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ORIGINAL ARTICLE

Effects of early-life experience on innovation and problem-solving in captive coyotes

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Abstract
Early-life experience often shapes behaviors like innovation and exploration. These behaviors are important to animals encountering novel food resources in diverse habitats, such as mesocarnivores in urban areas. To understand if early-life experiences impact later-life behavior, we examined how coyotes (*Canis latrans*) responded to a multi-access puzzle box at two life stages: pup (~ 7 weeks) and dispersal (~ 10 months). We first exposed pups, still living with their parents and littermates, to a baited puzzle box. At dispersal age, we again tested both these pups and an age-matched control group that was not exposed to the puzzle box as pups, both as individuals and with their pair-mate. We quantified problem-solving capability, latency to approach, and time spent in proximity to the puzzle box. Most pup litters solved two of the three access points, but no dispersal-age coyotes solved any access point. The amount of time dispersal-age coyotes spent near the box during pair-testing increased with (1) more time spent near the box during single-testing, (2) more time their pair-mate spent near the box during pair-testing, and (3) if their pair-mate came from a litter that previously solved the box. These results suggest that early-life experience and social interactions influence exploratory behavior at dispersal age, but coyotes exhibit increased avoidance behavior at this life stage, which corresponds with the life stage that overall survivorship decreases. Our study provides insight into how early-life experiences shape adult behavior in mesocarnivores.

Significance statement
Exploratory behaviors, including risk-taking and problem-solving, are likely important characteristics for urban-dwelling species, such as coyotes, but how development and sociality influence these traits is poorly understood. Therefore, we presented coyotes with a puzzle box as pups with their littermates and again at dispersal age, both individually and with their pair-mate. Three of four litters solved the puzzle box when housed with their littermates, but no coyotes solved at dispersal age when housed alone or with their pair-mate. Notably, there was a general decrease in exploratory behavior and innovation from pup to dispersal age. However, we found that previous experiences during puzzle-box trials positively influenced the amount of time coyote pairs spent near the puzzle box at dispersal age. Our results suggest that pursuing food resources in novel situations may be constrained by developmental processes, possibly in response to prioritizing future opportunities to reproduce.

Keywords Ontogeny · Development · Life stages · Social learning · Facilitation

Introduction

Anthropogenic disturbance and urbanization are expanding globally, and wildlife is increasingly living in the resulting novel environments. This widespread expansion of human-modified ecosystems has affected the biodiversity and abundance of species living in urban environments, including rodents, reptiles, birds, and carnivores (Hamer and Mcdonnell, 2010; Baxter-Gilbert et al. 2019; Fidino et al. 2020). In adapting to urban landscapes, many species display shifts in behavior, diet, and life-history

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traits (McDonnell and Hahs 2015; Seress and Liker 2015; Kujiper et al. 2016; Henke-von der Malsburg et al. 2020). These shifts can help species survive and even thrive in novel environments. For example, urban striped field mice (*Apodemus agrarius*) are better at problem-solving than rural individuals (Mazza and Guenther 2021) and wild sulphur-crested cockatoo (*Cacatua galerita*) living in urban areas developed innovative behaviors used to open household waste bins (Klump et al. 2021). In particular, generalist mesocarnivores like raccoons (*Procyon lotor)*, spotted hyenas (*Crocuta crocuta*), and coyotes (*Canis latrans*) have become adept at living in urban environments through increased ecological opportunities and changes in approach behavior (Ordeñana et al 2010; Breck et al 2019; Turner et al 2019; Larson et al 2020).

Problem-solving, the act of overcoming an obstacle to access a resource (Rowell et al. 2021), and innovation, the ability to solve new problems or invent novel solutions to existing problems (Reader and Laland 2003), may be key to surviving in anthropogenic landscapes (Ducatez et al. 2020). These traits can be characterized via trials involving puzzle boxes (Reader et al. 2016; Johnson-Ulrich et al. 2021; Rowell et al. 2021). While single-access puzzle boxes are appropriate for determining problem-solving abilities, multi-access puzzle boxes have different ways of solving access points to receive a food reward and are more often used to test innovation (Auersperg et al. 2011; Johnson-Ulrich et al. 2018; Daniels et al. 2019; O'Connor et al. 2022). When puzzle boxes are first presented to an animal, the boxes are also novel objects and can therefore be used to measure an animal's exploratory behavior. Exploratory behavior defines an animal's response to novel objects or settings and is an integral first step in problem-solving and innovation (Réale et al. 2007; Auersperg et al. 2011; Breck et al. 2019; Jacobson et al. 2022).

Puzzle boxes have been used in a variety of species, such as smooth-coated otters (*Lutrogale perspicillata*) (Ladds et al. 2017), Asian short-clawed otters (*Aonyx cinereus*) (Saliveros et al. 2020), skunks (*Mephitis mephitis*), raccoons (Daniels et al. 2019; Stanton et al. 2021), and Asian elephants (*Elephas maximus*) (Jacobson et al. 2022). Research testing captive coyotes with single-access puzzle boxes showed that they were not only capable of solving different types of puzzle boxes for a food reward but are also capable of social learning—showing shorter latencies to approach and solve and higher success rates after observing successful peer demonstrators (Young et al. 2019). Furthermore, the study found that dominant coyotes within a mated pair had a shorter latency to approach times and were more persistent in their interactions with the puzzle boxes, suggesting social facilitation and exploratory behavior may enhance problem-solving abilities. While fundamental to our understanding of problem-solving in urban-adapted mesocarnivores, the research on problem-solving has primarily focused on adults and lacks an understanding of other life-history stages.

How early-life experiences influence behavior at later life stages is understudied (Rowell et al. 2021). Behavioral traits that are often linked to innovation, such as exploration, are consistent across different ontogenetic stages in some species, such as the Eurasian harvest mice (*Micromys minutus*; Schuster et al. 2017) and zebra finch (*Taeniopygia guttata*; Wuerz and Krüger 2015). Yet even in these species, there are differences across other behavioral traits that correlate to innovation; boldness was not consistent over ontogenetic stages in zebra finches but was consistent in the mice. Early-life experiences could influence later-life behavior in other mammals, like mesocarnivores, especially if those experiences occurred when young individuals are still with their parents and littermates. For example, coyote pups began to mirror their parent's risk-taking behavior during foraging as their parents became more habituated to human presence and less risk-averse (Schell et al. 2018). Habitat selection for developed areas as adults is also related to natal home range characteristics in coyotes (Zepeda et al. 2021), suggesting that early life experiences could influence how mesocarnivores select resources later in life. However, whether similar patterns are observed for other behavioral traits, such as innovation and problem-solving, remains unknown.

After dispersal, social interactions with conspecifics may also influence mesocarnivore behavior. Social facilitation influencing foraging behavior has been documented in diverse animals, such as sheep (*Ovis aries*) and barnacle geese (*Branta leucopsis*; Michelena et al. 2009; Kurvers et al. 2012). Therefore, exploration, innovation, and problem-solving behavior in mesocarnivores may also depend on social context. This is a critical gap in knowledge and important for us to understand because expanding urbanization will provide more opportunities to pursue novel food resources for urban-dwelling mesocarnivores such as coyotes and their young.

Coyotes are an ideal North American species for understanding how mesocarnivores adapt to and thrive in novel environments. They typically live in packs consisting of a male–female mated pair and offspring from the given year. Coyotes have experienced rapid range expansion in the past century (Hody and Kays 2018). Expansion is likely a result of several factors; coyotes can modify their behavior and foraging strategy to obtain food resources (Wong and Candolin 2014; Stanton et al. 2021; Parsons et al. 2022b), will consume anthropogenic food resources when available (Ordeñana et al. 2010; Larson et al. 2020), and exhibit different behaviors in different habitats. For example, urban coyotes are bolder and more exploratory than their rural counterparts (Breck et al. 2019; Brooks et al. 2020), a pattern also observed in other taxa including birds (Audet et al. 2016; Preiszner et al. 2017) and rodents (Vrbanec et al.

2021). Coyotes are also capable of problem-solving for food resources (Young et al. 2019; Parsons et al. 2022a). The breadth of knowledge related to coyote behavior and their ubiquity in North American urban centers provides an excellent opportunity to evaluate how exploration, innovation, and problem-solving behavior develop in young coyotes and vary by social context. Thus, we ask two key questions: (1) Does early-life problem-solving experience impact problem-solving behavior later in life, and (2) Do social rank and social facilitation influence problem-solving later in life in concert with early life experience?

To better understand what role early-life experience may play on later-life behavior, we conducted a controlled puzzle box experiment with captive coyotes. We first presented coyotes with a multi-access puzzle box as pups and then presented them with the same puzzle box at a later life stage—dispersal. The multi-access puzzle box was presented at dispersal age to individual coyotes and then again when they were housed with their pair-mates. By testing coyotes with the same puzzle box at sequential life stages, we were able to characterize how early-life experience influenced their problem-solving, innovation, exploration, and persistence at dispersal age when coyotes in the wild would begin forming territories with a newly acquired mate or become transients (Harrison 1992). By also testing coyotes with their pair-mate at dispersal age, we were able to characterize the added component of social facilitation on problem-solving, innovation, and response behaviors to the puzzle box. Based on previous research on social facilitation of problem-solving and foraging behavior in coyotes (Schell et al. 2018; Young et al. 2019), we predicted that (1) pups from litters that solved the puzzle box would be more likely to solve that same puzzle box later in life, relative to pups from litters that were either unsuccessful in solving or not exposed to the puzzle box as pups, (2) dominant coyotes with higher social rank would approach more quickly and spend more time exploring the puzzle box than subordinate coyotes when tested at dispersal age, and (3) coyotes would spend more time exploring the puzzle box during pair-testing if they had a pair-mate that spent more time exploring the puzzle box. Findings from this study contribute to our understanding of the interplay between early-life experience as pups and social facilitation in the context of problem-solving and innovation at dispersal age.

Methods

Study site

This study was conducted at the USDA – National Wildlife Research Center's Predator Research Facility in Millville, Utah, USA. The facility maintains about 90 adult coyotes in outdoor enclosures (0.1–1.0 ha), typically housed as male–female pairs. At around 9 months of age, coyotes are paired with a mate selected for genetic diversity within the colony, and the coyotes will remain in these mated pairs throughout their lifespan. The facility's husbandry methods aim to maintain coyote behavior similar to that observed in wild coyotes (Shivik et al. 2009).

Each coyote housed at the facility is fed 650 g of commercial mink food (Fur Breeders Agricultural Cooperative, Logan, Utah, USA) scattered throughout the enclosure at least six days per week by animal care staff. This feeding protocol was continued by the experimenter throughout the study so that coyotes became habituated to the experimenter's presence. Water was provided ad libitum.

Experimental apparatus

We used a multi-access puzzle box to assess problem-solving, innovation, exploration, and persistence (Parsons et al. 2022a). The puzzle box was a cube (45.7 × 45.7 × 45.7 cm) with three access points along three sides (Fig. S1). The sides were made of clear PVC sheeting, and the top, bottom, and backside were composed of white PVC sheeting. Of the three access points, one door pushed inward via a hinge on the bottom, another pulled outward via a racquetball handle and bottom hinge, and the third swung outward via a side hinge when a wooden dowel was removed from the outside. Each pup litter, dispersal-age singleton, and coyote pair, had their own puzzle box for the duration of a ten-trial testing block. Puzzle boxes were cleaned and stored outside in between testing blocks to eliminate potential odor cues during subsequent testing.

Subjects

A total of 18 coyote pups from six litters participated in the study. Four of the six litters were first presented a puzzle box at ~ 7 weeks of age with their parents and littermates as part of a complementary study (Parsons et al. 2022a). The remaining two litters were not presented with a puzzle box at that time and served as controls for dispersal-age trials. Thus, we had three testing groups: those from litters that solved the puzzle box as pups (solvers; $n = 9$ coyotes: 5 F, 4 M), those from litters that were exposed but failed to solve the puzzle box as pups (non-solvers; $n = 3$ coyotes: 2 F, 1 M), and those that were not exposed to a puzzle box as pups (no-boxers; $n = 6$ coyotes: 2 F, 4 M) (Fig. 1).

Experimental procedure

The experiment consisted of three phases of puzzle box testing: (1) pups (~ 7 weeks of age), except in the no box control group, (2) dispersal age (~ 10 months of age)

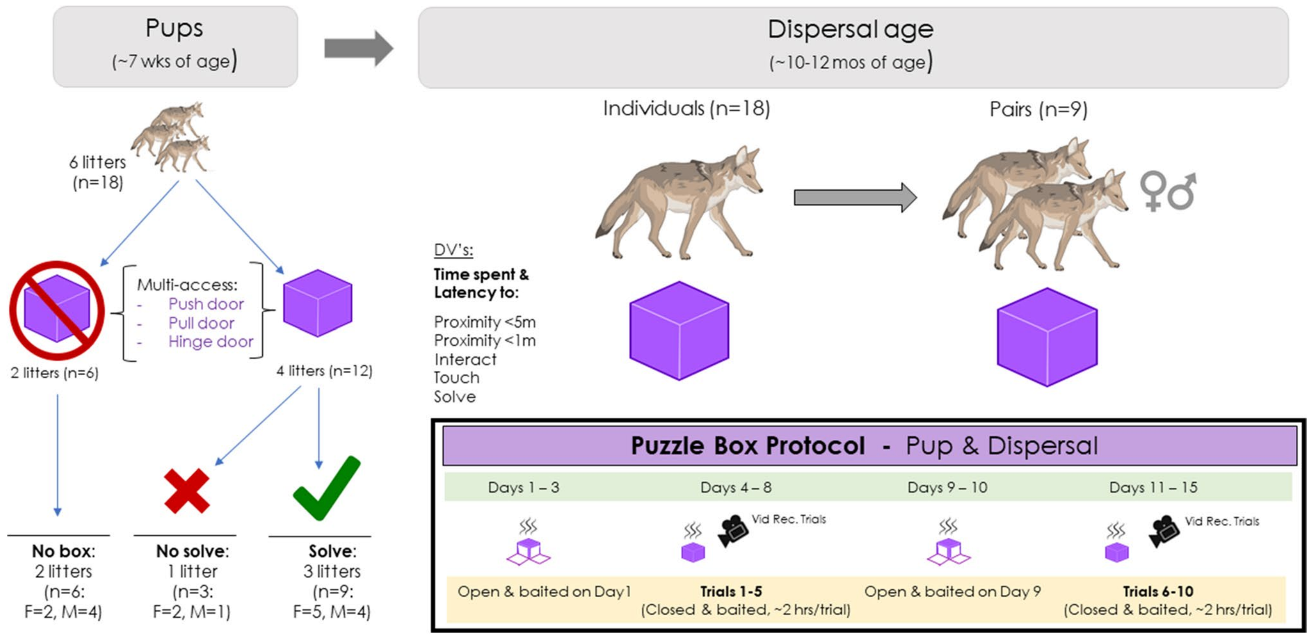

Fig. 1 Diagram of the experimental procedure. Four litters of pups underwent puzzle box trials around seven weeks of age, while two litters did not. The litters of pups presented with a puzzle box either solved (solve) or failed to solve (no solve). Those pups not presented with a puzzle box served as controls for the dispersal-age trials (no box). Puzzle box trials were also run at dispersal age (around 10 months old) for all three groups (solve, no solve, no box). Trials were first conducted on individuals (single-tested) and then while housed with their pair-mate (pair-tested). Each puzzle box trial was for 3 h and repeated for ten video-recorded trials. Coyote images were adapted from Biorender.com

Table 1 Information on the captive coyotes used in the study. The first column shows the mated pairs (female + male identification), with additional columns detailing the litter identification (solve, non-solve, no box) and dominant individual within each pair based on feeding trials (social rank). Coyote identification is a coded number, with the first two digits representing the year of birth (e.g., 20 = 2020), the third digit representing the litter, and the final digit representing sex (odd for male, even for female)

Coyote IDs	Female litter ID	Male litter ID	Social rank
2000 + 2031	Solve 1	Non-solve 1	Female
2010 + 2001	Solve 2	Solve 1	Female
2030 + 2025	Non-solve 1	No box 2	Female
2032 + 2013	Non-solve 1	Solve 2	Male
2040 + 2027	No box 1	No box 2	Male
2042 + 2051	No box 1	Solve 3	Female
2050 + 2011	Solve 3	Solve 2	Male
2052 + 2021	Solve 3	No box 2	Female
2054 + 2023	Solve 3	No box 2	Female

when housed singly (single-tested), and (3) dispersal age (~ 11 months of age) when housed and tested together with their pair-mate (pair-tested) (Fig. 1, Table 1). In all three phases of testing, the puzzle box protocol consisted of ten trials, conducted as one trial per day over 15 days (Fig. 1). To reduce object neophobia, the puzzle box remained in the enclosure throughout the 15-day period and was placed inside the enclosure and left open with food inside for three consecutive days preceding the first trial. Similarly, to minimize context-specific neophobia at dispersal age, coyotes were placed in unfamiliar enclosures with the puzzle box already present inside. During both life stages of testing, the box remained in the enclosure throughout the 15 days over which testing occurred, which included leaving it for two days in between trials 5 and 6 with the doors open and food inside for logistical reasons and to further reduce neophobia.

In each trial during all three phases, the box was baited with a food reward inside and all access doors were closed. We used the coyotes' normal food as the food reward because the captive coyotes are highly motivated to receive this food (Mettler and Shivik 2007). A small amount of food was placed immediately in front of the three doors and a small amount of peanut butter was placed on each door's access point to encourage interaction. During each trial, coyote behavior was video recorded for 2 h after the box was baited and the experimenter left the vicinity. At the end of each trial, the doors were opened and the food reward was removed. To control for motivation, all experimental trials were conducted before daily feedings, and daily food rations were not given until at least 2 h had passed following the end of each trial. To minimize bias, the researcher conducting trials was blind to which experimental group each coyote belonged.

During the latter half of pair-testing trials, coyote pairs underwent a supplemental test to determine social rank. This test was administered immediately before coyotes received their daily food ration to ensure that this test did not influence puzzle box response behavior. Social rank was quantified via five consecutive winner-loser trials for food dominance (300 g mink food). During each trial, the experimenter placed the food on the ground only when both coyotes were visually focused on the experimenter and each coyote was approximately equidistant from the experimenter. The experimenter then backed away toward the exit and the coyote who obtained the food first or displaced its pair-mate in at least 4 of the 5 trials was identified as the dominant coyote within the pair, and the other was identified as the subordinate (Table 1). This social rank test has been previously validated in coyotes, wolves (*Canis lupus*), and domestic dogs (*Canis familiaris*) (Scott and Fuller 1965; Fox 1972; Johnson and Balph 1990; Mettler and Shivik 2007; Young et al. 2019).

Video coding of trials

We quantified the latency to approach and the time spent in proximity to the puzzle box (< 5 m, < 1 m, and interacting) from the video recordings of coyote behavior using Behavior Observation Research Interactive Software (BORIS, Friard and Gamba 2016). The latency measures began when the experimenter exited the enclosure and closed the gate and ended when the coyote approached the box within 5 m, 1 m, and interacted with the box. Interacting with the puzzle box was defined as head-directed attentive exploratory behavior within 1 m of the box including prolonged investigation via vision and/or olfaction and touch-based exploration (licking, biting, pawing). To minimize observer bias, coders were blind to experimental conditions. Only one person coded all videos of mate-pairs but an additional three people helped code videos of individuals. All coders were trained on the same five videos and only worked independently once > 95% agreement was met on coding data.

Statistical analyses

We used mixed-effect cox proportional hazard models ("coxme" package in Program R version 4.1.0 (R Core Team 2021)) for both the single-tested and pair-tested latency to approach measures (Therneau 2020). For the single-tested data, we generated a set of multiple models (simpler to more complex) to examine the effects of past puzzle box experience as a pup (solver, non-solver, or no box), sex, and social rank (dominant or subordinate), on each of the latencies to approach and interact with the puzzle box. We included random effects of coyote ID to account for repeated measures and individual variability. For the pair-tested data, we maintained the same specifications for a set of multiple models but included the additional factors of latency to approach when single-tested, past puzzle box experience of the pair mate as a pup and latency to approach of the pair mate when pair-tested. We then used AICc model selection to identify the top models describing these associations.

For the time spent interacting with the puzzle box, we used mixed-effects beta regression models ("glmmTMB" package in Program R version 4.1.0 (RCore Team 2021)) to identify factors that influenced the proportion of time that coyotes spent within 5 m and 1 m of the puzzle box (Brooks et al. 2017). During single-testing, coyotes interacted with the puzzle box very infrequently, so our models failed to converge and provide sufficient parameter estimates for interaction behavior; therefore, we did not include models for interaction with the puzzle box while single-tested. We were able to generate models for the proportion of time spent within 5 m and 1 m of the puzzle box during single testing. We again tested the effects of past puzzle box experience as a pup, sex, and social rank, on time spent within 5 m or 1 m of the puzzle box. We included a fixed quadratic effect of trial number to account for habituation and a random effects of coyote ID to account for repeated measures. For the pair-tested data, we maintained the same model specifications but included the additional factors of time spent within proximity when single-tested, past puzzle box experience of the pair-mate as a pup, and time spent within proximity of the pair-mate when pair-tested. We then used AICc model selection to identify the top model describing these associations for the 5 m, 1 m, and interaction data. We used the DHARMa package (Hartig 2022) to examine the model fit and residual diagnostics of linear mixed-effects models. Results showing averages include standard error (± SE).

Results

Of the four litters that were exposed to a puzzle box as pups, three litters successfully solved the puzzle box and consumed the food reward, while one litter did not. Each of the three litters solved two doors: the push door and the wooden dowel door. The three litters solved the puzzle box 4, 8, and 9 times over the 10 trials. Adults never interacted with the puzzle box during these trials and spent < 0.5% of the time within 1 m of the puzzle box. We could not determine individual ID from the videos but all coyote pups in litters that successfully solved the puzzle box were observed to interact with the puzzle boxes. None of the coyotes in any group solved any of the access doors for the puzzle box at dispersal age, neither when single-tested nor when pair-tested. For this reason, we focused our results on factors that influenced the following: (1) exploration, which was measured as the latency to approach the puzzle box within 5 m, 1 m, and interact with the puzzle box; and (2) persistence, which was measured as the time spent within 5 m, 1 m, and interacting with the puzzle box.

During the 180 single coyote trials, individuals failed to approach within 5 m during 32 trials (17%), within 1 m during 78 trials (43%), or interact with the puzzle box within 141 trials (78%). Coyotes spent an average of 6.3% (±0.5%) of the trial time within 5 m, 2.0% (±0.2%) of the trial time within 1 m, and 0.2% (±0.1%) of the trial time interacting with the puzzle box.

During the 180 paired coyote trials, individuals failed to approach within 5 m during 24 trials (13%), within 1 m during 93 trials (52%), or interact with the puzzle box during 148 trials (82%). Coyotes spent an average of 4.3% (±0.4%) of the trial time within 5 m, 1.1% (±0.2%) of the trial time within 1 m, and 0.1% (±0.03%) interacting with the puzzle box. This overall lack of exploratory behavior by dispersal-age coyotes limited our statistical power. Residual checks indicated that model assumptions were appropriately met for 5 m models during both single and paired trials. However, 1 m and interaction models both suffered from zero inflation that we were unable to account for. This poor model fit is unsurprising given the lack of interactions and also highlights why the null model performed best for 1 m and interaction data (see below). These model fit issues support a general pattern of lack of exploratory behavior by dispersal-age coyotes.

Exploratory behavior and persistence

Exploratory behavior, measured as latency to approach the puzzle box, did not respond to any tested covariates. Previous puzzle box experience, coyote sex, and social rank did not influence the latency to approach within 5 m, 1 m, or interact with the puzzle box during single or pair testing. Latency to approach during single testing, the pair mate's puzzle box experience, and the pair mate's latency to approach also did not influence latency to approach the puzzle box during pair testing (Table S1).

The null models, including only the random effects of coyote ID and trial number, were also the top models for the proportion of time spent within 5 m, 1 m, and interacting with the puzzle box when single-tested (Table S2). The null model was also the top model describing the proportion of time spent within 1 m of the box and interacting with the box when pair-tested (Table S2). For all these cases, we documented no influence of puzzle box experience, coyote sex, social rank, or partner's puzzle box experience on behavior.

The full model was the top model for pair-tested coyotes for the proportion of time spent within 5 m of the puzzle box. This model included past puzzle box experience as pups (solver, non-solver, no box), social rank (dominant, subordinate), sex, past puzzle box experience of the pair-mate as a pup, the proportion of time spent within 5 m when single-tested, the proportion of time their partner spent within 5 m during pair-testing, trial number, and random effects of coyote ID (Table 2). Specifically, the proportion of time that a coyote spent within 5 m of the puzzle box when pair-tested, was higher for those that had a pair-mate that belonged to a litter that had previously solved the puzzle box ($z = 2.379$, $p = 0.017$) or had previously been exposed to a puzzle box but not solved it ($z = 2.061$, $p = 0.039$), those that spent more time within 5 m of the puzzle box themselves when single-tested ($z = 2.166$, $p = 0.030$), and those whose pair-mates spent more time within 5 m of the puzzle box during pair-testing ($z = 3.425$, $p = 0.001$) (Table 3; Fig. 2).

Table 2 AICc comparison for mixed-effects beta regression models fitted to describe the factors influencing the proportion of time captive coyotes spent within 5 m of the puzzle box when pair-tested. Model comparison was based on AICc, and the model with the lowest AICc value, the full model, was retained and identified as the best fit (bold). Each model included random effects of coyote ID and trial number to account for repeated measures and individual variability

Model	Np	AICc	ΔAICc	ωi
Past PB + Social rank + Sex + Partner's Past PB + Time spent < 5 m (single-test) + Partner's Time spent < 5 m (pair-test)	**13**	**−903.57**	**0**	**0.88**
Past PB + Social rank + Sex + Partner's Past PB + Time spent < 5 m (single-test)	5	−898.00	5.57	0.05
Null	12	−896.39	7.18	0.02
Past PB	7	−895.00	8.57	0.01
Past PB + sex	8	−894.92	8.65	0.01
Past PB + social rank	11	−894.56	9.01	0.01
Past PB + social rank + sex + partner's past PB	8	−893.84	9.73	0.01
Past PB + social rank + sex	9	−893.09	10.48	0.00

Table 3 Mixed-effects beta regression model coefficients for the full model describing the proportion of time coyotes spent within 5 m of the puzzle box when pair-tested. Significant factors are indicated in bold

Variable	Estimate	SE	*z*	*p*
(Intercept)	− 4.162	0.298	− 13.958	< 0.001
Trial number	− 0.326	0.286	− 1.141	0.254
Trial number—quadratic	0.482	0.279	1.728	0.084
Past PB (non-solver)	− 0.393	0.33	− 1.188	0.235
Past PB (solver)	0.011	0.246	0.044	0.965
Social rank (subordinate)	0.027	0.244	0.109	0.913
Sex (male)	0.32	0.231	1.381	0.167
Partner's Past PB (non-solver)	**0.671**	**0.326**	**2.061**	**0.039**
Partner's PAST PB (solver)	**0.616**	**0.259**	**2.379**	**0.017**
Time spent < 5 m (single-test)	**2.366**	**1.092**	**2.166**	**0.03**
Partner's time spent < 5 m (pair-test)	**3.901**	**1.139**	**3.425**	**0.001**

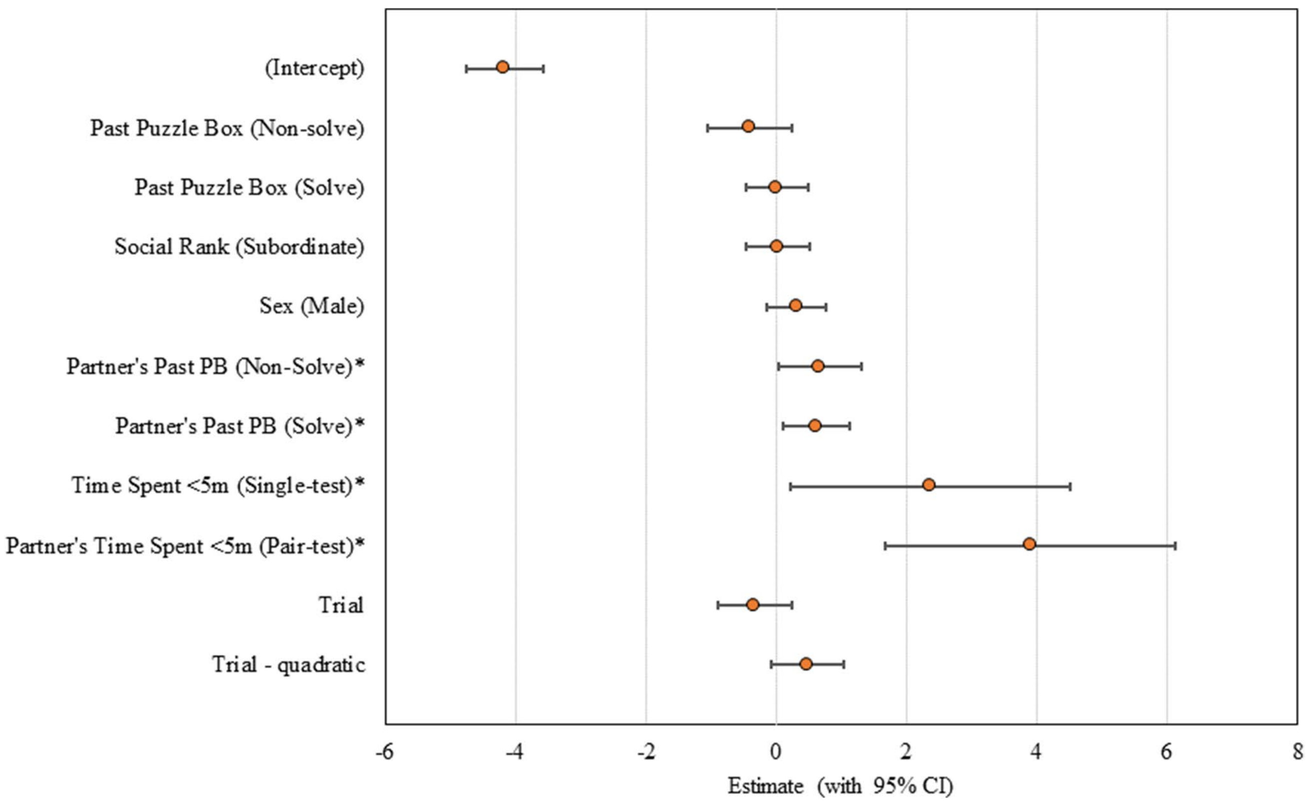

Fig. 2 Forest plot depicting parameter estimates with 95% confidence intervals for the full mixed-effects beta regression model describing the proportion of time coyotes spent within 5 m of the puzzle box when pair-tested. Significant factors are indicated with an asterisk

Discussion

This study sought to characterize the role early-life experiences play on later-life behavior concerning problem-solving, innovation, exploration, and persistence. Our results contradicted two of our predictions that were based on previous studies. First, coyotes from litters that solved the puzzle box were not more likely to solve that same puzzle box later in life, relative to coyotes that were either unsuccessful in solving or never exposed to the puzzle box as pups. Surprisingly, none of the coyotes solved any of the puzzle box doors when tested at dispersal age, neither as individuals nor with their pair-mates. Second, dominant coyotes did not explore the puzzle box more than subordinate coyotes at dispersal-age testing. Our data supported our third prediction: puzzle box response behavior increased during pair-testing when a coyote's pair-mate spent more time in proximity to the box. During pair-testing, we observed a significant increase in the time that dispersal-age coyotes spent within 5 m of the puzzle box for coyotes that had (1) spent more time within 5 m of the box when single-tested, (2) a pair-mate that had spent more time within 5 m of the box when pair-tested, and (3) a pair-mate from a litter that had previously solved the puzzle box as a pup. While we primarily aimed to characterize the impact of early-life exposure to a cognitive task on later-life behavior, we have also illuminated an innate decline in exploratory behaviors that may accompany dispersal age; our results suggest an increase in avoidance behavior as pups reach dispersal age. This age corresponds with the time in which coyotes become sexually viable, many leave their natal home ranges, and many do not survive to adulthood (Davison 1980; Windberg et al. 1985; Holzman et al. 1992; Gehrt 2006).

Our main findings suggest that the likelihood to investigate or engage with the puzzle box was socially facilitated and context-dependent. The ability of coyote pups to solve the puzzle box may have been contingent upon their ability to interact with the puzzle box as a group. Problem-solving is socially facilitated via peer demonstrators in coyotes (Young et al. 2019), and cooperation in spotted hyenas (Drea and Carter 2009), Asian elephants (Li et al. 2021), peach-fronted conures (*Eupsittula aurea*; Torres Ortiz et al. 2020), giant otters, and Asian small-clawed otters (Schmelz et al. 2017), amongst other species (Duguid and Melis 2020). Since pups collectively engaged the puzzle box with their littermates, it is possible that the coyote pups that successfully produced the actions required to open a puzzle box door failed to effectively associate their actions with the rewarding outcome. Alternatively, early-life problem-solving success and innovation we predicted to facilitate later-life problem-solving and innovation may have been countered by cautionary behavior emerging at dispersal age. The puzzle box was potentially perceived as a novel object at dispersal age, resulting in neophobic responses. This result is similar to behavioral traits of boldness and docility in yellow-bellied marmots (*Marmota flaviventris*) developing independently across successive life stages (Petelle et al. 2013). These findings suggest that the development of behavioral traits may allow individuals to behave adaptively at age-specific times. As juveniles living with their parents and littermates, coyotes have a generally safe environment to be more explorative, while at dispersal age, coyote behavior may be constrained by their life history strategy—the benefit of pursuing novel food opportunities may not outweigh the risk of increased mortality and loss of reproductive opportunity associated with such pursuit, particularly given the short lifespan of coyotes in the wild (Davison 1980; Windberg et al. 1985; Holzman et al. 1992; Gehrt 2006; Sol et al. 2013; Healy et al. 2019).

Surprisingly, social rank (i.e., dominant versus subordinate within a mate-pair) did not significantly influence puzzle box response behavior in any of our models. This result contrasts previous research with captive coyotes, which showed that dominant coyotes show reduced neophobia toward a novel object, fladry, compared to subordinate coyotes (Mettler and Shivik 2007) and exhibit reduced neophobia and increased persistence in a puzzle box task (Young et al. 2019). A dominance test may not have been appropriate for coyotes at ~ 10 months of age; first-year pair-mates may not have formed strong pair bonds as the tests were conducted before the pair-mates first engaged in mating behavior or had a litter. Alternatively, it is possible that dominance was accurately defined but coyotes may not have had sufficient time to become more exploratory and less risk-averse at this age in the context of puzzle box response behavior compared to their subordinate counterparts (Johnson and Balph 1990; Mettler and Shivik 2007).

Another alternative explanation is that coyotes may still exhibit collective social behaviors at dispersal age, like when they were housed with their littermates. In this scenario, despite having a dominant-subordinate relationship, pair-mates may approach or avoid objects similarly, overshadowing any impact of social rank on puzzle box response behavior. We observed similarities in puzzle box response behavior between pups and dispersal-age coyotes when tested with their pair-mates. Coyotes solved the puzzle box with their littermates and coyotes at dispersal age spent more time near the box during pair-testing when they had a pair-mate who came from a solving litter and spent greater amounts of time close to the box. Together, these results suggest that social contexts facilitate increased exploratory behavior.

Social facilitation can enhance exploration and innovation. Ravens (*Corvus corax*) exhibit social facilitation, as they have been found to spend more time close to and manipulating novel objects when they encounter them in a social context versus when alone (Stöwe et al. 2006). As pups, coyotes may mitigate risk via collective exploration of the puzzle box as a group with their littermates, while at dispersal age, coyotes may have utilized social information acquired from observing their pair-mate explore the puzzle box. Relying on such social information may have reduced their perception of neophobic risk and increased the motivation to approach and explore the puzzle box. This lends support to the social information hypothesis, which suggests that intrinsic neophobia can be overcome via social information and social facilitation (Forss et al. 2017). Similarly, coyotes paired with less exploratory mates may have reduced their own exploratory behavior in response to the behavior of their mate. Here, we observed socially facilitated exploratory behavior in captive coyotes that extends across life stages from pup to dispersal age; however, more information is needed to determine the impacts of social bonding within mated pairs across developmental stages.

As young animals in the wild mature, many will disperse from their natal ranges due to increased social pressure, limited resource availability, and limited breeding opportunities (Holekamp 1984; Harrison 1992; Gese et al. 1996; Behr et al. 2020). The fitness costs of dispersal can be high; animals will likely have to respond to increased predation pressure, decreased nutritional states, and higher stress levels as they navigate through unfamiliar areas with novel and unpredictable stimuli. The average age at death of foxes (*Vulpes vulpes*) that dispersed to establish a new range was significantly lower than the average age at death of foxes that did not disperse (Woollard and Harris 1990). During dispersal, mortalities increased for ruffed grouse (*Bonasa umbellus*) due to increased predation (Yoder et al. 2004), barn owls (*Tyto alba*) due to vehicular collisions (Massemin et al. 1998; Boves and Belthoff 2012), American martens (*Martes americana)* due to poor nutritional state and body condition (Johnson et al. 2009), and several species of snakes due to a combination of predation and anthropogenic-related mortality (Bonnet et al. 1999). Additionally, previous findings have demonstrated that subadult and adult spotted hyenas and captive-bred swift foxes (*Vulpes velox*) that exhibited fewer risk-taking behaviors were more likely to survive in the wild than their bolder counterparts (Bremner-Harrison et al. 2004; Greenberg and Holekamp 2017; Turner et al. 2019). Thus, it is likely that innate behavioral changes expressed during maturation led to reduced participation during puzzle-box trials at dispersal age compared to the high degree of interaction and solving at pup age.

Another factor that may have influenced the change in puzzle box response behavior from pup age to dispersal age may stem from differences in age-related experiences in captivity. Life experience involving interactions with humans impacts persistence behavior in canids (Lazzaroni et al. 2019), and captive coyotes had varying experiences with humans across life stages. As pups, the coyotes had minimal interaction with humans at the facility. Although we utilized coyotes from a facility that practices minimal human interactions to preserve wild coyote behaviors (Shivik et al. 2009), by the time the study coyotes reached dispersal age, they were repeatedly captured, handled, vaccinated, and transported among enclosures. This may have increased their cautionary behavior during research-related interactions. Previous research has characterized the influence of human socialization in problem-solving tasks by canids (Brubaker et al. 2017). While human interactions are considered to enhance the problem-solving performance of captive animals (Tomasello and Call 2004; Whiten and van Schaik 2007), this could be dependent on whether the humans are offering motivation or assistance (Lazzaroni et al. 2019). In our study, human interactions were entirely independent of puzzle box trials. Thus, the type of human socialization of coyotes in our study was unlikely to facilitate willingness to interact with the puzzle box.

It is also possible that problem-solving and persistence at dispersal age were influenced by the size of the puzzle box and the context in which it was encountered. Previous work has indicated that adult captive coyotes are more cautious around larger novel objects compared to smaller ones (Windberg 1996), and the puzzle box used in our study may have been too large to overcome avoidance behavior when coyotes were tested at dispersal age. The design and therefore size of the puzzle box was made to ensure all doors could open to access one food reward and that multiple doors could be opened without interference with one another within a trial. Alternatively, dispersal-age coyotes may have been overly cautious in an unfamiliar enclosure. Previous studies have also shown that avoidance and neophobia of novel objects were lower in unfamiliar enclosures compared to familiar enclosures (Windberg 1996; Harris and Knowlton 2001), so captive coyotes are often moved to an unfamiliar enclosure for the start of new experiments at the facility. We placed dispersal-age coyotes in new, unfamiliar enclosures where the puzzle box was already present at the start of trials to minimize context-specific neophobia. However, coyotes at dispersal age may exhibit different cautionary behavior because all environments are unfamiliar during dispersal. Future studies may benefit from using a smaller puzzle box, such as the one used in Young et al. (2019), which was approximately half the size of the one used here, or by allowing coyotes more time to become familiar with the object before testing.

Overall, our conclusions were limited by small sample sizes paired with the low level of exploratory behavior exhibited by dispersal-age coyotes. Experimental work with carnivores is logistically challenging and frequently has limited sample sizes. These limitations reduced our ability to detect smaller changes in behavior and limited our modeling approaches. We were also unable to construct too complex models given we only had 18 study subjects. We were further limited by a lack of participation by these 18 subjects as indicated by the high number of zeros for the time within 1 m and time interacting with the puzzle box.

Because our data supported only one of our three predictions, our study highlights how a continued investigation into exploratory and problem-solving behavior in carnivores can further challenge the canonical understanding of generalist carnivore capabilities. Generalist carnivores are often considered highly adaptive and use novel landscapes, including anthropogenic landscapes throughout the world (Bateman and Fleming 2012). While we did not observe problem-solving in dispersal-age coyotes, we detected limited exploratory behavior, which is a key first component to solving novel problems. Our results indicate that young coyotes dispersing into novel habitats may struggle to adapt to novel food and environmental resources due to limited exploratory behavior. However, the presence of other coyotes with experience in the anthropogenic landscape may facilitate social learning by dispersing coyotes (Young et al. 2019). Additionally, our experiment covered a short time period and coyotes were being fed their regular diet throughout the experiment. Therefore, motivation to solve the foraging task was likely lower than it would be in wild coyotes dispersing into new habitats.

The expectation of high innovation in urban carnivores has been challenged in other contexts as well. Comparing innovative behaviors with a multi-access puzzle box between spotted hyenas living in rural areas, urban areas, and areas undergoing rapid urbanization, researchers concluded that, contrary to their predictions, rural hyenas were the most innovative of the three groups (Johnson-Ulrich et al. 2021). Although other factors such as food motivation and availability may have influenced these findings, the authors suggest that this is likely attributed to higher motor diversity and flexibility amongst rural hyenas as there was little difference between problem-solving success amongst the three groups. These findings contest the paradigm that urban landscapes present food resource opportunities that are more complex and challenging than those experienced in rural areas. Our study results, along with those found by Johnson-Ulrich et al. (2021), emphasize the importance of life stage and environmental and social context in foraging, which has been observed in other species as well (Michelena et al. 2009; Kurvers et al. 2012). These contexts likely interact in affecting exploratory and problem-solving behavior, and further research should explore these patterns. For example, an interesting next step would be to continue to follow individuals into later life stages, through senescence.

Our study provides a foundational understanding of the interplay between early-life experience, social facilitation, and problem-solving behavior. We showed that coyote pups are capable of problem-solving and innovation when encountering novel foraging opportunities as a litter, but that this success does not predict future success. We observed a greater degree of exploratory behavior when coyotes were with a pair-mate who exhibited a high degree of exploratory behavior and had exposure to problem-solving early in life. Additionally, we illuminated a developmental increase in avoidance behavior as coyote pups reached dispersal age and exhibited reduced exploratory behaviors, compared to that observed at pup age. Together, these findings demonstrate the importance of understanding how, and when, coyotes use social cues to negotiate risk-reward tradeoffs during novel food resource opportunities. Characterizing the ontogeny and social facilitation of exploration, persistence, and innovation can help identify contexts where coyotes are most likely to cause challenges both in conservation efforts and human-wildlife conflict. Identifying these contexts will aid managers in identifying likely problem coyotes, allowing them to implement mitigation efforts.

Data sharing

All data generated or analyzed during this study are included in this published article Tables S3 and S4.

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Author contribution ACG contributed during the investigation and led analysis, writing, reviewing, and editing efforts. MAP contributed during conceptualization, developing methodology, analysis, and reviewing and editing. JKY led funding acquisition and conceptualization and contributed to developing methodology, analysis, reviewing, and editing.

Declarations

Ethics approval All applicable national and institutional guidelines for the use of animals were followed and approved by the USDA-National Wildlife Research Center's Institutional Animal Care and Use Committee (QA-3151).

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