



Problem-solving ability in wild raccoons, *Procyon lotor*, in relation to external factors and individual traits

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The cognitive process of innovation in animals produces new or modified behaviours in response to new challenges. Common raccoons rely on their problem-solving ability to exploit anthropogenic resources that are not freely available. As a result, they are often involved in human–wildlife conflict. We used two food extraction tasks of varying difficulty levels to measure problem-solving ability in wild raccoons living in three Canadian protected areas. We conducted experiments in two distinct locations within each park based on human footprint: recreation and preservation zones. We also looked at the effect of the presence of conspecifics and of two behavioural traits (exploratory diversity and persistence) on performance. Performance differed between the puzzles, with one of them being easier to solve based on success rate and time to success. The zone (presence of humans) did not affect problem-solving performance, while there was a tendency for solving time to increase with the presence of conspecifics. Exploratory diversity was positively related to success rate and time taken to solve. Contrary to predictions, persistence did not improve performance. There were also individual differences in performance in term of success rate and time to completion. We encourage using multiple concurrent tests to evaluate problem solving with wild individuals. Overall, we provide additional evidence that raccoons are apt problem-solvers, with the potential to adapt to new foraging opportunities, and a relevant species to study innovation in mammals.

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Innovative problem solving, which is overcoming an obstacle to attain a goal through a cognitive process, can help wildlife thrive in environments where there are novel challenges (Barrett et al., 2019; Griffin & Guez, 2014; Griffin et al., 2017; Pearce, 2008). Innovation is a hard concept to define (Ramsey et al., 2007; Reader et al., 2016); in this study we focus on the individual process (Ramsey et al., 2007), not the occurrence of a new behaviour in a population's repertoire (Reader & Laland, 2003). Problem solving has often been tested to evaluate behavioural flexibility and is considered to be adaptive as it opens foraging opportunities (Daniels et al., 2019; Johnson-Ulrich et al., 2022; Lea et al., 2020). As a cognitive trait, problem solving differs among individuals in a consistent manner, akin to behavioural personality traits (Boogert et al., 2018; Cauchoix et al., 2018; Griffin et al., 2015; Sih & Del Giudice, 2012).

The cognitive ecology framework considers how environmental factors affect cognition, and in turn, we can study how cognition affects fitness (Cauchard & Doligez, 2023; Huebner et al., 2018; Lea

et al., 2020; Mettke-Hofmann, 2014; Thornton & Truskanov, 2022). For this reason, it is important to conduct cognitive studies in ecologically relevant settings such as a species natural habitat (Healy & Rowe, 2014; Horn et al., 2022; MacDonald & Ritvo, 2016; Morand-Ferron et al., 2016; Pritchard et al., 2016; Thornton et al., 2014). Among factors that modulate behaviours in natural conditions is the presence of conspecifics (Brown et al., 2009), with competition and social interference potentially reducing cognitive performance (Stanton et al., 2022). In contrast, observational conditioning, social learning and mitigation of predation risk can improve problem-solving performance (Donaldson et al., 2012; Feyten et al., 2021; Papaj et al., 2019; Prange & Gehrt, 2004; Shettleworth, 2010; Young et al., 2019). Another factor that can affect wild animals' cognitive processes is exposure to humans and anthropogenic landscapes (Benson-Amram et al., 2022; Cook et al., 2017; Goumas et al., 2020; Johnson-Ulrich et al., 2022; Owen et al., 2017; Papaj et al., 2019; Schell et al., 2021; Wong & Candolin, 2015). For example, urban populations of many species perform better than rural ones in cognitive tasks (grey squirrel, *Sciurus carolinensis*: Chow et al., 2021a; birds: Griffin et al., 2017; raccoon, *Procyon lotor*: MacDonald & Ritvo, 2016; yellow mongoose, *Cynictis*

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penicillate: Müller & Pillay, 2023). Other studies have been more equivocal regarding the effect of urbanization. Under high levels of disturbance, urban house finches, *Haemorhous mexicanus*, performed better in problem-solving tasks than rural ones, but human disturbance itself greatly reduced performance overall (Cook et al., 2017). In one study, spotted hyaenas, *Crocuta crocuta*, in rural habitat were more innovative than urban ones (Johnson-Ulrich et al., 2021). Finally, within urban populations of Eurasian red squirrels, *Sciurus vulgaris*, an increase in human-built structures reduced problem-solving success (Chow et al., 2021b).

More innovative species are better at solving problems and predisposed to use anthropogenic resources, which might lead to more conflicts with humans (Barrett et al., 2019; Greggor et al., 2016; Lowry et al., 2013). Considering that cognitive traits can modulate human–wildlife conflicts, they are often overlooked by wildlife managers as they tend to only see the ‘big picture’: the population effect of mitigation methods and net results to stakeholders. However, conservation actions and their efficacy are tightly linked to wildlife behaviour and cognition (Greggor et al., 2014, 2020). For example, by identifying intraspecific variations in problem-solving ability, we can implement more targeted mitigation methods towards problematic individuals (Barrett et al., 2019; Swan et al., 2017). Understanding the behaviour of target species and the extent of their cognitive abilities is key to the efficiency and efficacy of nonlethal mitigation methods (Barrett et al., 2019; Blackwell et al., 2016; Goumas et al., 2020; Macdonald, 2016; Marzluff & Swift, 2017). Unfortunately, carnivores are under-represented in cognitive studies, compared to birds and primates (Benson-Amram et al., 2022; Daniels et al., 2019; Johnson-Ulrich et al., 2022). This is problematic as carnivores are often involved in human–wildlife conflicts (Bergstrom, 2017; Carter & Linnell, 2016; Expósito-Granados et al., 2019; Lozano et al., 2019; Sillero-Zubiri & Laurenson, 2001; Treves & Karanth, 2003).

The common raccoon is an omnivorous member of Carnivora, of medium size and part of the informal category of mesopredators (Buskirk & Zielinski, 2003; Glas, 2016; Hadidian et al., 2010; Prugh et al., 2009). Although relatively benign compared to other instances of human–wildlife conflict affecting peoples’ livelihood and security, raccoons are often maligned as an unruly source of annoyance and fear (Barrett et al., 2019; Justice, 2021; Pacini-Ketchabaw & Nxumalo, 2016; Pettit, 2010). Reasons to want to reduce contact rate between humans and raccoons include disease transmission risk, unwanted habituation, damage and interaction with pets (Bateman & Fleming, 2012; Beasley & Rhodes, 2008; Hadidian et al., 2010; Prescott, 2011; Rosatte, 2000). Conflicts with raccoons can also raise ethical issues and social turmoil within communities (Luther, 2013). The behaviour of the raccoon is not well understood in conflict situation, and information on its responses to different control strategies is incomplete and scattered (Curtis & Hadidian, 2010). The raccoon can adapt to complex and changing environments, such as rural and urban areas (Bozek et al., 2007; Daniels et al., 2019; Prange et al., 2004). It has a reputation for being ‘intelligent’ and, more specifically, is capable of innovative problem solving (Daniels et al., 2019; Stanton, 2020; Stanton et al., 2022).

Physical challenges, such as puzzle box paradigms, are popular and proven ways to assess problem-solving ability (Barrett et al., 2019; Benson-Amram et al., 2022; Boogert et al., 2018; Daniels et al., 2019; Griffin & Guez, 2014; Johnson-Ulrich et al., 2022; Reader et al., 2016; Washburn et al., 2017). Puzzle boxes usually involve food extraction, which make them ecologically relevant because raccoons have learned to take advantage of anthropogenic food resources (Barrett et al., 2019; Daniels et al., 2019; MacDonald & Ritvo, 2016). They often overcome similar types of physical challenges to attain food, such as opening a cooler, accessing

leftovers in a trash can or entering a cabin. Exposing subjects to different task difficulties (effort required to solve the task, e.g. time or number of actions), such as different puzzles or a multi-access box, allows researchers to explore variation in problem-solving ability (Auersperg et al., 2011; Daniels et al., 2019; Johnson-Ulrich et al., 2022). The context in which an experiment is conducted also sheds light on the ecological conditions that can affect problem-solving performance, especially in comparative experimental designs (Johnson-Ulrich et al., 2022). Apart from the rural–urban dichotomy, cognitive studies will benefit from research in many other environments to obtain a more refined understanding of the impact of external factors on cognitive traits.

Using puzzle boxes, we can quantitatively assess behavioural traits that potentially influence problem solving, such as exploratory diversity and persistence. Exploratory (or motor) diversity is the repertoire of actions exhibited by an animal while attending to a task and has been linked to problem-solving success (Griffin & Guez, 2014). Raccoons, having high dexterity, have the potential to express high exploratory diversity (Daniels et al., 2019). Higher exploratory diversity generally improves problem-solving performance (Daniels et al., 2019; Griffin & Guez, 2014). Persistence is commonly defined as the extent to which individuals engage with a device, measured as the time spent interacting with it, or the number of attempts (e.g. Griffin & Guez, 2014; Johnson-Ulrich et al., 2018). Raccoons show high levels of persistence, measured as the total duration of time spent working on a puzzle on their initial trial, which is positively correlated with success (Daniels et al., 2019). Higher persistence has also been linked to increased problem-solving success in spotted hyaenas (Benson-Amram et al., 2013, 2014; Benson-Amram & Holekamp, 2012).

Our objective was to evaluate problem solving in wild raccoons to assess how external (exposure to humans, presence of conspecifics, task difficulty) and internal factors (exploratory diversity, persistence) affect their performance. We used two single-access puzzle boxes: a cubic one with a door and latch (hereafter the Box), and one involving sliding and rotating concentric tubes (the Tube). Using two tests allowed us to assess convergent validity: a ‘good’ performance at one test should be reflected in the other as well (Boogert et al., 2018). We compared raccoons in their natural habitat, exploring two categories of locations (hereafter, the zones) differing by the level of human structures and activities: recreation and preservation zones of national parks. Zone, puzzle type and the presence of conspecifics are the external factors hypothesized to influence problem-solving performance. We predicted that, in recreation zones, success rate would increase and time to success would decrease, indicating better problem-solving ability. We also made similar predictions (improved success probability and time to solve) with the Tube puzzle in comparison with the Box, and in the presence of conspecifics in comparison with being alone. We also hypothesized that there is a link between behavioural traits (exploratory diversity and persistence) and problem solving, predicting that higher values for both would increase success probability and lower solving time. We further hypothesized that behavioural traits differ between the zones, with higher exploratory diversity and persistence in recreation zones. Finally, we expected individual variation in performance and predicted that individual performance would be correlated between the two tasks.

METHODS

Locations

We conducted field work in collaboration with the society responsible for managing Québec’s national parks (Sépaq) in the

south of the province. We selected three parks with ‘severe’ raccoon nuisance problems (Denis, 2017): Îles-de-Boucherville (hereafter referred to as IDB), Yamaska (YAM) and Plaisance (PLA). Raccoon density is very high in these parks (approximately 25–60 individuals/km²), especially in campgrounds (approximately 50–100 individuals/km²) based on past inventories and recent assessments (Lefebvre, 1998; Dellarosa, 2012; R. Charest, personal communication, 23 January 2019). These parks are relatively small (8–28 km²), adjacent to or around large bodies of water (river or lake) and encompassed in mostly urban or agricultural territories. We studied two site categories based on park zoning: intensive recreation zones and preservation zones. Recreation zones were characterized by human activity throughout the day and evening, the presence of camping sites, vehicles circulation at low speed (<20 km/h), campfires, dumpsters and a mosaic of ground cover (gravel or paved roads, parking, forest, fields, buildings, playgrounds). Therefore, recreation zones had higher indirect human disturbances, as defined by Chow et al. (2021b). Preservation zones were accessible to the public strictly by walking and biking trails during daylight, and with extensive forest cover. Distances between both zones ranged from 4 to 9 km (straight line) at each park. We ran the experiments for three summers (earliest–latest dates: 31 May–14 September) during 2019–2021. Plaisance park was not visited in 2021. From the start of the field season to the end, we ran the experiments approximately 5 nights/week without breaks longer than two nights, regardless of the weather. We baited and activated the puzzles prior to sunset, to have the experiments ready when the raccoons started foraging. The experiment was inactivated either when the puzzle was solved or when the period of activity ended (corresponding roughly to sunrise).

Experimental Set-up

We conducted experiments with wild raccoons using species-oriented baits (a few drops of custom odour bait, half a can of sardines or cat food and one marshmallow), but all wildlife could interact with both experimental devices. We installed the puzzles out of view from visitors, but easily accessible to the animals. Using the same type of puzzle (standardized method) as in other studies (Benson-Amram et al., 2016; Benson-Amram & Holekamp, 2012) facilitated comparison of our results with similarly conducted experiments (Krashennikova et al., 2020). The Box puzzle measured 30 cm per side and was made from steel mesh. There was one door with a sliding latch (Fig. 1a). To solve this problem, a raccoon had to slide the latch and pull on the door. The Tube puzzle consisted of two horizontal plastic tubes, with one sliding over the other (inner

tube: 50 cm long, 6 cm in diameter; outer tube: 34 cm long, 7 cm in diameter), requiring the animal to slide and turn the outermost tube to align two holes (approximately 5 × 10 cm) and access the food in the inner tube (Fig. 1b). The Tube is a new type of puzzle in studies of raccoon cognition. Both necessitate two consecutive actions that can be performed with the paws, mouth or muzzle of the animal. However, the Box requires the actions to be performed in a specific order, making it potentially more difficult to solve. Both puzzles were always presented concurrently.

The experiments were noninvasive; animals voluntarily approached or walked away from the apparatus. This ensured that only motivated animals participated in the trials. Each trial included all of an individual's interactions with a puzzle in a single night. Within a trial, an attempt to solve the puzzle began when an animal approached to within one body length of the puzzle; the attempt immediately ended when the animal either opened the puzzle (recorded as a successful trial) or withdrew more than a body length away from the unopened puzzle. We considered the puzzle to be solved when a raccoon gained access to the food in the puzzle with its paw, even if it did not immediately consume the reward. Whenever a puzzle was successfully opened during a trial, it was de facto disabled until the next trial (newly baited and closed on a subsequent evening). If all attempts within a trial ended with a withdrawal, the trial was recorded as unsuccessful. We cleaned any leftovers and replenished the puzzles before each night of trial.

Video Recording and Analysis

We recorded raccoons' interactions with the puzzles using motion-triggered night vision cameras (Argus 2, Reolink, Hong Kong), set up 3–4 m away. We also assessed the presence of conspecifics based on the video recordings. As soon as there was at least one other individual visible during a trial, the focal animal was classified as being ‘with conspecifics’. This was an imperfect measure, as there was no way to know whether there were raccoons behind the field of view of the camera or hidden by vegetation, but it does consider conspecifics that were closer, and thus more likely to have an influence on the focal subject. We quantified performance in problem-solving ability from the videos using the following measures: (1) success to solve the puzzle or not (binomial) and (2) time to completion (continuous) using successful attempts. We also calculated exploratory diversity as the number of unique actions directed at the puzzle boxes (see Appendix, Table A1; Benson-Amram et al., 2013, 2014; Daniels et al., 2019; Johnson-Ulrich et al., 2018). The exploratory diversity score accounts for noncontact actions that allow information gathering



Figure 1. Two puzzle boxes used to assess wild raccoons' problem solving and learning abilities. (a) A cubic steel box (in the closed position) that required (1) sliding the latch and (2) opening the door, in that order, to solve the puzzle. (b) Two sliding tubes (in the open position) that required (1) rotating and (2) sliding one of the tubes, in no specific order, to solve the puzzle.

(perception), as well as actions involving physical contact that could result in opening the puzzle. Finally, we evaluated persistence as the number of attempts an individual made within a trial, i.e. how many times the focal subject returned in a single night (including the initial attempt) until successfully opening the puzzle or giving up.

Individual Identification

Raccoons were identified through careful observation of the video footages by a single observer (L.L.), based on relative size to the puzzles, body characteristics (fur, tail, limbs) and scars and injuries, in a manner similar to [Chow et al. \(2021a\)](#) with grey squirrels. We conducted an intrarater reliability test (Cohen's kappa) on a small subset of recordings from the site with the highest activity level (IDB, recreation zone). We obtained 87% agreement ($\kappa = 0.851$) for intrarater reliability testing, corresponding to 'almost perfect' agreement ([Landis & Koch, 1977](#)). Most juveniles were excluded because they showed little initiative and were indistinguishable from each other in the videos, often interacting together with the devices, and therefore making it difficult to track each individual. We were unable to differentiate individuals by sex; therefore, we did not control for sex differences. [Daniels et al. \(2019\)](#) did not find a sex difference in problem-solving rate in their study on captive raccoons.

Statistical Analysis

We performed generalized linear mixed-effects models (GLMM; [Mundry, 2017](#)) with appropriate distribution and link functions depending on the response variable of interest. To assess the effect of zone, the presence of conspecifics, puzzle type, exploratory diversity and persistence (independent variables) on problem-solving success probability (dependent variable), we used a binomial distribution with the logit link function. We included as random terms individual and park to control for the repeated measurements. We used Akaike's information criterion (AIC; [Burnham & Anderson, 1998](#)) to select the most parsimonious model from all combinations of the five predictor variables. Using only successful trials, we performed GLMMs with a gamma distribution and log link function to test the effect of the zones, presence of conspecifics, puzzle type, exploratory diversity and persistence on time to success (continuous dependent variable). We also included individual and park as random terms. As above, we used AIC to select the most parsimonious model and performed hypothesis testing using the best model. Two final GLMMs tested for an effect of zone and presence of conspecifics (including their interaction) on the behavioural traits exploratory diversity and persistence. Both showed a Poisson distribution with a log link function. Finally, we calculated the phi coefficient as a measure of association between each individual's performance on the two tasks measured as success or not (binary outcome). We used the 'lme4' (1.1–31), 'MuMIn' (1.47.1) and 'irr' (0.84.1) packages with RStudio (2022.12.0, [Rstudio Team, 2022](#)). We set the significance level at $\alpha = 0.05$ or smaller and present means \pm SD.

Ethical Note

Experimental design and devices did not compromise the health and welfare of wildlife in any significant way. Research was approved by Concordia University Animal Research Ethics Committee (certificate 30011464), under Québec government scientific annual permits for research involving wildlife (2019-04-02-005-00-S-F, 2020-05-19-007-00-S-F, 2021-05-11-007-00-S-F). The permits and certificate covered live-trapping activity, but this was

ultimately not necessary for this study. We also obtained authorizations to conduct the research within each national park we visited.

RESULTS

We recorded 114 wild raccoons in three parks, for a total of 199 trials. The park with highest number of trials was IDB (100 trials), followed by YAM (84 trials) and PLA (15 trials). Raccoons interacted with the Box on 117 trials and with the Tube on 82 trials. Preservation and recreation zones were fairly equally represented in the data, with 105 and 94 trials, respectively. On 119 trials, the focal raccoon was alone, and on 81 trials, the focal individual was with at least one conspecific (average = 1.7 conspecifics). None of the raccoons was identified in both zones within a park, indicating that there was probably little movement during the summer.

The overall problem-solving success rate was 28%. Mean (\pm SD) total trial duration was 103 ± 178 s (range 3–1441 s). A single attempt lasted on average 60 ± 95 s. On three occasions, raccoons found an alternative solution to open the Box (2% of successful trials), either by reaching through the side mesh (accomplished only by smaller raccoons), or by toppling over the Box and causing the door to open randomly. The only other species to interact with the puzzles was the striped skunk, *Mephitis mephitis*, with eight interactions overall (6 times with the Box, 2 times with the Tube). None of these resulted in success (giving-up time: 48 ± 55 s; number of attempts: 1.4 ± 0.7 , range 1–3 attempts; exploratory diversity: 1.8 ± 1.7 , range 0–4).

When exploring success rate, the most parsimonious model based on AIC criteria included zone, puzzle type and exploratory diversity. Running a GLMM using these three predictor variables, we found an effect of puzzle type and exploratory diversity ([Table 1](#)). The Tube puzzle success rate (51%) was 4.3 times higher than for the Box (12%; [Fig. 2](#)). When an individual attempted both tasks and solved only one, 90% of the time it was the Tube. While success probability increased with exploratory diversity, persistence did not have a significant effect ([Fig. 3a](#)).

The most parsimonious model to predict time to solve the puzzle included all predictors except zone. Puzzle type, presence of conspecifics, exploratory diversity and persistence all significantly affected the time to solve ([Table 2](#)). Time to solve was lower with the Tube puzzle and in the absence of conspecifics ([Fig. 4](#)). Time to successfully complete each task increased with exploratory diversity and persistence ([Fig. 3b](#)).

We tested whether raccoons behaved differently in each zone and in the presence of conspecifics. Mean exploratory diversity was 2.3 ± 1.5 (range 0–7) and differed between the zones ($\beta = -0.391$, $CI = -0.681, -0.101$, $P = 0.0083$). The interaction term between zone and conspecifics was also significant ($\beta = 0.484$, $CI = 0.217, 2.228$, $P = 0.0259$), with higher exploratory diversity expressed when alone in the preservation zone and lower exploratory diversity expressed when alone in the recreation zone ([Fig. 5a](#)). Mean number of attempts, indicative of persistence, was 1.6 ± 1.1 (range 1–6) and did not differ significantly between zones ($\beta = 0.064$, $CI = -0.945, 0.026$, $P = 0.0636$) or in the presence or absence of conspecifics ($\beta = -0.080$, $CI = -0.412, 0.252$, $P = 0.6374$; [Fig. 5b](#)).

Table 1

Binomial distribution GLMM looking at the effects of zone, puzzle types and exploratory diversity on success probability by raccoons performing cognitive tasks

Variable	Beta	Lower CI	Upper CI	P	z
Zone	1.496	-0.149	3.140	0.0746	1.783
Puzzle	3.932	1.533	6.332	0.0013	3.212
Exploratory diversity	1.113	0.399	1.826	0.0023	3.056

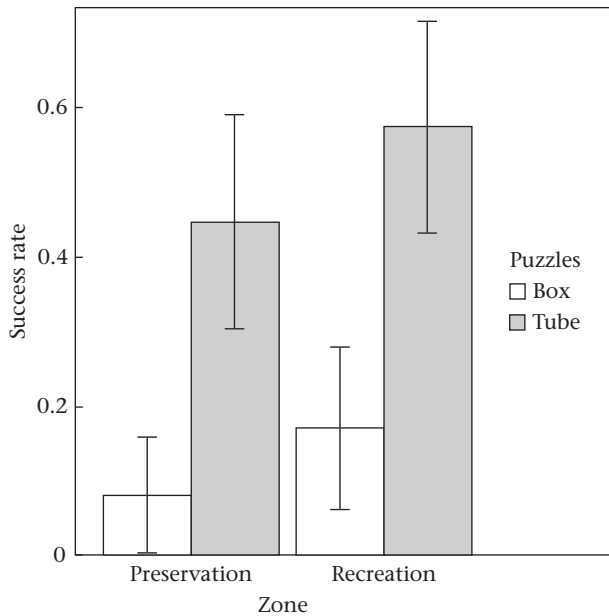


Figure 2. Comparison of problem-solving success rate from raccoons tested in recreation and preservation zones, by different puzzle types. Mean \pm 95% CI.

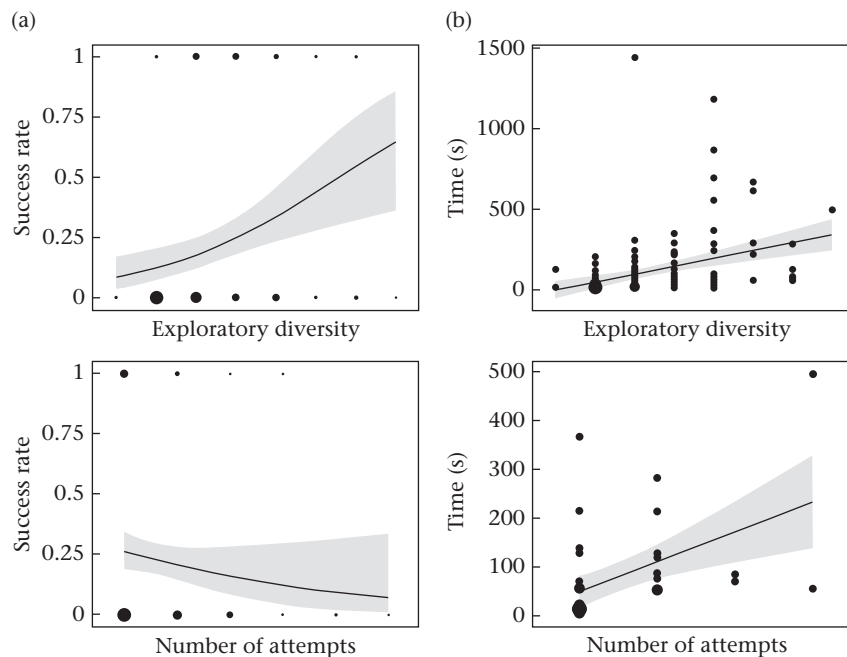


Figure 3. (a) Success rate and (b) time to successfully open the puzzles, in relation to exploratory diversity and persistence (number of attempts).

The interaction term between the factors was also not significant ($\beta = 0.460$, CI = $-0.028, 0.949$, $P = 0.0648$).

Among raccoons that only interacted with one puzzle ($N = 39$), 92% did not solve the puzzle. A minority of individuals (14%) succeeded on both tasks: 42% solved only one and 45% solved none. Success rate for one puzzle was related to success for the other, as calculated by the phi coefficient ($\phi = 0.241$, $N = 75$, $P = 0.0377$).

DISCUSSION

We assessed problem-solving ability in wild populations of raccoons and evaluated how external factors (the proximity to

humans, puzzle types, presence of conspecifics) and behavioural traits (exploratory diversity and persistence) influenced their performance. We monitored ~ 200 trials over three summers in three protected areas. Many individual raccoons voluntarily interacted with the puzzles, and there might have been a local enhancement effect, attracting more raccoons as the season advanced (Shettleworth, 2010). There was a stark contrast in success rate as well as time and number of attempts to solve between the two puzzle types. Based on both measures (solving probability and time), the Tube was easier to solve than the Box. The difficulty of each puzzle may influence the results on variability in problem-solving success (Daniels et al., 2019). The Tube was more befitting to trial-and-error solution, with a higher probability of solving due to chance (Thornton et al., 2014). Because raccoons showed better performance with the Tube, some individuals probably adopted a trial-and-error approach, rather than solving the puzzle by insight (reasoning, representation, planning; Seed & Mayer, 2017; Stanton et al., 2017). This difference between the two puzzles highlights the importance of testing cognitive abilities using multiple tests; convergent results using multiple different tasks provides more robust and coherent conclusions.

The physical and social environments, as well as human presence, have the potential to influence an individual's cognitive performance (Boogert et al., 2018; Goumas et al., 2020). In terms of fitness, recreation zones could be higher-value patches; thus, in-

dividuals that are better able to exploit such resources would have an advantage (Doligez & Boulinier, 2008; Storch & Frynta, 1999). The two zones, recreation and preservation (which differed in the amount of human activity and number of structures), did not influence success rate or time to achieve success. In comparison, MacDonald and Ritvo (2016) found a stark difference in problem solving, using a different task, in urban and rural raccoons (77% versus 0% success, respectively). In contrast, direct and indirect human disturbances decreased solving success in red squirrels (Chow et al., 2021b) and house finches (Cook et al., 2017). Our studied subpopulations (in each zone of each park) are unlikely to form distinct evolutionary units, which could explain the absence

Table 2
Gamma distribution GLMM looking at the effects of puzzle type, presence of conspecifics, exploratory diversity and persistence on resolution time by raccoons performing cognitive tasks

Variable	Beta	Lower CI	Upper CI	P	t
Puzzle	-2.134	-2.393	-1.876	<0.0001	0.132
Conspecifics	-0.533	-0.818	-0.248	0.0002	-3.665
Exploratory diversity	0.208	0.141	0.274	<0.0001	6.075
Persistence	0.553	0.415	0.690	<0.0001	7.881

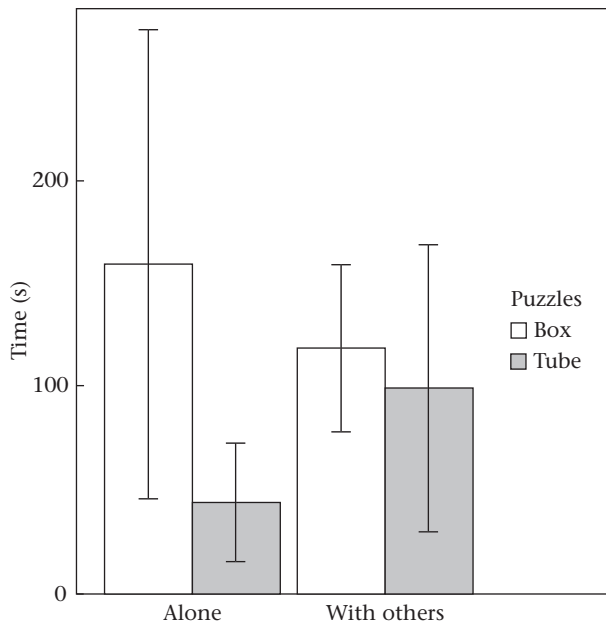


Figure 4. Time to successfully open the puzzles by wild raccoons in the presence of conspecifics or not, by different puzzle types. Mean \pm 95% CI.

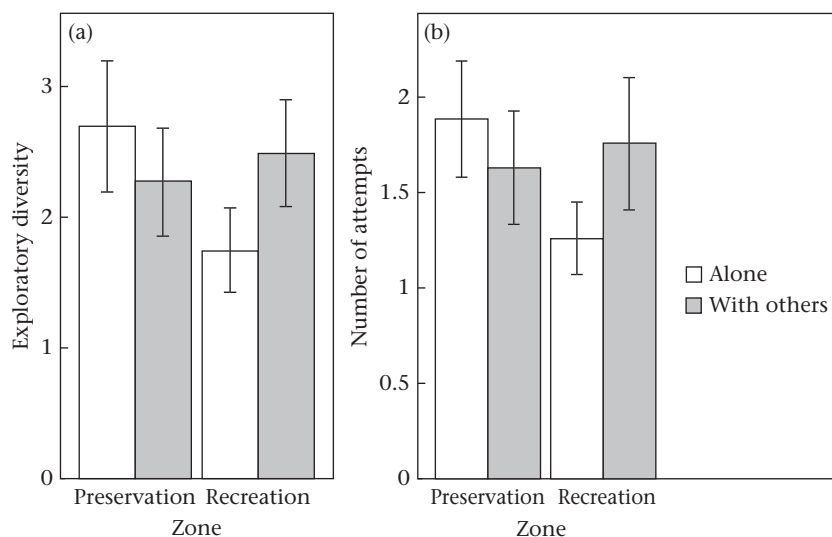


Figure 5. (a) Exploratory diversity exhibited by raccoons in the two study zones, whether they were alone or with conspecifics. (b) Number of attempts to solve the puzzles, indicative of persistence, in the two study zones, whether raccoons were alone or with conspecifics Mean \pm 95% CI.

of significant differences in problem-solving success. Even though we did not see any individual in two different zones, the raccoons from both zones in a single park can arguably be considered as being from the same population, due to the relatively small size of the parks and the absence of significant physical barriers.

We found a significant difference in time to success in the presence of conspecifics but no difference in success rate. The presence of conspecifics also reduced the exploratory diversity exhibited by focal raccoons in the recreation zone. Conspecifics can be seen as potential competition (Feyten et al., 2021; Stanton et al., 2022). Considering that there are no known raccoon predators in the study area and that the raccoons are habituated to humans, intraspecific competition might have caused a slight increase in awareness and distraction that resulted in less exploration and longer solving time, but ultimately it would not be enough to affect success probability. We found no evidence that the presence of conspecifics reduced solving time in order to maximize efficiency in the face of competition, as found by Chow et al. (2021b) for Eurasian red squirrels.

We found that exploratory diversity was positively correlated with success rate, as in Daniels et al. (2019) for captive raccoons using different puzzle boxes. The same relation between exploratory diversity and problem solving exists in other species (spotted hyaenas: Benson-Amram & Holekamp, 2012; birds: Griffin & Guez, 2014; chimpanzees, *Pan troglodytes*: Massen et al., 2013; yellow bellied-marmots: *Marmota flaviventris*: Williams et al., 2021; but see Asian elephants, *Elephas maximus*: Jacobson et al., 2022). The mechanisms involved are still unclear, and there might be a connecting variable (between exploratory diversity and problem solving) that is responsible for the relationship (Seed & Mayer, 2017). Time to success increased with exploratory diversity, which might simply mean that more time handling the puzzle means more time to try new actions. A more detailed analysis of the sequence and types of actions exhibited could shed light on this interaction. For example, are the subjects discarding an action when unsuccessful as in a real trial-and-error approach or is it more random, with no distinctive pattern? Or are there alternating sequences of passive (observations) and active (touching the puzzle with a body part) behaviours?

There was a weaker effect from persistence, and we only found an effect on time to success, which increased with the number of

attempts. Persistence has often been positively linked to problem-solving success (Benson-Amram et al., 2013; Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014; Jacobson et al., 2022; Johnson-Ulrich et al., 2018; Thornton & Samson, 2012; Young et al., 2019), including in raccoons (Daniels et al., 2019). We argue that the

proxies used to assess persistence have often been confused with work time (an issue also mentioned by [Chow et al., 2016](#)). However, an individual having a shorter work time to solve a problem should not be considered a less persistent one. Number of attempts, as we used, is less biased, but our results could be explained by more innovative raccoons solving in fewer attempts than less innovative ones. The ideal test for persistence would be to calculate the number of attempts at an unsolvable task to assess persistence, then submit the same individual to another solvable puzzle (e.g. [Rao et al., 2018](#)).

Individual variation in problem solving is well established in carnivores ([Benson-Amram et al., 2022](#)) and other taxa ([Griffin & Guez, 2014](#); [Rowell et al., 2021](#)), and our results concur with this. We found a correlation between the performance at each puzzle, indicating that some individuals were better on both tasks. Previous studies on wild and captive raccoons also found that individuals tend to solve multiple tasks, or none at all ([Benson-Amram et al., 2022](#)). A similar conclusion was reached for Eurasian red squirrels ([Chow et al., 2021b](#)). From a management point of view, this supports the idea that individual behaviour differences must be considered when choosing management strategies ([Merrick & Koprowski, 2017](#); [Swan et al., 2017](#)).

There are a few limitations to our experiment, some of them being inherent to the study of wild animals. First, we did not know or control for participating individuals' previous experiences ([Morand-Ferron et al., 2016](#); [Stanton et al., 2022](#)). Second, participation was voluntary and subject to various motivational factors such as hunger, breeding status and competition ([Griffin & Guez, 2014](#); [Morand-Ferron et al., 2016](#); [Stanton et al., 2022](#)). Third, some personality traits (e.g. boldness) may increase the likelihood of participation or performance in cognitive tasks ([Boogert et al., 2018](#); [Sih & Del Giudice, 2012](#); [Stanton et al., 2022](#)). Technology will contribute to future cognitive studies by helping identify individuals and remotely conduct and monitor experiments ([Griebling et al., 2022](#); [Pritchard et al., 2016](#)). More abundant and reliable studies on a diversity of species will enrich the field of animal cognition. As an added benefit, animal cognition studies have the potential, when properly explained and shared with the public, to generate appreciation and empathy towards wildlife ([Barrett et al., 2019](#)), and contribute to more serene human–wildlife coexistence. Additionally, nonlethal mitigation techniques, devised using our knowledge on animal cognition, can help transition the human–raccoon relationship from a paradigm of conflict to one of tolerance and acceptance ([Barrett et al., 2019](#); [Frank, 2016](#)). To design effective nonlethal methods, more research is needed in ecologically relevant contexts, especially on the cognitive basis of behaviour exhibited by problematic individuals.

Author Contributions

Louis Lazure: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft. **Robert B. Weladji:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

Data Availability

The data for this study are available on Figshare (<https://figshare.com/s/0a736d7e137ad759fd86>).

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.06.015>.

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Appendix

Table A1

Ethogram of observed actions performed by raccoons interacting with puzzle boxes used to quantify exploratory diversity (adapted from Daniels et al., 2019)

Behaviour	Description
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
Dig	Use paws to dig around the puzzle box
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 towards self
Pull knob	Use mouth or paws to move knob of door solution towards self
Push with arms	Use limbs to move puzzle box away from self
Push with head	Place head against puzzle box and move forward
Raise	Use nose or paws to move ledge of window solution up
Reach with paw	Place paw through puzzle box 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