



Social Learning of Avoidance Behaviors: Trap Aversion in Captive Coyotes

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Abstract – Social learning can help animals gain knowledge rapidly and may enhance survival. In species that are subjected to capture in foothold traps and then lethally removed, such as the coyote (*Canis latrans*), learning to avoid traps is critical to survival. Here, we tested social learning of trap avoidance behavior in three experimental scenarios with captive coyotes. In the first experiment, coyotes observed an unfamiliar coyote get captured in a foothold trap (i.e., demonstrator) or did not observe a demonstrator and were therefore naïve to traps. The coyotes that observed a demonstrator showed similar latencies to approach the trap and be captured as coyotes without a demonstrator. In the second experiment, coyotes observed their trap-naïve mate get captured in a foothold trap while housed together. These coyotes had longer latencies to approach the trap and be captured than their mates. In the third experiment, demonstrator coyotes were housed separately in an enclosure adjacent to two other enclosures – one housing their mate and one housing an unfamiliar coyote. Here, unfamiliar coyotes had longer latencies to approach the trap and get captured than the mates of the demonstrator coyotes. These results suggest that coyotes have limited ability to socially learn avoidance behavior, with familiarity and proximity of the demonstrator influencing the ability of coyotes to use social learning. Thus, the different results emerging from this study may reflect behaviors related to territoriality and pair-bonds.

Keywords – Avoidance behavior, *Canis latrans*, Cognition, Wildlife management

Social learning is a form of learning from observation of or interaction with other individuals (Galef & Giraldeau, 2001; Galef & Laland, 2005). Social learning of avoidance behavior broadly allows individuals to avoid danger, with most research focused on predator avoidance (Galef & Laland, 2005; Griffin, 2004). Social learning has also been demonstrated as a mechanism for animals to develop object avoidance (Herzog & Hopf, 1984; Lore et al., 1971; Lovén Wallerius et al., 2020; Mineka & Cook, 1998). These studies indicate that individuals can learn to avoid or fear an object based on demonstrator interactions with the object. For example, domesticated rats (*Rattus norvegicus*) learned to avoid a candle faster after watching a conspecific learn to avoid the flame than control rats that did not observe a conspecific (Lore et al., 1971); rhesus monkeys (*Macaca mulatta*) developed a fear of snakes more quickly after observing a social companion exhibit fearful behavior towards snakes (Mineka & Cook, 1998); and common carp (*Cyprinus carpio*) showed avoidance of fishing gear after observing a conspecific get caught (Lovén Wallerius et al., 2020).

Learning from conspecifics is common in animal species, but it is also important for individuals to be selective from whom they are learning (Kendal et al., 2014; Laland, 2004). Social relationships can

affect how readily information can be transferred through social learning (Coussi-Korbel & Fragaszy, 1995). Familiarity may facilitate social learning (Lachlan et al., 1998) and allow observers to be more effective learners (Swaney et al., 2001). This is likely because familiar individuals spend more time together facilitating more opportunities to learn and because it may be more advantageous to learn from socially familiar individuals that live in the same environment. For example, naïve mates of black-backed jackals (*Canis mesomelas*) were more likely to learn to avoid cyanide traps when their mates already learned to avoid them (Brand & Nel, 1997). While an animal may learn avoidance behavior more readily from a familiar individual, other factors, like the strength of the relationship between individuals, also contribute to whether socially transmitted behaviors persist within observers or become part of the culture within an animal population (Aplin et al., 2015; Cantor & Whitehead, 2013).

Hunters and fishers suggest that the wildlife they aim to harvest learn how to avoid harvest devices, such as fishhooks and traps. The experience of having a coyote (*Canis latrans*) that is difficult to trap, or “trap shy,” is well known and discussed throughout the trapper and scientific communities but has not been considered in the context of avoidance behavior or social learning (Barker, 1968). Coyotes are often the focus of management actions because they are the most common predator on domestic sheep (*Ovis aries*) within the United States (National Animal Health Monitoring Agency, 2015) and may also be a source of human-carnivore conflicts in urban areas (Poessel et al., 2017). Conflicts between carnivores and livestock, people, and their pets are global issues that impact economics, human health and safety, and wildlife management. In the United States alone, domestic sheep and lamb depredation totaled over 500,000 animals and resulted in an economic loss of 102 million USD in 2014 (National Animal Health Monitoring Agency, 2015). In many parts of the world, trapping is a commonly used removal technique to manage carnivores after a conflict occurs. These techniques include foothold traps, snaring, and poisoning with toxicants (Shivik et al., 2005).

For coyotes to learn trap avoidance, they first need to be able to recognize a trap set as an object to avoid. Studies have shown coyotes can begin to recognize and subsequently avoid trap locations (Andelt, 1985; Conner et al., 1998). This suggests prior non-lethal experience with traps can affect future behavior and trap efficacy, much like how fish that have been caught and released are more likely to avoid fishing gear afterward (e.g., Takahashi & Masuda, 2021). Yet, we lack an understanding of how coyotes learn to recognize traps as something to be avoided.

Several factors may affect trap efficacy. Coyote capture rates are inconsistent in relation to age, sex, season, breeding status, trap density, and the location of the traps within a home range (Sacks et al., 1999; Wilson et al., 2011; Windberg & Knowlton, 1990). Although territorial coyotes and transient females may be less likely to be captured in central, core areas of home ranges (Wilson et al., 2011), this may merely be an artifact of trap densities and resulting encounter rates. In a high-density area, there was no effect of coyote age on trap vulnerability (Conner et al., 1998). However, juveniles (< 1-year-old) may be captured at higher rates than predicted in a lower density population (Sacks et al., 1999). Thus, social learning may help coyotes to learn to recognize and avoid traps. Coyotes that are older or in more dense populations are likely to have had opportunities to observe other coyotes in traps. Because coyotes are territorial, if they observe a coyote in a trap, it is likely to be a packmate in the same territory or a neighbor along the territorial boundaries. These possible scenarios highlight the importance of ascertaining if there is social learning to avoid traps and whether avoidance behavior differs by the relationship with the conspecific that is observed. If coyotes are socially learning to avoid traps, this could have profound implications for managing coyotes because foothold traps are one of the most common tools to capture coyotes for management actions.

Here, we determine if social learning is a mechanism for learning trap-avoidance behaviors in coyotes. We aimed to determine (1) if trap avoidance can be learned by observing conspecifics; and (2) whether social familiarity of and physical proximity to demonstrators affect social learning of avoidance behavior by observers. We hypothesize that coyotes will avoid foothold traps via social learning and that social learning will be stronger when the demonstrator being observed is related to and in proximity of the observer.

Method

Ethics Statement

All research met humane standards and was approved by the U.S. Department of Agriculture (USDA) - National Wildlife Research Center's Institutional Animal Care and Use Committee (QA-2626 and QA-3356).

Subjects and Housing

The study was conducted with captive coyotes at the USDA-National Wildlife Research Center's Predator Research Facility in Millville, Utah, USA. The facility houses up to 95 adult coyotes for research purposes, maintained as male-female pairs in outdoor enclosures that range in size between 1000-10000 m². Each enclosure contains at least one PVC-den box and two or more shade tables (0.6 m tall x 0.8 m wide x 1.2 m long), created of wood posts and plywood. The coyotes are provided 650 g of a commercial mink food diet at least six days a week and water *ad libitum*.

Coyotes at the facility are captured occasionally for routine veterinary care or to move animals among enclosures for research purposes. For these captures, animal care staff and volunteers arrive at the enclosure in a capture truck, enter the enclosure with capture nets and brooms, form a line across the enclosure, and slowly walk towards the coyote. The coyote will then enter the PVC-den box on the opposite end of their enclosure and the den-box opening is then closed off so the coyote can no longer exit the box. Any handling or veterinary care is then conducted in observation buildings or at the main animal care building and not in sight of other coyotes.

Experiment 1 – Unfamiliar Coyotes in Adjacent Enclosures

To evaluate social learning of trap avoidance in socially unfamiliar coyotes, tests were conducted using two sets of seven, 1000-m² interaction enclosures, each set configured as one central enclosure surrounded by six adjacent enclosures (Figure 1). Three demonstrator coyotes (2 males, 1 female) were chosen that were classified as bold individuals based on interactions and observations of animal care staff at the facility. These coyotes were selected to facilitate coyotes interacting with the traps as demonstrators for this study. Excluding coyotes that were the mates or siblings of the demonstrator coyotes, we next randomly selected 27 other adult coyotes from the colony but two did not end up participating, one each in trials 1 and 3, because we could not capture and move them. We divided the 25 remaining adult coyotes into two groups: observer (8 males, 8 females) and control (6 females, 3 males). Observer coyotes were housed individually in the surrounding enclosures with a clear view of a single demonstrator coyote that was housed alone in the center enclosure (Figure 1). Control coyotes were located in enclosures >150 m away and out of sight from the demonstrator enclosure. We assigned three coyotes as controls when each set of observer trials was running ($n = 9$).

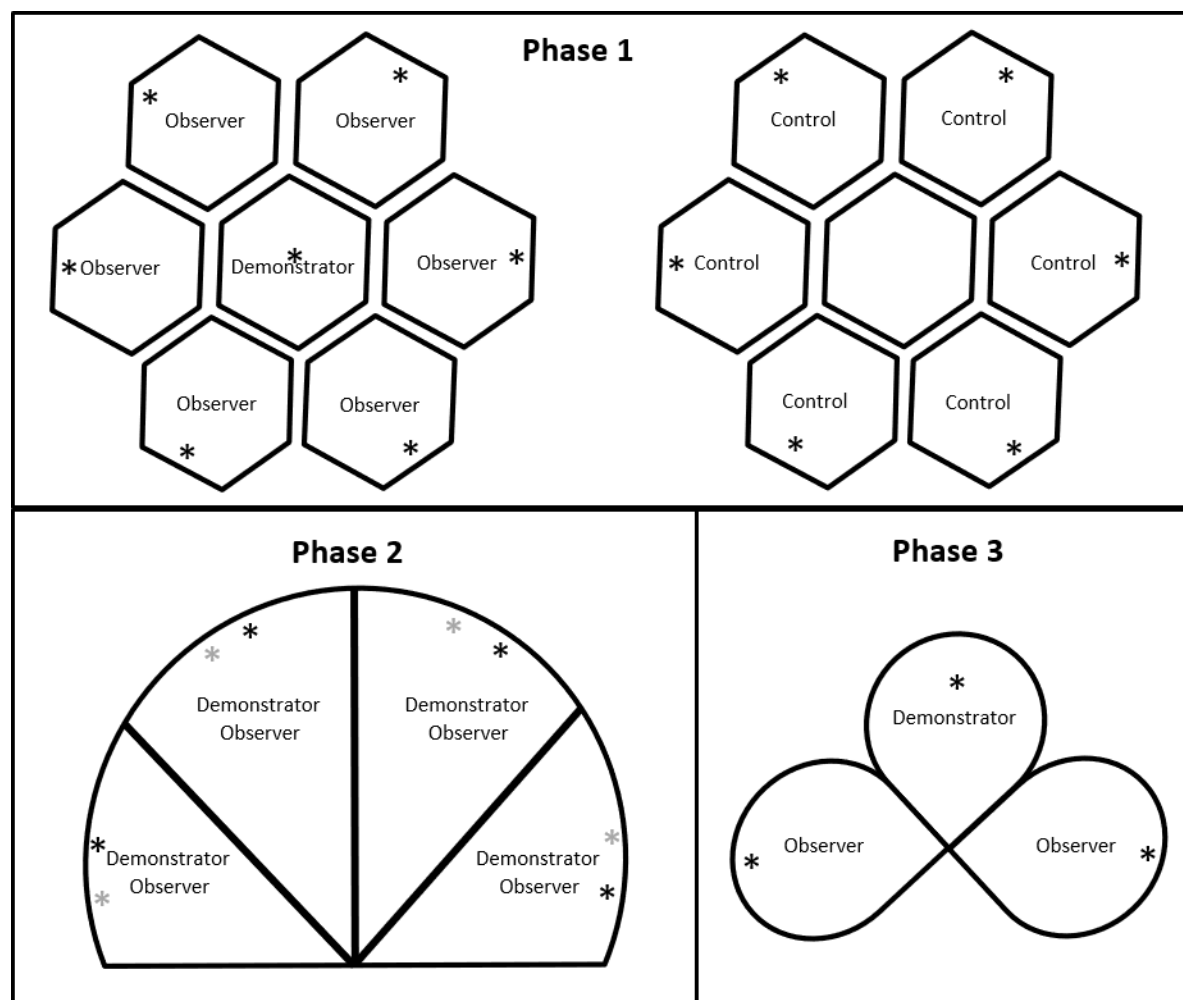
We used Victor #3 soft-catch foothold traps fitted with a trap tranquilizer tab device (TTD) containing 600 mg propiormazine (Balsler, 1965; Sahr & Knowlton, 2000) set in the center of the demonstrator enclosure in a dirt-hole set. A dirt-hole set is a trap buried in front of a small 45° hole with scent attractant placed in the hole. The researcher was visibly obscured from the coyotes when setting each trap using several 1 x 2 m plywood sheets held in place by a second person. A camera trap (Browning Strike Force HD, Model BTC-5HD or Bushnell Aggressor, Model 119836) was used to record the coyote interacting with the trap set. The camera was programmed to record 30-s videos. We used two different commercially available trapping lures: Government Call (O'Gorman's lure) was used for the first two trials and Trails End (Carmen's Lures) was used for the third trial to avoid bias due to the coyotes' smelling remnants from the trap sets of previous trials. Traps for the observer and control coyotes were set with the same lure as their demonstrator coyote. Sets and lures mimicked traps set in the wild.

At the start of each test, we released the demonstrator coyote into the enclosure with the trap. The coyote was observed for up to three hours or until the coyote was captured by the trap, whichever came

first. The springs of each trap make a small noise when triggered and the coyote in the trap typically becomes agitated trying to pull free, activity and sound that would be detected by the observers. Once the coyote was captured, the elapsed time was recorded, and the coyote was released from the trap after 10 min. This 10-min interval afforded time to ensure the observer coyotes to see the demonstrator in the trap but before the tranquilizer took effect. The tranquilizer helped the coyote rest while it recovered after being removed from the trap. The coyote was then removed from the trap and enclosure, checked for trap-related injuries, and held in a small cage for several hours while it recovered from the effects of the tranquilizer. Demonstrator coyotes were then released into an enclosure that already held their mate, away from the interaction enclosures where observers were housed. This procedure was designed for animal welfare and colony management purposes but also simulated the lethal removal of captured coyotes in the wild.

Figure 1

Diagrams of enclosures housing captive coyotes during Experiments 1, 2, and 3.



Note. The general location of the trap is denoted with an asterisk (*), with the general location of the dummy set is denoted in gray for Experiment 2. Enclosures are not drawn to scale.

Observer and control coyotes were tested one day after the demonstrator test was completed. Both groups of coyotes were first rotated to a new enclosure, to reduce avoidance behavior due to a new disturbance (i.e., the trap set) in a familiar enclosure (Figure 1; Harris & Knowlton, 2001). Traps were modified by removing one jaw from the trap to allow the trap to be set off without actually clamping onto

the coyote's foot. This also prevented the observer and control coyotes from continuing to socially learn from neighbors that set off their traps and meant we did not need to remove any coyotes after they set off a trap for welfare monitoring. The modified traps were set before observer and control coyotes were released, using the same dirt-hole set method and scent that was used with the demonstrator coyotes. As before, the person setting the traps was hidden from view of coyotes using plywood boards held by a second person and camera traps were set to record activity at all trap sets.

All observer and control coyotes were released into the enclosures simultaneously and allowed to directly interact with the trap sets for up to three hours. Individual coyote trials ended earlier if the coyote set off the modified trap. After three hours, trap sets that were not set off were covered with sheets of plywood. This 3-hr process was considered Day 1. Traps that were not set off on Day 1 were also uncovered for three hours on Days 2, 3, 4, 8, 16, and 32. To ensure a lure scent was present and to mimic procedures commonly used when trapping coyotes in the wild, additional lure was added on Days 8, 16, and 32. The test was terminated after Day 32 or earlier if a coyote set off the trap. Trials ran between July and October of 2016.

We measured the observers' latency to approach the trap and latency to when coyotes set off the trap. Latency to approach was calculated as the time from when the coyote was released into the enclosure to the time the coyote directly investigated the set, defined as the coyote digging in the hole and/or the coyote stepping nearly on top of the trap. The latency to setting off the trap was based on the time the trap was set off by the coyote. Latency times accumulated across days for coyotes that did not approach or set off the trap on Day 1. For example, latency to approach time started at 0 min on Day 1 and 180 min on Day 2.

Experiment 2 – Familiar Coyotes in Shared Enclosures

To evaluate socially familiar coyotes in proximity to one another, we randomly selected 12 mated male-female adult pairs that had not been exposed to traps previously. The mated pairs were each housed in .01-km² pie-slice-shaped enclosures, four pairs at a time because there were only four pie enclosures at the facility (Figure 1). We set camera traps and a functioning Victor #3 Soft catch foothold trap with a dirt hole set and lures as previously described within each enclosure. The same lure within each mated pair throughout their trials. Coyotes were present in the enclosure while the traps were set, but we used the same plywood shielding technique previously described to prevent coyotes from directly observing any trap being set. Trials ran between June and October 2017.

Each pair was directly observed for three hours following the trap set, but observations ended earlier if one of the coyotes was captured. The individual that set off the trap became the demonstrator, while the uncaptured mate became the observer. Demonstrator coyotes were left in the trap for approximately 10 min to allow time for the tranquilizer to take effect and the observer coyote to witness how its mate behaved in the trap. Demonstrators were removed from the trap, checked for trap-related injuries, held for observation until the effects of the tranquilizer wore off, and returned to the enclosure within 12 h. Coyotes were housed as pairs after the initial trapping for logistical purposes with colony management. Trap sets were removed from the enclosure following the capture of the demonstrator. The day following the capture of the demonstrator, two trap sets were placed in the enclosure using the same technique and dirt-hole set previously described. A modified trap was set in the same location as the functioning trap had been the day before, while a second, dummy set was placed at least 30 m from the modified trap, at a similar distance to any enclosure fencing boundaries. The dummy set was prepared in an identical manner to the modified trap but without a buried trap. This was to ensure there were two locations with the lure in case one animal dominated a site. The pair was then left to interact with the two sets for three hours. If neither coyote set off the trap after three hours, both sets were covered with plywood for the remainder of the day. This was considered Day 1. The sets were also uncovered on Days 2, 3, 4, 8, 16, and 32, but the experiment ended sooner if the observer coyote set off the modified trap.

For the initial presentation, if neither coyote set off the trap within the 3-h timeframe (i.e., neither coyote became the demonstrator), the trap set was covered with plywood for the remainder of the day, and

then uncovered for three hours for up to three subsequent days. If neither coyote was captured within four days, the trap was removed. Some pairs were presented a trap on another occasion in which the trap was set in a different location but in other cases, the pair was removed from the study. We attempted this relocation of a trap if we noted the pair of coyotes did not use the area of the enclosure where the trap was previously set (versus actively avoided the trap set).

Like Experiment 1, we recorded the latency to approach and set off each trap via video recordings obtained from our cameras. We defined the time a modified trap was set off (i.e., tripped) as when it was tripped but needed a new definition for the dummy sets where there was no trap. For dummy sets, we defined the time the trap was set off by the location of a coyote's foot at the trap site and if the coyote was actively digging or smelling the hole. Latency times accumulated across days for coyotes that did not approach or set off the modified trap on Day 1.

Experiment 3 – Familiar vs Unfamiliar Coyotes in Adjacent Enclosures

To compare socially familiar coyotes to unfamiliar coyotes when not in a shared enclosure, we used a similar design and recorded the same data as described in the two earlier experiments; however, there were some differences in the design for logistical reasons. First, for the design of this experiment, two coyotes each observed one demonstrator coyote. The demonstrator coyote was housed in one of the clover enclosures, a tear-dropped-shaped 1000-m² enclosure, with the two observers housed in the adjacent enclosures, one on each side of the demonstrator within the same 3-enclosure cluster (Figure 1). One of the observer coyotes was the mated partner of the demonstrator and the other was a randomly selected and unrelated coyote to the demonstrator. The two observer coyotes were of the same sex, opposite that of the demonstrator. In total we tested six observers (4 males, 2 females), who viewed three demonstrators (2 females, 1 male). Second, we were unable to use TTDs on the traps because the experimental research permit for TTDs was discontinued. (All TTDs had to be returned to USDA for destruction before this experiment began.) The demonstrator coyote was still held in the trap for 10 minutes before we removed it from the trap and enclosure. Third, after the demonstrator was removed from the enclosure and checked for potential trap-related injuries, we placed the coyote back in its enclosure on the same day. This was done for logistical reasons because there was no tranquilizer that the coyote needed to recover from, and we were limited on alternative spaces for housing the demonstrator coyotes at the facility at the time of testing. Finally, we changed the lure after observing two potential demonstrator coyotes show no interest in interacting with the commercial lures. Instead, we used a private trapper's homemade mixture that consisted of ground-up mice brains. This lure was used for all demonstrators and test coyotes. Like in the other two experiments, all coyotes used in this experiment were naïve to traps. The day after the demonstrator was captured, the observer coyotes were swapped into each other's enclosure and tested. The same dirt-hole set and lure was used for the demonstrator and observer coyotes. This video shows an example of an observer coyote tripping a modified trap: <https://doi.org/10.6084/m9.figshare.19929752.v1>. If an observer coyote did not get captured during Day 1, the trap was covered with plywood and the coyote was retested on days 2, 3, 4, 8, 16, and 32. The trial ended earlier than Day 32 if the coyote set off the trap. We recorded latency to approach and capture events using camera traps. Trials ran between July and November 2021.

Data Analysis

We modeled variation in latency to approach and latency to be captured using Cox proportional hazards models in program R ('survival' package; Therneau, 2021) for each experiment (R Core Team, 2021). This survival model allows for time-to-event data to be right censored so that we could include coyotes that did not get trapped with those that did. Thus, observer coyotes were coded as "dead" when they set off a modified trap in Experiments 1-3 and right censored if they did not set off a trap. For Experiment 2, we also coded data for when each coyote set off the dummy trap set. We evaluated coyote survival by observer treatment effects for (1) observer and demonstrator coyotes during all experiments and (2) observer and demonstrator coyotes at the dummy sets in Experiment 2. We used linear models when we could not meet

the assumptions for Cox proportional hazards models. Due to the small sample size in Experiment 3, we only summarize results about related and unrelated observer coyotes. Results are presented as average \pm SE.

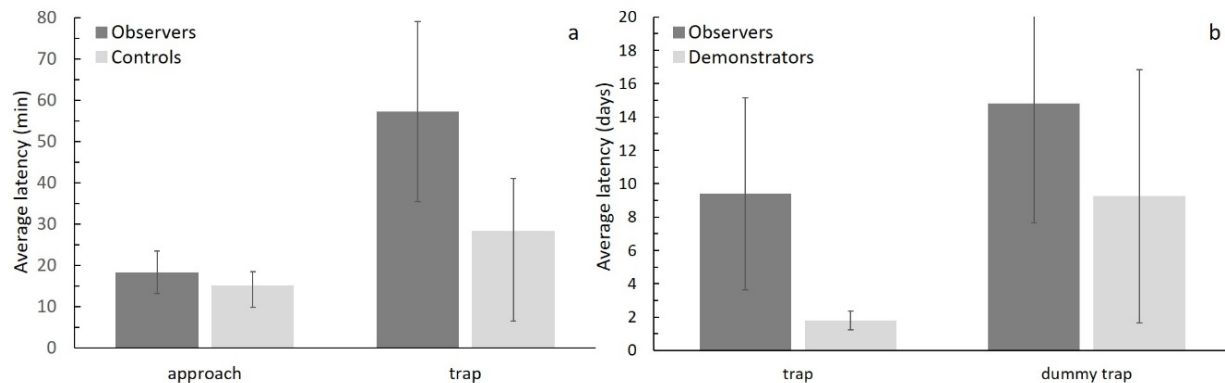
Results

Experiment 1 – Unfamiliar Coyotes in Adjacent Enclosures

The three demonstrator coyotes were caught at 6-min, 8-min, and 34-min after trap placement. We were unable to use one coyote assigned as an observer because it could not be captured by animal care staff to be moved to a new enclosure on the first day of trials. Of the remaining observers ($n = 17$), all but one was captured, with 14 captured on Day 1 and two captured on Day 2 (Figure 2). All control coyotes were captured on Day 1 ($n = 9$). We had to exclude two coyotes that were captured from data analysis because the camera trap system failed, and we were not able to determine the time of capture for latency metrics; one was a control coyote captured on Day 1 and one was an observer coyote captured on Day 2. We found no significant difference in latency to approach (Wald test: $H_1 = .79$, $N = 23$, $p = .37$) or latency to capture (Wald test: $H_1 = 1.5$, $N = 23$, $p = .22$) in control versus observer coyotes. The Cox proportional hazard model failed the Schoenfeld residual test for proportionality when including latency to approach as an explanatory factor for latency to capture, so we instead used a linear model and found a significant effect of latency to approach on latency to capture ($\beta = .9794$, $SE = 0.0524$, $p < .001$).

Figure 2

Average latency (in minutes or days \pm SE) for captive coyotes to approach or get caught in a trap during Experiments 1 and 2.



Note. (a) In Experiment 1, observer coyotes ($n = 14$) were able to watch a demonstrator get captured before encountering a trap, and latency to approach and latency to get captured were compared to control coyotes ($n = 8$), that had not observed a conspecific get trapped. Illustrated results do not include (1) one observer coyote that did not get caught, and (2) one control and one observer coyote where the camera trap system failed, and we could not obtain latency times for capture and approach. (b) In Experiment 2, a trap was placed in an enclosure with a male-female mated pair of coyotes, and the first coyote captured served as the demonstrator ($n = 10$). We compared latency to initial capture for demonstrator and observer coyotes for the real set and a dummy set, where no trap was set but the site was dug out and the lure was placed. Illustrated results show average latency times for coyotes that were captured ($n = 5$ observers, $n = 10$ demonstrators for first capture; $n = 5$ observers, $n = 4$ demonstrators for dummy captures). Four demonstrator coyotes were also recaptured in real traps (latency: 15.5 ± 6.4 days).

Experiment 2 – Familiar Coyotes in Shared Enclosure

One pair of coyotes was not trapped after two, 4-day attempts and was further excluded from the study. Two other pairs were re-tested for an additional 4-d interval and demonstrator latency was measured as the accumulative number of days the trap was set across the two trials. Ten coyotes were captured and served as the demonstrators (7 males, 3 females; $1.8 \pm .6$ days to capture). Five of the 10 mates that were observer coyotes were subsequently captured (3 males, 2 females; 3.4 ± 2.3 days to capture; Figure 2). The

latency to first capture was significantly different between demonstrator and observer coyotes (Wald test: $H_1 = 10.52$, $N = 20$, $p = .001$). We could not prevent demonstrator coyotes from interacting with traps during observer trials since they were housed together. Interestingly, we found no difference in the survival estimates of demonstrator coyotes recaptured and observer coyotes captured in a modified trap (Wald test: $H_1 = .51$, $N = 20$, $p = .470$). There was also no difference in latency to capture in a dummy versus modified trap by observer (Wald test: $H_1 = .02$, $N = 20$, $p = .900$) or demonstrator coyotes (Wald test: $H_1 = .27$, $N = 20$, $p = .600$) (Figure 2).

Experiment 3 – Familiar vs Unfamiliar Coyotes in Adjacent Enclosures

Four demonstrator coyotes (1 male, 3 females) were not captured across their four days of 3-h trials and removed from the study. Three demonstrator coyotes were captured on Day 1 (female), Day 2 (female), and Day 3 (male). Resulting data trends suggest similar latency to approach times by familiar and unfamiliar observers, but unfamiliar observer coyotes took longer than the mate observer to be captured (Table 1).

Table 1

Latency (in minutes) for captive coyotes to approach and get captured in a trap in Experiment 3.

Demonstrator		Observers			
Sex	Latency to Trap	Latency to Approach		Latency to Trap	
		Mate	Unfamiliar	Mate	Unfamiliar
female	4	82	29	363	903
male	421	17	544	41	1133
female	209	7	31	67	764

Note. Observers were either the paired mate of the demonstrator (mate) and an individual who was unfamiliar with the demonstrator (unfamiliar). The two observers were the same sex, but opposite to the demonstrator. Four other demonstrator coyotes did not get trapped and were therefore removed from the study.

Discussion

We investigated the role of social learning in trap avoidance by captive coyotes across different social and spatial contexts. Overall, our results suggest that captive coyotes have a limited ability to socially learn avoidance behavior of traps after viewing one demonstration. Instead, individual behavioral traits may best predict the likelihood of trap avoidance behavior. Individual variation is supported by the behavior observed across demonstrator coyotes. The length of time for demonstrators to be captured varied across experiments even though the same techniques were used. In all experiments, some demonstrator coyotes were never captured and removed from the experiment. Demonstrator coyotes were not selected at random but from those in the colony that are typically considered to be bolder and more investigative according to the animal care staff. Yet even these coyotes, categorized with some similar behavioral characteristics, showed variation in latency to approach and be captured.

Similar approach times between control and observer coyotes in all three experiments suggest the lure was an attractant to the captive coyotes and may have prevented avoidance behavior from emerging. These captive coyotes rarely encounter dangerous objects or situations and may have been more attracted to the lure than they were repelled by a potentially negative consequence. However, latency to approach was not correlated to latency to capture in the first experiment and while approach times may have been impacted by the attraction to the lure, coyotes could easily approach without being captured if they learned to avoid the trap itself. We had expected observer coyotes to evade setting off the trap after watching a demonstrator because the demonstrators showed substantial distress behavior for the 10 min they were in a trap. Most demonstrators vocalized, pulled, bit at the trap, and thrashed. Some were also aggressive towards animal care staff when we removed the coyote from the trap – a behavior that is atypical with the captive

coyotes maintained in the colony. However, we found no difference in latency to capture the coyotes that either observed a neighboring demonstrator coyote get captured in Experiment 1 or in the latency to capture observer and recapture demonstrator coyotes in Experiment 2. This suggests asocial learning (i.e., trial and error) were also likely poor. We detected a difference in latency to capture demonstrator and observer coyotes in Experiment 2 and a trend towards shorter latency to capture a mate observer versus an unfamiliar observer coyote in Experiment 3. Thus, our results suggest social learning of object avoidance may exist but only to a small extent, when neighbor coyotes can observe a territorial neighbor or their mate in close physical proximity.

The role of physical proximity in social learning of avoidance behavior may be related to coyote territorial behavior. Coyotes live in territorial social groups that are maintained by 2 – 4 adult coyotes over long periods. Territorial location remains constant across time (Young et al., 2006), with new individuals or pairs filling in vacant territory spaces (Gese, 2001). Thus, neighboring packs would be familiar with one another, constantly communicating territorial boundaries and checking for incursions. This may create a system in which coyotes readily learn from familiar neighbors. This was similar to the study design used in Experiment 3, where an unrelated coyote was housed adjacent to a mated pair and the latency to capture was significantly longer than for the mate of the demonstrator. Although our sample size was too small to allow statistical analyses, because so many coyotes had already participated in one of the two earlier experiments or failed to perform as a demonstrator in Experiment 3, the resulting pattern for all three sets of coyotes was robust: unfamiliar coyotes had longer latency to capture times than the mate of the demonstrator coyote.

Our experimental design differed from territorial tenure observed in the wild during Experiment 1. To ensure coyotes were unfamiliar to the demonstrator, the captive coyotes were not neighbors before the experiment and the mates of the demonstrators were not in proximity to the mates or testing enclosures. The observer coyotes did not have time to establish relationships with the coyote serving as a demonstrator or other neighboring observer coyotes. In this experimental scenario, the observer coyotes did not socially learn to avoid traps although there was a nonsignificant trend in longer latency to capture times relative to control coyotes. Nonetheless, the lack of a statistical significance between control and observer coyotes in latency to capture times suggests unfamiliar coyotes do not pay enough attention to their neighbors to result in social learning of object avoidance when all the surrounding coyotes are unfamiliar. This could explain why unfamiliar coyotes seemingly learned to avoid traps in Experiment 3 but not in Experiment 1. Territorial observation could be more prominent when the neighbors are a mate-pair and therefore facilitate social learning.

Proximity to familiar individuals seemed to matter as exhibited by results of Experiment 2 when coyotes were housed together. When coyotes were housed together, the observer mate had longer latency to capture than their demonstrator mate. These results are more similar to other studies that have shown familiarity improves learning in a wide range of taxa (e.g., Coussi-Korbel & Fragaszy, 1995; Guillette et al., 2016; Schwab, Bugnyar, & Kotrschal, 2008; Schwab, Bugnyar, Schloegl et al., 2008). However, these results could have emerged if coyotes within a pair have dominance structures that affect trap-site access. It is unclear if the demonstrator coyote in Experiment 2 was simply the dominant coyote and able to prevent the observer coyote from accessing the trap set. In a social learning study associated with a positive food reward, most food-dominant captive coyotes rarely allowed their mate access to the puzzle box and associated food reward (Young et al. 2019). Yet, in this experiment, there was no positive food reward with the site that a food-dominant coyote may have guarded against its mate. The use of two trap sites during the observer testing was used to provide access to two spots but coyotes were similarly interacting and captured at both sites. While some observer coyotes were captured shortly after observing their demonstrator mate get captured, there was no difference in latency to capture an observer coyote and latency to recapture the demonstrator mate, or in latency to capture demonstrator and observer coyotes at the dummy set. In hindsight, we may have been able to tease apart this potentially confounding issue by removing the demonstrator mate after capture but were unable to do this at the time of the experiment due to logistical constraints of available housing of the captive coyotes at the facility. The other alternative is to allow unfamiliar coyotes to access the same traps but there is a risk of unfamiliar coyotes physically

attacking one another if in a shared space and we were unwilling to attempt this experimental scenario. Thus, more information on how dominance hierarchical structures influence social learning is still needed for coyotes.

The experiments were carried out over 32 days to ensure sufficient time was allocated for the observer or control coyotes to get captured. In doing so, we observed several coyotes avoid capture until the last or second to last day of tests. For example, two coyotes were captured in a modified trap on the final testing day (Day 32) during Experiment 2; one was a demonstrator and one an observer. Both of these coyotes, and two more (1 demonstrator, 1 observer) were also captured on Day 32 in dummy sets. Similarly, two observer coyotes were not captured until Day 16 and 32 in Experiment 3. These data suggest that memory may play a role in the extent to which information obtained via direct experience, observations, and social learning shapes avoidance behavior. Most of our understanding of retention of learned responses has been studied in the context of foraging (Ferrari et al., 2010; Mangel, 1990; McNamara & Houston, 1987; Weschler, 1998) and responses to predators. Memory is thought to be most easily retrieved when conditions are constant (Dunlap et al., 2009), or for as long as the learned information is relevant (Brydges et al., 2008; Pravosudov & Clayton, 2002). The captive coyotes in this study experienced constant environmental conditions during the period of testing, so it is unclear what alternative extrinsic or intrinsic factors may be at play in determining retention of learned information related to avoidance.

For logistical reasons associated with colony management, we used different types of enclosures across the experiments. Pie enclosures, where the familiar demonstrator and observer coyote were housed together during Experiment 2, were about ten times larger than the interaction and clover enclosures, where single-housed observer coyotes were in adjacent enclosures to the demonstrator in Experiments 1 and 3, respectively. The smaller enclosures used in Experiments 1 and 3 may have led to higher trap-encounter rates than in the larger enclosures, whereas longer latency to capture during Experiment 2 may have resulted from coyotes being more easily able to avoid trap sites by being housed in larger enclosures, more similar to wild territorial behavior (Kamler & Gipson, 2000; Wilson et al., 2011). In Experiment 2, coyotes may have been avoiding the specific location of trap sets but not learned more generally to avoid traps. We used the smaller size enclosures in Experiments 1 and 3 to ensure observer coyotes could view the demonstrator. The use of familiar pairs in Experiment 2 allowed us to better simulate capture experiences in wild coyotes, where territories consist of >1 individual that would have relatively equal access to traps in their range. However, it prevents us from making direct comparisons across experiments.

Although enclosure size may have played a role, it was evident that coyotes could avoid being trapped in any of the enclosures. Coyotes avoided capture for up to 32 days in all three enclosure types. However, almost every coyote approached a trap and during Experiment 2, there was no significant difference in latency to capture in a dummy set and modified trap for demonstrator or observer coyotes, implying coyotes were not learning avoidance behavior in our experiments. Nonetheless, there was a trend in that, on average, demonstrator coyotes interacted with dummy sets in fewer days than for the real, modified traps (Figure 2), suggesting they may have detected a difference in the risk between set types and learned some avoidance behavior toward real traps. This could also be attributed to coyotes learning to avoid the specific location where it was originally trapped because Experiment 2 was our only experiment where the same location was used for the trap that captured the demonstrator and the trap available to the observer. Indeed, Eurasian lynx (*Lynx lynx*) subjected to capture in foot snares and box traps followed by chemical immobilization took more than four times as long to return to the capture patch as compared to randomly selected patches within their home ranges (Moa et al., 2001). However, location avoidance was unlikely to have been the reason for longer latency metrics in our study because both the demonstrator and observer coyotes set off (i.e., triggered) the trap at the same spot. Further, trappers often set traps in the same location after a successful capture. Even so, further studies that can better distinguish the roles of location and object are warranted, along with methods that avoid issues associated with enrichment for captive animals. Future studies may want to test in captivity without the use of lures or in the wild, where coyotes may be more fearful of humans and more likely to utilize avoidance behavior (Darimont et al., 2015; Kitchen et al., 2000).

Finally, due to experimental design and limitations with sample sizes for each experiment, we could not evaluate sex or age differences in these experiments. We only used adult coyotes in this study and excluded juveniles. Although used a mixture of male and female coyotes within each experiment, we did not design the study to evaluate potential sex differences. Instead, we focused on boldness to assign demonstrator status in Experiments 1 and 3, while the coyotes self-selected for demonstrator status in Experiment 2. Interestingly, males comprised most coyotes first captured in Experiment 2, when coyote pairs were housed together. These experiments establish the first tests of the role of social learning in avoidance behavior of coyotes. More studies to evaluate whether there are differences between sexes or among age classes are needed.

Conclusions

The ability for coyotes to potentially learn trap avoidance from conspecifics could have implications for research and management. Coyotes are notoriously difficult to capture and previous studies have already shown the influence of age, sex, season, breeding status, trap density, and the location of the traps within a home range. Here, we examined social learning of avoidance behavior and the roles of social familiarity and spatial proximity. Our results indicate it may be difficult for coyotes to socially learn to avoid traps except from territorial neighbors. This may make it difficult for researchers to capture coyotes from neighboring packs for studies of spatial dynamics or by managers tasked with capture and removal of coyotes in areas where there are conflicts. Managers and researchers may find higher success rates by utilizing a variety of trap sets, including passive trap designs such as snares that do not require the use of scent to lure a coyote into the trap. Our results and how they could impact capture success should be considered in study design and methods of capturing coyotes and possibly other canids.

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