Cognition of common mammal mesopredators and implications for their management

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ABSTRACT

Cognition of common mammal mesopredators and implications for their management

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Concordia University, 2023

An animal's cognitive abilities can modulate its interaction with humans and exacerbate conflicts. Mesopredator mammals demonstrate innovation and learning through their behaviour, especially in a generalist and widespread species like the common raccoon (*Procyon lotor*). The aim of this thesis is to combine wildlife management with the study of cognition to provide better coexisting conditions between humans and mesopredators. I first conducted a narrative synthesis to characterize the contexts in which conflicts occur with the raccoon, the red fox (*Vulpes vulpes*) and the striped skunk (*Mephitis mephitis*), and a meta-analysis to rigorously evaluate the efficacy of the mitigation techniques in reducing the intensity of conflicts. Although lethal interventions are regularly applied with relatively high efficacy, many nonlethal options are also effective. Many methods are based on a profound understanding of animal behaviour and cognition. Shifting toward cognitive studies, I experimentally tested problem-solving and learning performances of wild raccoons in three Québec national parks. I demonstrated innovative problem-solving in raccoons, and that task difficulty level has a clear effect on success probability and time to solve the problem. Higher exploratory diversity was linked to success, but not persistence. I also found evidence of learning, by an improved performance in term of success probability over consecutive trials. Raccoons living in a zone of the park more affected by the human presence also present more pronounced learning performance, which likely relates to their strong propensity to forage on human food. There are also indications that the improved performance gained through learning is retained over the winter season. Indeed, we found the success rates of the last trial from a summer to be similar to that of the first trial of the following summer. Basing mitigation interventions on scientifically proven methods and better integration of animal behaviour, may improve mesopredators management. Expanding our knowledge of cognition in common species contributes to our appreciation and tolerance toward wildlife. Overall, my findings could facilitate reaching a balanced coexistence between humans and mesopredators.

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Dedication

Je dédis cette thèse à ma famille :

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Contribution of authors

I was the main investigator for all the research work and as first author, responsible for the conception, data analyses, the writing of chapters related to this thesis and the writing of this thesis. The chapters 2, 3 and 4 were co-authored by Robert Weladji, PhD who contributed with the experimental design, the analyses as well as editing the manuscripts.

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List of Abbreviations

ANOVA:	Analysis of variance
CTA:	Conditioned taste aversion
GLMER:	Generalized linear mixed effect regression
GLMM:	Generalized linear mixed model
HWC:	Human-wildlife conflict
IUCN:	International union for conservation of nature
MELCCFP:	Minister of the Environment, the Fight Against Climate Change, Wildlife and Parks
SE:	Standard error
Sépaq:	Société des établissements de plein-air du Québec

Raccoon at Îles-de-Boucherville National Park, Boucherville, Québec, 2020 © Emily Collins

Chapter 1. General introduction

1.1 Human-wildlife conflicts

Interactions between the human species and non-human animals take on different forms in different settings. In a world that is increasingly urbanized and populated by *Homo sapiens*, conflicts between human and wildlife (so called human-wildlife conflicts, HWC) are becoming more common, as evidenced by the growing literature and communications on the subject. The context where those conflicts happen are varied (Distefano 2005; IUCN 2020; Nyhus 2016; Redpath et al. 2012; Torres et al. 2018) and subject to be amplified under global climate changes (Abrahms et al. 2023). Animals that are more often cited in HWC are large carnivores, elephants and primates (Distefano 2005; Inskip and Zimmerman 2009; Nyhus 2016; Seoraj-Pillai and Pillay 2017; Torres et al. 2018).

Human-wildlife conflicts can happen during nature-oriented activities, when the goals of humans (leisure, relaxation, access to nature) are negatively impacted by wildlife through disease transmission, annoyances such as odour and noise, food stealing, damages to material, or fear (Hudenko 2012; Jacobs 2012). Conversely, wildlife needs (food, space, reproduction, survival) are disrupted by human presence and activities (Green and Giese 2004; Knight and Gutzwiller 1995; Reed and Merenlender 2008; Taylor and Knight 2003). Recreational activities within protected areas affect wildlife activity pattern (Patten and Burger 2018) and frequently lead to HWCs. Outdoor activities are among the main contexts of HWC in Québec (Prescott 2011). Protected areas, like national parks in the Sépaq (Société des établissement de plein air du Québec) network, combine the dual objectives of preserving biodiversity and give access to nature to the public (Sépaq 2023). Protected areas in themselves do not prevent HWCs and may even be an important cause of conflict in parts of the world (Anthony and Szabo 2011; Nyhus 2016; Woodroffe and Ginsberg 1998).

Much has been done to manage HWCs in the past, and a lot of management actions are based on one-to-one transmission of information, as I learned discussing the topic with various stakeholders. There is a need for evidence-based interventions to tackle HWCs (Treves and Santiago-Ávila 2020). It is even more important considering poorly informed mitigation measures can worsen a conflict (IUCN 2020). Solutions are varied and can be preventive or reactive, simple or complex, cheap or costly, lethal or not (DiStefano 2005; Torres et al. 2018).

Systematic surveys and meta-analysis are powerful tools to search and synthetize research evidence (Koricheva et al. 2013; Pullin and Stewart 2006). They have covered topics such as wildlife conservation, natural resources management, animal behaviour and more recently HWC (e.g., Inskipp and Zimmermann 2009; Kansky et al. 2014; Seoraj-Pillai and Pillay 2017; Snijders et al. 2019). A systematic review will be useful in exploring the link between mitigation methods and the animal behavioural responses to determine the efficacy of the intervention (Greggor et al. 2016).

1.2 Mesopredators

Mesopredators are midranking predators within an ecosystem (Prugh et al. 2009). More restrictive definitions only include members of the order Carnivora, weighing between 1-15 kg (Buskirk and Zielinski 2003, Gehrt and Clark 2003, Roemer et al. 2009). In addition, a mesopredator cannot self-regulate its population density, in comparison to large apex predators (Wallach et al., 2015). In Québec, mammal mesopredators are a recurring source of nuisance to protected areas users and no mitigation measure has yielded satisfactory results so far (Dellarosa 2012; Denis 2017a,b). Within those parks and in the south of the province in general, common raccoons (*Procyon lotor*, rarely called northern raccoons), striped skunks (*Mephitis mephitis*) and red foxes (*Vulpes vulpes*) exhibit widely varying behaviours between and within species, are widely distributed and abundant, and are involved in frequent interactions with humans (Fournier 2013; Prescott 2011). In term of HWCs, mesopredators are less studied than larger or apex predators (Lozano et al. 2019).

Raccoons, family Procyonidae, are abundant in North America and are well established elsewhere in the world following successful albeit accidental introductions. The distribution of the raccoon extends from the Canadian boreal forest to Central America, and it was introduced in Europe and Asia, approximately 100 and 50 years ago, respectively (Lotze and Anderson 1979, Ikeda et al. 2004). The favourable geographic areas for raccoons under future climate scenarios will expand significantly to the north (Larivière 2004; Louppe et al. 2019). During winter in Canada, raccoons do not hibernate but become less active, and winter severity is inversely correlated to overwinter survival (Pitt et al. 2008; Reid 2006). Raccoons are generalist, known as active problem-solvers and can adapt to complex and changing environment (Bateman and Fleming 2012; Daniels et al. 2019; Prange et al. 2003). They are omnivorous and opportunistic foragers, and are well adapted and successful in anthropogenic landscapes such as rural and urban areas (Bozek et al. 2007; Daniels et al. 2019; Hadidian et al. 2010; Lotze and Anderson 1979; Prange et al. 2004). Raccoons have a reputation of being "intelligent" (Cole 1907; Daniels et al. 2019; Justice 2021; Pettit 2010). The behaviour of the pervasive raccoon is not very well understood in conflict situations, and information on their responses to different control strategies is incomplete and scattered (Curtis and Hadidian 2010). The red fox was originally found in North America, Europe, North Africa, and Asia and was introduced to Australia in the nineteenth century, making it the terrestrial carnivore with the widest geographical distribution (Larivière and Pasitschniak-Arts 1996; Macdonald and Reynolds 2004). It is strictly carnivorous and mostly nocturnal (Larivière and Pasitschniak-Arts 1996). It is discrete, widespread and adaptable to different habitats, including highly anthropogenic ones (Larivière and Pasitschniak-Arts 1996). The striped skunk distribution is limited to North America; in the USA it overlaps with four other skunk species in the genus *Mephitis*, *Spilogale* and *Conepatus* (Wilson and Reeder 2005). It is primarily insectivorous but is nevertheless highly opportunistic (Wade-Smith and Verts 1982). The striped skunk is mainly crepuscular and nocturnal (Wade-Smith and Verts 1982).

Mesopredators are interesting to study because of their relatively high cognitive abilities. Among the three species aforementioned, the raccoon is especially renowned for is mental prowess (Bozek et al. 2007; Daniels et al. 2019; Prange et al. 2004; Stanton 2020; Stanton et al. 2022). Much less cognitive work has been conducted on red foxes and striped skunks. We could liken the cognitive abilities of red foxes to other Canidae, but most studies involved captive animals. Wolves (*Canis lupus*) and dogs (*Canis familiaris*) show some skills, but no higher form of cognition (Berghänel et al. 2022). Few studies also specifically targeted the striped skunk, but they tend to show comparable cognitive performance to other mesopredators (Stanton et al. 2021). The relatively high cognitive abilities of some mesopredators can increase the risk that they get involve in HWC, because they find ways to exploit anthropogenic resources (Benson-Amram et al. 2022; Goumas et al. 2020; Schell et al. 2021). Finally, common species are important to study because of their ecological impact as widespread keystone components of their communities (Lidicker 2015). None of the three species has a threatened status either at the global, federal or provincial levels (Government of Québec 2023; Government of Canada 2023; IUCN 2023). Globally, according to the IUCN Red List (2023), the striped skunk and red fox are considered stable, and the raccoon is increasing.

1.3 Cognition

Carnivores' cognition tends to be understudied compared to other taxa (Benson-Amram et al. 2022). However, their ecological and behavioural diversity makes them stimulating research subjects and allows comparative cognitive studies. In addition, exposure to humans can drive changes in their behaviour and cognitive abilities (Benson-Amram et al. 2022) which makes them good candidates to study the impact of anthropogenic changes.

The field of animal behaviour is replete with terms with inconsistent definitions. For this reason, it is important to establish the definitions of the terms that are used in this thesis and put them in relation to one another. Cognition is the process by which animals interpret, retain, and act on information collected through their senses (Morand-Ferron et al. 2016; Shettleworth 2010), and it has the potential to modulate HWC (Barrett et al. 2019; Blackwell et al. 2016; Higham and Shelton 2011; Lowry et al. 2013; Sarmento and Berger 2017). Cognitive process can lead to an innovation, which is the invention of a new behaviour or modification of an existing one (Griffin and Guez 2014; Reader et al. 2016). Ramsey and colleagues (2007) add that the innovation cannot be the result of social learning or environmental induction. Innovation is required to solve a new problem, which helps wildlife thrive in environments where there are novel challenges (Barrett et al. 2019; Griffin et al. 2017). Innovation can be considered at the individual level (as we do in this thesis) or at a higher level (group, population or species; Ramsey et al. 2007). Problem-solving consists in finding a novel mean to reach a goal when direct means are unavailable, and it is a sign of behavioural flexibility (Barrett et al. 2019; Benson-Amram et al. 2022; Griffin and Guez 2014; Lea et al. 2020; Seed and Call 2010). Behavioural flexibility is the ability to adapt efficiently to variation in environment, by altering its behaviour, freed from intrinsic constraint (Audet and Lefebvre 2017; Coppens et al. 2010; Lea et al. 2020). Learning is a change in response (behaviour) to a stimulus (Chow et al. 2016; McFarland 2014; Papaj et al. 2019). It is the mechanism by which innovation is consolidated and integrated in the behavioural repertoire (Daniels et al. 2019; Ramsey et al. 2007). There are multiple variants of learning, and this thesis is interested in operant learning, when the animal learns of a predictive relationship between an action and an outcome (Griffin et al. 2015).

Both problem-solving and learning are highly contextual and vary between individuals. Cognitive performance varies with taxonomy (Benson-Amram et al. 2016, 2022), and between populations and individuals (Barrett et al. 2019; McDougall et al. 2006; Merrick and Koprowski 2017; Thornton and Lukas 2012). The environment has an immense influence on the cognitive process (Owen et al. 2017). Innovation and learning can be adaptive as they can provide access to novel resources, particularly in relation to human induced changes (Benson-Amram et al. 2022; Daniels et al. 2019; Johnson-Ulrich et al. 2022; Lea et al. 2020; Papaj et al. 2019). Learning is part of a raccoon foraging strategy (Dalgish and Anderson 1979), and probably for other species as well, and is involved in food extraction tasks. As a result, cognition allows organisms to adapt to novel or changing environment (Mettke-Hofmann 2014, Sol et al. 2016). We need to be careful when drawing conclusions from animal cognition studies, assessing cognitive skills on the basis of their adaptive value for the study species and not from an anthropocentric viewpoint (Bräuer et al. 2020).

With its apparent intelligence, the common raccoon started to be considered an interesting model to study behaviour at the start of the 20th century (Cole 1907, 1912, 1915; Davis 1907; Gregg and McPheeters 1913). Practical and scientific considerations slowly contributed to the demise of the raccoon as a study subject about two decades later (Pettit 2010). For many years onward, we saw a handful of mostly laboratory-based studies of the raccoon cognition (Dalgish and Anderson 1979; Davis 1984; Elder and Nissen 1933; Johnson and Michels 1958; Michels et al. 1961; Warren and Warren 1962). Meanwhile, more abundant studies focused on other aspects of the raccoons' behaviour like foraging, dispersal and mating mostly out of public health interests and nuisance concerns (e.g., Beasley and Rhodes 2010; Hauver et al. 2010; Judson et al. 1994; Reynolds et al. 2015; Robert et al. 2012; Rosatte et al. 2010). The cognitive buffer analysis states that large brain size relative to the body is associated with better cognitive abilities (Sol 2009) and that holds true within Carnivores (Benson-Amram et al. 2016). Raccoons fit in this paradigm as a potentially performing species because of their relatively large brain and neuron density (Jardim-Messeder et al. 2017). Even within raccoons, those that are better problem-solvers exhibit more cells in the hippocampus region of the brain (Jacob et al. 2021), and urban raccoons exhibit higher relative brain size (Anderson 2020).

1.4 Linking behaviour and management

Wildlife managers often overlook animal behaviour when addressing HWCs (Berger-Tal et al. 2011; Blackwell et al. 2016; Caro 2007; Edelblutte et al. 2022; McDougall et al. 2006).

They tend to only see the big picture: the population effect of mitigation methods and net results to stakeholders. In reality, conservation actions and their efficacy are tightly linked to wildlife behaviour and cognition (Greggor et al. 2014, 2020; Merrick and Koprowski 2017). Merging behavioural studies with conservation is regarded as a way to optimize protected area planning and wildlife management (Blumstein and Fernández-Juricic 2010; Berger-Tal and Saltz 2016; Caro and Sherman 2011; Graeme 2019; Greggor et al. 2016; Marzluff and Swift 2017; Mumby and Plotnik 2018). Information about cognition helps with conservation measures by shedding light on the motivation and obstacles for engaging in a behaviour (Edelblutte et al. 2022; Mumby and Plotnik 2018) and the various stages of the cognitive process (Barrett et al. 2019; Greggor et al. 2014). Although more and more recognized as important, the connection between behaviour and conservation has been understudied (Barrett et al. 2019; Berger-Tal et al. 2016; Blumstein and Fernández-Juricic 2004; Merrick and Koprowski 2017). Greggor et al. (2016) highlighted research priorities for the integration of the two domains, including questions on the behavioural responses to human recreation activities, protected area management and behavioural characteristics involved in conflicts. From a research standpoint, studying behaviour in wild settings informs us on the ecological drivers of cognition (Cauchoix et al. 2017; Fehlmann et al. 2020; Griffin et al. 2017; MacDonald and Ritvo 2016). High cognitive abilities can have an adverse effect on the species itself, as it can lead to more conflicts with humans (Barrett et al. 2019; Greggor et al. 2016). Furthermore, if we can identify intraspecific variation in cognitive ability, we can implement more targeted mitigation method toward problematic individuals (Barrett et al. 2019; Swan et al. 2017).

1.5 Partnership and stakeholders' engagement

Human-wildlife conflicts are often more about discordance between different (human) group of interests (Peterson et al. 2010; Redpath et al. 2015). This is why stakeholders' engagement is important to truly address the roots of conflicts (König et al. 2021; Marchini 2014; Nyhus 2016; Treves et al. 2006, 2009). Researchers also need to partner with wildlife managers to optimize the use of all the data they can obtain in the field. And in the end, researchers need to reach out to various stakeholders with easily comprehensible and practical recommendations (Sutherland and Wordley 2017).

In the specific context of this thesis, managers of protected areas and experts in wildlife control and trapping are identified as stakeholders on the topic and were contacted to obtain their point of view and possibly access unpublished documentation. Sépaq has been involved in the research project from the start, including discussion on the scope of the study, research questions and methodology for the experimental stage. We contacted wildlife control professionals and trappers through their respective associations in Québec, to obtain additional literature on which they might base their practices and to have their opinion on the subject. Contacting stakeholders is an essential albeit overlooked part of systematic reviews (Haddaway et al. 2017; White and Ward 2010).

All field work for this thesis was conducted in collaboration with Sépaq in national parks in southern Québec (Fig. 1.1). In January 2019, we met with the head of conservation which gave us the greenlight to go ahead, working directly with parks management. I selected parks with the most severe HWC issues with raccoons (Fig. 1.1). The parks themselves are divided in zones based on usage, from intensive recreation to extreme preservation zones, through service areas. Three field seasons were conducted in Yamaska and Îles-de-Boucherville national parks, two seasons in Plaisance national park, and only exploratory field work was done in Oka national park.

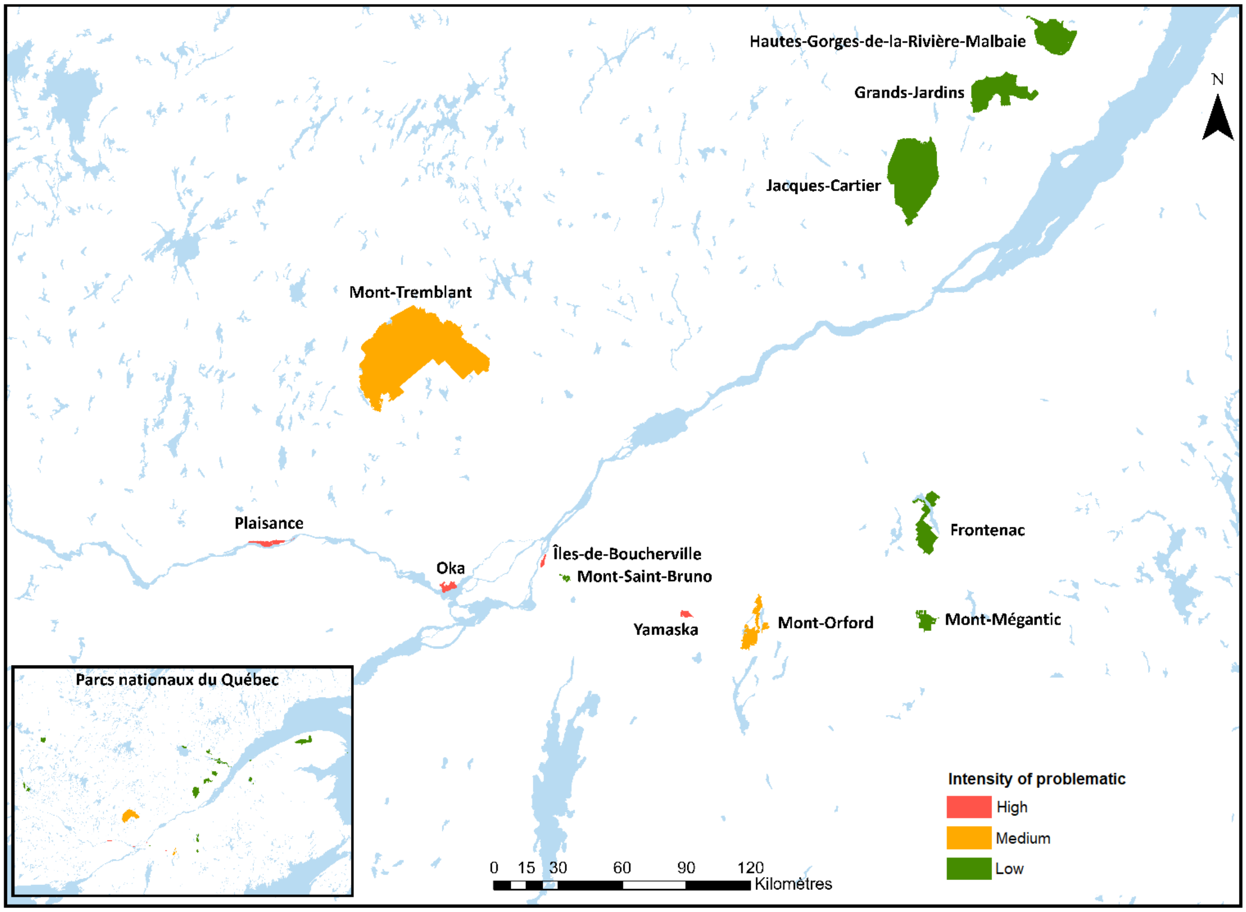


Figure 1.1 National parks in southern Québec categorized according to severity of HWC involving raccoons (source: Denis, 2017a).

Concordia University, Sépaq and the Québec Minister of the Environment, the Fight Against Climate Change, Wildlife and Parks (MELCCFP) all emitted permits and authorizations to conduct the research.

1.6 Objectives

With this thesis I aimed to assess two cognitive traits in a common nuisance species (the raccoon) and use that information to improve current mitigation methods applied to conflicts between mesopredators and humans. To achieve this goal, I took two main approaches. First, I looked to available information through a systematic search to define conflicts between humans and mesopredators, and evaluated mitigation strategies used in the past. Then I set up an experimental study to obtain behavioural data on raccoons when they are exposed to cognitive tasks. Through these experiments, I studied their cognitive abilities, more precisely problem-solving and learning. I finally combined information about mesopredators management and their cognition to integrate the two fields. Combining all those results, I set out to link the study of cognition to the management of wildlife. This gives my results more relevance when translated into the context of HWC that requires management actions. Because this project was developed with the input of various stakeholders, I will seek out opportunities to offer practical management input based on the results of these studies. I will be able to make recommendations about which mitigation methods would be the most appropriate to deal with the innovative raccoon in many conflictual situations in Québec.

Objective 1: Describe the context in which HWCs involving three common species of mammal mesopredators happen and evaluate the efficacy of various mitigation methods to decrease these HWCs. In chapter 2, I conducted a narrative synthesis with the papers collected through a systematic search. I applied rigorous search and review protocols, based on available standards. I searched for mitigation methods applied on the common raccoon, the red fox and the striped skunk, and extracted information about the conflict, the context, the publication and the mitigation methods. I followed with a meta-analysis on the efficacy of experimentally tested methods. Meta-analytical calculations summarized which methods were efficient or not. Finally, I highlighted the limitations and knowledge gaps in literature pertaining to this subject.

Objective 2: Study the problem-solving ability of raccoons (chapter 3), under the hypothesis that problem-solving will vary in relation to external factors and behavioural traits. My sub-objectives were 1) to compare raccoons foraging in different zones of protected areas based on the human activity, 2) compare raccoons foraging alone or with conspecifics, 3) estimate the between individuals' variability in problem-solving, and 4) test two different cognitive tasks (puzzles). Raccoons are excellent study subjects because they are already known to have good cognitive abilities (relative to other mammals), are abundant in southern Québec and are involved in frequent conflicts with humans. Studying cognition in wild animals, free to interact with the experimental devices, puts those results in an ecologically relevant framework.

Objective 3: Study the learning ability of raccoons (chapter 4), under the hypothesis that learning will vary in relation to external factors and behavioural traits. I used the same experimental setup as the previous objective, evaluating problem-solving performance on two cognitive tasks over consecutive trials. I identified raccoons individually from the video records and was able to document if they participated in the experiment on different nights, which were considered trials. I considered the effect of exposure to humans (different zones within the parks) and task difficulty. I also explored the effect of two behavioural traits on learning: persistence and exploratory diversity. Finally, we predict that learned solution will be retained for long periods, so I tested for the effect of the off-season (no experimentation for many months between field seasons) on their performances. Evaluating learning in addition to problem-solving offered a better picture of the raccoons' cognitive abilities and how it can explain their success in different environments.

Chapter 2. Methods to mitigate human-wildlife conflicts involving common mesopredators: A meta-analysis

Lazure, L. and Weladji, R.B. 2023. Methods to mitigate human-wildlife conflicts involving common mesopredators: A meta-analysis. Journal of Wildlife Management. e22526.

2.1 Abstract

Conflicts between humans and mesopredators are frequent and widespread. Over the last decades, conflicts have led to the development and application of different mitigation methods to diminish the costs and damage caused by such conflicts. We conducted a systematic literature search and meta-analysis to assess the influence of different mitigation methods on 3 common nuisance species: raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and striped skunks (*Mephitis mephitis*). A majority of the studies, from 1963–2022, were conducted in North America, followed by Australia, and Europe. The predation of wildlife species of conservation concern by nuisance species is the main reported source of conflict in the published literature. Lethal control is the most commonly tested method and is generally effective at reducing conflicts based on the calculated effect size. Barriers have mixed effects, with electric fences and nest exclosures both being effective, whereas conventional fences seem to be less effective. Repellents mimicking predators (e.g., guard animal, predator smell) are also effective. Conditioned taste aversion is a promising approach, but no precise product or chemical has proven to be effective. Many interventions suffered from a lack of validation through experimental approach. Research on human-mesopredator conflict mitigation would benefit from repeated studies using the same methods in similar contexts thus reducing heterogeneity in the results and by testing new and innovative methods.

2.2 Introduction

In the era of the Anthropocene, coexistence between humans and wildlife inevitably leads to interactions. They vary in scale and intensity, and can be positive, negative, or neutral (Peterson et al. 2010, Prescott 2011, Nyhus 2016, Lozano et al. 2019, Hill, 2021). The term human-wildlife conflict (HWC) is used when there is a real or perceived threat to humans or their interests, leading to negative effects on humans and frequent retaliation against fauna (International Union for Conservation of Nature [IUCN] 2020, Su et al. 2022). Human-wildlife conflicts often prompt the introduction of mitigation measures, which seek to reduce, contain, or remove damages (Messmer 2000, Marchini 2014, Conover and Conover 2022).

Increasing human tolerance to interactions with wildlife would be an important first step to deal with HWCs but is either underemphasized or overlooked completely (Messmer 2000, Treves et al. 2009, Curtis and Hadidian 2010, Baruch-Mordo et al. 2011, Dubois et al. 2017). Historically, lethal solutions have been put forward to mitigate HWCs (Treves and Naughton-Treves 2005, McManus et al. 2015), and their use persists today. Lethal methods have the advantage of directly decreasing the size of the problematic population, thus reducing the risk of damage in the short-term (Drake 2014). A survey among ranchers in Wyoming, USA, demonstrated that lethal methods were perceived to be more effective than nonlethal ones against a range of predators, including foxes (Scasta et al. 2017). It has also been reported to be more simple and cheaper to implement, but it is not always the case (McManus et al. 2015). It is often an effective method that yields concrete welfare benefits for remaining animals (Hampton et al. 2018). Despite its extensive use, lethal management has been increasingly unpopular and controversial with the public and is currently under regulatory oversight and ethical considerations (Liss 1997, Reiter et al. 1999, Dubois et al. 2017, Boulet et al. 2021, Conover and Conover 2022*)*. Lethal control remains more acceptable against mesopredators compared to more charismatic megafauna (Glas 2016) and is more acceptable toward introduced or pest species (van Eeden et al. 2020). Acceptability also differs by the demographics and attitudes toward wildlife of the person surveyed (van Eeden et al. 2019, Baker et al. 2020).

For social acceptability and ethical considerations, nonlethal management approaches should be considered if not currently prioritized in mitigating human–wildlife conflicts (Shivik 2006, Drake 2014). Even for the control of large predators, nonlethal approaches are favored by the public, from rural to urban areas in Ohio, USA (Stanger et al. 2022). Such methods are novel and largely untested, or established but understudied, and their effectiveness needs to be compared to lethal methods in a scientifically-sound manner (Sillero-Zubiri et al. 2007). Nonlethal methods include physical barriers (i.e., any structure that can impede access to a particular place or object [fences, exclosures]), aversive and disruptive stimuli, guard animals and conditioned taste aversion (CTA; Treves and Karanth 2003*,* Baker et al. 2007a). Apart from barriers, nonlethal methods are often based on cognitive mechanisms such as learning, neophobia (fear of novelty), and categorization (process of classifying or differentiating cues; Greggor et al.

2014). For example, by combining food with a chemical compound resulting in a negative stimulus, CTA draws on the cognitive mechanisms of association and learning (Schulte 2016, Snijders et al. 2021). Although animal cognition is extensively studied, its applicability to wildlife management has been the subject of less investigation.

In North America, 3 native mammalian species are often mentioned in HWCs: the common raccoon (*Procyon lotor*), the striped skunk (*Mephitis mephitis*), and the red fox (*Vulpes vulpes*; Gehrt et al. 2010, Bateman and Fleming 2012, Glas 2016). The distribution of the raccoon extends to Central America, and it was introduced in Europe and Asia, approximately 100 and 50 years ago, respectively (Lotze and Anderson 1979, Ikeda et al. 2004). The red fox was originally found in North America, Europe, North Africa, and Asia and was introduced to Australia in the 19th century, making it the terrestrial Carnivore with the widest geographical distribution (Larivière and Pasitschniak-Arts 1996, Macdonald and Reynolds 2004). Among terrestrial vertebrate species in the United States, raccoons, striped skunks and red foxes rank respectively 2nd, 3rd and 10th in the number of complaints received by the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) Wildlife Services between 2014-2021 (Cassini 2022). Those species qualify as mesopredators: a midranking predator within an ecosystem (Prugh et al. 2009). More restrictive definitions only include members of the order Carnivora, weighing between 1-15 kg (Buskirk and Zielinski 2003, Gehrt and Clark 2003, Roemer et al. 2009). In addition, a mesopredator cannot self-regulate its population density, in comparison to large apex predators (Wallach et al., 2015).

Under the mesopredator release hypothesis, environmental changes, including anthropogenic effects, drive large carnivores away from a territory, releasing competition and creating an expansion in density or distribution of mesopredators (Crooks and Soulé 1999, Prugh et al. 2009). This can lead to more frequent HWCs with mesopredators as they become more pervasive in an area (Curtis and Hadidian 2010). These common species are important to study because of their ecological influences as widespread keystone components of their communities (Lidicker 2015). Literature on human-carnivore conflicts is strongly biased toward large species (such as wolves, bears, and big cats), whereas the medium-sized families Mephitidae and Procyonidea are underrepresented (Lozano et al. 2019). Furthermore, we included raccoons, red foxes, and striped skunks in the same study because any mitigation method used against one could be relatively easily adapted to the others. We excluded coyotes (*Canis latrans*) from the study despite them being sometimes classified as mesopredators (Buskirk and Zielinski 2003, Prugh et al. 2009, Bateman and Fleming 2012, Glas, 2016). Due to their larger size, the severity of the conflicts and more negative human perception (Fox 2006, Curtis et al. 2007, Bateman and Fleming 2012, Elliot et al. 2016), they require mitigation methods that are not easily transferable to the 3 selected species. Furthermore, with the range contraction of wolves (*Canis lupus*) and other large carnivores in North America (Berger and Gese 2007, Ripple et al. 2014), coyotes are now functionally and ecologically apex predators in many ecosystems (Crooks and Soulé 1999, Roemer et al. 2009, Prugh et al. 2009, Wallach et al. 2015).

A lot of HWC management actions are based on a limited and informal transmission of information based on discussions with various stakeholders (e.g., trappers, pest control professionals, protected area managers, municipal service managers). Human-wildlife conflict management is very context-dependent, so the accumulation of studies produces a *corpus* of data from experiments varying in terms of species, habitats, sample characteristics, research designs, analytic strategies, and sampling errors (Cooper and Hedges 2009, IUCN 2020). An ideal HWC management plan needs to select appropriate mitigation methods and tools and elaborate on their known (or unknown) effectiveness (Can 2021). Systematic surveys and meta-analyses are powerful tools to regroup and synthetize research evidence (Pullin and Stewart 2006, Koricheva et al. 2013, Pullin et al. 2013). In the past, they have covered topics such as wildlife conservation, natural resources management, animal behaviour and more recently HWCs (Inskip and Zimmermann 2009, Kansky et al. 2014, Seoraj-Pillai and Pillay 2016, Snijders et al. 2019). A systematic review is therefore important in exploring the link between mitigation methods and the animal behavioural responses to determine the efficacy of the intervention (Greggor et al. 2016).

Here, we present an analytical review of mitigation methods toward 3 common mammal mesopredators (raccoon, red fox, striped skunk). Our objectives were to survey the mitigation methods that have been tested and the context in which the studies have been conducted, obtain a general picture of their efficacy, and identify knowledge gaps.

2.3 Methods

We first conducted a systematic literature search and then conducted a meta-analysis on a subset of selected studies (Pullin and Stewart 2006). We designed a rigorous search methodology to handle unavoidable challenges in exploring an ecologically and sociologically complex topic such as inconsistent reporting, and disparity in the methods and contexts between studies (Inskip and Zimmermann 2009, Holland et al. 2018).

2.3.1 Literature Search

We followed the guidelines and standards for systematic reviews and maps (Haddaway et al. 2018; Appendix 2.7.1). We gathered articles and other documents published in English and French in Web of Sciences, ProQuest, bioRxiv, and Google Scholar. In addition, we consulted 35 websites related to wildlife conservation and management (Appendix 2.7.2). In search engines, we combined 2 keywords: 1 corresponding to the focus species (common or scientific name) and 1corresponding to the topic of interest, among the following terms: conflict, control, habituation, mitigation, nuisance, persecution, pest, and problem. Additionally, we analysed the reference sections of found articles allowing us to incorporate additional articles in our study. We first screened the retrieved literature based on their title, then the abstract and finally the full text. Inclusion was conservative, meaning that when in doubt, we included an article to be reviewed in the next stage. An article containing quantitative data on a method's effectiveness was eligible for inclusion. We included studies with before–after, control–impact or a combined research design, and that explicitly stated the studied population, intervention, comparison and outcome (Berger-Tal et al. 2019). Causes of exclusion at the full-text screening stage included: incompatible goal of study, wrong species or context, issue in research design, missing methodological details, unreported sample size, inadequate comparators, and not reporting new data.

2.3.2 Data extraction and synthesis

We read selected studies and coded extracted data to manage the discrepancy in measures from one study to another (Table 2.1). We assigned each study to a conflict type: wildlife killing (when the mesopredator preys are species of conservation concerns, which conservationists are monitoring or actively managing for their protection), livestock killing, disease spread, vehicle collision, annoyance, or multiple concurrent conflicts. We did not quantitatively evaluate the severity of conflicts for each publication. Instead, we described the severity using criteria reported by previous studies (Inskip and Zimmerman 2009, Seoraj-Pillai and Pillay 2016), which was quite subjective given that only limited information was provided by each study. We categorized mitigation methods in the following categories (and sub-categories within parenthesis): lethal methods (poison, shooting, traps), barriers (conventional fences, electric fences, exclosures), repellents (competitor signals, predator signals, sensory stimuli, guard animals), CTA (different chemical compounds), diversionary feeding, reduction of attractants, and the combination of more than one method applied simultaneously. We then recorded if these methods were reported by the authors as successful at reducing HWCs, made them worse or had no effect. We collected metadata on a variety of aspects of the study, including bibliographical information, study year, location characteristics, target species, and intervention (Snijders et al. 2019). We calculated descriptive statistics of the metadata, allowing us to better understand the published literature on human-mesopredator conflicts and its management.

Table 2.1 Extracted data from selected publications after systematic literature search on mitigation of conflicts with common mammal mesopredators to describe literature on human-mesopredators conflicts, describe the context of the conflicts, report mitigation experiments, and calculate effect sizes.

Literature	Conflict	Mitigation	Effect size
Authors	Habitat	Method (main types)	Sample size
Country	Species	Method (sub-types)	Mean of control/after group
Journal (or type of publication)	Human antagonist	Experimental design	Mean of treatment/before group
Title	Severity of conflict	Response variables	Standard deviation of control/after group
Year of publication	Type of conflict	Duration of experiment	Standard deviation of treatment/before group
		Effect as reported by authors	
		Variation (%) of outcome	

The selected studies covered different contexts, species, methods, durations, and response variables. As a result, heterogeneity (confounding factors) in the data is high and raises issues of comparability. To address these concerns, we took 4 precautions: we described the different contexts and methods seen in the literature; we analysed the data at different levels, by mitigation methods and by species; we explored the potential of publication bias and knowledge gap; and we carefully and conservatively interpreted the results.

We organized the data and determined the response variables used by the authors to test mitigation efficacy. This could reflect a direct (e.g., mesopredator density) or indirect (e.g., survival of a prey species) effect. We then calculated the mean results, the standard deviations and sample sizes for the control and treatment.

2.3.3 Estimating effect sizes

To assess the effectiveness of mitigation methods, we calculated the Hedges' d effect size from each study (Rosenberg et al. 2013). We extracted the mean of conflict metric when mitigation was applied (treatment, Y_t) or not (control, Y_c) and applied the following formula:

Eq. 2.1

$$d = \frac{\bar{Y}_t - \bar{Y}_c}{\sqrt{\frac{(n_t - 1)s_t^2 + (n_c - 1)s_c^2}{n_t + n_c - 2}}} J$$

where, n is the sample size, s is the standard deviation, and J is a correction for small sample size.

Eq. 2.2

$$J = 1 - \frac{3}{4(n_t + n_c - 2) - 1}$$

Hedges' d effect size ranges from −∞ to +∞. We interpreted the magnitude of effect size using the following conventional and expanded rule of thumb (Cohen 2013, Sawilowsky 2009): 0.2 small, 0.5 medium, 0.8 large, 1.2 very large and 2.0 huge. The directionality (positive or negative) was interpreted depending on the metric calculated in each study.

We calculated the sampling variance (v_d) as (Rosenberg et al. 2013):

Eq. 2.3

$$v_d = \frac{n_1 + n_2}{n_1 n_2} + \frac{d^2}{2(n_1 + n_2)}.$$

We calculated a grand mean effect size ($\bar{\theta}$) by combining effect sizes using a random effects model (Rosenberg et al. 2013):

Eq. 2.4

$$\bar{\theta} = \frac{\sum w_i \theta_i}{\sum w_i},$$

with variance

Eq. 2.5

$$s_{\bar{\theta}}^2 = \frac{1}{\sum w_i}.$$

We used the inverse of the variance to weight observations:

Eq. 2.6

$$w_i = \frac{1}{s_i^2}$$

We conducted categorical meta-analyses where categorical variables were treated as random effects because we expected the true effect may vary among studies (Gurevitch and Hedges 1999, Borenstein et al. 2009). We refer to methods which mean effect size with 95% CI are positive, to be effective. Alternatively, a method will be considered more effective relative to another if its mean effect size is higher. After obtaining Hedges' d effect size values, we calculated heterogeneity to characterize the data in more details. We calculated 2 distinct relative measures:

Eq. 2.7

$$Q_T = \sum w_i \left(\theta_i - \bar{\theta}\right)^2$$

and

Eq 2.8

$$I^2 = max\left[0.100 \times \frac{Q_T - (n-1)}{Q_T}\right].$$

The Q test (Q_T) assesses the heterogeneity among effect sizes, by following a chi-square distribution (Huedo-Medina et al. 2006). I^2 describes the percentage of variation across studies that is due to heterogeneity rather than chance (Higgins et al. 2003) and is complementary to Q_T (Huedo-Medina et al. 2006). A significant Q_T or high I^2 suggest that there may be some additional unexamined factor influencing the effect sizes (Higgins and Thompson 2002).

We used the MetaWin software (version 3.0.7) to perform the meta-analysis calculations (Rosenberg 2022). We also assessed whether the outcome reported by the authors (i.e., was the effect of the mitigation method good, bad, mixed, or neutral) aligned with calculated effect sizes. To do this, we calculated a 1-way analysis of variance comparing effect sizes of the 4 possible outcomes. We followed up with a post hoc Tukey Honestly Significant Difference, to do pairwise comparisons between the outcomes reported in the publications. We conducted a linear regression between effect size and experiment duration (squared root days) to determine if long-term mitigation methods yielded higher effect sizes than short-term techniques. We used R (4.2.3, R Core Team 2023) to calculate the analysis of variance and linear regression, and set the significance level at $\alpha = 0.05$.

2.3.4 Assessing publication bias

We used a rank correlation test (Spearman's ρ) to determine whether there was a significant correlation between sample size and effect size, which would suggest a bias toward publication of tests with larger effects (Begg and Mazumdar 1994, Branton and Richardson 2011). We also performed a cumulative meta-analysis, ordered by year of publication (Leimu and Koricheva 2004). We randomly assigned orders to experiments published within the same paper. We also used 2 methods to estimate the number of missing studies necessary to change the results of the meta-analysis from significant to nonsignificant. We performed the trim and fill procedures to find unpublished results (Møller and Jennions 2001, Jennions and Møller 2002). We used 3 estimators (R_0, L_0, Q_0) and reported the 3 results (Duval and Tweedie 2000, Shi and Lin 2019). We also calculated a fail-safe number (Rosenberg method, N_+) to estimate the number of unreported non-significant studies needed to change an overall significance to non-significance (Rosenthal 1979, Rosenberg 2005, Branton and Richardson 2011). We will compare N_+ to Rosenthal (1979) rule of thumb of $5k + 10$ (k = number of studies in the meta-analysis) indicating vulnerability to publication bias. We calculated Spearman’s ρ with the program R (4.2.3, R Core Team 2023) and ran the other analyses with MetaWin (Rosenberg 2022).

2.4 Results

2.4.1 Attribute of literature

As expected, we obtained a low specificity (proportion of retrieved material judged relevant; Pullin and Stewart 2006; Appendix 2.7.3). We retained 218 experiments from 148 different published sources in the descriptive review (Appendix 2.7.4). The 3 oldest papers selected are from Balser et al. (1968), Chessness et al. (1968) and Mann (1968). There was a steady increase (from 0.5–1.43 times) in the number of papers over the decades up until the 2000s, and a plateau between the 2000s and 2010s. Scientific journals were the main source of data (129/148), followed by proceedings (7), reports (5), thesis (5), patent (1) and book (1). Among peer-reviewed articles, wildlife management journals were the most common including The Journal of Wildlife Management (21/129), Wildlife Society Bulletin (11), Wildlife Research (11), Biological Conservation (10) and Journal of Applied Ecology (9) with all other sources representing <5 each. The United States was the most represented country in the literature (74/148; Fig. 2.1), followed by Australia (38), the United Kingdom (11) and Canada (7).

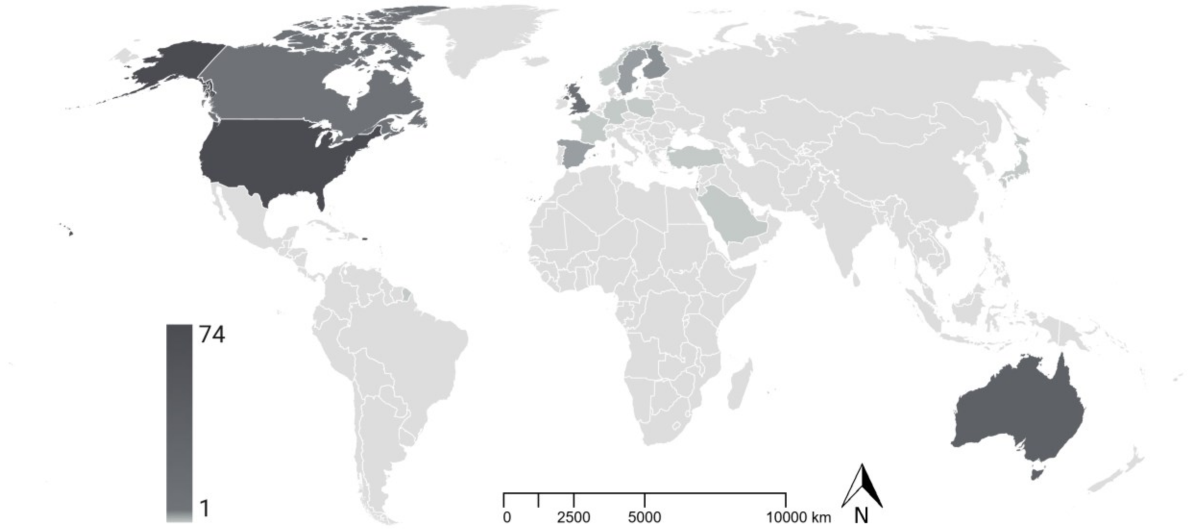


Figure 2.1 Source countries of studies found through the systematic review from 1968 to 2022 regarding mitigation methods to manage human-wildlife conflicts involving raccoons, red foxes and striped skunks. The legend represents the number of articles per country. Scale is only true at the Equator.

2.4.2 Mesopredator-human conflicts description

The red fox was the most common subject of the studies (106/218), followed by raccoons (38) and striped skunks (15). An additional 59 studies looked at mitigation aimed at multiple species, including ≥2 of the species of interest. In North America, all 3 species were identified in the publications, often concomitantly (raccoons in 36 studies, striped skunks 14, red fox 12, and 58 studies with more than 1 species). In Australia, Europe and the Middle East, all interactions were about the red fox. Overall, severity levels qualified as either low or moderate. Most experiments related to conflicts over wildlife killing (154), especially predation of shorebirds and turtles' nests. Other type of conflicts that prompted testing mitigation methods were livestock killing (19), annoyance or nuisance (6), risk of disease transmission (6) and collision with vehicles (3). In urbanized settings, material damage and annoyance were the most common form of nuisance. Some conflicts were multifaceted (7), and 22 studies did not report a specific conflict. Different types of conflicts affected all species, but foxes were involved in all livestock killing and multifaceted conflicts and were never reported as a source of annoyance. Wildlife managers were the most common human antagonists in conflicts with mesopredators (156), whereas farmers and ranchers were the second most affected group (20). Other groups (< 6 each) included: public health managers, pest control professionals, hunters, drivers, and the general public. No specific human antagonists were identified in 20 studies. Studies were most commonly carried out in forested habitats (62), followed in order by agricultural lands (32), seashores (32), prairies (26), wetlands (25), arid regions (12), urban/suburban areas (11), freshwater habitats (7), in captivity (4) and in 7 studies, it was not determined.

2.4.3 Mitigation methods

A wide range of mitigation methods has been tested, with lethal methods representing 112 studies. The relative number of lethal method evaluations remained between 36 and 86% every decade up until the 2020s. The other represented mitigation methods were barriers (36), repellents (26), CTA (19), and diversionary feeding (9). Most studies (121) collected data ≥1 year from the start of the experiment. Very few (6) tested immediate effects (<1 day). On average, experiments and the monitoring of effects lasted slightly > 3 years. A majority (58%) of the studies measured mitigation effects (response variable) through indirect measures such as nest success, prey population size and predation rates. Most experiments were designed as control–impact (122), others being before–after (38) or the combination of both designs (43). A remaining 15 studies did not provide information on the study design or involved another type of study (e.g., modelling).

2.4.4 Effectiveness of interventions

We included 137 experiments in the meta-analysis, from 88 distinct publications. Mean global effect size was 1.019 (95% CI = 0.830–1.209), which is a large effect. Heterogeneity measures were $Q_T = 213.07$ (df = 136, $P < 0.001$) and $I^2 = 36.17\%$. When we pooled all species together, some mitigation methods stood out as being effective (Fig. 2.2). Lethal methods produced a large effect size (ES = 1.161, 95% CI = 0.899–1.424; Fig. 2.2). Exclosures over nests (ES = 1.219, 95% CI = 0.714–1.723) and electric fences (ES = 1.192, 95% CI = 0.607–1.777) seemed to be effective, whereas traditional fences were not (ES = 0.224, 95% CI = -0.587–1.034). Guard animals (ES = 1.983, 95% CI = 0.132–3.834) and predator smells (ES = 1.415, 95% CI = 0.356–2.473) were very efficient methods to repel mesopredators, whereas competitor mimics (ES = -0.934, 95% CI = -2.457–0.590) and lights (ES = -0.105, 95% CI = -2.312–2.103) were not. Conditioned taste aversion was effective (ES = 0.849, 95% CI = 0.262–1.436), but no single product was sufficiently tested to prove to be a good option. Diversionary feeding (ES = 0.387, 95% CI = -0.556–1.329), reduction of attractants (ES = 1.437, 95% CI = -0.650–3.524) and the combination of >1 method (ES = 1.242, 95% CI = -0.480–2.964) all had non-significant results. Other mitigation methods that were reported in the literature but were not included in the meta-analysis (either not tested, not adequately reported or insufficient sample size) are: field borders, sensory-based repellents, fertility control, human presence, and other combinations of different methods.

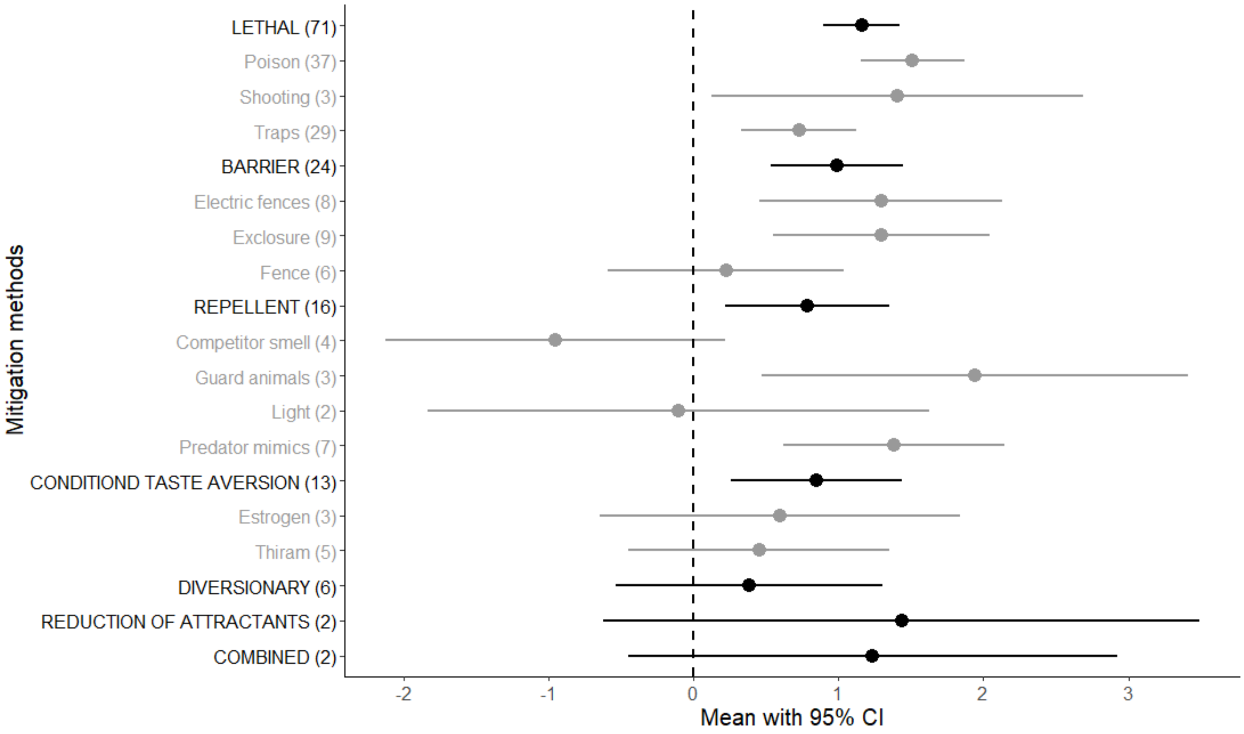


Figure 2.2 Effect sizes (mean with 95% CI) by types (black) and sub-types (if *n*>1; grey) of mitigation methods against human-wildlife conflicts involving raccoons, red foxes and striped skunks, following a meta-analysis covering 1963-2022. The sample size is within the parenthesis next to the methods.

An analysis by species showed that mitigation methods tended to be successful against raccoons (ES = 1.213, 95% CI = 0.712–1.715, *n* = 20) and red foxes (ES = 1.138, 95% CI = 0.852–1.425, *n* = 65). Lethal methods and repellents showed very large effect sizes against raccoons, unlike barriers and CTA (Table 2.2). Barriers, diversionary feeding, reduction of attractants and repellents did not show significant effect size against red foxes; on the other hand, CTA and lethal methods (more precisely the use of poison baits) had very large effect sizes (Table 2.2). There have been less experiments conducted with skunks, and there was no indication that mitigation methods have been successful (ES = 0.128, 95% CI = -0.696–0.951, *n* = 8). The efficacy of mitigation also differed depending on the type of conflict (Table 2.3).

Table 2.2 Effect size with 95% CI and sample size of different types and sub-types of mitigation methods effect, following a meta-analysis on 3 common mammal mesopredators. CTA = conditioned taste aversion.

Species	Mitigation	Effect size	95% CI	Sample size
Raccoon	Barriers	0.764	-0.689–2.218	3
	CTA	0.695	-0.501–1.891	4
	Estrogen	0.608	-0.935–2.150	3
	Lethal	1.323	0.398–2.248	7
	Traps	1.306	0.230–2.382	6
	Repellents	1.835	0.776–2.894	5
	Predator mimic	2.037	0.775–3.299	4
Red fox	Barriers	0.426	-0.646–1.498	6
	Exclosures	0.800	-0.755–2.354	3
	Fences	-0.143	-1.929–1.643	2
	CTA	1.195	0.349–2.042	8
	Thiram	0.081	-0.649–1.538	5
	Diversionary feeding	1.376	-0.135–2.887	3
	Lethal	1.375	0.971–1.778	38
	Poison	1.657	1.191–2.123	30
	Shooting	1.342	-0.459–3.143	2
	Traps	0.081	-0.932–1.094	6
	Reduction of attractants	1.439	-0.787–3.665	2
	Repellents	0.033	-0.976–1.043	7
	Competitor mimic	-1.404	-3.228–0.421	2

	Guard animals	1.373	-0.664–3.410	2
	Light	-0.105	-2.092–1.883	2
Striped skunk	Lethal	0.570	-0.525–1.664	3
	Traps	0.647	-0.539–1.834	2
	Repellents	-0.078	-0.947–0.790	3
	Predator mimic	0.226	-0.633–1.084	2

Table 2.3 Effect size with 95% CI and sample size of mitigation efforts on different type of conflicts involving common mammal mesopredators. CTA = conditioned taste aversion.

Type of conflict	Effect size	95% CI	Sample size per type of mitigation used
Annoyance	-0.347	-2.145–1.451	2 Repellent
Vehicle collision	-0.057	-1.129–1.015	3 Barrier
Disease spread	1.153	0.248–2.059	4 Lethal 1 CTA
Livestock killing	0.939	0.137–1.740	5 Repellent 2 Reduction attractants 2 Lethal 1 Barrier
Multiple concurrent conflicts	0.657	-0.624–1.937	2 Lethal 1 Barrier
Wildlife killing	1.080	0.864–1.297	61 Lethal 18 Barrier 11 CTA 6 Diversionary feeding 3 Not defined 2 Combined
Not defined	1.061	0.449–1.673	9 Repellent 2 Lethal 1 CTA

When considering the effect sizes, 75% study results were positive, 14% neutral, and 11% negative. Reported outcomes were mostly positive (62% of experiments), while a third (33%) of the studies reported no effect or mixed results of mitigation methods, and 5% obtained worse results following mitigation actions. The mean effect sizes difference was very strong between the reported outcomes ($F_{3,127} = 23.68$, $P < 0.001$): better (ES = 1.618, 95% CI = 1.418–1.817, n = 82), mixed (ES = 0.750, 95% CI = 0.189–1.311, n = 11), none (ES = 0.037, 95% CI = -0.264–0.337, n = 33) and worse (ES = -1.494, 95% CI = -2.266–-0.722, n = 6). Most pairwise comparisons showed moderate to very strong evidence that they differed, except for better versus mixed (P = 0.059) and mixed versus none (P = 0.400) that showed moderate to no evidence. There were little to no evidence of a relation between experiment duration and effect size ($F_{1,123}$ = 0.05, P = 0.826; Fig. 2.3). Direct (ES = 0.956, 95% CI = 0.646–1.266, n = 48) and indirect (ES = 1.053, 95% CI = 0.873–1.288, n = 89) measures yielded similar effect sizes.

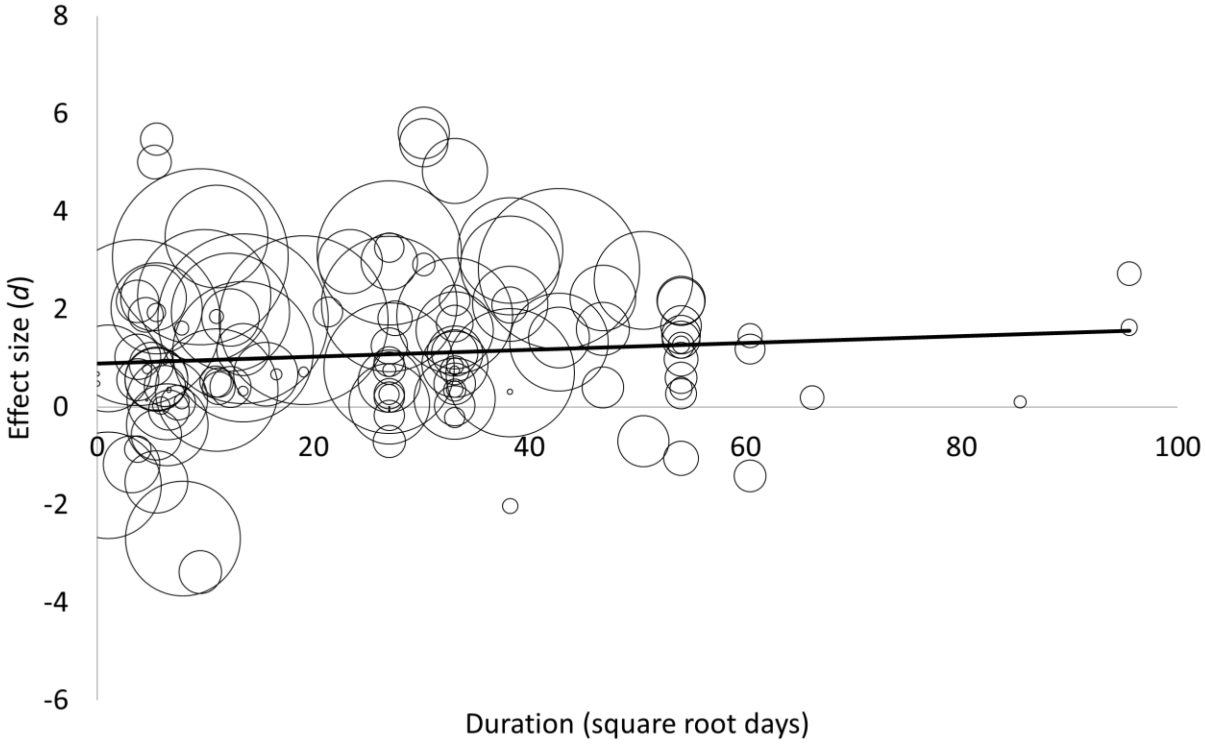


Figure 2.3 Scatterplot, including trendline, of effect size (*d*) versus total study duration (square root days) of mitigation methods against human-wildlife conflicts involving red foxes, raccoons and striped skunks, following a meta-analysis covering 1963-2022. Symbol size is proportional to the variance (V_d) weight of each effect size.

2.4.5 Publication bias

There is strong evidence that studies with larger effect sizes were more likely to be published than those with smaller effect sizes (Spearman's $\rho = 0.32$, $P < 0.001$; Koricheva et al. 2013). In the cumulative analysis, we attained a significant and positive effect size (the 95% CI was >0) starting at the combination of 8 studies (published by 1972). The global effect size reached a very high level (>1) and remained there by the 79th study (published in 2008). The trim and fill method found missing studies ($n = 2$) with only 1 (R_0) of the 3 calculated estimators, reducing the mean effect size to 0.956 (95% CI = 0.760–1.152). The fail-safe number $N_+ = 2{,}448$ is higher than the threshold set at 655, indicating more stable and robust results.

2.5 Discussion

Lethal methods have been the focus of most of the mitigation evaluations and that they proved to be effective. Based on our results, nonlethal alternatives that also contribute to reducing conflicts include nest exclosures, electric fences, and some variations on CTA and repellents. We are still lacking data on behavioural based mitigation, and from studies conducted in urban and suburban settings.

2.5.1 Conflicts with mesopredators

Raccoons, red foxes and striped skunks are found in various habitats, and their carnivorous or omnivorous diets make them important predators of other species of conservation and agricultural interest; wildlife and livestock killings are the most often reported source of conflicts, in all regions of the world. Mesopredators are known to often prey on eggs from bird and turtle nests (Conover and Conover 2022). Mitigation was generally effective when the goal was to control livestock and wildlife killing, and disease spread. On the contrary, vehicle collisions, annoyance and nuisance, and complex conflicts (>1 type) were more difficult to mitigate.

2.5.2 Effectiveness of mitigation methods

We calculated a significantly positive ES for 74% percent of studies. This is high considering studies on large carnivores did not find most mitigation methods effective in protecting livestock (Eklund et al. 2017) and would indicate that conflicts with mesopredators are easier to manage. There was not a significant relationship between the duration of an experiment and the reported effectiveness of mitigation methods. This could be explained by the nature of the target species, especially raccoons. Animals with high cognitive abilities have the potential to find a solution to circumvent an imperfect mitigation method (Blumstein 2016, Barrett et al. 2019). It is possible that long-term application, consistency, and repetitions are necessary for successful mitigation.

Combining different methods is one area where testing has not been explicit and sufficient to draw conclusions, but some propose that it might be the key to dealing with problematic animals (Madden 2004, Shivik 2006, Blackwell et al. 2016, Miller et al. 2016, Baynham-Herd et al. 2019). Our very limited sample (*n* = 2) of studies combining multiple methods does not allow to draw any conclusion on effectiveness. Multiple methods must be deployed simultaneously, must be designed, and installed with a particular species in mind, and must be modified periodically to avoid habituation by target species (Treves and Karanth 2003, Baker et al. 2007*b*). A combination of techniques might also be more effective and last longer (Stringham and Robinson 2015, Miller et al. 2016). A random rotation of methods could also avoid habituation (Greggor et al. 2014), and multiple methods can account for individual behaviour differences (Merrick and Koprowski 2017).

2.5.2.1 Lethal practices

Lethal management practices commonly include shooting, trapping (either immediately lethal, or followed by euthanasia), and poison. Lethal methods show high efficiency in addressing HWCs involving raccoons or red foxes. They are also the most common methods used to address conflicts related to wildlife killing and disease spread, and probably influence the large positive effect sizes associated with these conflicts (Table 2.3). This efficiency might be limited in time, such as in Rosatte et al. (2007) control campaign, which saw a return to pre-control population levels after only 1 year. Baiting campaigns, especially against the red fox in Australia, and lethal trapping give out relatively consistent results. Shooting for control and hunting tend to have a positive effect as well, but with more variability in the results. Controlling at the population level through lethal practices is very labour-intensive and must be maintained over the long-term (Conover and Conover 2022). On the other hand, individual-based (selective) lethal methods can be more challenging but might be more readily socially accepted (Swan et al. 2017). Although lethal methods can be effective, their social and ethical concerns should incite wildlife managers to explore nonlethal methods before implementing lethal actions. Lethal control is negatively perceived by an increasing portion of the public and warrants a conservative approach in its application (Treves and Naughton-Treves 2005). For proponents of animal rights ethics, lethal methods should not even be considered, whereas a cost-benefit analysis might make it the best option for proponents of conservation or welfare ethics (Hutchins 2007, Hampton et al. 2018), which still makes them relevant albeit unpopular.

2.5.2.2 Barriers

Two main types of barriers are used as mitigation methods: fences and exclosures. Fences are a traditional and widely used method to keep wildlife away (Breitenmoser et al. 2005, Hayward and Kerley 2009, Somers and Hayward 2012, Vantassel and Groepper 2016). The addition of electric wires is common, and Khorozyan and Waltert (2019) reported a sustained positive effect of electric fences against larger carnivore species. Exclosures, as described in the literature, are relatively small devices placed on the ground, commonly used to protect birds or turtles' nests for the duration of incubation (Yerli et al. 1997, Mabee and Estelle 2000, Beaulieu et al. 2014, Stringham and Robinson 2015, Bougie et al. 2020). Our results indicate that electrical fences and exclosures are more effective against mesopredators than regular fences. Electrical fences should be designed to optimize efficiency based on height and tension (Tsukada et al. 2019, Honda 2022), however there are obvious limitations to an electric fence versus a non-electric fence. Other than the increased cost, the reliability of the electrical system (e.g., faulty wires, limited battery life, insufficient solar power) can potentially reduce their efficacy. Care must be taken when considering barriers, because when applied at large scales they can have unintended, negative consequences such as limiting movement of other species, disrupting daily activity and migration, causing injuries, or impending gene flow (Somers and Hayward 2012, Schell et al. 2021).

2.5.2.3 CTA

Our results indicate an overall positive effect of CTA, but this is when considering results from many different chemicals and in different contexts. The application of conditioning is typically aimed at being aversive to a unique target species and relies on using the appropriate product (Snijders et al. 2021). We therefore cannot point to an effective chemical to use with mesopredators in general or for a specific species, thus highlighting the need for more research on the subject. Nevertheless, CTA is promoted as a relevant tool to manage endangered species rehabilitation, pest or invasive species, crop-raiding, and animal tourism (Sarabian et al. 2023). Snijders et al. (2021) offer guidelines in implementing a CTA program.

2.5.2.4 Diversionary feeding

In line with our results, the review by Kubasiewicz et al. (2016) concluded that supplementary food is inconsistently taken by target species (mammals, birds); and even when taken, it does not always reduce conflicts. Diversionary feeding was partially successful to protect duck nests using dead fish to lure skunks in Utah (Crabtree and Wolfe 1988), but inefficient against mesopredators in another experiment in North Dakota (Conover et al. 2005). A study on larger carnivores indicated that supplementary feeding even led to an increase in damage (Khorozyan and Waltert 2019). Over longer periods of time, supplemental feeding may have a counterproductive effect by increasing local population size (Conover and Conover 2022). There is also a risk of spreading disease by concentrating individuals at a feeding site (Castillo et al. 2011, Møller et al. 2014). Due to the poor success reported, the high cost, and the risk of worsening conflicts by using diversionary feeding, a thorough evaluation of the target species and context of HWC is essential if this mitigation should be considered (Kubasiewicz et al. 2016, Conover and Conover 2022).

2.5.2.5 Repellents

Repellents are a very appealing method to the public because they are nonlethal and seen as humane (Liss 1997). Methods mimicking predators (smell or sound, guard animal), were more efficient than methods mimicking competitors and artificial lights, underlining that incorporating biologically relevant stimuli to the target animal might be more successful (Baker et al. 2007b). In a comparison of multiple methods, chemical repellents yielded the best results against larger carnivore species, but with huge variability between studies (Miller et al. 2016). Chemical repellents also wear off over time and need to be reapplied (Conover and Conover 2022). The effect of repelling strategies is thought to be short-term and labor-intensive, with animals habituating (Draulans 1987, Vantassel and Groepper 2016, Khorozyan and Waltert 2019, Petracca et al. 2019, Conover and Conover 2022) or acquiring a coping mechanism through their cognition (Daniels et al. 2019, Barrett et al. 2019). In addition, because of their conspicuous visual, olfactory or auditory components, repellents can disturb other wildlife and people (Conover and Conover 2022).

Fear conditioning, through frightening devices, is a variation of the repellent methods, as it teaches animal to anticipate a negative consequence (aversive stimulus) by responding to a neutral stimulus (Greggor et al. 2020). The creation of a landscape of fear implies that an animal will avoid or reduce its activities in an area where perceived risks are higher (e.g., predation) and secured places within the habitat are removed (Conover and Conover 2022). Fear conditioning is difficult to implement, because managers must be cautious about what associations are being taught and habituation may occur (Greggor et al. 2020). Against species with higher cognitive capacities, frightening devices that incorporate different sensory stimuli may be among the most promising nonlethal mitigation methods to test (Blumstein 2016). Some other repelling mitigation methods that were not tested within the systematic review include: pyrotechnics, effigies and scarecrows, sounds, bright or flashing lights, lasers, reflectors, shock collars, fladry and flags, gas-guns, drones, motion activated devices, predator models, ultrasounds, hazing by humans and *high-pressure water sprayers* (Smith et al. 2000, Baker et al. 2007b, Reidinger and Miller 2013, Blumstein 2016, Conover and Conover 2022). Fladry barriers seem effective against larger canids (Musiani et al. 2003, Young et al. 2019, Windell et al. 2021), therefore this might have potential against foxes.

2.5.2.6 Reduction of attractants

Attractive signals (most often food odours) are often at the root of HWCs. The distribution of carnivores in urban and agricultural areas is closely related to anthropogenic food resources (Rivest and Bergeron 1981, Prange et al. 2004, Curtis and Hadidian 2010). Although our measure of the effect size from a single paper is imprecise, sound waste disposal appears to be very effective in reducing conflicts with the red fox (Bino et al. 2010). Generally, feeding wildlife poses high risks of causing conflicts and should be avoided in most cases (Dubois and Fraser 2013, Griffin and Ciuti 2023). Management already integrates this principle in some contexts (national parks, campgrounds, cities), but more research is required to validate this approach.

2.5.2.7 Other potential methods

Other mitigation methods were not included in our meta-analysis due to a lack of published studies evaluating them, such as: fertility control (Ransom et al. 2014), evolutionary traps involving attracting a target species to a fitness negative resource or situation, thus reducing survival or reproductive success (Robertson et al. 2017), chemical camouflage consisting in covering naturally attractive odour with non-rewarding odours (Selonen et al. 2022), or translocation (Massei et al. 2010; Hill et al. 2023).

Because some methods such as barriers and population reduction measures (e.g., trapping and poison-baiting campaign) might have far-reaching and unintended consequences, a targeted approach towards problematic individuals (selective management, profiling) might be sufficient and is increasingly favored (Sillero-Zubiri et al. 2007, Curtis and Hadidian 2010, Swan et al. 2017, Barrett et al. 2019, Conover and Conover 2022). For innovative species or individuals, there is a risk that mitigation efforts create novel challenges, therefore only providing a temporary solution (Barrett et al. 2019). The integration of cognition in developing innovative mitigation methods is needed and could be promising (Greggor et al. 2020).

2.5.3 Improving reporting

Good data analysis and reporting is dependent on properly conducted studies and experiments (Warburton and Norton 2010, Reddiex and Forsyth 2006). In our meta-analysis, we had to exclude 62% of the studies at the full-text screening level, mostly due to issues with the study design, choice of comparative treatments and goal of the study itself. These are missed opportunities to learn, what Warburton and Norton (2010) called a failure to increase knowledge and achieve outcomes. The literature on the mitigation of human-mesopredators conflicts has increased over time and will likely increase in the coming years as seen in the HWC literature in general (Su et al. 2022). Wildlife management publications remain favoured scientific outlets to evaluate and report management practices and techniques, however, it still lacks in its diversity of contexts studied. Although a variety of habitats is covered in the literature, research in urban settings is underrepresented considering that mesopredators are strongly associated with cities in the wildlife management and animal behaviour fields (Prange et al. 2004, Bateman and Fleming 2012, Drake 2014, Barrett et al. 2019, Schell et al. 2021). Additionally, most studies come from North America, Australia, and a few European countries. Red foxes and raccoons are found in numerous countries as native and introduced species (Lotze and Anderson 1979, Larivière and Pasitschniak-Arts 1996, Hohmann et al. 2002, Ikeda et al. 2004, Stope 2023). This could be due to a language barrier but searching French literature did not contribute a single study to the meta-analysis data set. A single thesis from Québec (Bélanger-Smith 2014) and 1 article from France (Lieury et al. 2015) were published in English.

Heterogeneity measures suggest that there is substantial heterogeneity and that all studies do not share a common effect size. This level of heterogeneity makes it more strenuous to draw overall conclusions (Higgins and Thompson 2002), which is explained by the variety of species, contexts and methods used in the analysis. Measures of robustness against publication bias (trim-and-fill method and fails-safe number) do not indicate vulnerability. On the other hand, we believe that the early positive effect of mitigation measures, as reported by the cumulative meta-analysis, is explained by a bias of publishing highly successful methods. It is essential to publish unsuccessful methods and the reason why these methods were unsuccessful (Dubois 2019). A meta-analysis on the effectiveness of road-kill mitigation also showed a publication bias toward significant effectiveness in peer-reviewed publications (Rytwinski et al. 2016). Transparency (by sharing inefficient or failed mitigation experiments and attempts) and more transdisciplinary approaches will contribute to finding solutions to HWCs (König et al. 2020). As in many other disciplines, we highlight the importance to publish results in easily accessible repositories, such as scientific publications. On the other hand, pest control specialists and wildlife managers might not always be able to conduct in-depth research or have access to scholarly publications, therefore great efforts should be deployed to broadcast relevant results to them, and even accompany them in integrating review findings in their own practices (Haddaway et al. 2017). In relation to the meta-analysis itself, the complexification of experimental design and data analysis renders difficult the extraction and interpretation of data from more recent papers. Complex models with multiple covariables complicates the extraction of means and standard deviations from control and experimental samples, necessary to calculate effect size.

2.6 Management implications

Human-wildlife conflicts are complex and not easy to solve, and a poorly informed or designed intervention can make matters worse. There is no magic bullet to resolve HWC, and a single technique cannot be expected to work in all situations. Mitigation methods need to be chosen based on the species involved, the environment within which it exists, and the type of conflict. In many cases, highly technical interventions are not practical within the socioeconomic constraints of developing countries or rural communities, but we demonstrate that rather simple and accessible methods can be efficient. The integration of more animal behaviour and cognition studies has the potential to lead to more targeted and efficient mitigation methods, and steer away from lethal interventions. Successful mitigation methods should facilitate respectful engagement with wildlife by considering a species ecological requirements, behaviour and preferences to find a common solution to conflicts.

2.7 Appendices

Appendix 2.7.1 ROSES review report

Systematic review report following the Reporting standards for systematic evidence syntheses (ROSES) guidelines, on the effect of mitigation methods to manage conflict with 3 common species of mammal mesopredators: common raccoons (*Procyon lotor*), red fox (*Vulpes vulpes*) and striped skunk (*Mephitis mephitis*).

Background

During nature-oriented activities, the goals of humans (leisure, relaxation, access to nature) are sometimes negatively influenced by wildlife (disease transmission, annoyances such as odour and noise, damages to material, fear). Conversely, wildlife needs are disrupted by human presence and activities. Recreational activities within protected areas frequently lead to human-wildlife conflicts (HWC), and wildlife managers often overlook animal behaviour when addressing such situations (McDougall et al. 2006, Caro 2007, Berger-Tal et al. 2011, Blackwell et al. 2016).

Behavioural data sheds light on motivations and obstacles for engaging in risky behaviours (Mumby and Plotnik 2018) and the various stages of the cognitive process (Greggor et al. 2014, Barrett et al. 2019), thereby influencing the effectiveness of conservation measures. When behavioural elements are not considered, conflict mitigation methods against species with high cognitive abilities are often only temporarily successful (Barrett et al. 2019). Mitigation methods based on behaviour are varied (Shivik and Martin 2000) and can be aversive (stimuli causing a negative experience paired with specific behaviours), disruptive (undesirable stimuli that alter the behaviour) or involve some form of training to attain cooperative mitigation (Barrett et al. 2019). Different species require different approaches (Vantassel and Groepper 2016) and, at a finer scale, conflicts can be addressed more precisely with problem individuals if they can be identified (Merrick and Koprowski 2017, Swan et al. 2017). Cost, feasibility, and acceptance are also to be considered in addition to effectiveness when devising a management intervention (Snijders et al. 2019).

Québec's network of protected areas offers good opportunities to shed light on the role of animal behaviour in HWC. Mammal mesopredators (1-15 kg; Prugh et al. 2009) are a recurring source of nuisance to park users and no mitigation measure has yielded satisfactory results so far

(Dellarosa 2012; Denis 2017*a,b*). Within those parks and in the south of the province in general, raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*) and red foxes (*Vulpes vulpes*) exhibit varying behaviours between and within species, are widely distributed and abundant, and are involved in frequent interactions with humans. The behaviour of the pervasive raccoon is not very well understood in conflict situation, and information on their responses to different control strategies is incomplete and scattered (Curtis and Hadidian 2010). Common species are also important to study because of their ecological significance as widespread keystone components of their communities (Lidicker 2015).

Stakeholder engagement

The main stakeholder is the national parks authority (Sépaq). The network of protected areas has been involved in the research project from the start, including discussion on the scope of the study, research questions and methodology for the experimental stage. They will be notified regularly through the systematic review process. Pest management experts will be contacted to obtain additional literature on which they might base their practices and to have their opinion on the subject.

Questions

What mitigation methods have been tested to deal with conflict with the 3 target mesopredator species?

What type of conflict did it address?

Which methods proved effective?

Over what period of time was it effective?

Search components (population, intervention, comparator, outcome [PICO])

Population = Free-living raccoons, red foxes, stripped skunks involved in human-wildlife conflicts.

Intervention = Techniques or devices intended to prevent the occurrence, or reduce the frequency or intensity, of conflict.

Comparator = No intervention in time, space or both. Alternative intervention in time, space or both.

Outcome = Human-wildlife incidents (e.g., number of complaints, attacks, undesired close encounters), material damage, predation, approach of human-populated areas.

Searches

We will gather articles and other documents through a search on different search engines, in English and French: Web of Sciences, Google Scholar (if no new relevant article is found after going through 10 pages, the search is completed), ProQuest, bioRxiv. In addition, we will consult 21 websites related to wildlife conservation and management.

We expect a low specificity (proportion of retrieved material judged relevant). We will browse the references sections of articles for further references. We will search all possible combinations of the following keywords:

Term 1: species common name or scientific name

Term 2: conflict, control, habituation, mitigation, nuisance, persecution, pest, problem

We will not make an *a priori* selection of benchmark studies.

Screening strategy

We will first screen the retrieved literature on basis of title then abstract and finally full text. Inclusion will be conservative, meaning that when we are in doubt, we will include an article to be reviewed in the next stage. We will automatically transfer articles with relevant titles but no abstract to the full text screening stage. For consistency checking, all research was conducted or reviewed by the senior author.

Inclusion

Refer to PICO for inclusion criteria. We will provide reasons for exclusion at full text screening level.

Appraisal

We will include any study that fit comply to the PICO criteria and has been published in peer-reviewed journals. Studies that have not been published in peer-reviewed journals need to have been rigorously conducted and analyzed, based on the scientific method and before–after and control–-intervention study designs. We will qualify the 3 categories of study as high, medium and low quality in the synthesis.

Data synthesis

Description of the conflicts will be a narrative synthesis, but we will assess the effectiveness of mitigation method quantitively. We will code extracted data, to manage the discrepancy in measures from one study to another. We will qualitatively evaluate the intensity of severity based on the authors' statements in their article. We will define the types of conflict according to Peterson et al. (2010). Human-wildlife conflict measures will depend on each study. These can be number of complaints, number of animals trapped or killed, extent of damages, percentage of survey respondent reporting conflict. We will record mitigation techniques only if they were implemented (not proposed) and quantitative results are available. We will record if they were successful at reducing HWC, had no effect, or worsen the situation. We will calculate the effect size (Eklund et al. 2017).

Appendix 2.7.2 Websites consulted for systematic literature search on the effect of mitigation methods to manage conflict with mammal mesopredators.

Animal Damage Control [ADC, under the U.S. Deparmtent of Agriculture]. <www.aphis.usda.gov/aphis/ourfocus/wildlifedamage>. Accessed 20 May 2020.

Canadian Parks and Wilderness Society. <http://cpaws.org>. Accessed 20 May 2020.

Center for Conservation and Research. <www.ccrsl.org>. Accessed 20 May 2020.

Commonwealth Scientific and Industrial Research Organisation (CSIRO). <www.csiro.au/en/Publications>. Accessed 24 April 2023.

Conservation Evidence. <www.conservationevidence.com>. Accessed 24 April 2023.

Database Carnivore Ecology and Conservation. <www.carnivoreconservation.org>. Accessed 20 May 2020.

Defenders of Wildlife. <https://defenders.org/publications>. Accessed 20 May 2020.

Department of Environmental Science, Policy and Management, University of California Berkeley. <https://ourenvironment.berkeley.edu>. Accessed 20 May 2020.

Department of Renewable Resources, Government of the Northwest Territories, Canada. <www.enr.gov.nt.ca/en/resources>. Accessed 20 May 2020.

Environment and Climate Change Canada. <www.canada.ca/en/environment-climate-change.html>. Accessed 18 May 2023.

Fauna & Flora International. <www.fauna-flora.org/documents>. Accessed 20 May 2020.

Food and Agriculture Organisation of the United Nations. <www.fao.org/publications/en>. Accessed 20 May 2020.

Institute for Wildlife Studies. <www.iws.org>. Accessed 20 May 2020.

IUCN-Directory of Specialist Groups, Red List Authorities, Task Forces of the Species Survival Commission [SSC]. <www.iucn.org/ssc-groups>. Accessed 20 May 2020.

IUCN–Human Wildlife Conflict Task Force [HWCTF] Document Library. <www.hwctf.org/resources/document-library>. Accessed 17 April 2023.

IUCN–World Commission on Protected Areas [WCPA]. <www.iucn.org/theme/protected-areas/publications>. Accessed 20 May 2020.

Little Blue Society – Human-Animal Conflict Resolution. <www.littlebluesociety.org>. Accessed 20 May 2020.

Nature Conservation Foundation. <http://ncf-india.org>. Accessed 20 May 2020.

National Wildlife Research Center – [NWRC, under the U.S. Department of Agriculture]. <www.aphis.usda.gov/aphis/ourfocus/wildlifedamage/programs/nwrc/sa_publications/ct_research_gateway>. Accessed 20 May 2020.

Organisation for Economic Co-operation and Development [OECD] iLibrary. <www.oecd-ilibrary.org>. Accessed 20 May 2020.

Parks Canada. <www.pc.gc.ca/en/index>. Accessed 20 May 2020.

Research Institute for Agriculture, Fisheries and Food. <www.ilvo.vlaanderen.be/language/en-US/EN/Research.aspx#.WnRSwa7ibIU>. Accessed 20 May 2020.

The Nature Conservancy. <www.nature.org>. Accessed 20 May 2020.

United Nations Environment Programme. <www.unenvironment.org>. Accessed 20 May 2020.

U.S. Environmental Protection Agency. <www.epa.gov>. Accessed 20 May 2020.

U.S. Fish & Wildlife Service. <www.fws.gov>. Accessed 20 May 2020.

U.S. Government Publications. <www.science.gov>. Accessed 20 May 2020.

U.S. National Park Services. <www.nps.gov>. Accessed 20 May 2020.

W.A. Franke College of Forestry & Conservation, University of Montana. <www.cfc.umt.edu/research/default.php>. Accessed 20 May 2020.

WildCRU. <www.wildcru.org/research/theme/all-projects>. Accessed 20 May 2020.

Wildlife Conservation Society. <https://library.wcs.org>. Accessed 20 May 2020.

WildSmart. <www.wildsmart.ca>. Accessed 20 May 2020.

World Wildlife Fund [WWF]. <www.worldwildlife.org>. Accessed 20 May 2020.

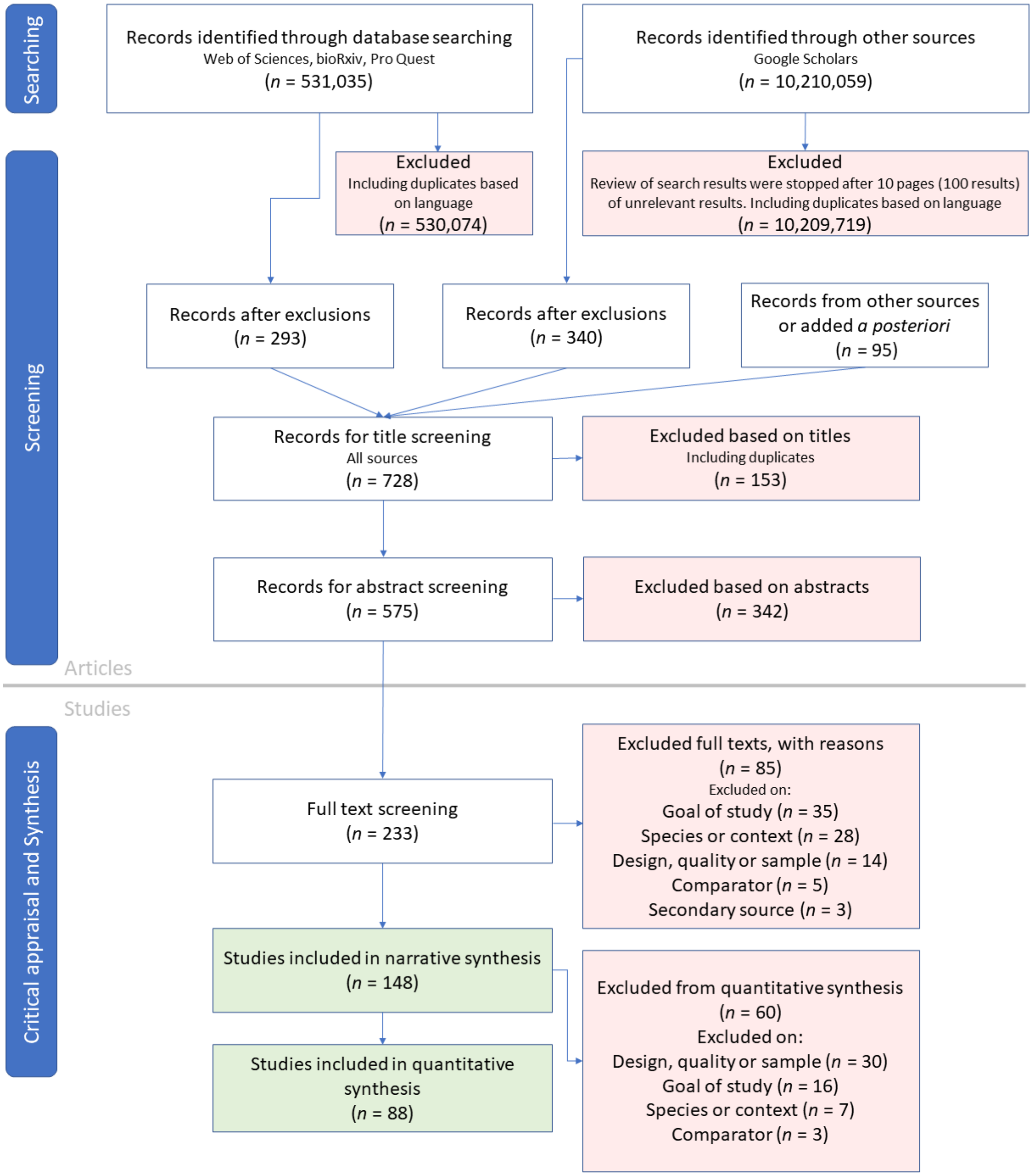
Yale School of Forestry and Environmental Studies. <http://environment.yale.edu>. Accessed 20 May 2020.

Zoological Society London [ZSL]. <www.zsl.org/science/publications/scientific-publications>. Accessed 20 May 2020.

Appendix 2.7.3 Figure A2.1

Figure A2.1 Systematic search flow diagram based on the ROSES (Reporting standards for systematic evidence syntheses) form including the number of selected articles or studies for each step. The diagram was used to conduct the narrative synthesis and the meta-analysis on the effectiveness of mitigation methods toward 3 common mesopredators: common raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*) and striped skunk (*Mephitis mephitis*).

Haddaway N.R., B. Macura, P. Whaley, and A. S. Pullin. 2017. ROSES flow diagram for systematic reviews. Version 1.0. DOI: 10.6084/m9.figshare.5897389



Appendix 2.7.4 Studies included in the systematic review analysis and the meta-analysis on the effectiveness of mitigation methods toward 3 common mesopredators: common raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*) and striped skunk (*Mephitis mephitis*). Studies included in the meta-analysis are marked with (*).

Abraham, C. J. 1996. Non-toxic animal repellent. U.S. Patent Serial Number 5554377. U.S. Patent and Trademark Office, Alexandria, Virginia, USA.

Amundson, C. L., and T. W. Arnold. 2011. The role of predator removal, density-dependence, and environmental factors on mallard duckling survival in North Dakota. The Journal of Wildlife Management 75:1330–1339.

Amundson, C., M. Pieron, T. Arnold, and L. Beaudoin. 2013. The effects of predator removal on mallard production and population change in northeastern North Dakota. The Journal of Wildlife Management 77:143–152.

Antworth, R. L., D. A. Pike, and J. C. Stiner. 2006. Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. Biological Conservation 130:10–15.

Baker, P. J., and S. Harris. 2006. Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? European Journal of Wildlife Research 52:99–108.

Baker, S. E., P. J. Johnson, D. Slater, R. W. Watkins, and D. W. Macdonald. 2007. Learned food aversion with and without an odour cue for protecting untreated baits from wild mammal foraging. Applied Animal Behaviour Science 102:410–428.

*Balser, D. S., H. H. Dill, and H. K. Nelson. 1968. Effect of predator reduction on waterfowl nesting success. The Journal of Wildlife Management 32:669–682.

*Banks, P. B. 1999. Predation by introduced foxes on native bush rats in Australia: Do foxes take the doomed surplus? Journal of Applied Ecology 36:1063–1071.

*Banks, P., A. Newsome, and C. Dickman. 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. Austral Ecology 25:283–291.

Barrull, J., I. Mate, M. Salicrú, J. Palet, J. G. Casanovas, J. Gosàlbez, and J. Ruiz-Olmo. 2014. Differential response of a carnivore community to predator control: A spatio-temporal observational study. Italian Journal of Zoology 81:271–279.

*Beasley, J. C., Z. H. Olson, W. S. Beatty, G. Dharmarajan, and O. E. Rhodes Jr. 2013. Effects of culling on mesopredator population dynamics. PLoS ONE 8:e58982.

*Beaulieu, G., D. Austin, and M. L. Leonard. 2014. Do nest exclosures affect the behaviour of piping plovers (*Charadrius melodus melodus*) and their predators? Canadian Journal of Zoology 92:105–112.

*Bélanger-Smith, K. 2014. Evaluating the effects of wildlife exclusion fencing on road mortality for medium-sized and small mammals along Québec's Route 175. Thesis, Concordia University, Montréal, Québec, Canada.

*Bengsen, A. 2014. Effects of coordinated poison-baiting programs on survival and abundance in two red fox populations. Wildlife Research 41:194–202.

*Bennett, C., S. Chaudhry, L. Gilmer, S. Lee, E. Peterson, J. Rajkowski, K. Shih, S. Subramaniam, R. Wells, J. White et al. 2009. Excluding mammalian predators from diamondback terrapin nesting beaches with an electric fence. Thesis, University of Maryland, College Park, Maryland, USA.

Berry, O., D. Algar, J. Angus, N. Hamilton, S. Hilmer, and D. Sutherland. 2012. Genetic tagging reveals a significant impact of poison baiting on an invasive species. The Journal of Wildlife Management 76:729–739.

*Bino, G., A. Dolev, D. Yosha, A. Guter, R. King, D. Saltz, and S. Kark. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. Journal of Applied Ecology 47:1262–1271.

Bolton, M., G. Tyler, K. Smith, and R. Bamford. 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding suc4cess on wet grassland nature reserves. Journal of Applied Ecology 44:534–544.

*Bougie, T. A., N. W. Byer, C. N. Lapin, M. Z. Peery, J. E. Woodford, and J. N. Pauli. 2020. Wood turtle (*Glyptemys insculpta*) nest protection reduces depredation and increases success, but annual variation influences its effectiveness. Canadian Journal of Zoology 98:715–724.

Burke, R. L., M. Vargas, and A. Kanonik. 2015. Pursuing pepper protection: Habanero pepper powder does not reduce raccoon predation of terrapin nests. Chelonian Conservation and Biology 14:201–203.

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*Chesness, R. A., M. M. Nelson, and W. H. Longley. 1968. The effect of predator removal on pheasant reproductive success. The Journal of Wildlife Management 32:683–697.

*Chodachek, K. D. 2003. Evaluation of repeated removal of mammalian predators on waterfowl nest success and density. Thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

*Coates, T. D. 2008. The effect of fox control on mammal populations in an outer urban conservation reserve. Australian Mammalogy 30:51.

Conner, L. M., and G. Morris. 2015. Impacts of mesopredator control on conservation of mesopredators and their prey. PLoS ONE 10:e0137169.

*Conover, M. R. 1987. Reducing raccoon and bird damage to small corn plots. Wildlife Society Bulletin 15:268–272.

*Conover, M. R. 1990. Reducing mammalian predation on eggs by using a conditioned taste aversion to deceive predators. The Journal of Wildlife Management 54:360–365.

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Crabtree, R. L., and M. L. Wolfe. 1988. Effects of alternate prey on skunk predation of waterfowl nests. Wildlife Society Bulletin 16:163–169.

*Davey, C., A. R. E. Sinclair, R. P. Pech, A. D. Arthur, C. J. Krebs, A. E. Newsome, D. Hik, R. Molsher, and K. Allcock. 2006. Do exotic vertebrates structure the biota of Australia? An experimental test in New South Wales. Ecosystems 9:992–1008.

Dexter, N., and A. Murray. 2009. The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. Wildlife Research 36:252–261.

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Chapter 3. Wild raccoons (*Procyon lotor*) problem-solving evaluation in relation to their environment and individual traits

Lazure, L. and Weladji, R.B. Wild raccoons (*Procyon lotor*) problem-solving evaluation in relation to external factors and individual traits. Animal Behaviour. *In review.*

3.1 Abstract

The cognitive process of innovation in animals produces new 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, 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 another evidence that raccoons are apt problem-solvers, with a potential to adapt to new foraging opportunities, and that they are also a relevant species to study innovation in mammals.

3.2 Introduction

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 (Reader et al., 2016; Ramsey et al., 2007); in this study we focus on the individual process (Ramsey et al., 2007), not the occurrence of a new behaviour into 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 return 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; Thornton et al., 2014; MacDonald & Ritvo, 2016; Morand-Ferron et al., 2016; Pritchard et al., 2016). 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). On the other hand, observational conditioning, social learning and mitigation of predation risk could improve 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 process is the exposure to humans and anthropogenic landscapes (Benson-Amram et al., 2022; Goumas et al., 2020; Johnson-Ulrich et al., 2022; Lea et al., 2020; Owen et al., 2017; Papaj et al., 2019; Schell et al., 2021; Wong & Candolin, 2015). For example, it has been demonstrated in many species that urban populations perform better than rural ones in cognitive tasks (grey squirrels, *Sciurus carolinensis*, Chow et al., 2021a; various birds, Griffin et al., 2017; raccoons, *Procyon lotor*, Macdonald & Ritvo, 2016; yellow mongooses *Cynictis penicillate*, Müller & Pillay, 2022), but this is not always the case (see Johnson-Ulrich et al., 2022). 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 abilities can modulate human-wildlife conflicts, this trait is 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 cognitive ability, we can implement more targeted mitigation methods toward 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 underrepresented 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-sized 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 conflicts affecting people livelihood and security, it is 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, 1998). 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 environment, such as rural and urban areas (Bozek et al., 2007; Daniels et al., 2019; Prange et al., 2004). It has a reputation of 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 the 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 type of physical challenge to attain food, such as opening a cooler, accessing leftovers in a trash can, or entering a cabin. Exposing subjects to different task difficulties, such as different puzzles or a multi-access box, allows to explore variation on problem-solving abilities (Auersperg et al., 2012; Daniels et al., 2019; Johnson-Ulrich et al., 2022). The context within which the 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 quantitively assess behavioural traits that potentially influence problem-solving, such as exploratory diversity and persistence. Exploratory (or motor) diversity is the repertoire of behaviours 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). 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 present high levels of persistence, measured as total duration of time spent working on a puzzle on their initial trial, which positively correlates to success (Daniels et al., 2019).

Our objective is to evaluate problem-solving in wild raccoons to assess how external (exposure to humans, presence of conspecifics and task difficulty) and internal factors (exploratory diversity and persistence) affect their performance. We used two single-access puzzle boxes: a cubic one with a door and latch (hereafter the Box), and another one involving sliding and rotating concentric tubes (the Tube). 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. Using two tests allows to assess convergent validity: a “good” performance at one test should be reflected in the other as well (Boogert et al., 2018). 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 will increase and time to success will 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 will 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 expect individual variation in the performance, and predict that individual performance will be correlated between the two tasks.

3.3 Methods

3.3.1 Locations

We conducted field work in collaboration with the society responsible of managing Québec's national parks (Sépaq) in the south of the province. We selected three parks with "severe" raccoon nuisance problems (Denis, 2017b): 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/km^2), especially in campgrounds (approximately 50–100 individuals/km^2) based on past inventories and recent assessments (Lefebvre, 1998; Dellarosa, 2012; R. Charest, personal communication, 23 January 2019). These parks are relatively small (between 8 and 28 km^2), adjacent to or around large bodies of water (river or lake) and encompassed in mostly urban or agricultural territories. Two site categories are studied based on the parks' zoning: intensive recreation 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). 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 4–9 km (straight line) at each park. We ran the experiments for three summers (earliest–latest dates May 31–Sept. 14) between 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).

3.3.2 Experimental Set-up

We conducted experiments with wild raccoons using species-oriented baits, but all wildlife could interact with both experimental devices. We installed the puzzles out of view from visitors, but easily accessible to the animals. The Box puzzle was similar to models used with other carnivore species in captivity or in the wild (Benson-Amram et al., 2016; Benson-Amram & Holekamp, 2012). Using the same type of puzzle (standardized method) will facilitate the comparison of our results to similarly conducted experiments (Krasheninnikova et al., 2020). The Box measures 30 cm a side and is made from steel mesh. There is 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 consists of two horizontal plastic tubes (50 cm long and 6 cm diameter for the inner tube, and 34 cm long and 7 cm diameter for the outer one), one sliding over the other, requiring the animal to slide and turn the outermost tube to align two holes (approximately 5 x 10 cm) and access the food in the inner tuber (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.

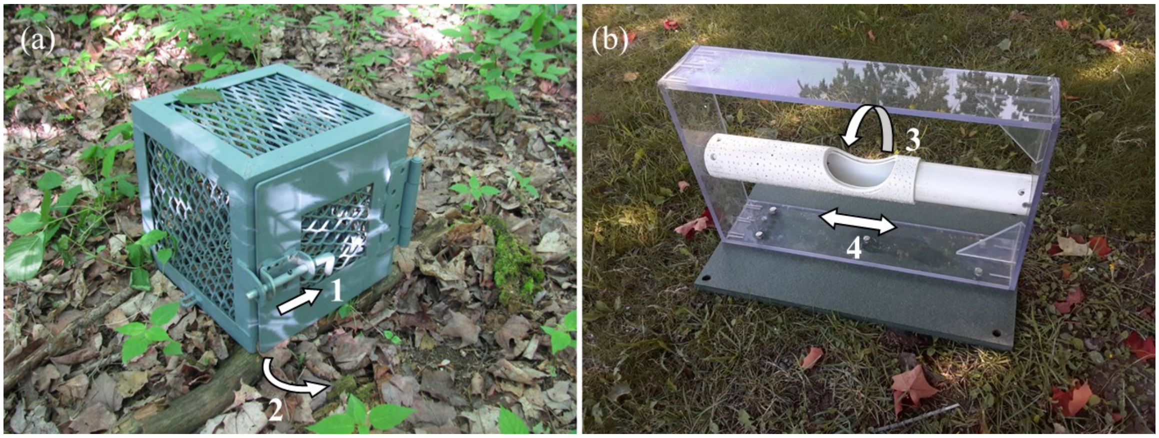

Figure 1. Two puzzle boxes used to assess wild raccoons problem-solving and learning abilities. (a) A cubic steel box (closed on the picture), requiring sliding the latch (1) and opening the door (2), in this order. (b) A sliding tube (open on the picture), requiring to rotate (3) and slide (4) the other tube in no specific order.

The experiments were non-invasive; animals voluntarily approached or walked away from the apparatus. This ensures that only motivated animal participated in the trials. A trial included all the interactions of an individual with a puzzle in a single night. Within a trial, an attempt 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 by moving more than a body-size away from the unopened puzzle. We considered the puzzle to be solved when a raccoon opened it enough to have direct access to the food with its paw, even if they did not immediately reach in and consumed the reward. Whenever a puzzle was successfully opened during a trial, it was *de facto* disabled until the next trial (new bait installed and puzzle 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.

3.3.3 Video Recording and Analysis

We recorded the interactions with motion triggered night vision cameras (Argus 2, Reolink, Hong Kong), set up between 3–4 m away. The presence of conspecifics was also assessed based on the video recordings. As soon as there was at least one other individual visible during a trial, it was classified as "with conspecifics". This was an imperfect measure, as there was no way to know if there were raccoons behind the field of view of the camera or hidden by vegetation, but it does consider conspecifics that are closer, 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 behaviours directed at the box (Appendix 1; Benson-Amram et al., 2013, 2014; Daniels et al., 2019; Johnson-Ulrich et al., 2018). The exploratory diversity score accounts for behaviours without contact that allow the gathering of information (perception), as well as behaviours with 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 it came back in a single night (including the initial attempt) until successfully opening the puzzle or giving up.

3.3.4 Individual Identification

Raccoons were identified through careful observation of the video footages by a single observer (LL), based on relative size to the puzzles, body characteristics (fur, tail, limbs), and scars and injuries, in a similar manner to Chow et al. (2021b) with grey squirrels. We conducted an intra-rater reliability test (Cohen's kappa) on a small subset of recordings from the site with the highest activity level (IDB, recreation zone). Most juveniles were excluded because they showed very little initiative and were impossible to tell apart from the videos, often interacting together with the devices, therefore creating confusion to track one individual at a time. We were unable to differentiate the individual by sex, and therefore did not control for the sex-difference. Daniels and colleagues (2019) did not find a sex difference in problem-solving rate in their study on captive raccoons.

3.3.5 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 dependant variable). We also used AIC with these models to select the most parsimonious one, and performed hypothesis testing using the best model. Two final GLMMs tested for an effect of the zone and the presence of conspecifics (including their interaction) on the behavioural traits (exploratory diversity and persistence). Both have a Poisson distribution with log link function. We finally calculated the phi coefficient as a measure of association between the performances of individuals 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 ± standard deviations.

3.3.6 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 with each national park we visited.

3.3 Results

We recorded 114 individual wild raccoons in three parks, for a total of 199 trials. The most represented park is IDB with 100 trials, followed by YAM with 84 and PLA with 15. Animals interacted with the Box on 117 trials and 82 with the Tube. Preservation and recreation zones are fairly equally represented in the data with 105 and 94 trials respectively. On 119 trials the raccoon was alone, and with at least one conspecific on 81 others (with an average of 1.7 conspecifics). We obtained an 87% agreement ($\kappa = 0.851$) for intra-rater reliability testing, corresponding to an "almost perfect" agreement (Landis & Koch, 1977). None of the raccoon was identified in both zones within a park, indicating that there is probably little movement in the summer.

The overall problem-solving success rate was 28%. Total duration of trials was between 3–1441 s, with a mean (± SD) of 103 ± 178 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 (but only smaller raccoons were able to do it) or by toppling over the whole Box (and the door randomly opened). The only other species to interact with the puzzles was the striped skunk (*Mephitis mephitis*), with eight interactions overall (6x Box and 2x Tube). None of these resulted in a success, with an average giving up time of 48 ± 55 s, 1–3 attempts (1.4 ± 0.7) and exploratory diversity between 0–4 (1.8 ± 1.7).

When exploring success rate, the most parsimonious model based on the 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).

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* value	z value
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

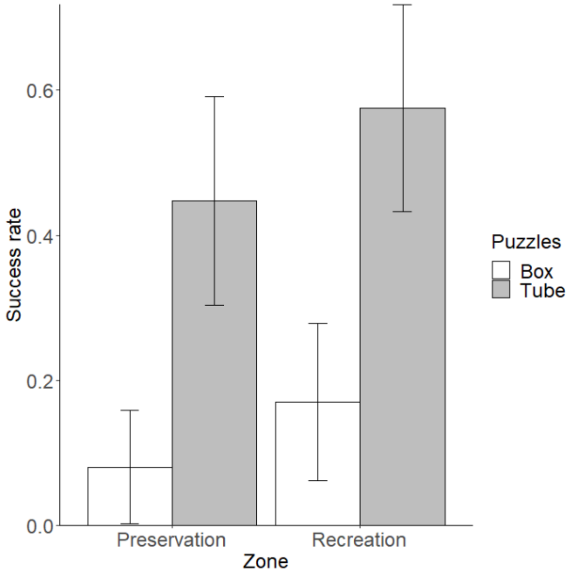

Figure 2. Comparison of problem-solving success rate from raccoons tested in recreation and preservation zones, by different puzzle types. Mean ± 95% CI.

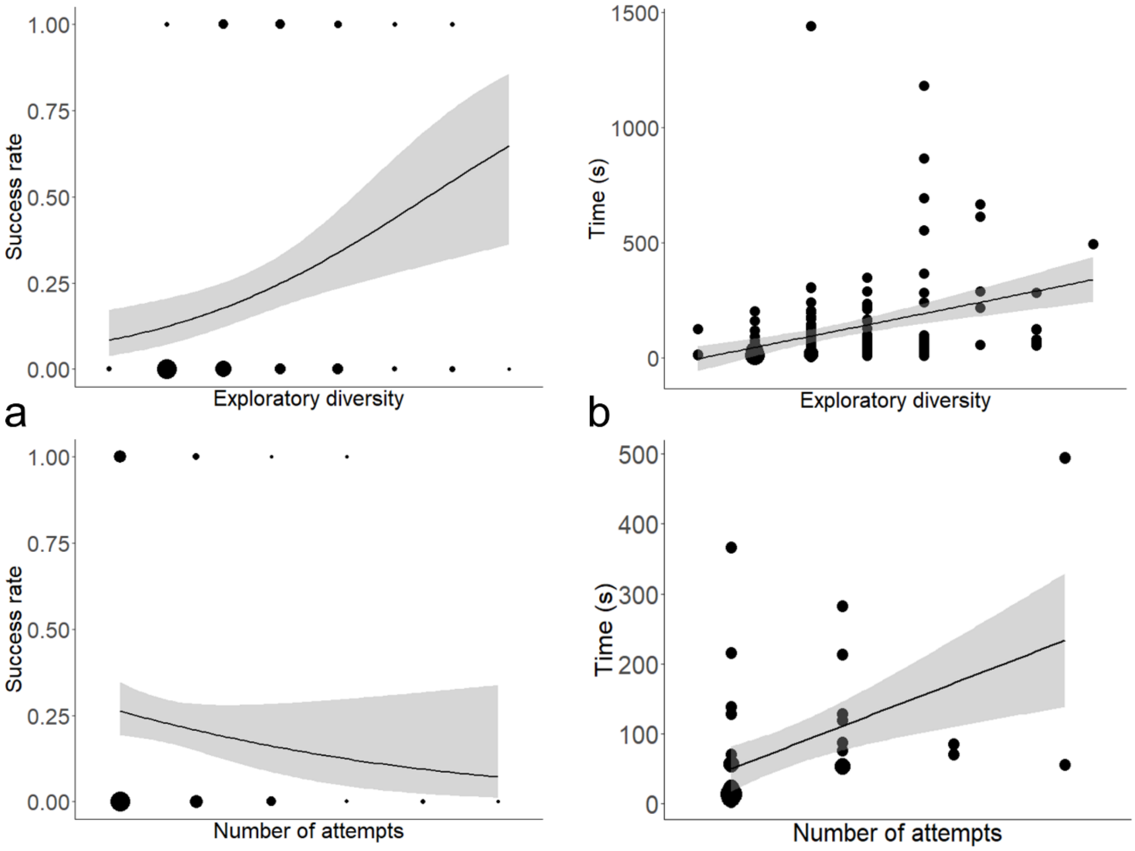

Figure 3. (a) Success rate and (b) time to successfully open the puzzles, in relation to exploratory diversity and persistence (number of attempts).

The 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 showed significant effect on 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 the tasks increased with both exploratory diversity and persistence (Fig. 3b).

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* value**	**t value**
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

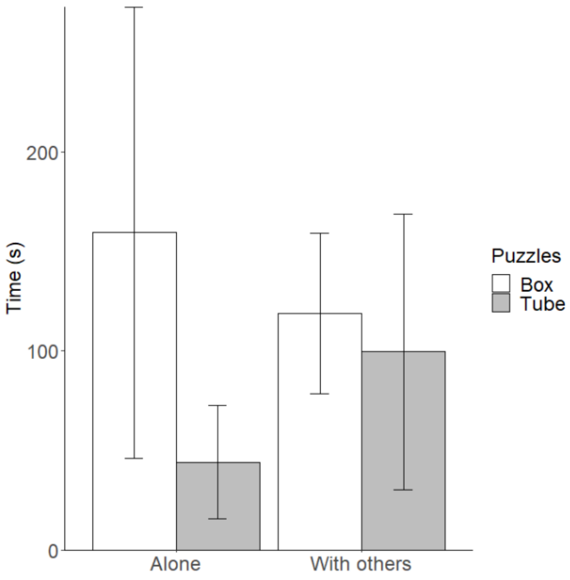

Figure 4. Time to successfully open the puzzles by wild raccoons in the presence of conspecifics or not, by different puzzle types. Mean ± 95% CI.

We tested if raccoons behaved differently in each zone and in the presence of conspecifics. Overall, exploratory diversity was between 0–7, with a mean of 2.3 ± 1.5. Exploratory diversity was different between the zones (β = -0.391, CI = -0.681, -0.101, *P* = 0.0083), and the interaction term between zone and conspecifics was also significant (β = 0.484, CI = 0.217, 2.228, *P* = 0.0259; Fig. 5a). Number of attempts, indicative of persistence, was between 1–6, with a mean of 1.6 ± 1.1. It was not significantly different between the zones (β = 0.064, CI = -0.945, 0.026, *P* = 0.0636), and in the presence of conspecifics or not (β = -0.080, CI = -0.412, 0.252, *P* = 0.6374; Fig 5b). The interaction term between the factors was not significant either (β = 0.460, CI = -0.028, 0.949, *P* = 0.0648).

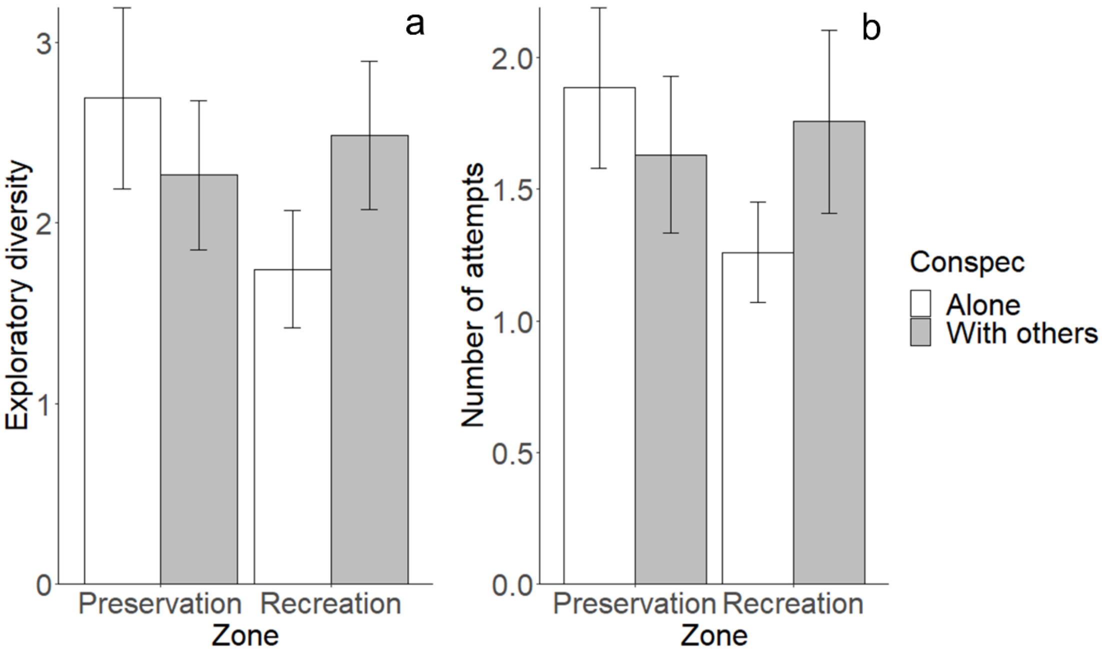

Figure 5. (a) Exploratory diversity exhibited by raccoons in the two study zones, whether they were alone or with conspecifics. (b) Number of attempts to solve the puzzles, indicative of persistence, in the two study zones, whether raccoons were alone or with conspecifics Mean ± 95% CI.

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

3.4 Discussion

We assessed problem-solving ability in wild populations of raccoons and evaluated how external factors (the proximity to humans, puzzle types, and presence of conspecifics) and behavioural traits (exploratory diversity and persistence) influenced their performance. We monitored almost 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 advances (Shettleworth, 2010). There was a stark contrast in success rate, as well as time and number of attempts to solving, between the two puzzle types. On every measure, 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 is more befitting to trial-and-error solution, with a higher probability that a solution is found due to chance (Thornton et al., 2014). Because performance was better with the Tube, it would be indicative that a trial-and-error approach is adopted by some raccoons, rather than some sort of insight (reasoning, representation, planning; Seed & Mayor, 2017; Stanton et al., 2017). This difference between the two puzzles highlights the importance of testing cognitive abilities with multiple tests.

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 term of fitness, recreation zones could be higher-value patches, and individuals able to exploit such resource by their cognitive capacity would have an advantage (Doligez & Boulinier, 2008; Storch & Frynta, 1999). We did not find that the zones (which differed by the amount of human activity and structures) influenced either the success rate or time taken to achieve success. As a comparison, Macdonald and Ritvo (2016) found a stark difference in problem-solving, using a different task, in urban and rural raccoons (77 vs 0 % success respectively). Our studied sub-populations (in each zone of each park) are unlikely to form distinct evolutionary units. 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 from the same population, due to the relatively small size of the parks and absence of important physical barrier.

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 no known raccoon predator is present in the study area, and that they seem quite habituated to humans, intraspecific competition might cause a slight increase of awareness and distraction that resulted in less exploration and longer solving time, but ultimately it is not enough to affect success probability.

We found that exploratory diversity is positively correlated to success rate, just like Daniels and colleagues (2019) with captive raccoons, using different puzzle boxes. The same relation between exploratory diversity and problem-solving exists in other species (spotted hyaenas, *Crocuta crocuta*, Benson-Amram & Holekamp, 2012; various birds, Griffin et al., 2014;

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 behaviours exhibited could shed light on this interaction.

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 & Holekamp, 2012; Benson-Amram et al., 2013; 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 and colleagues, 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, which would indicate 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). From a managing 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 do not know or control for the previous experiences of the participating individuals (Morand-Ferron et al., 2016; Stanton et al., 2022). Second, participation is voluntary and subject to various motivational factors such has 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 to the public, to generate appreciation and empathy toward 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 context, especially on the cognitive basis of behaviour exhibited by problematic individuals.

3.5 Appendix

Table A3.1. Ethogram of observed behaviours expressed by raccoons interacting with the puzzle boxes, used in quantifying exploratory diversity. Adapted from Daniels et al. (2019).

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 toward self
Pull knob	Use mouth or paws to move knob of door solution toward self
Push with arms	Use limbs to move puzzle box away from self
Push with head	Place head against puzzle box and move forward
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

Chapter 4. Exposure to humans and task difficulty levels affect wild raccoons (*Procyon lotor*) learning

Lazure, L. and Weladji, R.B. Exposure to humans and task difficulty levels affect wild raccoons (*Procyon lotor*) learning. Behavioral Ecology. *Submitted.*

4.1 Abstract

Cognition helps wildlife exploit novel resources and environments. Raccoons (*Procyon lotor*) have successfully adapted to human presence in part due to their cognitive abilities. However, close interactions between humans and wildlife can create conflicts. A better understanding of the raccoon's behavioural flexibility and learning ability could improve the mitigation of those conflicts. Learning can be evaluated over multiple exposures to a cognitive task. Our objective is to evaluate wild raccoons learning in contexts varying in terms of exposure to humans (recreational and preservation zoning within protected areas) and task difficulty. We used two food extraction tasks to measure how problem-solving performance varied between trials based on success probability (number of successful trials divided by total number of trials) and time to solve the puzzles. We also looked at the effects of two behavioural traits, exploratory diversity and persistence, on performance. We found strong evidence for learning over consecutive trials in terms of improved success probability. Improvement in terms of success probability and solving time was more pronounced with the initially easier task. The success probability increased over trials only in the recreation zones. There was no evidence for an effect of behavioural traits. The improved performance that we attribute to learning was also maintained over consecutive years. We provide additional evidence that raccoons can learn how to solve a problem, resulting in a more effective solution in consecutive trials. Finally, we consider the management implications of dealing with raccoons that can learn solutions to access anthropogenic resources.

4.2 Introduction

Species in the order Carnivora are often involved in human–wildlife conflicts (Sillero-Zubiri and Laurenson 2001; Treves and Karanth 2003; Carter and Linnell 2016; Bergstrom 2017; Expósito-Granados et al. 2019; Lozano et al. 2019). Raccoons (*Procyon lotor*) are medium-sized members of Carnivora and are considered mesopredators (Buskirk and Zielinski 2003; Prange and Gehrt 2004; Prugh et al. 2009; Glas 2016). They are generalists in terms of diet and habitat

(Lotze and Anderson 1979; Bozek et al. 2007) and are well adapted and successful in anthropogenic landscapes such as rural and urban areas (Prange et al. 2004; Bozek et al. 2007; Hadidian et al. 2010; Daniels et al. 2019). Raccoons are often vilified as a pest species, despite the severity of conflict being relatively benign compared to other cases of human–wildlife conflicts (Pettit 2010; Pacini-Ketchabaw and Nxumalo 2016; Barrett et al. 2019; Justice 2021). Reasons to want to reduce the contact rate between humans and raccoons include reduced disease transmission risk, unwanted habituation, damage and interaction with pets (Rosatte 1998; Beasley and Rhodes 2008; Hadidian et al. 2010; Prescott 2011; Bateman and Fleming 2012; Glas 2016).

The behaviour of raccoons in conflict situations is poorly understood, and data on their responses to different control strategies are fragmented and insufficient (Curtis and Hadidian 2010). The need for conservation actions and their efficacy is tightly linked to wildlife behaviour and cognition (Greggor et al. 2014; Goumas et al. 2020). Understanding and considering learning is essential in devising successful mitigation measures based on repellents or conditioned-taste aversion (Greggor et al. 2020). A manager could theoretically take advantage of a nuisance animal's learning ability by conditioning it to adopt an appropriate behaviour (Greggor et al. 2014). The relatively high learning abilities exhibited by raccoons make them good candidates for conditioning (Snijders et al. 2021).

Learning is a difficult concept to define but is characterized by a change in cognitive state resulting from experience (Pearce 2008; Shettleworth 2010) and persists for a certain time (Domjan, 2000). There are multiple variants of learning, and this study is interested in operant learning, where the animal learns a predictive relationship between an action and an outcome (Shettleworth, 2010; Griffin et al. 2015). Sequentially, it is the ability to acquire, consolidate and retrieve information (Papini and Torres 2017). Learning permits the integration of innovations in the behavioural repertoire (Ramsey et al. 2007). Memory of learned knowledge may fade over time (Shettleworth 2010), for example, during prolonged periods of disuse such as overwinter (Mateo and Johnson 2000; Mateo 2010). Learning is a form of phenotypic plasticity and can be subject to selective forces. Unambiguous cues, such as the presence of food in proximity to humans, and rapid feedback, make learning especially susceptible to selective pressure (Sih 2013). As a cognitive process, learning ability differs among individuals in a consistent manner, akin to behavioural personality traits (Sih and Del Giudice 2012). Understanding learning may enhance our ability to predict how wildlife will adapt to environmental changes (Owen et al. 2017). Learning is highly contextual, and environmental characteristics can shape cognitive performance, which supports wildlife in adapting to new challenges (Greggor et al. 2014; Owen et al. 2017; Chow et al. 2021b), especially in a rapidly changing human context (Sih 2013; but see Greggor et al. 2019). Through learning mechanisms within its lifespan, an individual will adjust its behaviour to avoid risks and take advantage of opportunities (Snell-Rood 2013; Sol et al. 2013; Fehlmann et al. 2021).

Learning is almost exclusively studied through experiments because naturalistic observations are blind to the experience of the individual (Domjan 2000). Learning has been studied more extensively in laboratory settings, but there is still work to perform in ecologically relevant contexts (Thornton et al. 2014; Greggor et al. 2020). Physical challenges, such as the puzzle-box paradigms, are popular and proven ways to assess one's performance in cognitive tasks (Reader et al. 2016; Washburn et al. 2017; Barrett et al. 2019; Daniels et al. 2019; Johnson-Ulrich et al. 2020; Benson-Amram et al. 2022). Puzzle boxes are ecologically relevant because raccoons have learned to take advantage of anthropogenic food resources, often overcoming similar types of physical challenges to obtain rewards (Bateman and Fleming 2012; MacDonald and Ritvo 2016; Barrett et al. 2019; Daniels et al. 2019). In addition, the most biologically relevant and sensory salient experiences are learned faster (Shettleworth 2010). Food is also a central problem in human–wildlife conflicts (Donaldson et al. 2012), making the experiment contextually relevant. Problem-solving tasks are often used to study learning, and an animal with high cognitive abilities could perform well in both (Griffin and Guez 2014); however, there does not seem to have a clear relationship between problem-solving and learning (Seed and Mayer 2017). Using more than one test allows us to assess convergent validity: a "good" performance at one test should be reflected in the other as well (Boogert et al. 2018). Reproducing experiments with different populations in various natural settings is also important to study the effect of the environment on cognitive abilities (Healy and Rowe 2014; Morand-Ferron et al. 2016; Pritchard et al. 2016; Horn et al. 2022; Johnson-Ulrich et al. 2022; Thornton and Truskanov 2022).

Learning is part of a raccoon foraging strategy (Dalgish and Anderson 1979) and is also involved in food extraction tasks (Daniels et al. 2019). We hypothesize that successful raccoons will exhibit operant learning and predict a relationship between trial numbers and success probability, time to successful completion of the tasks, and exploratory motor diversity. In addition to trial number, we will test for the effect of the puzzle type and the human exposure (recreation versus preservation zones). We predict that learning improves faster (higher increase in success probability and reduction in solving time over consecutive trials) with the task being easier to solve in the first interaction and that it will be more important (higher success probability increase and quicker solution over consecutive trials) in recreation zones compared to preservation zones. Finally, we hypothesize that the period of time between field seasons has a negative effect on the retention of learning. We predict that the first interactions the following year will be less successful than the last ones from the previous year.

4.3 Methods

4.3.1 Field work

We conducted experiments in three protected areas located in the south of the province of Québec (all located around latitude 45.6° N and between longitude 72.6° and 75.2° W): Plaisance (28 km^2), Îles-de-Boucherville (8 km^2) and Yamaska (13 km^2) national parks. These parks are considered to have a high density of raccoons, causing "severe" nuisance problems (Denis 2017; Dellarosa 2012). All these parks are relatively small, encompassed in mostly urban or agricultural territories, and border large bodies of water (river or lake). Two site categories are studied based on management zoning: preservation and intensive recreation zones. Recreation zones were defined by the presence of camping sites, vehicle circulation at low speed (<20 km/h), campfires, dumpsters, and a mosaic of ground cover (gravel or paved roads, parking, forest, fields, buildings, playgrounds). Preservation zones were strictly accessible to the public by walking and biking trails, with extensive forest cover. We ran the experiments for three summers (earliest-latest dates May 31–Sept. 14) between 2019–2021. Plaisance Park was not visited in 2021 because of its lower raccoon activity compared to the two other parks and lower accessibility.

We used species-specific baits, but all wildlife could interact with the devices (we only recorded eight interactions by stripped skunks in addition to raccoons). The experiments are non-invasive; animals voluntarily approached the apparatus and left. This ensures that only motivated animals participated. Raccoons were trap-shy, and although tested, capture-marking did not prove efficient in identifying individuals. Raccoons were identified solely by LL through careful observations of the video footage, based on their size relative to the puzzles, body characteristics (fur, tail, limbs), marking when available, and scars and injuries, in a similar manner to Chow et al. (2021a) with Eastern grey squirrels (*Sciurus carolinensis*). Juveniles were excluded because they showed very little initiative and were impossible to tell apart from the videos, often interacting together with the devices, therefore creating confusion to track one individual at a time. It was also impossible to identify an individual as a juvenile one year and as a grown adult on consecutive ones.

We used two puzzle box tasks to test problem-solving abilities. Raccoons trying to open containers (e.g. plastic boxes, bags, bottles, trash bins) is a common occurrence when they are exposed to humans, making this task contextually relevant. The first puzzle we used (hereafter, the Box) is similar to the model used with other carnivore species (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2016). Using the same type of puzzle will facilitate the comparison of our results to similarly conducted experiments (Krasheninnikova et al., 2020). The Box measured 30 cm a side and was made from steel mesh. There was one door with a sliding latch. To solve this problem, a raccoon had to slide the latch and pull on the door. The second puzzle (hereafter, the Tube) consisted of two horizontal plastic tubes (50 cm long in total and 7 cm diameter), one sliding over the other. It required the animal to slide and turn the outermost tube to align two holes (approximately 5 x 10 cm) and access the food in the inner tuber. Both necessitated two consecutive actions that can be performed with the paws, mouth, or muzzle of the animal.

4.3.2 Video analysis

We considered the puzzle to be solved when a raccoon opened it enough to have direct access to the food with its paw, even if it did not immediately reach in and consume the reward. An attempt began when an animal approached within one body length of the box and ended when the animal moved more than a body length away from the puzzle or when it opened the puzzle. A trial included all attempts at opening a puzzle within a single night. We recorded interactions with night vision cameras (Argus 2, Reolink, Hong Kong) set up 3–4 m away. We quantified cognitive performance in problem-solving ability from the videos. We used two response variables to quantify problem-solving efficacy: 1) success (binomial) when the subject opens the puzzle (or not) to have direct access to the bait and 2) time to success (continuous), which is the cumulative time from the first interaction until the puzzle opening within a trial. Two discrete terms representing behavioural traits were included in our models: persistence is the sum of all attempts, including the one when the puzzle is solved, and exploratory diversity is the number of unique behaviours directed at the puzzles. We calculated exploratory diversity in a similar manner to previous studies (Benson-Amram and Holekamp 2012; Benson-Amram et al. 2013, 2014; Johnson-Ulrich et al. 2018; Daniels et al. 2019). The exploratory diversity score accounts for behaviours without contact that allow the gathering of information (perception), as well as behaviours with physical contact that could result in opening a solution (Table 1).

4.3.3 Data analysis

We performed a generalized linear mixed-effect model (GLMM) to examine how success changed over successive trials. We used a binomial distribution with the logit function and included the fixed covariates zone and puzzle type in interaction with trials. Individual and year were included as random effects. To assess the effect of trial number on time to solve the cognitive puzzles, we ran a GLMM using only successful trial data. We used a Gamma distribution with the log function. We explored interactions between trials and zone, as well as between trials and puzzle type. Year and ID were included as random terms, and the model was optimized using the Nelder-Mead optimizer from the R package "nloptr" (Nelder and Mead 1965; Johnson 2014).

To see if persistence (number of attempts) at a task changed over trials, we performed a GLMM with Poisson distribution and log link function, controlling for repeated measures within an individual by including ID as a random term. We also calculated the success probability and mean number of attempts on unsuccessful trials (as a proxy of persistence) for each individual and tested for a correlation with a Kendall rank correlation coefficient. To see if exploratory diversity changed over trials, we performed a GLMM with Poisson distribution and log link function, controlling for repeated measures within an individual by including ID as a random term.

We used a log-likelihood ratio test, comparing a model with year as a random effect to one without, while keeping the fixed effect structure constant (lmtest package; Zeileis and Hothorn 2002). We also performed McNemar's Test (with continuity correction) to determine if the proportions of success significantly differed when matching pairs of subjects (Fagerland et al. 2014) at their last trial from the year was different from the first of the next year. We used the program R to run all statistical analyses (4.2.3, R Core Team 2023).

4.4 Results

We recorded 331 trials from 67 individual raccoons. The minimum number of trials (by individual, by puzzle) was 1, the maximum was 10, and the mean (± S.E.) was 2.7 ± 0.1. Thirty-five individuals interacted with the same puzzle three times or more. Not all individuals interacted with both puzzles. The percentage of raccoons that did not solve the puzzles was 66% for the Box, 27% for the Tube, and 17% for neither.

The data revealed a positive relationship between success probability and trial number ($\beta = -0.798$, CI = -1.180, -0.416, *P* <0.001). Overall, the probability of success increases by 4% in each consecutive trial. There was very strong evidence that the relationship between success probability and trial number differed with puzzle type ($\beta = 0.752$, CI = 0.475, 1.028, *P* <0.001), with an overall success probability almost twice as high (1.95 times) on the Tube (Fig. 1A). There was also very strong evidence for a relationship with zone ($\beta = 0.921$, CI = 0.598, 1.244, *P* <0.001), with an improvement in consecutive trials from raccoons in the recreation zone but a slight negative trend in the preservation zone (Fig. 1B).

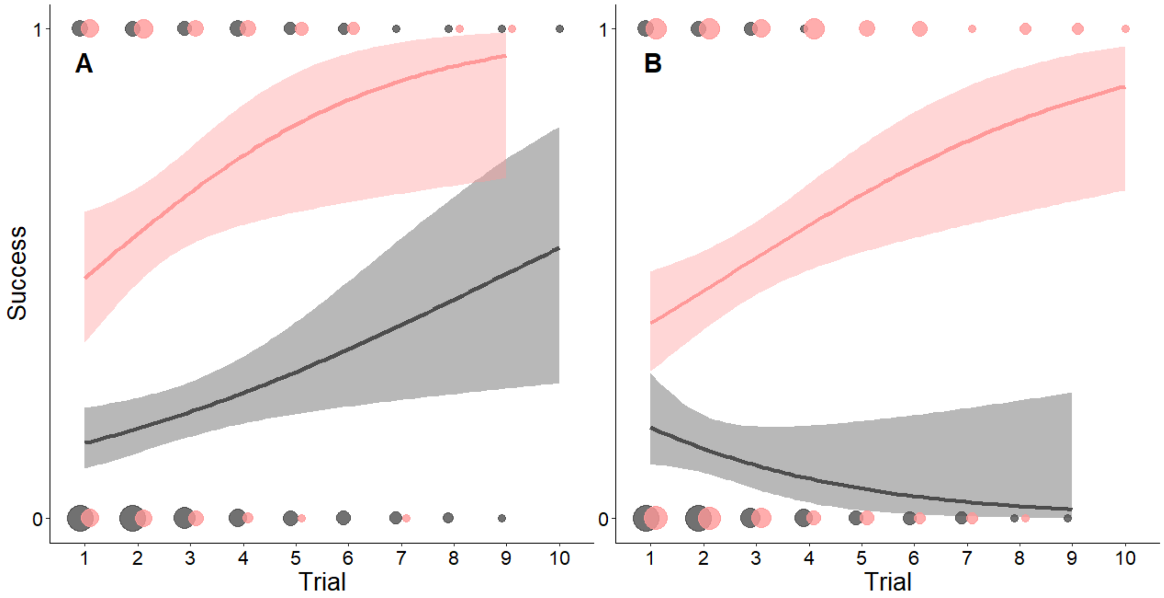

Figure 4.1. Logistical regression lines (mean ± 95% CI) of success probability of wild raccoons trying to solve cognitive puzzles on consecutive trials. **A**: Comparison between the Tube puzzle (red) and the Box puzzle (gray). **B**: Comparison between raccoons in the recreation zone (red) and the preservation zone (gray). Points are dodged horizontally to avoid overlap.

The solution time ranged from 2 s to 36 m 46 s. We only included 72 successful trials in the time model. There was no evidence that the number of trials was related to time to success (β = 0.131, CI = -0.346, 0.609, *P* = 0.589). There was however very strong evidence that there is an interaction between trials and both puzzle types (β = -0.264, CI = -0.389, -0.139, *P* <0.001) but little evidence of such interaction with zone (β = -0.189, CI = -0.636, 0.258, *P* = 0.406). The linear regression slopes indicate a decrease in solving time of -11.3 s per trial with the Tube and an increase of 0.3 s per trial with the Box (Fig. 2). Although there was little evidence to be significant, we see a slight decrease in time to success in the preservation zone but almost none in the recreation zone.

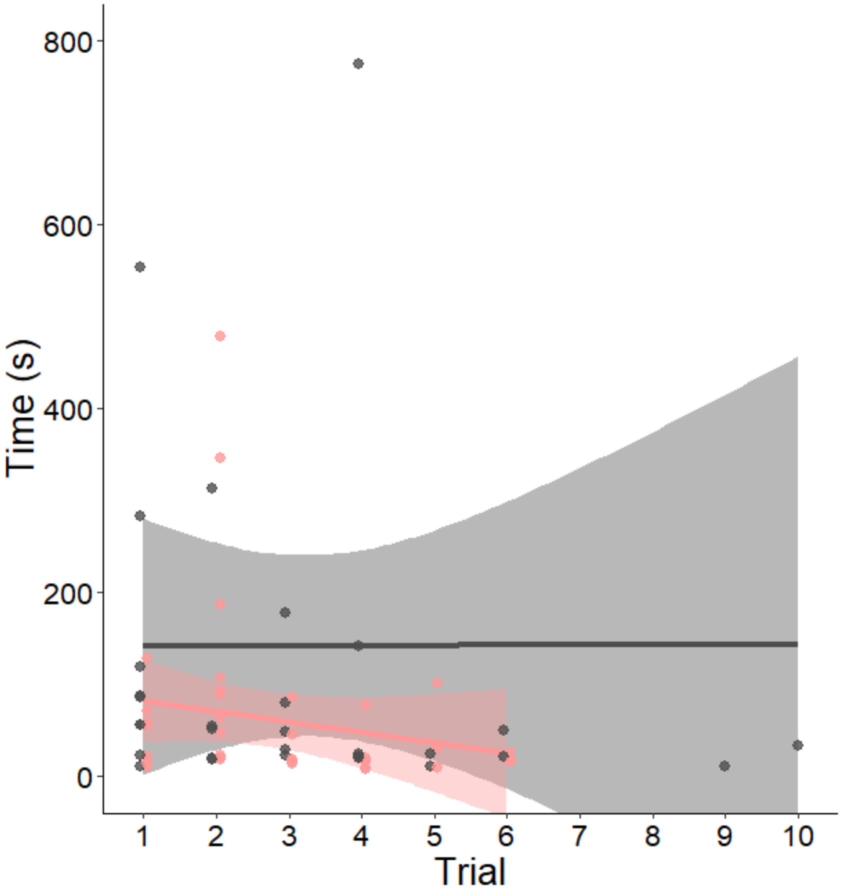

Figure 4.2. Linear regression line (mean ± 95% CI) of time (s) to successfully solve cognitive puzzles by wild raccoons over consecutive trials. Comparison between the Box puzzle (gray) and the Tube puzzle (red). One outlier for the Box puzzle is not shown but was included in the analysis (coordinates 5, 1297). Points are dodged horizontally to avoid overlap.

Sniffing represented the most common behaviour scored using the ethogram (33%, Table 1). There was no evidence that the number of behaviours was associated with trials (*P* = 0.665). This remained true when we only looked at successful trials (*P* = 0.928). The number of attempts also did not vary on successive successful trials (*P* = 0.222). There was weak evidence that there is a negative correlation between an individual mean number of attempts and mean success probability (tau = -0.192, *P* = 0.051).

Table 4.1. Ethogram of observed behaviours expressed by raccoons interacting with the puzzle boxes, used in quantifying exploratory diversity, and frequency observed among all interactions (*n* = 948). Adapted from Daniels and colleagues (2019).

Behaviour	**Description**	**Frequency (%)**
Bite	Open mouth and close teeth around a puzzle box feature	1
Circle	Move around puzzle box within arm's length	9
Climb	Raise body vertically along the puzzle box	8
Dig	Use paws to dig around the puzzle box	3
Lick	Open mouth and move tongue onto a puzzle box feature	1
Pull box	Use limbs to move puzzle box toward self	5
Pull knob	Use mouth or paws to move knob of door solution toward self	3
Push with arms	Use limbs to move puzzle box away from self	1
Push with head	Place head against puzzle box and move forward	1
Raise	Use nose or paws to move ledge of window solution up	<1
Reach with paw	Place paw through puzzle box to retrieve food reward	6
Slide	Use mouth or paw to move knob of slide solution to the left	6
Sniff	Draw in air through the nostrils to detect a scent	33
Stand on	Position body on top of the puzzle box	4
Touch	Place paw on a puzzle box feature	19

Few individuals participated in consecutive years (n = 16). The mean success probability increased over trials and increased year after year (Fig. 3). Models differed significantly with or without year as a random factor (log-likelihood ratio test: $\chi^2 = 15.5$, $P = <0.001$). Comparing the last trial from a given year to the first trial of the next year, we found no evidence of a change in the proportion of success ($\chi^2 = 0.8$, $P = 0.371$).

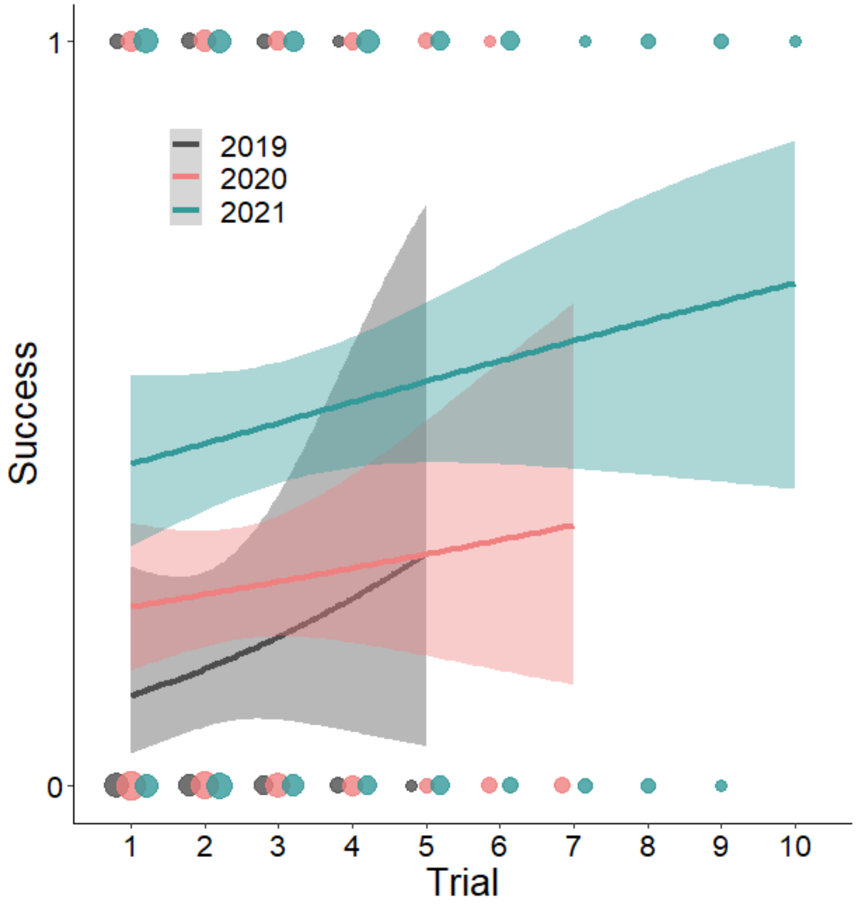

Figure 4.3. Logistic regression line (mean ± 95% CI) of success of wild raccoons taking part in cognitive tasks over consecutive trials in three separate field seasons (2019-2021, see legend). Points are dodged horizontally to avoid overlap.

4.5 Discussion

We tested the learning ability of wild raccoons by exposing them to two cognitive tasks on multiple nights. Raccoons demonstrated learning capabilities over consecutive trials by improving their success probability. This result fits in the idea that generalist species have high innovative potential and learn fast (Henke-von der Malsburg et al. 2020). This is indicative of an overall learning capacity in raccoons, as previously demonstrated (Dalgish and Anderson 1979; Daniels et al. 2019; Galois 1996; Stanton et al. 2022). This ability to learn indicates an evolved predisposition in raccoons (Shettleworth 2010; Fawcett et al. 2012), that is possibly reflected in the cellular architecture of their brains (Jacob et al. 2021). Like many studies of learning in animals, food was again successfully used as a positive reinforcer with raccoons (Galois 1996; Daniels et al. 2019; Morton 2021; Stanton et al. 2021, 2022).

In the initial trial, the two puzzles were not solved at the same rate or speed (Fig. 1A, 2A); thus, we concluded that each task was not as challenging. The improvement of performance (over consecutive trials) is different in terms of success probability and time to solve between the two puzzles. This shows that task difficulty can constrain learning. Practically, it highlights the importance of using different tasks when we want to quantify learning ability.

There is also an effect of the zone on the problem-solving success probability. Raccoons in the recreation zones, which are more exposed to anthropogenic food resources, tended to improve their success probability over trials, while the performance of raccoons in preservation zones decreased (Fig. 1B). More variable and complex environments favor learning and innovation (Mettke-Hofmann 2014; Henke-von der Malsburg 2020), and the recreation zone can be argued to be less predictable than the preservation zone. Anthropogenic changes can correlate with behavioural adaptations (Owen et al. 2017), but learning is not always optimal (Fawcett et al. 2012).

There is also no indication that raccoons lost acquired knowledge between seasons. Interestingly, they seem to perform as well, in terms of success probability, toward the end of a given season and the start of the next, basically continuing from the point where they left (Fig. E). This is indicative of long-term retention of learned solutions or memory (Papaj et al. 2019; Kirkpatrick et al. 2022). We show that their foraging-related information retention time spans many months. In previous experiments, raccoons retained their problem-solving knowledge over similar time periods: up to 147 days (Cole 1907) and up to 286 days (Davis 1907). Davis (1907) extrapolates that problem solving ability is preserved for more than a year. The memory window will vary considerably between species, individuals, and within an individual’s own age and state (Dunlap et al. 2009).

Exploratory diversity remained the same over trials, thus we did not support the inhibitory control hypothesis. Daniels et al. (2019) found that raccoons improved their performance both in terms of the speed of solving and by being more selective. A reduction in exploratory diversity, by removing unnecessary behaviours, would be indicative of inhibitory control (Reader et al.

2016). Inhibition is a cognitive mechanism of rejecting a behaviour while favoring an alternative (Hauser 1999). This implies that there is a behavioural cost (time, energy) in sampling many behaviours, which might not be significant in our study context (Papaj et al. 2019). The number of attempts within a trial did not change between trials. Raccoons, being described as 'stubborn', present high levels of persistence, which positively correlated with success in an experiment by Daniels and colleagues (2019). We did not find such a correlation, with more persistent individuals not being more successful.

The learning ability of raccoons, especially in human-altered habitats, represents a challenge in regard to managing conflicts, but it can also be an opportunity (Barrett et al. 2019; Schulte 2016). Our experiment involved a barrier (the puzzles) to access food, and we showed that a more difficult task has a lower success probability and slower learning. Practically, for someone who wants to block access to a resource by raccoons, it is probably worths investing in a barrier or locking device that involves more complex actions from the start, instead of trying the cheaper or more simple options. Learning can be based on different sensory inputs; odours in particular can affect learning processes (Schulte 2016). Conditioned taste aversion (CTA) is an approach that creates an association (learning) between a sensory cue and an aversive stimulus (Shivik et al. 2003; Snijders et al. 2021; Kirkpatrick and Hall 2022). Because we showed learning ability in the raccoons and relatively long-term retention, it opens the door to the mitigation of conflict through deterrent stimuli (Schakner and Blumstein 2013). Some authors (Proppe et al. 2016; St. Clair et al. 2019) proposed that learning principles can also mitigate transportation-caused wildlife mortality. On the other hand, habituation is a learning process that can attenuate an animal response to a repeated sensory cue (Blumstein 2016; Papaj et al. 2019). Overall, considering an animal learning capacity is essential for long-term deterrence (Schakner and Blumstein, 2013).

Studying wild raccoons allows the testing of animals in ecologically relevant contexts. A limitation, especially in learning studies, is that we have no information on the animal's background. Technological advances will help study learning by facilitating individual identification essential to study repeated attempts from the same individual. Griebling and colleagues (2022) present RFID tags and machine-learning assisted identification as candidate technologies for this challenge. Long-term and repeated experiments will inform us on the parameters influencing the learning and memorization of new knowledge. With the integration of cognitive knowledge on target species and technological advances, new mitigation methods can be devised to reduce the severity of conflicts with importune individuals in a paradigm of respectful coexistence with wildlife.

CHAPTER 5. General discussion

The goal of this thesis was to better understand the cognition of a common nuisance species in the context of protected and recreational areas in southern Québec and consider it within the larger framework of human-mesopredators conflicts. To achieve this goal, I performed a systematic review followed by a narrative synthesis and a meta-analysis on tested mitigation interventions on three common mammal mesopredators (Chapter 2). In the field, I tested the problem-solving ability of wild raccoons by exposing them to two different cognitive puzzles (Chapter 3). Further, I assessed their learning potential over consecutive trials using the same experimental setup (Chapter 4). Below, I review the main findings of my thesis and give some perspectives for future research.

5.1 The cognition of wild raccoons

In the past few years, some researchers have given greater attention to raccoon's cognition, and my thesis followed on those lines. By using comparable methods in slightly different contexts, I can compare my results and consider how the environment might affect cognitive abilities.

5.2.1 Problem-solving

Early experimental cognitive studies were already able to demonstrate the raccoons' very high cognitive abilities (Johnson and Michels 1958; Michels et al. 1961). There is little doubt that raccoons are innovative (Daniels et al. 2019; Stanton et al. 2017, 2022). Most of our results agree with previous studies on raccoons, fitting with the idea that this generalist species has higher innovative potential, exhibits greater behavioural flexibility, and learns faster than specialist species (Henke-von der Malsburg et al. 2020). There was weak evidence that the raccoons from each zone differed in term of problem-solving, performance being slightly better in the recreation zones. I did not see any raccoons in two different zones, the raccoons from both zones can arguably be considered from the same population. Comparing much more different groups of raccoons would probably underline their cognitive divergence, just like the striking problem-solving performance between urban and rural raccoons in Ontario (Macdonald and Ritvo 2016). Overall, it seems normal to detect behavioural differences between individuals and higher ecological levels (sub-populations, populations) of the same species because natural habitats are so complex, dynamic, and unpredictable that natural selection cannot provide a specific behaviour pattern appropriate for every conceivable situation (Fawcett et al. 2012).

5.2.2 Learning

Early experiments demonstrated the raccoons' learning ability (Johnson and Michels 1958; Michels et al. 1961), as well as very recent ones (Stanton et al. 2022). I observed that time to complete subsequent successful trials decreased on one of the tasks (reduction of 11.3 s/trial for the Tube puzzle), but not on the other (Box puzzle). In the study by Daniels and colleagues (2019), there was a reduction in solving time over consecutive trials. The reduction they measured was larger in absolute value (18.3 s faster at each trial); however this is not that meaningful considering all the experimental discrepancies between the two studies. Although different from our measures of operant learning, other experiments demonstrated that raccoons also exhibit reversal learning (Warren and Warren 1962; Stanton et al. 2021), which is closely matched to an animal behavioural flexibility. Interestingly, Galois (1996) demonstrated that raccoons learned to discriminate sensory cues in a foraging task conducted in southern Québec. This is relevant, because raccoons are major predators of nests (turtles and birds, see chapter 1), and is a demonstration that studying cognition can have practical management implications.

There was evidence that learning improved solving time in the recreation zone. For the reason mentioned before, I probably dealt with single populations of raccoons within each park. There is therefore little support that selective pressures would explain that the cognitive abilities differ between these groups at the genetic level. I hypothesize that the most likely explanation why the two zones (differing by the amount of human activities and structures) yielded different results is that the raccoons already possessing better learning ability tend to move toward sites with higher human activity to take advantage of anthropogenic resources, and that they further adapt through learning and phenotypic plasticity (Papaj et al. 2019; Snell-Rood 2013; Sol et al. 2013; Wong and Candolin 2015).

5.2.3 Interaction with other factors

There was a stark difference between the difficulty of the two puzzles. Daniels and colleagues (2019) also noticed big differences in success probability between different tasks. The initial difficulty of a task also had an influence on the learning trajectory. We also detected a higher exploratory diversity toward the Box (mean ± SE, 2.4 ± 0.2) than toward the Tube (2.0 ±

0.1) on the initial trials. This is not surprising because we evaluated the Box to be more challenging. This difference between the two puzzles highlights the importance of testing cognitive abilities with multiple tests.

We saw little evidence that the presence of conspecifics influenced problem-solving ability. Similarly, the presence of conspecifics did not significantly influence habituation to a testing device in wild urban raccoons (Stanton et al. 2022). This might be du to observational conditioning where an observer learns a stimulus-reward association by seeing a demonstrator perform the task (Papaj et al. 2019). The presence of conspecifics can also be seen as potential competition or cause social interference (Brown et al. 2009; Stanton et al. 2022). Social learning and the mitigation of predation risk are other mechanisms that could improve performance in the presence of conspecifics (Donaldson et al. 2012; Feyten et al. 2021; Prange and Gehrt 2004; Shettleworth 2010; Young et al. 2019), but that was not apparent from our results, and on the contrary, the presence of conspecifics increased solving time.

Racoon's exploratory diversity predicted success, which is similar to the findings from Daniels and colleagues (2019). In the context of this study, maybe that there was less cost in giving up due to the relative abundance of other food sources in the environment. However, we did not see a reduction in exploratory diversity over consecutive trials, as Daniels and colleagues saw using a multi-access box. They interpreted it as "selective expression" of behaviours as raccoons gained experience with the task. There was likely a difference on how we scored diversity: on their initial trial, they measured approximately seven different behaviours (between 6-8), whereas we measured 2.3 ± 0.1 (min 0, max 7). I doubt their raccoons were truly that more explorative from the start. Regardless of how we measured it, I did not see the same trend.

In my experiments, persistence did not predict success, which is contrary to results from Daniels and colleagues (2019). I believe there are often flawed methodology to quantify persistence and given the opportunity I would myself measure it differently. I argue that the proxies used to assess persistence have often been confused with work time (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 assign the same individual to a solvable puzzle (e.g., Rao et al. 2018).

5.2 Management implications

Managing conflicts involving species with high cognitive abilities is a challenge (Fehlmann et al. 2021). In chapter 1, I offer a robust synthesis of mitigation methods applied to conflicts involving three common mammal mesopredators. I also show that individual variations in raccoons opens the door to individual-based mitigation (Stanton 2020; Stanton et al. 2022). Interestingly, there seems to be some individuals that performed better on both tasks, worse on both, and fewer that were relatively better at only one task. This was also shown with captive and wild raccoons by other researchers (Daniels et al. 2019; Benson-Amram et al. 2022)

Lethal methods have been a staple of wildlife control for a long time, and many studies evaluated their efficacy. Generally, they offer effective ways to reduce the intensity of conflicts with mesopredators. Trapping followed by euthanasia seems to be the most reliable methods, but also the least disturbing to the rest of the ecological community, compared to shooting or poison-baiting campaign. Because of the stigma around lethal methods, a very strict and selective approach would be preferable (Swan et al. 2017). Selectively trapping problematic individuals will depend on behavioural data and cognitive strategies. Non-lethal methods are quite diverse, with many relying on cognitive traits. Efficacy seems to be more hit-or-miss (chapter 2), with some approaches even having detrimental effects (using conspecific odours and diversionary feeding). Because the suitability and efficacy of each method is highly context-relevant, I cannot make suggestion at-large. But the review and meta-analysis are an excellent starting point for managers to evaluate their options. The use of repellents is overall, a good idea. However, they are not all equals, and many variations have never been tested. We also demonstrate that a repellent should mimic a predator, and not a competitor, which might even attract more individuals. Learning ability of nuisance animals can reduce the efficacy of repellents through habituation and sensitization (Barrett et al. 2009; Blumstein 2016; Shivik et al. 2003). Conditioned taste aversion is very interesting because it is based on cognitive mechanisms. The relatively high learning abilities exhibited by the raccoons make them good candidates to conditioning (Schulte 2016; Barrett et al. 2019; Snijders et al. 2021). The downside is that it can be more complex and labour-intensive than other methods. Finally, barriers are a traditional method of limiting access to a resource. Because of the cognitive abilities and persistence of mesopredators, a regular fence is not a proven solution. Exclosures, which can be built more robust and close-fitting, can be effective. Electric fences also have better results but cannot be applied in all contexts and are more costly.

The review also highlighted limitations in the literature. On that topic, my main message to managers is to include an experimental, and hopefully long-term, approach to mitigation actions. This way, we can rigorously evaluate the efficacy of the methods, to solve a real conflict on the ground. Otherwise, this is wasted opportunities to advance the field of wildlife management (Warburton and Norton 2010). This data then needs to be analysed and shared through easily accessible repositories, preferably through a peer-review process (Sutherland et al. 2004). For researchers, I insist on two points, relating to aspect of data reporting that can result in publication bias or that can limit the applicability and future use of the data : (1) that the results of unsuccessful or simply less effective methods be shared, and (2) that data must be reported in a way that will allow future evaluation of mitigation methods (Cassey et al. 2004; Jennions and Møller 2002; Lortie et al. 2007; White and Ward 2010).

The cognitive tasks we exposed raccoons to in chapters 3 and 4, are a form of barrier they had to overcome. In this sense. the demonstration that task difficulty had a strong effect on problem-solving probability has an implication to deal with nuisance raccoons. If a manager chooses a form of physical barrier to restrict access to a resource (e.g. garbages), I would strongly suggest they implement an opening mechanism as difficult to open as possible from the start. Trying to cut on cost or labour by putting simple mechanisms (e.g. a single lever, a caliper) opens the door to problem solving by raccoons, with subsequent consolidation of the behaviour through learning. This could be the start of an "arm race", which has been documented by managers I talked to during this thesis. Additionally, switching between mitigation methods at regular intervals (exact timing to be determined) might counteract the effect of long-term learning by raccoons.

5.3 Ethical and social considerations

I found with my meta-analysis that lethal mitigation methods are quite effective at reducing human-mesopredators conflicts (chapter 1). However, social and ethical considerations reduce the attractiveness of those methods (Boulet et al. 2021; Conover and Conover 2022; Dubois et al.

2017; Liss 1997; Reiter et al. 1999, White and Ward 2010). On the contrary, Hampton and colleagues (2018) argued that lethal management can have more advantages in term of animal welfare when taking a consequentialist perspective. This is not to say that lethal management should be banned or not, and this thesis is not the place for such a debate. In “real life”, wildlife managers still tend to consider it in their toolkit, although its relative importance to nonlethal methods tend to diminish. Likely that a transition toward less lethal methods will represent an evolving compromise for the coming years.

My research benefited from discussions with various stakeholders, including, pest control professionals, protected areas managers, municipal services providers and fur trappers. In addition to formal scientific literature, it highlights the complexities of dealing with HWCs, and how context inevitably modulates these conflicts. More practically, I considered these interlocutors experiences, challenges and priorities, to ensure I can suggest practical and realistic mitigation measures. A more formal approach could take advantage of citizen science, where more abundant data can shed light on the efficacy of mitigation methods in various contexts while engaging the public in wildlife research and management (Ostermann-Miyashita et al. 2021; Silvertown et al. 2013).

Managers need to consider social factors if they want to solve HWCs, and there is a wealth of research on the topic (Dickman 2010; Glikman et al. 2022; König et al. 2021; Redpath et al. 2013; Treves et al. 2006). Human-wildlife conflicts are a matter of human perceptions and attitudes (Basak et al. 2023; Dickman et al. 2013) and are often ultimately conflicts between humans (Peterson et al. 2010; Redpath et al. 2015). For example, campers fearing mesopredators complain to protected areas managers who want to leave as much freedom to wildlife. In a national park context, there is therefore potential to reduce HWCs by orienting visitors’ attitudes and values toward a more mutualistic relationship with wildlife (Teel et al. 2010). Public education and enforcing laws are two primary methods to alter human behaviour, but just like interventions aimed at wildlife, we need to carefully assess their effectiveness (Baruch-Mordo et al. 2011). A combined approach addressing both the human and animal sides will likely reap the best benefits for both parties.

5.4 Future research directions

Many mitigation methods still need to be sufficiently tested to obtain more confidence on their effectiveness; there is a need to replicate studies and monitor long-term efficacy. By including cognitive information, there is also great potential to develop new methods (Greggor et al. 2014; Schakner et al. 2014). Among already known methods, there are a variety of repelling methods that can still be tested. Also, there are many chemicals that still need to be proven effective in the context of CTA. In Québec, examples of real opportunities for new or improved conflict management approaches include wildlife-proofing trash bins to manage nuisance in urban and national parks, using repellents to ward off animals denning on private properties, and applying CTA to reduce predation on the nest of birds and turtles of conservation value.

During the course of this PhD, I initiated two pilot-studies that did not make it into the thesis. They could potentially be a starting point for future research projects. First, I tried to expose captive raccoons from a wildlife rehabilitation center in Québec to the cognitive puzzles. This was intended to have more control over the experiments, using wild raccoons with little experience in captivity. It had the additional benefit of evaluating raccoons from different origins in the same context. The ongoing animal care conditions were however not appropriate for the experiments unless major changes, which were not feasible at the time. The second project was to evaluate how the presence of dogs in national parks affected the raccoon's behaviour. Sépaq started allowing dogs on leash in selected campgrounds a few years ago and they are currently studying their impact on a wide range of wildlife (Labbé 2022). I wanted to do a finer analysis of their impact on raccoons and did camera trapping in Oka and Yamaska national parks in 2021. I scrolled through 6183 photos obtained over 14 weeks in eight different sites, to find no significant difference in raccoon activity between sites allowing dogs or not. Resource limitation (cameras and time) did not allow me to continue with this project.

Because animal cognition is adaptive and context-dependant, field experiments have enormous values. As previously mentioned, different actors that manage wildlife as part of their work should contribute to this research by setting up their actions in a way that can reap valuable data to evaluate mitigation methods. The challenge remains to conduct rigorous experiments and proper analytical approaches to tease out the effects of different factors and of all the "noise" inherent to an uncontrolled experimental setup. New technologies, or novel application of existing ones, shows potential to advance the study of cognition in wildlife (Stanton et al. 2022; Swaisgood 2020). Griebling and colleagues (2022) offer a comprehensive review of technologies and applications in cognitive studies, stressing the barriers and solutions to their implementation. The main and most obvious advantages would be to identify individuals more easily (e.g., using artificial intelligence) and allow to remotely conduct experiments and observations. Including the individual level and considering within species variability in cognitive studies will benefit the understanding of drivers of natural selection, and the development of targeted mitigation interventions.

Interdisciplinarity is a response to the fragmentation of knowledge in different fields (Clark and Wallace 2015). Animal cognition is at is roots interdisciplinary research, resulting from the combination of animal biology and psychology (Boysen and Himes 1999; Shettleworth 2010). The same can be said about HWC management, a very complex issue (Gao and Clark 2023; Pooley et al. 2016; White and Ward 2010). Further integration and inclusion of other disciplines (social sciences, genetics, engineering, computer sciences, humanities and economics) will stimulate new ideas and approaches in both fields (animal cognition and HWC).

5.5 Conclusion

Bridging the gap between animal cognition and wildlife management can take many forms. In my thesis I focused on human-mesopredators conflicts, more specifically involving raccoons in protected areas in Québec in chapter 2 and 3. I demonstrated how cognition can contribute to conflicts by conferring an ability to exploit novel resources and situations. On the upside, this is also an opportunity to design mitigation measures that will consider an individual animal ability to solve problems and learn new associations. If societal values tend to frown upon lethal mitigation methods, then we need to better understand animal cognition to apply existing non-lethal methods effectively and develop new ones.

One beneficial side-effect of studying animal behaviour is the increased appreciation of their cognitive abilities by the general public (Barrett et al., 2019). Raccoons are particularly impressive in their success to thrive in different habitat and take root in new territories, which can be explained by their relatively high cognitive abilities (Daniels et al. 2019). The recognition of their intelligence and cognition fosters a heightened sense of esteem and respect for wildlife, and down the line increases the tolerance toward them. Empathy and tolerance will be major drivers toward a more sensible approach to HWC (Frank 2016; Kansky et al. 2016). Although we aim toward a peaceful and harmonious coexistence with wildlife, it is impossible to avoid conflicts, which are simply a component of human-wildlife interactions (Hill 2021). The objective of HWC management should not be to eliminate conflict, which is unrealistic, but rather to decrease its level of intensity to an acceptable level, which will be context dependent. A more realistic and workable view is therefore to consider our relationship with wildlife on a continuum, ranging from conflict to coexistence (Frank and Glikman, 2019). It is my belief that this thesis is a small but relevant step toward the coexistence end of that spectrum.

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