, 95\% \text{ CI} = 0.01, 0.12, P = 0.01$ ), whereas Orion’s performance varied across testing sessions and did not demonstrate an increase in win stay–lose shift responses (quasibinomial GLM with logit link:  $\beta = 0.02, 95\% \text{ CI} = -0.08, 0.12, P = 0.71$ ) (Fig. 4). However, Orion, along with Saturn (skunk), Pollux, Riegel, and Vega (raccoons), demonstrated a win stay–lose shift strategy (i.e., only one error made) multiple times in reversal testing (Table 1), albeit infrequent and not always repeated in succession.

## Discussion

Behavioral plasticity is expected to play an important role in the ability of animals to adapt to environmental variation (Metzke-Hofmann 2014) and is, therefore, likely to bolster their success in urban habitats (Ducatez et al. 2018). Here we measured the cognitive flexibility of three generalist mesocarnivores that are commonly found in urban habitats. All subjects across species typically required a low number of blocks (i.e., 2–3) to meet the 90% learning criterion and most demonstrated an ability to form and reverse associations. However, we observed differences in the response of subjects to testing and found moderate individual variation in reversal learning performance. This variation may be partially explained by an individual’s prior experience with the task, yet it did not affect an individual’s ability to improve their reversal learning across time. Intraspecific differences in cognitive flexibility may be also affected by traits outside of the scope of our study, including sex (Lucon-Xiccato and Bisazza 2014; Petrazzini et al. 2017), age (Johnson and Wilbrecht 2011; Tello-Ramos et al. 2018), temperament (e.g., bold vs. shy individuals; Mazza et al. 2018), and origin (Croston et al. 2017). Therefore, future research on the reversal-learning abilities of mesocarnivores would benefit from investigating the drivers of individual variation in testing performance among a single species with an increased sample size.

Raccoons generally showed engagement and success in this task. Most raccoons demonstrated rapid associative learning in that they learned to use the testing device and began passing blocks within their first testing session. Similarly, most raccoons completed several reversals and showed trends for improvement in reversal learning across time. These results join a growing body of literature that demonstrates the cognitive flexibility of raccoons and supports the notion that cognition and behavioral plasticity enables the heightened efficiency of raccoons to exploit urban habitats. For example, wild raccoons are able to solve novel foraging challenges associated with urban living (e.g., open garbage bins; MacDonald and Rivto 2016), demonstrate plasticity in social behavior (Prange

and Gehrt 2004; Prange et al. 2011), and have heightened opportunities for transmission of information in comparison to other urban mesocarnivores (e.g., group foraging, extended familial bonds, Gehrt 2004). Recent research employing the Aesop's Fable paradigm (Stanton et al. 2017) and multi-access puzzle boxes (Daniels et al. 2019) further confirms that raccoons can learn rapidly and are flexible in their problem-solving behavior.

Although our sample size for skunks was limited, we found that our skunk participants were willing to approach and engage with the device rather quickly. Nevertheless, they did not complete a high number of reversals and only one of three skunks demonstrated a trend towards improvement. Given their small body size and amount of reward received upon correct selections, we suspect that this deficit in performance may reflect a lack of food motivation and/or rapid satiation by skunks, rather than a particular learning barrier. For instance, skunks made a low number of errors in reversals and demonstrated a trend towards a win stay-lose shift strategy. In addition, our results generally align with the findings of Gossette et al. (1968) who reported that the reversal-learning performance of skunks, raccoons, and other mesocarnivores was similar. Because the cognition of skunks is generally under-investigated (but see Vonk and Leete 2017; Johnson-Ulrich et al. 2017), further research on the cognition of skunks, and how it relates to their urban adaptation, is currently needed. Additional comparative investigations of raccoon and skunk cognition may prove especially interesting because of the differences in their brain morphology (e.g., low relative brain size in skunks, high relative brain size and neuronal density in raccoons; Jardim-Messeder et al. 2017; Stankowich and Romero 2017), but this will require larger sample sizes of each species, as well as additional evidence linking mesocarnivore brain morphology with cognitive capacity (e.g., brain size and problem-solving ability; Benson-Amram et al. 2016).

Our results for coyotes are more ambiguous due to a low participation rate for this species. Although our single coyote participant, Orion, was capable of completing reversals, demonstrated a win stay-lose shift strategy in two of his reversals, and generally made a low number of errors, he exhibited wavering participation and a lack of improvement in testing. Captive coyotes at the same testing facility demonstrated behavioral plasticity in a similar operant conditioning study (Gilbert-Norton et al. 2009) and completed a problem-solving task with puzzle boxes (Young et al. 2019b). Moreover, wild, urban coyotes have shown behavioral plasticity in diet composition (Newsome et al. 2015) and activity patterns (Murray and St. Clair 2015). We, therefore, suspect that Orion's lack of improvement and the low participation by coyotes in this study may have been related to motivation and object neophobia, rather than a particular learning barrier or a lack of inhibitory control.

Neophobia towards the testing device in our study was not unexpected, because coyotes are generally known to be cautious of novel objects (Mettler and Shivik 2007; Windberg, 2008). However, we were surprised to find that captive coyotes continued to demonstrate neophobia toward our automated testing device despite our extensive efforts to habituate them to the experimental procedure. Although captive coyotes have been successfully habituated to testing apparatuses when a human investigator was involved and have demonstrated learning and flexibility in empirical studies of cognition (Gilbert-Norton et al. 2009; Young et al. 2019b), captive coyotes have also shown a lack of habituation to frightening devices that use a combination of light and sound stimuli (Darrow and Shivik 2009). Indeed, managers and livestock owners are known to employ these stimuli in conflict mitigation scenarios to successfully deter predation on livestock (e.g., Zarco-González and Monroy-Vilchis 2014; Lesilau et al. 2018). Similarly, in a recent problem-solving study, a puzzle box required modification to reduce the startle response by captive coyotes related to the noise made during door removal (Young et al. 2019b). The LED lights and motor-dispensing sound of our testing device also appeared to have startled the coyotes and may, therefore, explain why most of the coyotes never interacted with the device, despite showing interest and attempting to remove food from it (see ESM video 4 for example). Therefore, we recommend that future studies employing automated cognitive testing devices with coyotes reduce any unnecessary light and sound stimuli.

Although generalists may gain benefits from reduced neophobia and greater exploration, neophobia may also serve to protect individuals from the unknown potential dangers of new things (sensu the "Dangerous Niche Hypothesis", Greenberg 2003). In this way, coyotes may resemble other successful cosmopolitan generalists that show heightened aversion to novelty, such as rats (*Rattus spp.*) and corvids (*Corvus spp.*) because of their historic persecution by humans (Greenberg and Mettke-Hofmann 2001; Vernelli 2013; Greggor et al. 2016). However, unlike rats and corvids, urbanization may be relaxing pressure on coyotes and could explain why current research is revealing increased boldness in urban vs. rural coyotes (Schell et al. 2018, 2020; Breck et al. 2019; Brooks et al. 2020). Similarly, mixed findings on the cognitive and behavioral competencies of urban wildlife might imply that different cities impose different inter and intraspecific pressures, and that this may be sensitive not only to the natural history of a species, but also the degree of conflict animals face with the local human population (Griffin et al. 2017; Kozlovsky et al. 2017; Barrett et al. 2019; Schell et al. 2020). Indeed, enhanced cognition and behavior plasticity may be one of many strategies that facilitate exploitation of urban environments (Santini

et al. 2019; Sayol et al. 2020). Therefore, although cognition likely acts as a buffer (Sol 2009), we might expect diversification of the cognitive and behavioral strategies generalists use to exploit urban environments; some of which may demand more cognitive complexity, whereas others may be more cognitively simple (Davey 1989; McKinney 2006; Kozlovsky et al. 2017). In our study, we found only moderate individual variation in the number of errors made (i.e., explained 16% of variation), which may indicate similar levels of cognitive flexibility; however, we also observed behavioral differences among individuals and species that warrant further investigation. Experimental investigation of cognition in wild populations will continue to be invaluable in understanding urban adaptation and the co-evolutionary forces between humans and urban wildlife (Barrett et al. 2019; Schell et al. 2020).

Our study was limited by a small sample size of participants. Because we were unable to systematically encourage participation (e.g., food deprivation), we relied heavily on the interest and self-motivation of our subjects. Given this limitation, we were unable to generate enough subjects across traits of interest (e.g., sex, age, temperament, origin) to identify how these traits may have affected reversal-learning performance, and in most cases our analyses were limited in power. Furthermore, our protocol evolved over time as we gained experience working with these animals that have yet to be tested in this manner and, therefore, includes individuals that varied in prior testing experience. Thus, some of our results should be interpreted with caution. Nevertheless, the species-specific accommodations made during testing allowed us to adapt our methodology as necessary. Our study has, therefore, made important contributions to the field of comparative cognition and has expanded our ability to investigate the cognitive underpinnings of urban adaptation in a greater diversity of species. Automated protocols and testing devices, such as the one developed in our study and similar studies in birds (e.g., Bridge et al. 2019), remove the role of an experimenter and better enables research on cognition in the wild (Morand-Ferron, Cole, et al. 2015a, b), which is an important next step in understanding the adaptability of urban carnivores. Because carnivores represent an understudied yet diverse group of generalists and specialists that differ in their use of anthropogenic areas, including procyonids (e.g., raccoons vs. crab-eating raccoons (*Procyon cancrivorus*)), felids (e.g., bobcats (*Lynx rufus*) vs. Canada lynx (*Lynx canadensis*)), and ursids (e.g., black bears (*Ursus americanus*) vs. sun bears (*Helarctos malayanus*) or giant pandas (*Ailuropoda melanoleuca*)), this group can offer new insights in animal cognition and urban adaptation.

## Conclusion

Our study offers some support for the hypothesis that urban mesocarnivores are cognitively, and thereby behaviorally, flexible based on their performance in a classic reversal learning paradigm. Behavioral plasticity is expected to underlie the ability of generalists to persist in challenging environments, including urban habitats, where animals may be encountering novel, complex, and changing stimuli. The demonstrated ability of our subjects to form and reverse learned associations based on the cues of the paradigm suggests that they have the capacity to change their behavior in a flexible manner; however, there may be variation in this flexibility. Testing of wild individuals across urban–rural gradients, as well as in urban populations representing different human attitudes and behaviors towards wildlife, will be essential for linking flexibility in cognition to urban adaptation. Furthermore, variation in willingness of subjects to engage with novelty in this experiment serves as a reminder of the inter and intraspecific differences in exploration, and how such differences may reflect the different strategies of behavioral adaptation to urban habitats, even within a single group like generalists. Our study is an important first step in advancing current methodologies for the study of less-traditional species, and we expect that future studies of the cognition of wild mesocarnivores will benefit from automated testing devices like the one deployed in our study. Such contributions to our understanding of adaptation to urban habitats will advance our ability to mitigate human-wildlife conflict, conserve biodiversity in urban habitats, and elucidate the evolutionary trajectory of cognition in the Anthropocene.

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**Data availability** Data is available at <https://bit.ly/3lXbTFK>.

**Code availability** Code is available at <https://bit.ly/3lXbTFK>.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they do not have any conflict of interest.

**Ethics approval** This study was approved by the USDA National Wildlife Research Center's Institute for Animal Care and Use Committee (QA-2825).

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