Natural conditions and adaptive functions of problem-solving in the Carnivora

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Physical problem-solving paradigms are popular for testing a variety of cognitive abilities linked with intelligence including behavioral flexibility, innovation, and learning. Members of the mammalian order Carnivora are excellent candidates for studying problem-solving because they occupy a diverse array of socio-ecological niches, allowing researchers to test competing hypotheses on the evolution of intelligence. Recent developments in the design of problem-solving apparatuses have enhanced our ability to detect inter-specific and intra-specific variation in problem-solving success in captive and wild carnivores. These studies suggest there may be some links between variation in problem-solving success and variation in urbanization, diet, and sociality.

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Introduction

The ability to solve physical problems to maximize foraging efficiency is highly adaptive; all animals confront such problems while attempting to obtain food via interactions with the environment. For example, many animals living at high latitudes must break through a crust of snow or ice to access forage or water in wintertime [e.g. Ref. 1]. Unsurprisingly, physical problem-solving tasks are among the most widely used paradigms for testing animal cognition, especially with wild subjects [2–4]. These tasks test operant learning; animals learn to associate a motor behavior with a food reward. The apparatuses are usually novel to animals and as a result, problem-solving tasks are often used to test innovation, the ability to solve novel problems [5]. Problem-solving tasks are also used to measure memory, inhibition, and non-cognitive abilities such as motor diversity and boldness [6,7[•] ,8[•]]. More generally, problem-solving tasks are used to measure behavioral flexibility, an ability that is often defined much like fluid intelligence in humans: the ability to quickly and flexibly solve new problems [9]. Links among problem-solving, behavioral flexibility, and intelligence are supported by correlations between problem-solving success and various measures of brain size and executive function across species [6,10]. Recently, there has been growing interest in investigating problem-solving under natural conditions to elucidate the evolution of intelligence.

Four major hypotheses have been forwarded to explain the evolution of intelligence. The 'Social Complexity' hypothesis posits that these traits have been favored by selection to maximize social agility [11,12]. The 'Cultural Intelligence' hypothesis also suggests a key role for sociality but suggests that the main benefit of social living is the transmission of learned skills [13]. The 'Cognitive Buffer' hypothesis [14] suggests that greater intelligence is favored by natural selection to help animals cope with novel or unpredictable environments. The 'Ecological Intelligence' hypothesis suggests that enhanced cognitive abilities and larger brains evolve as a product of natural selection on cognition required for finding food, tool-use, and hunting [15,16]. Here, we review recent research that investigates the methods used to test physical problem-solving, and the conditions under which successful problem-solving occurs, in species of the mammalian order Carnivora (hereafter referred to as 'carnivores').

Why mammalian carnivores?

Although most field research on animal cognition to date has used either primates or birds as subjects, mammalian carnivores represent another excellent group in which to assess comparative problem-solving ability. Carnivores occupy a vast array of ecological niches, and consume diets ranging from plants, carrion, or insects to large herbivores. Many gregarious carnivores engage in cooperative foraging behavior and some live in surprisingly

complex societies. To date, species in both hyena and cat families have been identified as good model systems for exploring problem-solving and other aspects of animal intelligence [17,18], and brain-size has been found to be positively correlated with problem-solving ability among 39 species of zoo-dwelling carnivores [6]. Although some terrestrial carnivores form social groups that are comparable in size and complexity to those of primates, carnivores and primates last shared a common ancestor between 90 and 100 million years ago [19,20]. Therefore, carnivores offer the opportunity for an independent test of the hypothesis that demands imposed by social living have driven the evolution of both cognitive abilities and nervous systems in mammals. However, the cognitive abilities of carnivores, particularly wild carnivores, have seldom been the subject of systematic study, and they remain poorly understood. Striking differences separate carnivores and primates with respect to their limbs and feeding apparatus. Specifically, because most carnivores have teeth and skulls specialized for shearing, snipping, crushing and pounding, carnivores have much less need than primates or birds to develop tools for extracting or processing difficult foods. Recently, the cognitive abilities of captive carnivores have been tested using several novel paradigms, and some of these paradigms have then also been used successfully with carnivores in their natural habitats.

How do we test problem-solving in carnivores?

The most lauded examples of problem-solving in wild animals are those of novel tool-use, when an animal uses a new tool for the first time in its population. Novel tool-use has been the focus of much research because it may involve specialized cognition, such as learning about physical affordances, causal reasoning, and innovation [21,22]. In addition, if a species is capable of novel tool-use, its environment informs us about the evolution of intelligence (e.g. if the novel behavior is transmitted to other group members, this supports the Cultural Intelligence hypothesis).

Perhaps the most well-known example of tool-use by mammalian carnivores is use of rocks by sea otters (*Enhydra lutris)* to open hard-shelled prey [23]. Recently, innovative tool-use was reported in a wild dingo (*Canis lupus dingo*) [24], a wild striped skunk (*Mephitis mephitis*) [25], wild brown bears (*Ursus arctos*) [26], and wild polar bears (*Ursus maritimus*) [27]. However, because recorded instances of tool-use in the wild are rare and typically lack documentation on the emergence, development, and repeated use of tools, it can be difficult to make inferences about the cognition involved. Experimental tests of tool-use are also problematic because they require subjects to learn to use a researcher-chosen tool in a limited amount of time, conditions that do not emulate those in the wild and often result in 'failure' without meaningfully

informing us about cognition [e.g. Refs. 28,29]. Nevertheless, tool-use is not the only example of physical problem-solving by wild carnivores. For example, grizzly bears (*Ursus arctos horribilis*) break into logs to eat insects [30], Eurasian lynxes (*Lynx lynx*) cache meat by covering it with plant matter or snow [31], and monk seals (*Monachus schauinslandi*) dig and move rocks on the ocean floor to flush prey [32].

Examining cognition experimentally using problems that vary in their degree of difficulty can give us a broader view of problem-solving ability and allow us to examine the conditions and development of innovative problem-solving [33], especially when using designs that allow for repeated problem-solving by individual subjects. Single-access puzzle boxes (puzzle boxes with a single method to access a food reward) are commonly used to investigate problem-solving in carnivores (Figure 1a–c). Originally conceived by Thorndike in 1898 [34], who used puzzle boxes to test the intelligence of cats and dogs, puzzle boxes have experienced a resurgence in use with carnivores over a century later. Most experiments give subjects multiple trials, allowing for an examination of trial-and-error learning and known influences on successful innovation, such as motor diversity, persistence, motivation, and neophobia [33]. Benson-Amram and Holekamp [35] used a single-access puzzle box with a latch opening to test innovation in wild spotted hyenas (*Crocuta crocuta*). They found that motor diversity was linked with successful innovation, while neophobia limited innovation, laying the groundwork for future studies to continue investigating these influences. More recently, Borrego and Dowling [36°] used a single-access puzzle that required pulling on a rope to release a food reward (Figure 1a). Captive lions (*Panthera leo*) learned to use their jaws or front paws to pull the rope and retained their learning after a period of 24–33 weeks. This study is an excellent example of using a single-access design to assess learning, memory, and social facilitation related to problem-solving. Young *et al*. [37°°] investigated problem-solving in captive coyotes (*Canis latrans*). They initially used a single-access box that could be opened by pulling a handle to open a door. However, coyotes were frequently startled when the door fell open. In a second experiment they used a novel puzzle that required coyotes to remove a lid with the snout or paws to access a food reward (Figure 1c). This study represents a good example of adapting puzzle designs to meet the requirements of diverse species.

Puzzle boxes are also used to test cooperative problem-solving with apparatuses where handles or ropes must be pulled simultaneously by multiple individuals to access bait [38–41]. Cooperative problem-solving tasks add additional socio-cognitive demands because subjects must attend to the behavior conspecifics. For example, Borrego [40] investigated cooperative problem-solving by lions

Figure 1

Current Opinion in Behavioral Sciences
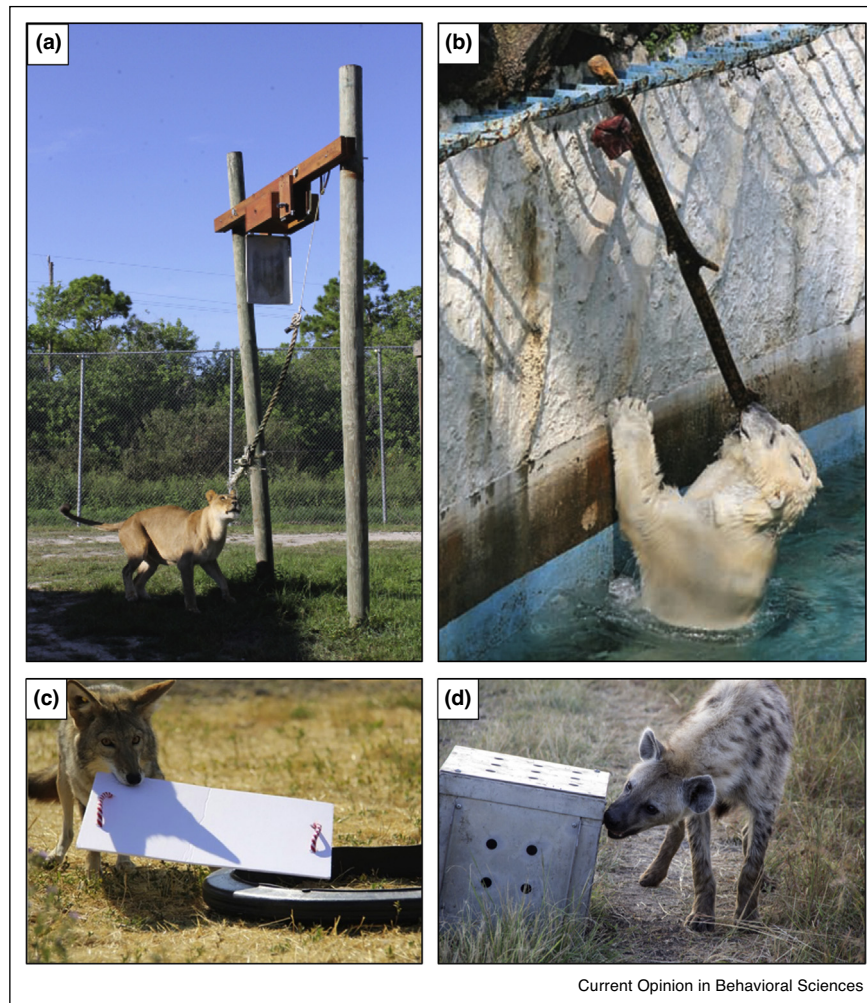
Carnivores solving motor problems. **(a)** A captive lionness interacts with a puzzle box (Reprinted from Borrego and Dowling [36*] with permission from Springer). **(b)** A captive polar bear uses a tool to retrieve a piece of meat (Reprinted from Stirling *et al.* [27] with permission from the Arctic Institute of North America, © Tennoji Zoological Gardens, Osaka, Japan). **(c)** A captive coyote pulls the lid off a puzzle (Reprinted from Young *et al.* [37**] under a CC0 1.0 license). **(d)** A wild hyena interacts with a multi-access puzzle box (Source: Lily Johnson-Ulrich).

after subjects had individually learned to open a puzzle box with a single latch. A second box with two latches (both of which had to be pulled simultaneously) was presented to pairs of lions. Lions were able to solve this cooperative puzzle box but showed no evidence of coordination.

Researchers are increasingly turning to multi-access puzzle boxes (MABs) to assess problem solving [42]. These puzzles allow subjects to use different motor behaviors to obtain food in a variety of ways and require repeated problem-solving to learn multiple puzzle solutions (Figure 1d, Figure 2). Importantly, they also allow researchers to observe a greater degree of variation in success than single-access boxes. For example, six out of seven captive brown bears (*Ursus arctos*) were able to learn

at least one solution to a MAB, but only three learned all four solutions (Z Johnson-Ulrich, PhD thesis, Oakland University). Eight out of 10 captive spotted hyenas (*Crocuta crocuta*) were able to solve a MAB once (Figure 2c), but only four learned all four possible solutions [8*]. Five of six African lions and seven out of nine snow leopards (*Panthera unica*) learned at least one solution to a MAB, while only one lion and none of the snow leopards learned all three solutions (VL O'Connor *et al.* unpublished). Thirteen of 63 meerkats (*Suricata suricatta*) learned one of three solutions to sequentially presented puzzle boxes, while only four solved all three boxes [43]. Finally, thirteen out of twenty captive racoons (*Procyon lotor*) learned at least one solution to a MAB, while seven solved all three MAB solutions (Figure 2a) [7*]. These MABs were also used to assess learning, inhibition, and

Figure 2

Current Opinion in Behavioral Sciences
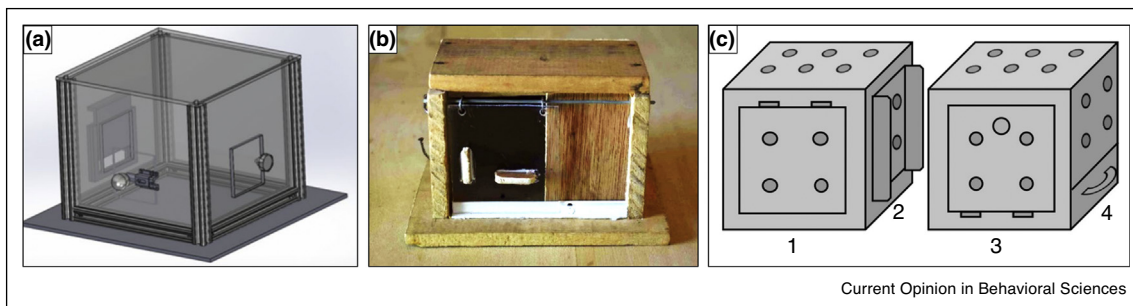
Examples of multi-access boxes used with carnivores. **(a)** A three-access MAB used with raccoons (Reprinted from Daniels *et al.* [7•] with permission from Springer). **(b)** A two-access MAB used with narrow-striped mongooses (Reprinted from Rasolofoniaina *et al.* [58••] under a CC BY 4.0 license). **(c)** A four-access MAB used with spotted hyenas (Reprinted from Johnson-Ulrich *et al.* [8•] with permission from Springer).

non-cognitive abilities such as motor diversity and persistence. Typically, subjects initially discover solutions through trial-and-error (wherein persistence and motor diversity enhance the likelihood of discovering a solution), and afterwards show increased efficiency in solving, indicating that they learn how to operate different solutions. Additional learning of new solutions shows repeated innovation. Despite predictions [44], repeated innovation did not correlate with inhibition of previously learned solutions in captive hyenas [8•]. Studies on wild (Figure 1d) and captive spotted hyenas found that measures taken from MAB performance were highly repeatable, which further validates the use of MABs for measuring cognitive traits in wild subjects [8•,45].

Lastly, some researchers combine observations of tool-use by wild carnivores with research on captive individuals. Stirling *et al.* [27] discuss anecdotal reports of tool-use by wild polar bears and contrast these with a report of innovative tool-use by a captive polar bear and experimental studies of tool-use by captive brown bears [46] and sloth bears (*Melursus ursinus*) [28]. Stirling *et al.* [27] provide a useful method for research going forward; researchers interested in physical problem-solving should continue to observe wild animals for examples of tool-use or other innovative physical problem-solving and use these examples to inform research in both captivity and the wild. Experiments using puzzle boxes and other apparatuses can then inform us in more detail about the traits of individuals (e.g. persistence and motor diversity), current environment (e.g. presence of conspecifics), and the ecological variables (e.g. sociality, urbanization, environmental change, etc.) that may influence physical problem-solving.

What ecological conditions promote successful problem-solving in carnivores?

Investigating the ecological conditions under which successful problem-solving occurs is critical because natural

selection can only act on traits to the extent to which they are expressed in an animal's natural environment [47]. In addition, environments that favor a high rate of problem-solving success or a high proportion of problem-solvers in a given population, very likely exert strong cognitive demands on their inhabitants [48]. Environments that are cognitively demanding for extant species may share similarities with the environment of evolutionary adaptedness (EEA) and can thus shed light on conditions under which problem-solving evolved.

Recent research on carnivore problem-solving has focused on three conditions: urbanization, domestication, and sociality. Urbanization has unprecedented effects on entire ecosystems and is increasing exponentially on a global scale. Within the Carnivora, many species have successfully adapted to urban environments [49]. The Cognitive Buffer hypothesis predicts that problem-solving abilities should be adaptive for responding to urbanization because cities present animals with many novel challenges [50]. Research with birds suggests that superior problem-solving abilities are correlated with urban adaptation [51], and highly urbanized carnivores such as bears, raccoons, and spotted hyenas are all successful problem-solvers compared to other carnivores [6,7•,50]. However, a study in raccoons found that, although urban raccoons were better at solving a familiar problem (opening a trash can), both urban and rural raccoons were equally adept at solving a novel problem (novel bucket task) [3]. In addition, a study of spotted hyenas found that both urban and urban-transitional hyenas were significantly worse at problem-solving than hyenas living in a natural environment, perhaps because a switch from hunting to scavenging among urban carnivores reduces the demand for problem-solving abilities [52•]. Taken together, these studies suggest that, although successful problem-solvers may be most likely to invade urban environments, urban environments themselves may not demand superior problem-solving abilities in carnivores.

These results fail to support the Cognitive Buffer hypothesis. Instead, many species may find urban environments to be much less challenging than natural ones with regards to foraging opportunities [51]. If this trend holds across the Carnivora, it would support the Ecological Intelligence hypothesis, which links problem-solving to foraging challenges.

The second condition is domestication, which, like urbanization, alters the selective demands on cognitive ability. Research has consistently found that wolves (*Canis lupus)* are much more successful problem-solvers than domestic dogs (*Canis lupus familiaris)*, a result apparently driven by greater motivation to interact with and explore test apparatus among wolves than dogs [53,54,55•]. The socioecology hypothesis of domestication suggests that this difference in motivation is likely driven by the difference in feeding ecologies because hunting requires much more persistence than scavenging [55•], and perhaps also more intelligence; among carnivores, hunting of vertebrate prey is one of the strongest positive predictors of larger brain volume [56]. These results also lend support the Ecological Intelligence hypothesis. However, in addition to motivational differences, dogs and wolves exhibit differences in social behavior. Dogs are much more likely to show human-directed gaze, a behavior that may result from selection for greater socio-cognitive skills in dogs during domestication [53].

As with domestication, the social context appears to be important in many carnivores tested on problem-solving tasks. Wild meerkats had higher rates of interaction with a two-option puzzle box, and were much less likely to abandon their attempt, after observing other meerkats manipulate or gain access to the puzzle box [57]. Spotted hyenas were faster to approach a puzzle box after seeing a demonstrator interacting with it (captive) or when a conspecific was present (wild) [39]. Only 60% of captive lions were successful at opening a novel puzzle box when physically and visually separated from conspecifics [36•]. However, when unsuccessful lions were allowed to access the puzzle box during a trial with a successful partner, 80% of previously unsuccessful lions went on to successfully open the puzzle box in subsequent trials. Similarly, 80% of captive coyotes that had the opportunity to observe a conspecific demonstrator opened a puzzle box, in part due to increased persistence [37••], while only 20% of coyotes with no demonstrator opened a puzzle box. In wild narrow-striped mongooses (*Mungotictis decemlineata*), 63% of individuals with a demonstrator solved a puzzle box (Figure 2b) compared to only 25% of individuals without a demonstrator [58••]. While social learning has not been tested in solitary carnivores, brain size correlates with the length of time that juveniles associate with their mothers after weaning, a period of time where juveniles are presented with many social

learning opportunities by their mothers [59,60]. These results generally support the Cultural Intelligence hypothesis and suggest that natural selection may have favored the use of social information during problem-solving by carnivores [13].

Interestingly, group size, a common proxy for social complexity, does not consistently predict problem-solving in carnivores. Within the genus *Panthera*, social lions outperform solitary leopards and tigers [61] and within the family Hyaenidae, social spotted hyenas outperform solitary striped hyenas (*Hyaena hyaena*) [62]; however, a study across 39 carnivore species, including members of *Panthera* and Hyaenidae, found no relationship between group size and problem-solving after controlling for phylogenetic relatedness [6]. The lack of any consistent relationship across the Carnivora is not surprising given that the Carnivora includes families such as Ursidae, whose members are solitary yet score highly for problem-solving ability [6], an observation that challenges the Social Complexity hypothesis. In addition, while the results described in Borrego and Gaines [62] and Holekamp *et al.* [63] are intriguing, there are many other socioecological factors that may vary among these species other than group size. For example, within the genus *Panthera*, species also vary in their hunting strategies (e.g. lions use a mix of ambush, stalking, and direct pursuits of prey, whereas leopards and tigers rely primarily on ambushing prey) [63]. In addition to living in larger groups, both spotted hyenas and lions are cooperative hunters.

Other research on the Social Complexity hypothesis has drawn attention to factors such as social bonds [12], inter-group conflict [64], or intra-group cooperation [65], rather than group size, as drivers of intelligence within social species. More cooperative behaviors are associated with, among other factors, larger brains in the Carnivora [66] and cooperative problem-solving has been tested in several species of social carnivores including lions [40], spotted hyenas [38], wolves [67], dogs [67], giant otters (*Pteronura brasiliensis*) [41], and small-clawed otters (*Aonyx cinerea*) [41]. Whereas all these species were able to solve the cooperative problem-solving tasks, only wolves and spotted hyenas showed evidence of actively coordinating simultaneous attempts. However, in all studies except Schmelz *et al.* [41] the social relationship between partners influenced success. Individuals that were closer in rank, had stronger social bonds, or showed greater social tolerance were more successful at solving cooperative puzzle boxes. These intraspecific results support predictions of the Social Complexity hypothesis with regards to the importance of social relationships.

Conclusions and future directions
Although research on problem-solving in carnivores is still in its infancy, recent results already provide some insights

on the evolution of intelligence in carnivores. Urbanization and domestication research offer some tentative support for the Ecological Intelligence hypothesis. In social carnivores, the strong effects of social facilitation and social relationships support predictions of the Cultural Intelligence hypothesis and Social Complexity hypothesis respectively. Taken together, foraging challenges and opportunities to learn socially about foraging challenges are strong predictors of problem-solving abilities in the Carnivora. Such research has been powered by developments in methodology that allow repeated examination of problem-solving within wild subjects and provide data on physical problem-solving success, innovation, learning, memory, and related behaviors such as motor diversity, persistence, and inhibition. However, research with captive subjects will continue to be useful for developing new paradigms, piloting research methods, supplementing data from wild individuals, and conducting fine-scale tests of learning and cognition during problem-solving.

We suggest several areas for future research with carnivores. First, while the breadth of species within the Carnivora that are included in tests of cognition continues to increase, testing an even broader array of species could have several distinct benefits. Phylogenetic sister-group comparisons within a single family or multiple species within a genus that vary in their ecological niches provide particularly useful data points because phylogenetic explanations for cognitive ability can be partially controlled (e.g. the bear family includes both obligate herbivores, obligate carnivores, and generalist omnivores). Likewise, comparisons of distantly related carnivore taxa, such as fissiped and pinniped caniform species, can potentially shed light on how a major evolutionary shift, switching from a terrestrial to an aquatic lifestyle, may affect problem-solving [68].

Second, further investigation of the relationship between social complexity, cooperation, social learning, and problem-solving in carnivores is warranted. The role of social facilitation in problem-solving success among solitary species (e.g. between parents and offspring) would provide an interesting test of the Cultural Intelligence hypothesis outside of gregarious carnivores. In addition, the intraspecific approach for testing the Social Intelligence hypothesis has been successful in other taxa [69] and could help shed light on the role of social complexity in shaping carnivore intelligence.

Finally, although the conditions of successful problem-solving may reflect the conditions under which problem-solving evolved, there has been virtually no research on the fitness consequences of variation in problem-solving ability [but see Ref. 70]. Investigating the strength of selection in different environments will allow researchers to draw stronger inferences about the kinds of

environments that exert selective pressure on problem-solving skills in extant populations. Ultimately, we look forward to seeing the future of research on carnivore problem-solving.

Conflict of interest statement
Nothing declared.

CRediT authorship contribution statement
Lily Johnson-Ulrich: Conceptualization, Writing - original draft, Writing - review & editing. **Zoe Johnson-Ulrich:** Conceptualization, Writing - original draft, Writing - review & editing. **Kay E Holekamp:** Writing - original draft, Writing - review & editing, Supervision.

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